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Vocal performance in the chipping sparrow: can a bird change his song?

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Vocal performance in the chipping sparrow: can a bird change his song?

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By

Meredith C. Miles

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Table of Contents

Abstract

Bird song is an animal signal that serves as the primary method of mate attraction in most songbirds, a group that accounts for the majority of bird species worldwide. While it has been established that there can be a wide range in song quality within a species, and that high-quality vocal performance tends to attract more mates, less is known about the effects of differing vocal performance on the behavior of other competing males. It also has not been established whether individual birds can alter their own vocal performance quality in response to different situations. In some birds that sing a trilled vocalization, it is possible to quantitatively define the vocal skill required to produce a given song. In this Honors Thesis, I explore these issues in the chipping sparrow (*Spizella passerina*), whose trilled vocalization facilitates measurement of the vocal skill required to produce a given song. I tested three competing hypotheses concerning the vocal performance of this species: (1) that individuals modulate their song quality in different competitive contexts, (2) that individuals differ from one another in their vocal performance and are unable to modulate their vocal performance, and (3) that individuals are neither different from one another nor modulate their vocal performance. Over the course of a single breeding season, chipping sparrows were captured, color-banded, and recorded as they sang spontaneously. In a playback experiment simulating territorial intrusions by both high- and low-quality males, tested birds did not modulate any aspect of their vocal performance outside of singing more often while a simulated intruder was also singing ($p=0.223$). In all contexts, the largest source of variation in song was attributable to inherent differences between individuals ($p<0.0001$). These results support the hypothesis that chipping sparrow song is highly variable from bird to bird, and that birds do not modulate their song based on vocal performance, despite recognizing the occurrence of the simulated intrusion and consequently increasing their rate of singing. However, they may be reacting aggressively to intruders by changing their behavior outside of song modulation. These findings are a reminder of the complex ways that sexual selection and competition interact to shape animal behavior, and offer numerous avenues for future study.

Introduction

Animal signaling and sexual selection

From a behavioral ecology standpoint, an animal signal is a behavior that conveys information to other individuals, which are typically conspecifics. Signals manifest in many different forms, including chemical and visual cues as well as auditory cues, the latter of which are usually produced as vocalizations. Theoretically, a signal must convey reliable information in order to be valuable to the individual receiving it. The ability for animals to “cheat” on certain signals does complicate the issue, presenting a paradox that is currently still being researched (Smith and Harper 2004).

Signaling is among the most prevalent mechanisms that support sexual selection in animal species. Most sexual signals are accomplished through ornamentation, such as the annual growth of antlers in cervids or the long tail growth in African widowbirds (Ploceidae: *Euplectes*), as well as through elaborate display or performance (Byers *et al.* 2010). Of course, establishing a given signal as sexually driven (implied here to be by female choice) requires that it meets some basic criteria of sexual selection, first proposed by Darwin (1859): that the males of the species possess the phenotypic trait to various degrees, and that females demonstrate a preference for particular versions of that trait.

Though there are numerous categories and classification schemes of animal signal, two key types are vital to informatively communicate individual fitness. One of these is the index signal, which directly correlates with individual quality and acts as an informative indicator of some aspect of the animal’s quality (Smith and Harper 1995). While index signals seem commonplace in nature, the number of studies that actually evaluate behaviors hypothesized to be index signals is limited. This is largely due to the fact that in order for an index signal to persist, it must be physically constrained in order to remain informative, and for many traits that seem to be index signals it can be difficult to pinpoint this physical constraint. However, the examples that do exist are both convincing and taxonomically varied. When funnel web spiders (Araneae: Hexathelidae) are preparing to fight over a web site, they can sense the weight of the potential opponent through vibrations along the web fibers; a larger spider will vibrate the web more, and if there is a large enough size discrepancy between the two competitors, they will not fight over the web at all (Grafen 1990). Index signals are also of great importance to sexual selection; for instance, female barn swallows (*Hirundo rustica*) prefer a mate that has a higher degree of tail streamer symmetry, which enhances flight dynamics (Møller 1998). Because of the inherent connection between streamer symmetry and flight ability, tail morphology becomes an informative signal to the discerning female swallow. The recipient of an index signal involved in sexual selection need not always be a possible partner; consider the case of the polygynous Montezuma oropendola (*Psarocolius montezuma*), which gathers in large social groups during the breeding season. In vocal contests to establish the social and mating hierarchy, the male oropendolas will produce a low-frequency note that is physically constrained by body size. The birds that call with the lowest frequency have a higher social rank in the flock, and mate with more females, though the vocal signal was not originally intended to be heard by the females in this case (Price *et al.* 2006).

Another method to communicate individual quality is the handicap signal, in which an animal will display a behavior or morphological trait that ostensibly reduces that individual's fitness, thereby indicating an ability to overcome the handicap (Zahavi 1975). The handicap can be simultaneously behavioral and morphological, as in the courtship display of the red grouse (*Lagopus lagopus*); the males annually grow a red comb over the eyes that is used in an energetically-costly performance for potential mates. In order to produce these sexual ornaments, testosterone levels are dramatically increased, even at the cost of immune function; grouse with more testosterone have larger combs and a lower level of T-cell-mediated immunity (Mougeot *et al.* 2004). Similarly, the impressive display of the great frigatebird (*Fregata minor*) has been hypothesized to serve as a handicap signal due to the potential energetic costs associated with inflating the brightly-colored gular pouch that serves as the species' primary sexual ornament (Dearborn *et al.* 2005). It is important to note that signal classification as index or handicap is not mutually exclusive; for example, the red grouse ornamentation acts as both. Although growing the red comb can compromise immune function, the ornament's pigment consists of diet-derived carotenoids, the production of which requires that the bird be able to both find sufficient food to extract the pigment and have enough energy to concentrate the pigment in the comb (Martinez-Padilla *et al.* 2007). Therefore, the comb is an informative index of the food-finding and energetic capabilities of a given male.

Sexual selection has long been recognized as a driving force for evolution in many vertebrate groups (Darwin 1859, Andersson 1994). Excepting sexual selection by combat, signaling is a vital component of this evolutionary process, allowing potential mates to communicate their fitness to one another and make an informed decision about the presence or absence of desirable traits. Many of these signals can be categorized as index signals, handicap signals, or a combination of the two, and establishing the origin and significance of these characteristics is an ongoing project.

Bird song as signal

Bird song is another example of a behavior that can function both as an index and handicap signal (Cardoso and Hu 2011), one that is employed by thousands of species worldwide to serve purposes including but not limited to mate attraction and territory defense. In order to sing, a bird must expend time and energy that otherwise could be allocated to more “valuable” behaviors like feeding. The bird is also producing a sound loud enough to be heard by a conspecific, which is prone to eavesdropping by predators. In this way, bird song is a handicap. It can simultaneously function as an index signal due to inherent connections between song quality and neurological or physiological ability; experimental tests on wild birds in the field and raised in a laboratory setting continue to emerge that support this claim (e.g. Ballentine 2004, Byers and Kroodsma 2009, Caro *et al.* 2010, Cramer 2013, Cramer *et al.* 2011). Studying this signal is not only valuable to understand avian behavior and ecology, but also serves to further elucidate fundamental issues of animal signaling.

Though the use of acoustic communication for mate attraction Class Aves, it is the songbirds (Order Passeriformes) that seem to have adopted vocal signaling as their primary method of breeding season interaction with conspecifics of both sexes. Across many songbird families, female preference is for males that sing well, though the females are often not directly selecting for singing ability in a mate. For example, male red-winged blackbirds (*Agelaius phoeniceus*) with larger song repertoires do acquire more females during the breeding season than those with smaller repertoires; however, their increased success is due to greater reproductive experience and higher territory quality, both of which are correlated with repertoire size in the species (Yasukawa *et al.* 1980). Bird song serves purposes beyond advertising to females, however; it is a multifunctional signal that can be used in competitive contexts as well. Northern mockingbirds (*Mimus polyglottos*) acquire a wide range of interspecific song imitations for their repertoire because large song repertoires aid in acquisition of mates, but also because they can use mimicry to drive interspecific competitors away from their breeding territories (Howard 1974).

How bird song is produced

Production of bird song relies on the syrinx, an upper-respiratory tract structure unique to birds but analogous to the larynx found in mammals (Goller 1998). Muscular contractions to force air through the bifurcated syrinx and eventually the bill allow for the production of vocal signals in birds, though the exact muscular mechanism for this is only now being unraveled (Larsen and Goller 2002). Minute muscle contractions along the syrinx allow for small-scale modulation of the sound being produced, while larger changes are mostly accomplished by shortening and lengthening the vocal tract by shifting the position of the neck or by employing rapid movements in the cranium, including opening and closing the bill (Westneat *et al.* 1993). While a high level of neurological coordination is required to produce many bird songs, the way in which many vocalizations are physically constrained cannot be understated. In an experimental test, Hoese *et al.* (2000) disabled or immobilized different aspects of captive sparrows' vocal tracts to determine that final sound production heavily relies on post-production sound modulation—that is, on movements of the respiratory tract above the syrinx, including bill motion.

Modern passerine bird song spans a diverse range of sound, from the complex repertoires of the mimids (mockingbirds and their allies) to the simple but physically demanding trills of certain emberizid sparrows. Because of this variation in song type across taxa, definitions of song quality will also be highly variable and species-specific; a high-quality song may be complex and provide a cognitive challenge to produce, or it may require far less brain power but more muscular acrobatics at the syrinx (Cardoso and Hu 2011). This divergence can occur at the family level or even within a single genus; for example, male song sparrow (*Melospiza melodia*) fitness is directly correlated with song repertoire size (Pfaff *et al.* 2007), while female swamp sparrows (*Melospiza georgiana*) solicit males that produce a song that is physically difficult to perform (Ballentine 2004). It can be difficult to define vocal performance quality in birds that employ complex songs involving a repertoire or innovation, because there is no precise physical correlation between syringeal structure and the vocal performance of these song types (Gaunt 1983). Without a physically-defined constraint on vocal performance, the information content of the signal can be difficult to infer.

On the other hand, bird song that is simplistic but physically challenging to produce is convenient to study because it is possible to quantify song difficulty (which then corresponds to quality of the signaler) according to measurable physical aspects of the song (Podos 1997). One such vocalization is the trill, which consists of rapid repetition of single-note syllables. Trills are commonplace in songbirds, either serving as the entirety of the song or as a single component of a more complex or variable song; trills are found in both song sparrow and red-winged blackbird song, but are one component of a larger vocal routine, while certain birds, including multiple species in Family Emberizidae (New World sparrows), exclusively employ trills for their vocal performance.

Bird song as communication with females

Vocal performance is known to play a large role in sexual selection in the passerines, but the information content of the signal—and the benefit to the receiver—appears to vary among species. When a female songbird is selecting a male, either a social partner or perhaps an extra-pair sperm donor, what is she looking for? Some studies suggest that the determining factor for picking a social mate will be direct benefits to the female, such as the quality of territory or the male's ability to care for the brooding female and her chicks, rather than the quality of flashy ornamentation for sexual display (Yasukawa *et al.* 2009). Other studies find evidence that females select based on preference for the male's genetic contribution; that is, they are concerned with finding a mate that will be able to sire reproductively fit offspring that will carry the female's genes into future generations (Weatherhead & Robertson 1979). This "sexy sons hypothesis" has been used in part to explain the prevalence of extra-pair fertilization in songbirds.

There is mounting evidence that female birds will base their selection of mates on different aspects of motor performance (Byers *et al.* 2010), which is demonstrated both through singing and other sexual displays, such as dancing (Martinez-Padilla *et al.* 2007) or structure-building (Madden *et al.* 2012). The quality of motor performance can be broadly defined by two key characteristics:

skill, or the ability to execute a complex behavior close to the physical limit of performance; and vigor, the ability to repeatedly perform a costly behavior (Darwin 1859). In various bird species, females display preference for both aspects of motor performance during vocal display; female swamp sparrows, for example, prefer to solicit males that perform challenging trilled songs (Ballentine 2004) as well as songs that conform to a typical song standard rather than introducing innovative vocal elements (Nowicki *et al.* 2001). Meanwhile, nearly all vocal performance in birds is demonstrative of vigor in motor performance; most males will sing intermittently throughout the day during the breeding season, especially while air conditions are favorable for transmission of vocal signal across a large distance. More extreme examples of vigor can be found in the highly stereotyped displays of lekking bird species, which will perform costly behaviors for many consecutive days for the opportunity to win mating rights with observing females (Reynolds and Gross 1990).

For many bird species, establishing the bounds of adult song performance occurs during the most biologically stressful period of the individual's development. Developmental stress itself affects nearly every physiological system (Spencer and MacDougall-Shackleton 2011), so it is unsurprising that experimental evidence also indicates that exposure to various stressors over the course of development in songbirds affects both song performance and eventually reproductive success. Because songbirds are highly altricial, hatching completely helpless and relying on parental care during the most sensitive period of life, good nutrition becomes key to proper development and growth. The "developmental stress hypothesis" for bird song, first outlined by Nowicki *et al.* (1998) posits that poor nutrition or exposure to toxins in the early life of a bird will compromise multiple and diverse body systems—including the neuromuscular systems underlying the performance of song. Flaws in song performance can therefore be connected with other physical and neurological defects in the male songbird that could compromise his ability to provide adequate parental care to any offspring he manages to produce. Experimental tests of this hypothesis suggest that this effect may indeed be real, often using toxins introduced environmentally or through direct manipulation to induce developmental stress. For instance, Carolina wrens (*Thryothorus ludovicianus*) breeding along a mercury-contaminated river in Virginia had a 34% reduction in reproductive success when compared to an unexposed control population (Jackson *et al.* 2011). These detrimental toxic effects are also reflected in avian vocal performance; both black-capped chickadees (*Poecile atricapilus*) and song sparrows exposed to nonlethal levels of polychlorinated biphenyls (PCBs) during development produced song that was significantly different from vocalizations performed by unaffected individuals (DeLeon *et al.* 2013). The developmental stress hypothesis can also be tested by using standard measurements that indicate body quality, including rate of mass gain during the developmentally-critical early life. This is the estimate of developmental stress used by Searcy *et al.* (2010) in a direct field test of the effects of early nutritional stress on female response to male swamp sparrows. Females increased the rate of copulation solicitation display as quantified in a copulation solicitation assay (Searcy 1992) when presented with males with a superior growth history than the developmentally challenged males. At least some of the females' ability to discriminate the developmental history of the males was coded in advertising song; inferior males differed in the average length of song, as well as a combined song metric that included trill rate, number of notes per syllable, and song stereotypy (Searcy *et al.* 2010).

What other roles can bird song play in sexual selection? Song could also be a coded signal to communicate that the male is in possession of a high degree of fine motor control to produce excellent song, which in turn might ensure any listeners that he is a physically competent individual. It is possible that song contains other hidden physiological information, such as immune quality. One more consideration is that bird song may not have evolved to be shared with females in the first place; it may have instead originated as an aggressive signal to communicate with competitive males and aid in territory defense, and females may have since evolved a preference for good song that had its origins in eavesdropping.

Bird song as communication with other males

The old paradigm of "singing for your mate" continues to be challenged with emerging research on competitive interactions between male birds mediated by song. There is evidence that some species can distinguish the songs of neighbors versus novel intruders; young song sparrows, for example, will increase the rate of aggressive behavior when confronted with an unknown song compared to a known neighbor's song (Searcy *et al.* 1981), or when hearing a known neighbor's song coming from an unfamiliar location (Godard 1991). When a territorial song sparrow male is presented with song or a visual intruder alone, he will not be inclined to behave in an overtly aggressive manner, but when presented with the stimuli in tandem he will go on the offensive

(Akcay *et al.* 2011). In this way, song augments other visual signaling methods to be a signal of aggression toward other male songbirds.

There is also evidence that a bird may shift his singing habits when faced with an intruder. The chiffchaff (*Phylloscopus collybita*), a European songbird that typically sings a slow song, will increase the speed of his syllable rate when presented with high-syllable rate playback, suggesting that song speed is an aggressive signal in this species (Linhart *et al.* 2013). Different species will alter other aspects of vocalization contextually to indicate aggressive intent, as in the song sparrow. In this species, males responded to a simulated intrusion (which included both a taxidermic mount and playback) with low-amplitude soft song in addition to aggressive wing-waving (Akcay *et al.* 2011). Soft singing in the song sparrow is considered to be an example of how soft song can function as a "vulnerability handicap": a signal that is effective due to the risks inherent in performing it, and therefore assumed to be informative (Laidre and Vehrencamp 2007). In this instance, performing a low-amplitude song is inaudible to the signal recipient unless the individual is very close to the bird producing the song, thereby increasing risk of attack on the part of the singer.

Birds are also able to use their ability to discriminate differences in song production to signal aggression to competitors. Song matching is a common example of this, in which a bird will respond to a singing intruder by shifting his natural song type to more closely match that of the intruder. This can either be by type matching, i.e. directly mimicking the type of song recently sung by the neighbor, or by performing a song in the intruder's repertoire that has previously been performed (Burt *et al.* 2001). Song matching has been observed in a number of common species in Europe and North America, including northern cardinal (Lemon 1968), great tit (Krebs *et al.* 1981), black-capped chickadee (Shackleton and Ratcliffe 1994), red-winged blackbird (Cramer and Price 2007), and western meadowlark (Falls 1985). In bird song where the difficulty (and thus, quality) of the vocalization is determined by physical constraints rather than the cognitive difficulties associated with maintaining a repertoire, mimicry, or innovation, individuals of some species may be inclined to match the physicality of their performance to the song of a singing rival. Swamp sparrows, which rely on a slow trilled song, will perform a more difficult trill in an aggressive context when compared with typical spontaneous song (DuBois *et al.* 2009).

The extent of male response to songs of differing quality or difficulty is still undetermined. While both male and female birds of some species seem to be able to discriminate between simple and challenging vocal performances (e.g. DuBois *et al.* 2010, Cramer and Price 2007, Illes *et al.* 2006, Goodwin and Podos 2013), differences in male vocal performances in response to intruder song quality has seldom been investigated. For the most part, male birds are inclined to respond more actively to a territorial intruder that is producing challenging, and therefore potentially threatening, song. In the swamp sparrow, for example, individuals increased the rate at which they performed singing, aggressive flying, and wing-waving behaviors when faced with a simulated intruder singing difficult song relative to a low-performance control (DuBois *et al.* 2010). The level of aggression with which a swamp sparrow will respond to an intruder also depends on the vocal performance of the individual responding to an intruder in the first place; while conducting an experiment to determine the extent to which aggressive behavior shifts in response to intruder vocal quality, Moseley *et al.* (2013) found that birds that produce challenging songs will respond more aggressively than those that do not. Chipping sparrows (*Spizella passerina*), a species typically considered to be both territorial and largely solitary during the breeding season, have even demonstrated an unprecedented inclination to form vocal "alliances" with neighbors to drive off territorial intruders (Goodwin and Podos 2014). In this case, the vocal alliance is always formed when a high-performance singer assists a low-performance neighbor to out-sing the intruder, further suggesting that these birds can discern the abilities of their conspecifics.

One important caveat to note is that in all of these studies, the differences in vocal performance that the birds were discriminating and responding to occurred on the between-bird, rather than within-bird scale. It remains to be seen whether these effects occur equally when an individual is performing low-difficulty spontaneous song in addition to song performed at the peak of physical constraints that is typically reserved for more aggressive interactions. Another avenue that has yet to be explored is the ability for an adult bird to shift his vocal performance based on the singing ability of an intruder or neighbor; thus far, published studies have evaluated aggressive behavior rate and the overall rate of singing in response to varying vocal quality, but not the within-bird vocal response. Conducting studies like these requires considerable prior work preparing song recordings and determining methods for appropriately quantifying vocal performance for different types of bird song.

Defining and measuring song quality

Defining the quality of an individual bird's vocal performance will vary between species, as different birds have different vocal styles, each with its own range of performance variables. In some groups, like the mimids, vocal quality and performance are largely defined by the size of the song repertoire, which may convey information about the individual's cognitive quality (Howard 1974).

In birds that regularly employ trills in their vocal repertoire, it is possible to define vocal quality using basic physical elements of that trill. This type of vocalization consists of a large number of syllables repeated consistently over the course of the song (Fig. 1). Each syllable in a song typically comprises a sweep through a small and consistent range of frequencies, and the

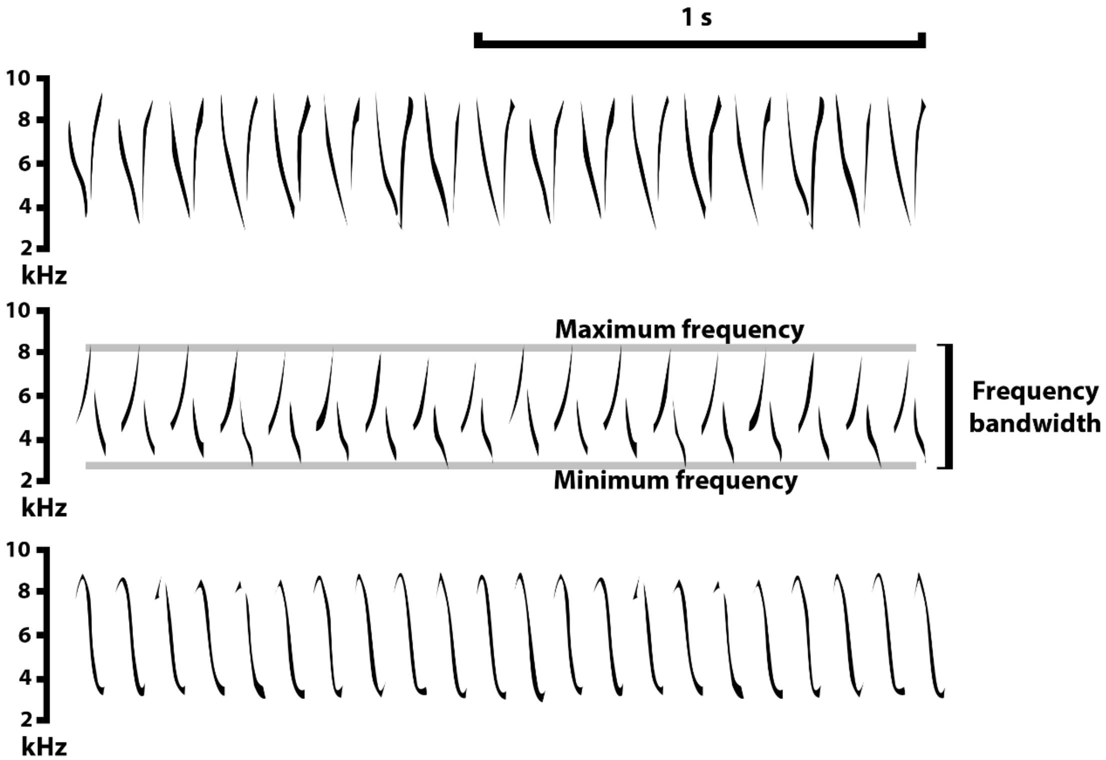

Figure 1. Three exemplars of chipping sparrow song visualized as change in frequency over time, with amplitude represented as the amount of black ink. Trill rate is the average number of syllables performed in a second, and frequency bandwidth is the difference between the average maximum and minimum frequencies, estimated by dragging a line over the top of bottom of the spectrogram.

spacing of the syllables through time in the song is similarly regular. These two qualities can be reliably and repeatably measured: the trill rate is the number of syllables produced per unit time of song performance, and the frequency bandwidth is the average range of frequencies occupied by the syllables in the song.

Producing a trill relies on rapid modulation of the gape size in the bill; opening the bill wider for each syllable will produce syllables with a wider frequency bandwidth, while opening and closing the bill faster will increase the trill rate for the song (Podos 1996). Because it is difficult to produce a vocalization using both a wide gape and very fast opening and closing of the bill, there is a trade-off between these two characteristics of trilled song that is physically constrained (Podos 1997). Plotting the trill rate against bandwidth for many songs sung by birds of a given species that employs the trill in its vocal performance should yield a triangular distribution, with individuals near the top of the distribution giving a vocal performance that best navigate the trade-off between trill rate and frequency bandwidth (Fig. 2). Individuals can be binned by frequency range, with the highest individual in each bin selected to be incorporated into a regression line fit to define the best possible performance. The distance between a given individual's vocal performance and a linear regression line fitted to these best exemplars in the distribution is that individual's vocal deviation, which is inversely related with difficulty of vocal performance (Podos 1997).

One potential critique of this method is to emphasize that a difficult performance is not necessarily the same as a high-quality performance. However, this criticism is gradually

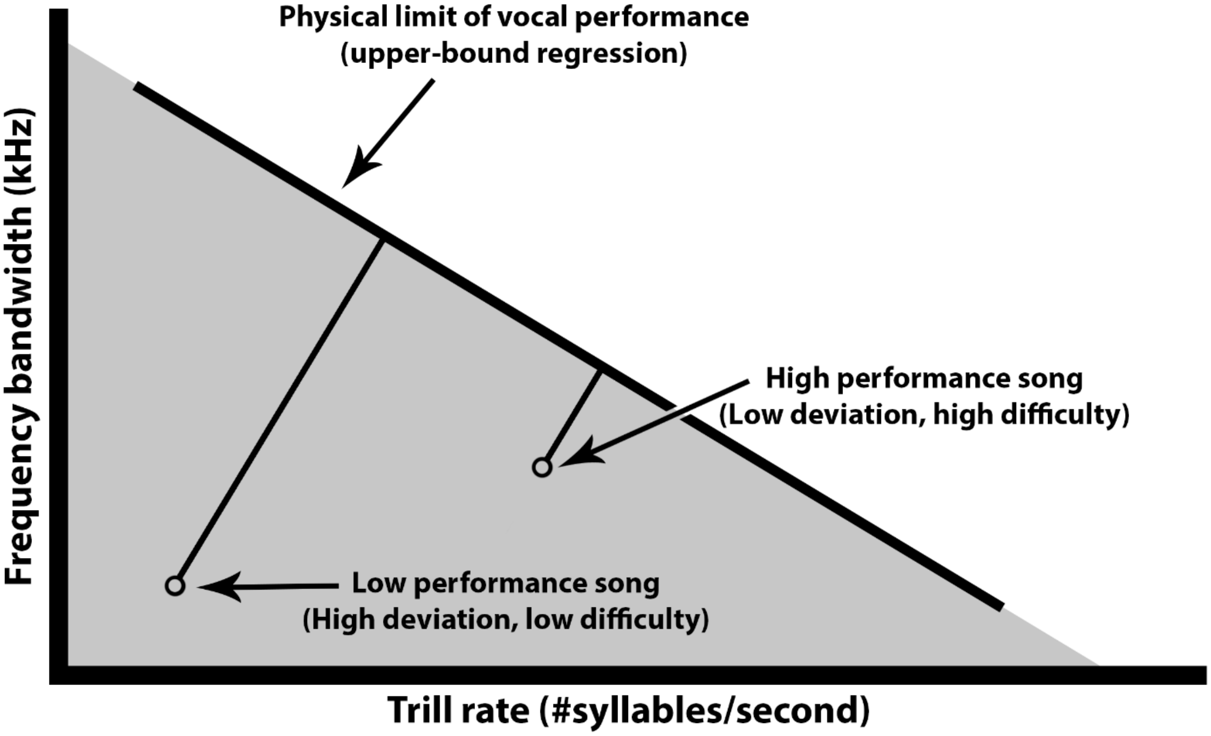

Figure 2. A hypothetical vocal performance distribution for trilled bird song. The gray triangle represents the entire possible range of combined values for trill rate and frequency bandwidth, which are physically limited to an upper-bound regression. The most difficult songs to perform are those with low deviance, measured as the orthogonal distance from the regression line. Adapted from Ballentine (2004).

becoming invalidated by a growing body of field research suggesting that there is a connection between the physical challenge inherent in a vocalization and its quality. Vocal deviation is a reliable predictor of age and body size in swamp sparrows, with older and larger males performing low-deviance, high-difficulty songs (Ballentine 2009). Additionally, females will solicit the males that can perform this challenging song more often than individuals that produce high-deviance trills in both swamp sparrows (Ballentine 2004) and Lincoln's sparrows (Caro *et al.* 2010). Among song sparrows, which will often end their song with a trilled phrase, older males will produce lower-deviance trills (Moore 2013). While these connections with age may suggest that it is possible for a bird to improve his singing over the course of a lifetime, it may be more likely that there is an inherent connection between vocal performance and fitness, and the better singers are simply the birds that survived to an older age. Indeed, other aspects of reproductive fitness have been indicated by vocal performance studies; house wrens that produce physically challenging songs have higher reproductive success (Cramer 2013) and male banded wrens that are good singers have a higher rate of extra-pair paternity than their musically-challenged counterparts (Cramer *et al.* 2011). For a full summary of species studied using this method, see Table 1.

While vocal deviation remains the most popular metric for determining difficulty of song performance for those birds that employ trills in their song, there are some other measurements that have potential for being connected with female and male response to vocal performance. These include such simple measurements as overall song duration, which may be connected with a bird's energy expenditure during an interaction that involves singing (Eberhardt 1994, Oberweger and Goller 2001), or the number of notes per syllable, which acts as an estimate of overall song complexity (Searcy *et al.* 2010).

Project Introduction

Among the emberizids, there are a few species that rely entirely on trilled song for vocal performance. While the most frequently studied is the swamp sparrow, the diminutive chipping sparrow is also a viable candidate for vocal performance studies. Chipping sparrows are distributed across the United States and tend to sing their distinct trill from a high perch in the middle of lawns or fields (Middleton 1998), making them easy to identify, observe, and record.

In this study, I aimed to investigate the function of vocal performance in competitive interactions between male chipping sparrows, with an emphasis on the potential of an individual to modulate his song based on context. Over the course of the 2014 breeding season, I recorded spontaneous song produced by a breeding population of chipping sparrows in central Maine while capturing and color-banding a subset of males for future recognition in the field. Known birds were later presented with multiple exemplars of both high- and low-quality rival song to test the three hypotheses concerning variation in chipping sparrow song: (1) that individuals can modulate their song quality, (2) that there is no modulation of song by the individual, but individuals differ from one another in vocal performance, and (3) that birds neither modulate their song nor differ from one another in vocal performance. I predicted results that would support hypotheses (1) and (2) but reject hypothesis (3): that birds would differ from one another in their vocal ability, and that when presented with a simulated intruder performing a low-deviation, high-difficulty song, a bird would produce a song of greater difficulty than he would when presented with a simulated intruder performing a high-deviation song.

Materials and Methods

Study time frame and location

This study was conducted between April and August 2014 on and around the Bates College campus in Androscoggin County, Maine (44.106512, -70.202011). Focal animals were adult male chipping sparrows (*Spizella passerina*) singing to defend a breeding territory, selected by canvassing likely habitat areas and following visual and auditory cues to locate individual birds. All song recording, bird capture, and playback experiments took place between 0600 and 1200 hours in fair weather.

Bird capture and sampling

Targeted netting efforts were made to capture familiar male chipping sparrows on the Bates College campus, using 30 mm mist nets in conjunction with song recordings played from an iPhone through a Radio Shack mini amplifier-speaker (Model #277-1008) combination and hand-painted chipping sparrow decoy model. After extraction from the net, each bird was banded with a size 1C federal metal band and a combination of three unique Darvic 2.8mm color bands for future identification in the field.

Following color banding, bill morphology of each individual was characterized by measuring three separate dimensions using analog calipers: culmen width (width of the bill measured at the front of the nares), culmen depth (the length of the bill from its tip to the front of the nares) and exposed culmen depth (the length of the bill from tip to base. The extent of rufous feathering on the cap was also measured with analog calipers to potentially provide further information about the individual’s age and condition.

Finally, each individual was blood sampled and weighed before being released. Blood samples were collected by puncturing the brachial vein with a needle and collecting blood in a capillary tube.

Spontaneous song recording

In order to establish a baseline collection of songs on which to base future vocal performance playback experiments, spontaneous chipping sparrow song was recorded throughout the spring and summer (n=425 songs from n=29 birds). All recordings were made with a battery-operated Marantz PMD-661 MKII recorder and Senneheiser ME67 shotgun-style condenser microphone operating from a target distance of 5-10m away from the bird.

While recording spontaneous song, the bird would be sighted and identified by color band combination or the absence of bands altogether. By mapping the territories of birds observed in the field using the ArcMap software package, it was possible to identify certain unbanded birds that maintained a territory surrounded by banded individuals.

Song analysis and characterization of song performance

Following methods developed by Podos (1997), all song recording files were reviewed and analyzed using the Cornell University RavenLite 1.0 [Update 22] audio software package. Each audio file was first reviewed to ensure that it contained songs that were clear enough to be accurately and repeatably measured.

To measure trill rate, i.e. the amount of syllables produced per unit time in a given song, the number of syllables was counted manually and divided by the duration of the song. Frequency bandwidth, or the average range of frequencies spanned over the course of the song, was measured by dragging a horizontal gridline to the frequencies that best approximated the maximum and minimum frequency of the song and then taking the difference between the two.

To construct the vocal performance distribution of the population, trill rate and frequency bandwidth were plotted against each other. The top performance song in each of 10 bins of trill rate was then visually identified and singled out to construct a regression line that would serve as the performance bound for the distribution. The orthogonal distance of a given individual's song from this line is the "vocal deviance" of the individual; high vocal deviance indicates a low quality song, while high quality songs are represented by lower vocal deviance. The vocal deterioration factor, or the average change in vocal deviation with each song repetition during a singing bout, was calculated as the slope of the regression line during that singing bout for that bird.

The vocal performance distribution for local birds was contextualized by supplementing my 425 locally recorded songs with an additional 10 open-source recordings from the Cornell Lab of Ornithology MacCaulay Library, using birds recorded in other areas in the United States (accession numbers listed in Appendix B).

Playback experiments with known birds

In order to determine if male chipping sparrows would modulate their song performance in response to simulated territory intrusions by both high- and low-deviance singers, multiple song examplars were engineered using a combination of RavenLite 1.0 and Audacity 2.0.6 software. Songs from the 25th and 75th percentile of the vocal performance distribution were selected and then modified to create three separate exemplars of good-bad song pairs to be presented to individuals in the field. Songs in a pair were identical in duration but varied in trill rate and frequency bandwidth and thus in vocal deviation.

Birds eligible for the playback experiment were individuals that could be positively identify based on a combination of color band combination (or lack thereof) in addition to territory and song perch location. Upon locating an eligible animal in the field, the song pair to which it would be exposed was randomly determined following elimination of any song pairs that included that individual's song or the song of a close neighbor. Additionally, the order in which each bird would be exposed to good or bad song was randomly determined.

The playback experiments took place on two consecutive days for each bird participating, though extra days were necessary in about 15% of the cases, if the bird was impossible to locate or did not remain for the entirety of a day's playback. Each day's playback experiment followed a "before-during-after" design, where a bird's song performance could be compared across different phases of the playback. Each bird was first presented with three minutes of a simulated intruder's song from a handheld Radio Shack mini amplifier-speaker combination at a distance of 5-10 m. To ensure that stimulus volume remained similar between playback phases and birds, a Radio Shack sound level meter (Model #2055) was used to confirm the playback volume. This distance would be maintained throughout the playback experiment. After three minutes of simulated intrusion, the bird would be allowed two minutes of response without the playback. Following this two-minute refractory period, the second simulated intrusion would begin and continue playback for three-minutes before another two-minute response period followed. On the following day, the same recording pair was presented but with the order of intruder quality reversed to allow for control of stimulus presentation order.

Songs recorded from focal birds during each phase of the playback experiment were analyzed for differences in trill rate, bandwidth, and orthogonal distance from the performance bound. Additionally, the overall singing rate was measured for each playback phase as the number of songs performed during the two- or three-minute period.

Data analysis

After the characterization of song metrics in RavenLite, all data were analyzed using a combination of Microsoft Excel, GraphPad Prism 6, and Minitab 17 software packages. For data used in parametric statistical analyses, the distributions were tested for normality and equal variances before proceeding. For the morphological characteristics measured on captured birds, a Pearson correlation matrix was used to check for any association between the variables. To establish the relationship between trill rate and bandwidth and determine the presence of a physical trade-off between the two characteristics, a linear regression was performed. Upper-bound linear regression was also used to generate the upper-performance bound equation later used in calculating vocal deviation. Due to the two-factorial design of the playback experiment, the bulk of analysis was performed using two-way ANOVA. The effect of both playback quality (good or bad) and phase (during or after) was tested for the dependent variables of trill rate, bandwidth, and vocal deviation in addition to song rate and vocal deterioration. A new metric, vocal deterioration was established to determine how a bird’s vocal performance changes over the course of a song bout and was calculated as the average slope of the regression line of vocal deviation over time, approximated as the song number performed (Fig. 3). To determine the relative variation in vocal performance on between- and within-bird scales, an intra-class coefficient of correlation (Lessels and Boag 1986) was calculated. All means are reported ± SEM.

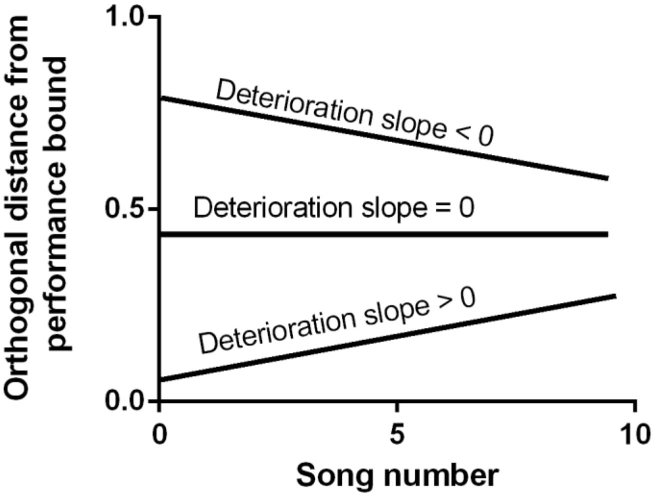

Figure 3. Three hypothetical scenarios for vocal deterioration, which is defined as the average change in vocal deviation as the song bout progresses through time. A deterioration slope greater than zero indicates decreasing quality (increasing deviation) over the song bout, while a slope less than zero indicates increasing quality.

Results

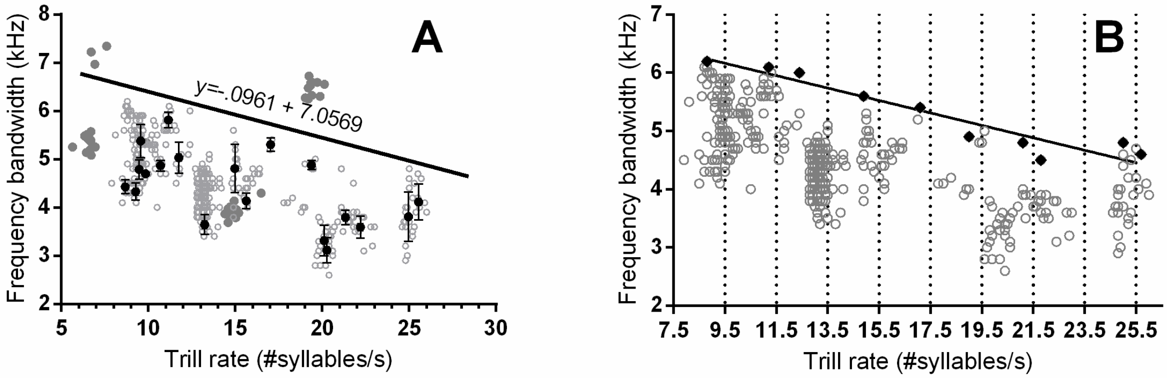

Figure 4. (A) Vocal distribution with upper performance bound (elevated above actual position for ease of view) for chipping sparrows recorded on and around the Bates College campus, with mean vocal performance (±SEM) for known birds in black (n=27), all songs recorded in light gray circles (n=426), and Macaulay Library recordings in dark gray (n=61; not included in calculating the performance bound). (B) Actual top performance songs used to calculate the linear regression for upper performance bound (black diamonds) with the ten trill rate bins delineated by dotted lines.

Vocal performance distribution

The Bates College chipping sparrow population recorded for use in developing a vocal distribution conformed to the strict physical trade-off between trill rate and bandwidth (m= -0.09162 ± 0.01066, r^2=.4018, p=.0004). The upper performance bound was determined by selecting the highest-bandwidth songs in each of ten trill rate bins and then calculating a separate regression using those points (Fig. 4). Vocal deviance, the orthogonal distance from a given point to the upper-performance regression line, occupied a range from 0 (at the points coinciding with the boundary) to 2.324 for individual songs, with a mean deviance of 0.8620 ± 0.02625 (n=426). Recordings sourced from the Macaulay Library to expand the distribution did not differ from local recordings in vocal deviation (t_{30}=0.7108, p=0.4827). A paired t-test comparing vocal performance in spontaneous song and song elicited by playback stimuli demonstrated that there was no shift in average bandwidth (t=1.125, p=0.3035), trill rate (t=1.759, p=0.1291) or vocal deviance (t=1.810, p=0.1203) for known individuals.

Morphology and vocal performance of captured birds

Targeted capture efforts on the Bates College campus yielded 9 male chipping sparrows captured and banded (Table 2). A Pearson correlation matrix revealed no statistically significant correlation between any two measured morphological traits (Table 3). There were moderately large positive but non-significant correlations between culmen width and tarsus length (r=0.58, p=0.100), culmen width and wing length (r=0.55, p=0.127), wing length and tarsus length (r=0.513, p=0.158), and culmen width and the length of the rufous cap (r=0.62, p=0.075).

Of the 9 captured birds, 5 returned and sang during recording sessions (Fig. 5). The three main song metrics of trill rate, frequency bandwidth, and vocal deviation were included in a correlation matrix with key morphological characteristics. The sample of only 5 birds made correlation analysis even weaker (requiring $|r| \geq 0.878$ for statistical significance), and again there was no statistically significant correlation between any two traits. However, rufous cap length and trill rate showed a fairly strong negative relationship (r= -0.725, p=0.166).

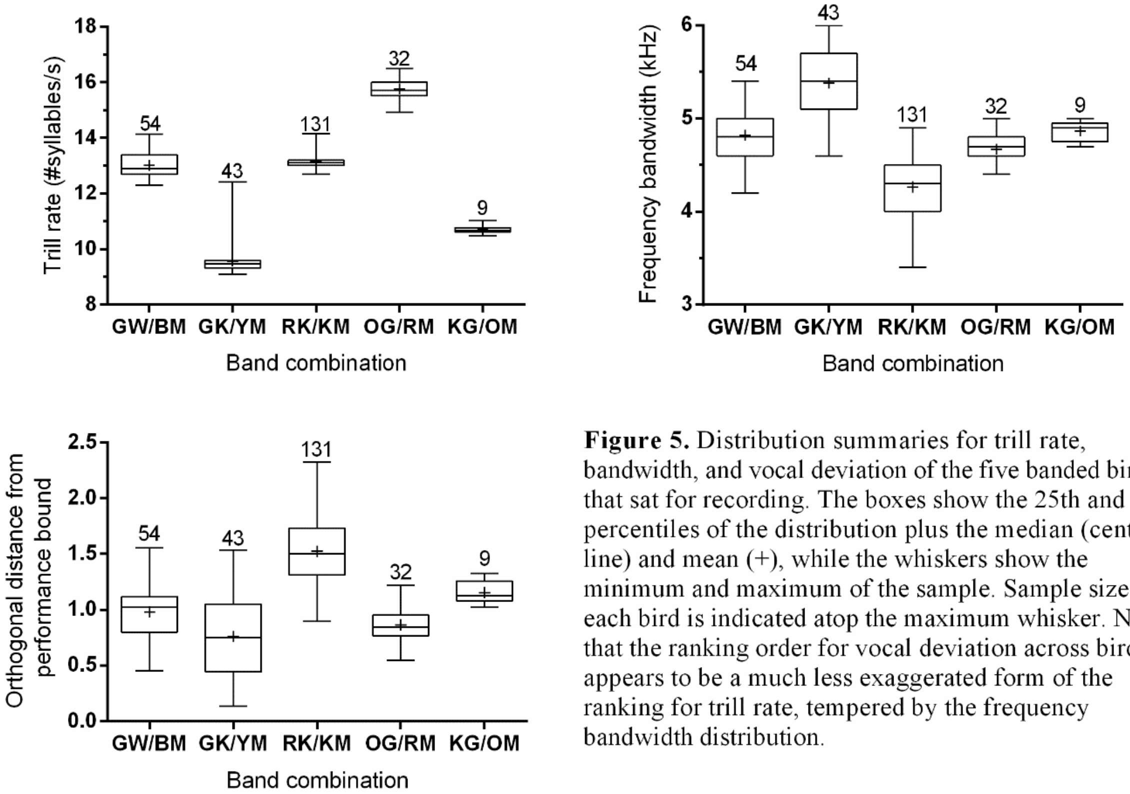

Figure 5. Distribution summaries for trill rate, bandwidth, and vocal deviation of the five banded birds that sat for recording. The boxes show the 25th and 75th percentiles of the distribution plus the median (center line) and mean (+), while the whiskers show the minimum and maximum of the sample. Sample size for each bird is indicated atop the maximum whisker. Note that the ranking order for vocal deviation across birds appears to be a much less exaggerated form of the ranking for trill rate, tempered by the frequency bandwidth distribution.

Within-bird vs. between-bird variation

Song recordings were obtained from a larger sample of birds, which were tentatively identified to the individual by a combination of color bands (a minority of birds) and territory and song perch location. Of 27 birds with at least 10 songs recorded, each appeared to have some variability in bandwidth but not in trill rate. Comparing the proportion of variability occurring between individuals rather than within the individual is valuable in distinguishing what vocal characteristics are more strongly rooted in a bird’s identity as opposed to those that can be modulated more freely. In three separate one-way ANOVAs in which each individual bird was a factor level, there was a significant effect of bird identity on song parameters related to vocal performance: trill rate ($F_{28,777}$=8237, p<0.0001), bandwidth ($F_{28,777}$=212.7, p<0.0001), and deviation ($F_{28,777}$=50.74, p<0.0001. An intra-class correlation coefficient (Lessels and Boag 1987) revealed that trill rate was extremely repeatable within birds (r=0.9938), with repeatably being lower but still significantly from zero for bandwidth (r=0.8894) and vocal deviation (r=0.6538). The difference in variation between trill rate and bandwidth is apparent in within-bird coefficients of variation; the coefficient of variation averaged across birds for bandwidth is more than twice as large as it is for trill rate (t=3.957, p=0.0002). While bandwidth is shown here to be the more-often varied aspect of vocal performance in trilling birds, this difference is also possibly compounded by the higher rate of error inherent in measuring frequency bandwidth.

Playback experiments

Of the 15 birds that could be identified in the field on multiple days using a combination of color banding, territory, or song perch, only 10 could be located on consecutive days for playback; of those birds, only 8 remained for the duration of the playback experiments.

As detailed in the Methods, three song pairs were engineered from previously recorded chipping sparrow songs to have consistent song length and song rate, and varied primarily through manipulation of trill rate rather than bandwidth (Fig. 6). Because of this, the difference between songs in a pair fell well outside the within-bird ranges for trill rate and deviation, but within the within-bird range for frequency bandwidth. The scale of the difference in deviance between pairs

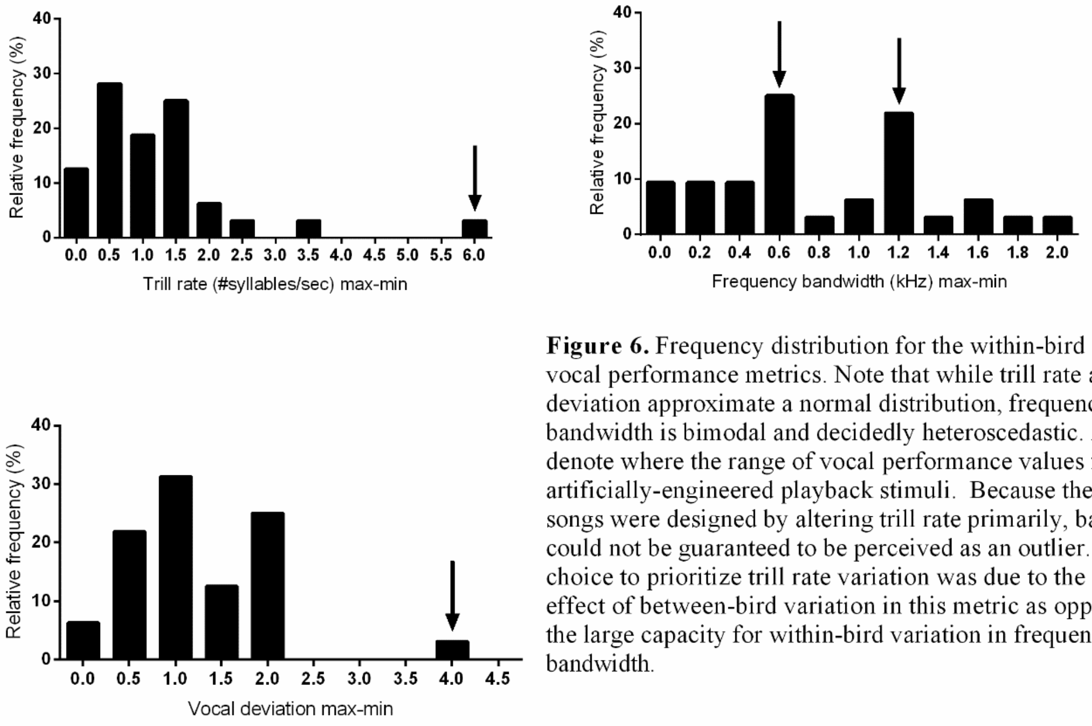

Figure 6. Frequency distribution for the within-bird range of vocal performance metrics. Note that while trill rate and vocal deviation approximate a normal distribution, frequency bandwidth is bimodal and decidedly heteroscedastic. Arrows denote where the range of vocal performance values fell in the artificially-engineered playback stimuli. Because the playback songs were designed by altering trill rate primarily, bandwidth could not be guaranteed to be perceived as an outlier. The choice to prioritize trill rate variation was due to the larger effect of between-bird variation in this metric as opposed to the large capacity for within-bird variation in frequency bandwidth.

of stimulus songs makes it possible that during the playback experiment, target birds would perceive that the simulated intrusions were sufficiently different to have come from two separate birds.

A set of 2-way repeated-measures ANOVA was used to check for both the effect of playback quality (either good or bad) and playback phase (song performed either during the playback or after the playback). Overall, these ANOVAs revealed no effect of either factor individually or interactively on trill rate, bandwidth, or vocal deviation (Fig. 7; Table 3), though there was a case of marginal nonsignificance in the effect of playback phase on trill rate ($F_{1,14}$=2.452, p=0.1397), which increased 0.3% during playback.

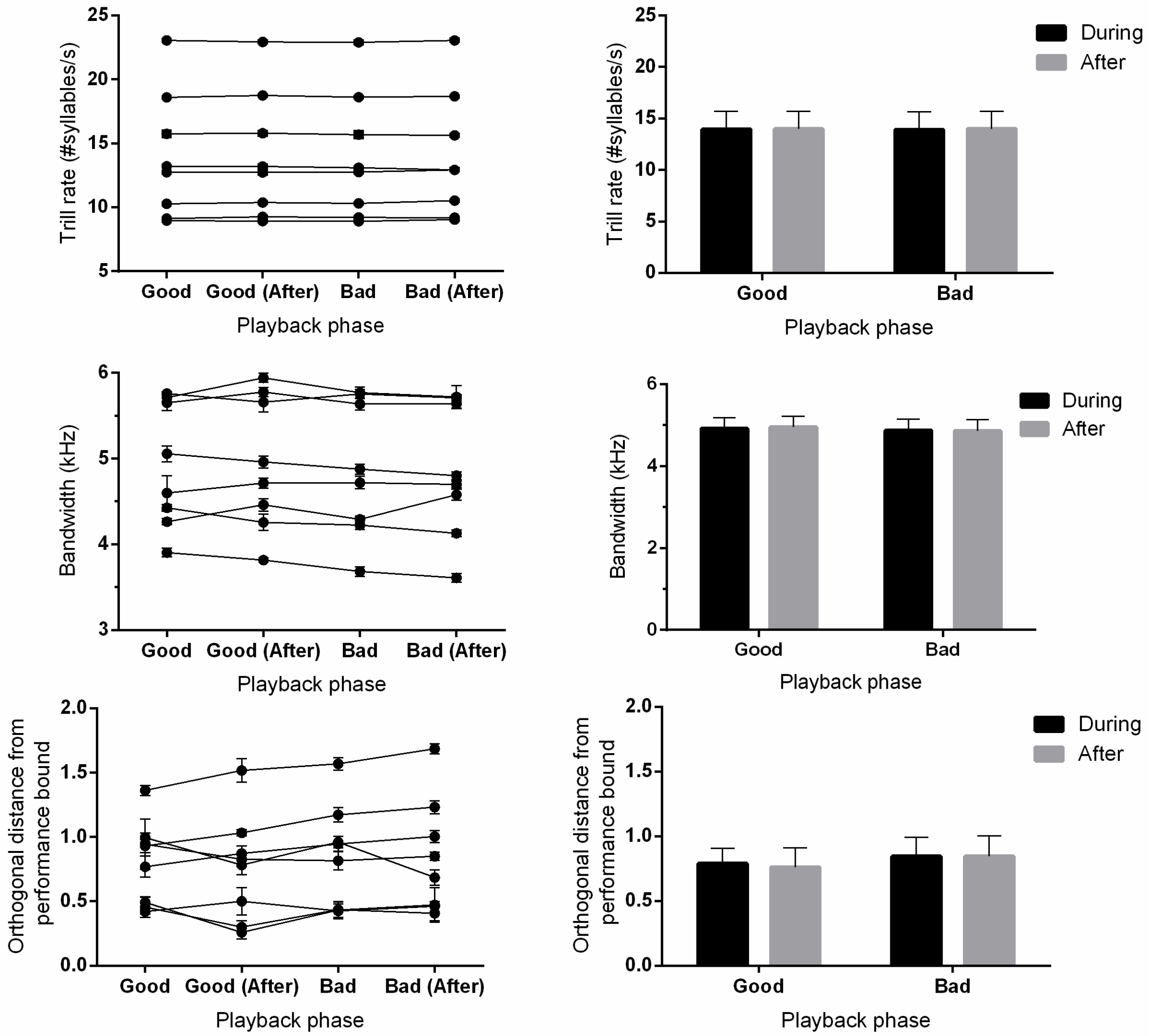

Figure 7. Mean (±SEM) trill rate, bandwidth, and vocal deviation for each bird (left) and in summary (right) during a playback experiment testing for modulation in vocal performance by stimulus quality (good or bad) and playback phase (during playback or after playback). There was no change in vocal performance in any of the three metrics (Two-way repeated measures ANOVA, p>0.05).

For trill rate, bandwidth, and vocal deviation alike, the largest source of variation was from the individual bird performing the song (between-subject factor of bird identity; $p<0.0001$). These results were not confounded by the order in which the good or bad playback stimuli were presented; the order of presentation, already randomized, also did not affect trill rate ($F_{1,14}$=<0.01, p=0.999), bandwidth ($F_{1,14}$=0.014, p=0.906), or vocal deviation ($F_{1,14}$<0.02, p=0.994).

The number of songs per minute did increase by 13% during playback when compared with the silent after-playback phase ($F_{1,14}$=6.60, p=.0223; Fig 8). Quality deterioration was moderately variable through the playback experiment (Fig. 9), with average vocal deviance remaining unchanged after playback but consistently negative during playback, indicating a gradual increase in vocal performance quality during these stimuli. These qualitative differences fell short of statistical significance, however ($F_{1,12}$=1.08, p=0.319).

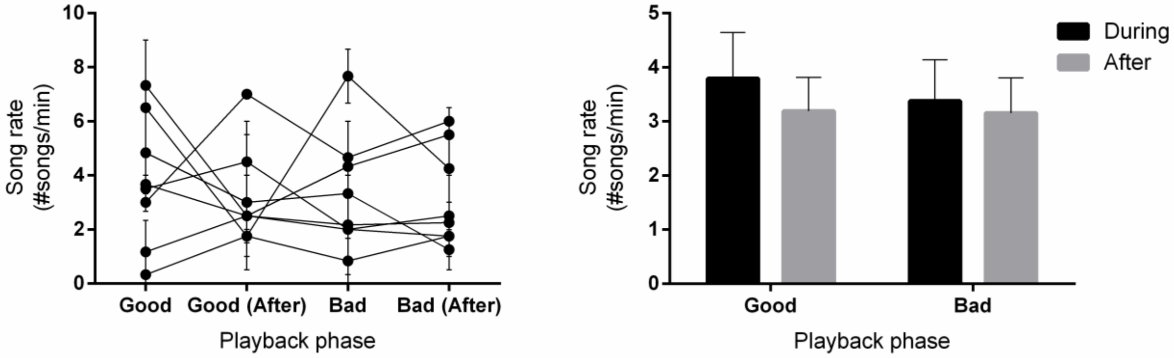

Figure 8. Mean (±SEM) song rate for each experimental bird (left) and in summary (right), averaged across birds. Two-way repeated measures ANOVA indicated an increase in song rate during playback ($F_{1,14}$=6.60, p=0.0223), no change in song rate by playback quality ($F_{1,14}$=0.09, p=0.7345), and no interaction between the two ($F_{1,14}$=0.12, p=0.734).

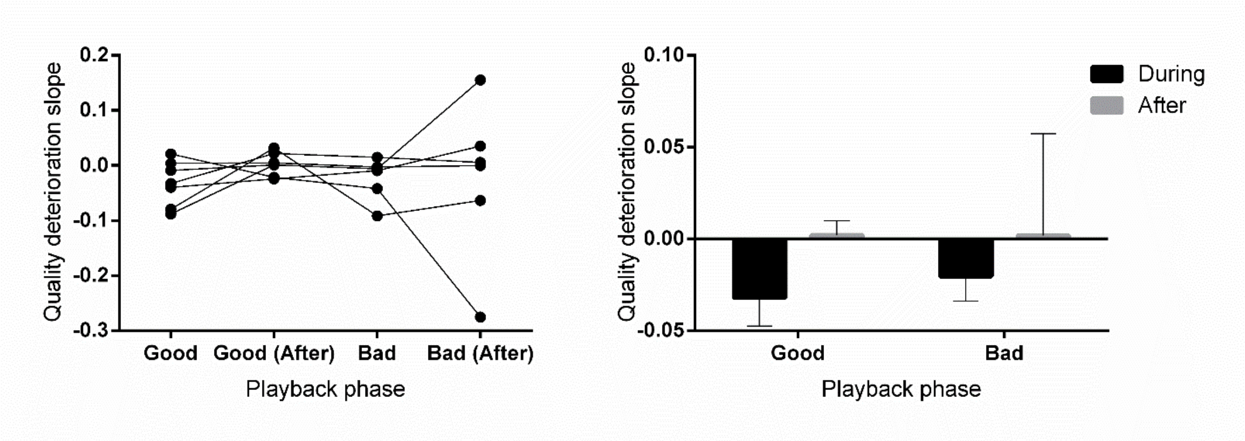

Figure 9. Mean (±SEM) rate of vocal deviation change over a singing bout for each experimental bird (left) and averaged across birds (right). There was no change in deterioration by playback quality ($F_{1,14}$=0.03, p=0.863) or phase ($F_{1,14}$=1.08, p=0.319), and no interaction between the two ($F_{1,14}$=0.05, p=0.829).

Discussion

Characterizing the population

A physical trade-off originally described for numerous sparrow genera by Podos (1997) and then later by other researchers (e.g. Ballentine 2004, Cramer and Price 2007, Cardoso *et al.* 2007) is clearly present in this population of chipping sparrows, which validates the use of vocal deviation as an accurate indicator of relative vocal performance. For both trill rate and bandwidth, within-bird variation was negligible when compared to the large-scale variation that occurred between birds. Notably, within-bird variation in bandwidth was significantly greater than that of trill rate, while individual birds differed considerably from each other in the key song metrics of trill rate, bandwidth, and vocal deviation. This suggests that although individual males do have a set range of vocal performance qualities that differ greatly from one bird to another, each male also does have the capacity to vary his vocal performance somewhat. The within-bird variation in song may have little effect on the behavioral response of rival males and mate-seeking females, however, since it is so much smaller than the between-bird variation.

Due to both time and personnel constraints, it was impossible to put in sufficient sampling effort required to capture numerous birds for banding and morphometrics. The small sample and corresponding low power make it difficult to interpret the nonsignificance in the correlation matrices for bird body measurements and song metrics. Most notably, the length of the rufous cap appeared to increase with increasing bill length and decrease with increasing trill rate. It is currently unknown whether the reddish cap of the chipping sparrow is used in sexual display whatsoever or if the subtle differences in male and female plumage are sufficient for this mark to be used in such a way. The significance of the distinct reddish-brown of rufous markings in general is also not completely understood. It is known to serve as a sexual ornament in species like the barn swallow (McGraw *et al.* 2004), but the pigment origin of rufous coloration is from melanin, easily manufactured by birds in the feather follicles (Ralph 1969). This means there is no obvious connection with fitness-defining traits like food-finding and metabolic ability, as is reflected in the red diet-derived carotenoid pigments (Hill 1990).

One other near-correlation of note was the negative relationship of culmen depth and trill rate. Because of the physically-controlled nature of maximum feasible trill rates, bill morphology is one of the key variables that can affect a given bird's ability to produce trills with a high syllable rate. A longer bill has more space that must be opened and closed to produce a single syllable, and will thus bring about a lower trill rate (Podos 2001, Huber and Podos 2006) all else being equal. Although there is no current research available on chipping sparrow bill size and food-finding ability, it is possible that a smaller bill size conveys some sort of fitness advantage to the individual and that female preference for high trill rate reflects this advantage.

Though no correlation was present connecting vocal metrics with key indicators of overall body size, such as tarsus length and wing length, this topic is certainly deserving of further research. Though within-population size variation in small songbirds is not obvious to the casual observer, it was recently discovered that the diminutive willow warbler's song decreases in pitch with increasing tarsus length (Linhart and Fuchs 2015).

Do individual chipping sparrows differ from one another in their vocal performance?

Among the birds involved in this study, variation in all aspects of vocal performance was overwhelmingly due to the effect of a given bird's identity rather than the playback circumstances during which he was recorded. Beyond differences in trill rate and bandwidth, individual chipping sparrows also sang notes of different shapes. This trait can be audible even to human observers, though the significance of note variety to the birds is unknown (Marler and Isaac 1960). The difference in song from bird to bird could be due to genetic makeup and developmental conditions, both of which may affect a male's attractiveness or value as a mate (Weatherhead and Robinson 1979), though little is known about the role of song variation in mate choice in this species.

Ontogeny of bird song

The extent to which genetic makeup affects intraspecific variation in bird song is still unknown. However, there is a well-established understanding of the role that ontogeny plays in shaping song before it can be employed to defend territory or warn of impending attack. The order Passeriformes is divided into two suborders: the oscine songbirds, which comprise most of the order, and the suboscines, which all occur in Family Tyrannidae. In the oscine songbirds, song learning is a social process and cannot be completed if the juvenile bird does not have the opportunity to listen to and copy adult song (Beecher 2010). In developing the full song of an adult songbird, a juvenile must go through two vital learning periods during which it will produce "subsong" as it learns to vocalize properly. The first of these two periods is the plastic phase, which lasts for most of the bird's juvenile life. As the young bird's brain develops, it listens to the songs around it and may make some attempts to imitate that song, but this song will be abbreviated and never given in the proper position associated with full adult song. The second phase, the crystallization period, takes place very quickly following the plastic phase. The timing of the crystallization period can vary highly from species to species; in some birds, song crystallizes during the first spring as the young bird establishes his territory, while in others crystallization may not occur until after the second spring (Konishi 1985).

Even in birds with simple songs like the chipping sparrow, often considered to have a “repertoire of one” from which to dip when choosing which song to sing, there can be a surprising amount of flexibility in song development. Adult male chipping sparrows will remain loyal to a single syllable type, varying the way in which that syllable is repeated in his trills, but the story is somewhat different for the juveniles; like many birds, young chipping sparrows go through a plastic phase of song learning during which they mimic the song of adult “tutors” around them before finalizing their song during the crystallization period early in the second year (Baptista and Gaunt 1997). During this plastic phase, each bird will experiment with singing a variety of songs that differ widely in note shape (Liu and Kroodsma 1999); to this date, there has been no research on the role of development in establishing trill rate and frequency bandwidth of adult song.

Liu *et al.* (2007) investigated chipping sparrow song development in juveniles reared with and without tutors, as well as in completely deafened birds. If allowed to develop normally, exposed to multiple songs of adult male tutors, a young chipping sparrow will maintain anywhere from 5 to 7 song signatures and practice these as subsong. The crystallization period occurs in late spring, after the juvenile has settled on a territory and dropped all song signatures from his repertoire except for the one that most closely resembles his closest neighbors. This is set as the individual's single song as an adult chipping sparrow. One might think that the several song types retained in the plastic phase of song learning require the presence of different vocal tutors to imitate, but sparrows raised in a sound-proof isolation chamber improvised 5 to 6 subsong types that were completely similar to the precursor-songs produced by juveniles raised with tutors. Juveniles captured during their second spring and then exposed to a single tutor's song experienced a brief instability in vocal repertoire before crystallizing their song to match the tutor's. Even in deaf birds, the juveniles experimented vocally to perform their own subsongs (though these were fewer and different than the subsong performed by birds with intact hearing) and dropped all song types but one during the crystallization period. This suggests that even though the precise development of a given song type would typically be reliant on the adult birds surrounding a newly-independent juvenile chipping sparrow, the neurological framework for song development and crystallization is there even with hearing removed.

In chipping sparrows hand-reared with live adult tutors provided at different life stages, the crystalized adult song more closely resembled a given bird's neighbors during the crystallization period rather than his early tutors (Liu and Kroodsma 1999). In this study, the father's song was not played for the juvenile sparrows and the birds did not produce vocalizations similar to the paternal song. However, chipping sparrow nestlings in the field developed songs that strongly resembled their father's song, likely because of his proximity. In some species, such as Darwin's finches, this trend can even be extended back a generation—offspring bird song will resemble the paternal grandfather, which presumably tutored the father, but not the maternal grandfather (Grant and Grant 1996). Overall, the evidence from oscine songbirds suggests that while the neurological foundation for learning and producing vocalizations is inherited genetically, the specific shape that a bird’s song takes as it develops is culturally inherited.

Effects of ontogenic challenges on reproductive success

Numerous constraints exist during avian development, especially in the realm of vocal performance. During development, birds grow a unique portion of their brain called the hyperstriatum ventrale (HVC), the size of which positively correlated with song repertoire size (DeVoogd *et al.* 1993). The HVC resides on the dorsal portion of the cerebrum and neighbors the hippocampus, a key brain region in spatial learning and memory (Sherry *et al.* 1992). In young song sparrows (*Melospiza melodia*), the development of these two areas may be subject to a trade-off. In an experiment involving captured adult birds, Sewall *et al.* (2013) administered a series of spatial learning tests to the sparrows and found that spatial learning error rate increased predictably in birds that had larger song repertoires. The authors do note that only the spatial learning rate was measured, and that the actual capacity for spatial memory in each bird could still be similar regardless of repertoire size. The fact that large repertoire size (a trait that is associated with high rates of female solicitation) actually comes at the cost of other neurological abilities is particularly interesting because it suggests that repertoire size may actually function as a handicap signal in these birds; a particularly fit song sparrow will be able to forego development in other areas of the brain in favor of growing the HVC, and if he can survive to reproduce in spite of the neurological handicap he may be displaying extraordinary fitness.

During development, introducing stressors to the young bird’s body can be reflected in aspects of its anatomy and physiology that are visible into adulthood. This “nutritional stress hypothesis" (Nowicki *et al.* 1998) poses that poor nutrition or inadequate food consumption in a bird's juvenile stage will in turn depress less-necessary aspects of the bird's development, which can include the growth of sensorimotor centers in the brain associated with singing. This early stress, which will be reflected in numerous body systems, may then be unintentionally communicated to females during vocalization. This hypothesis stands on a few key assumptions: (1) early nutritional stress affects the reproductive fitness of a bird, (2) vocal performance is affected by this nutritional stress, and (3) female listeners are able to detect the effects of nutritional stress encoded in song.

Nowicki and colleagues (2002) tested the first two assumptions of the nutritional stress hypothesis in a small sample of swamp sparrow nestlings. The captive birds were separated into two experimental groups and raised with vocal tutor recordings, but only one group of birds was fed to satiation; the second group was only fed to 70% satiation for 14 days, after which all birds were offered identical amounts of food. A growth gap in body mass was evident between the two groups of birds beginning on their sixth day of development, but this gap began to close once all birds were allowed to feed to satiation. Both groups crystallized their song at similar ages, but the effect of nutritional stress was evident in brain mass. The 14 days of less food left the experimental group with a significant decrease in the mass of their HVC and the robust nucleus of the arcopallium (RA), another brain region associated with song production. The nutritional stress group also copied the tutor songs less accurately than the control, indicating decreased vocal performance as a consequence of the decreased HVC and RA size. What is most remarkable about this study is the duration and extent of stress required to elicit a response in the nestlings; two weeks of not being fed to satiation resulted in impaired brain development and a decreased ability to copy tutor songs properly, a step that is key to producing quality songs as an adult. Both nutritional and corticosterone stress were later observed to limit HVC growth in a larger sample of zebra finches (*Taenopygia guttata*; Buchanan *et al.* 2004). The effect of nutritional stress on the physical components of vocal performance in trilled song has yet to be explored, but will be vital to determining the extent to which nutritional stress during development may affect a young songbird's ability to defend a territory, attract a mate, and reproduce in adulthood.

Of the many limitations imposed on a bird's song during ontogeny, one may be as simple as the difficulty in processing the auditory information contained in high-performance trills sung by tutors. During the sensitive plastic phase of song development in the swamp sparrow, from 15 to 106 days of age, young birds will attempt to mimic the songs of nearby tutors, even skipping over syllables in their own song when attempting to produce a physically impossible trill that has been modified digitally (Podos 1996). While this constraint was long thought to be purely physical, with the young sparrow cutting out syllables to accommodate the performance of a faster trill, new research suggests that early singing constraints may also have neurological origins. In swamp sparrows implanted with electrodes at sensorimotor centers of the HVC, the neurons fired reliably when the bird was played songs with natural trill rates, but the reliability of the neuron signaling deteriorated as the trill rate was artificially increased to exceed natural speeds (Prather *et al.* 2012). If this neurological limitation holds true in the chipping sparrow, which trills markedly faster than the swamp sparrow, then the constraints in song development are twofold: both the ability to hear and process syllable rate and the ability to produce those syllables are tested during song development.

Do chipping sparrows modulate their vocal performance in response to intruders?

The only circumstance that did effect a change in song performance was whether the bird was singing during playback or during the silent "reset" period following the intruder simulation. When playback was on, simulating the presence of a singing intruder, the sparrows increased the rate at which they sang by 13%. Focal birds also exhibited a very slight increase in trill rate and decrease in vocal deterioration, but neither of these was statistically significant. The rate of singing is one way a bird can increase the aggressiveness of his signaling based on circumstance (DuBois *et al.* 2010), and in a manner that is possibly less physically stressful or more physically feasible than ramping up the frequency bandwidth or trill rate of the song itself. The fact that the focal birds changed their singing rate in response to experimental playback of conspecific song demonstrates that they are attentive to territorial challenges and are capable of—and willing to—modulate at least one aspect of their singing behavior in response to our experimental protocol. Furthermore, this behavioral response to song playback supports the use of these particular edited chipping sparrow songs as playback stimuli. Consequently, the lack of focal birds' modulation of trill rate or bandwidth is not because the focal birds failed to recognize our playback as territory challenge by a conspecific.

Overall, the largest source of variation for all aspects of song measured was the individual identity of the bird; each bird studied behaved differently toward the playback. Clearly, other aggressive inclinations such as soft singing, wing-waving, attack flights, and angry "chip" vocalizations were not included as part of the behaviors assessed during this study.

Despite the presence of significant variability between birds in trill rate, frequency bandwidth, and vocal deviation alike, simulated back-to-back intrusions of birds singing high- and low-deviation song evoked no shift in any aspect of vocal performance by the focal territorial birds. Although sample sizes for the experiment were small, the p-values in the statistical output were so large—and lack of visual pattern in the graphs so apparent—that the lack of statistical significance seems likely to reflect a biological reality. The biological source of this lack of response is a far more complex matter, however. If the birds were to respond to the playback with modulation of vocal performance, they would have to (1) be able to discriminate vocal performance qualities in competing males, (2) be physically capable of modulating their own trill rate or bandwidth, and (3) be inclined to respond to this differential performance using song rather than some other signal.

Can male chipping sparrows discriminate between good and bad vocal performance?

The lack of evidence in this study that chipping sparrows can even distinguish between good and bad vocal performances is somewhat disconcerting; because a single researcher was present in the field for any given playback experiment, it was not possible to document other aspects of the birds' aggressive responses that are typically quantified in similar research, such as approach distance to a speaker or mount or a species-specific aggressive display (e.g. Ackay *et al.* 2013, Burt *et al.* 2001, Hof and Hazlett 2010, Linhart and Fuchs 2015, Mosely *et al.* 2013). Luckily, numerous existing studies do suggest that it is possible and even common for male songbirds to modulate behavior in response to changes in the vocalizations of competitors; the presence of a behavioral change in the presence of differing vocal abilities necessitates that the bird be able to distinguish between the vocal performances in the first place.

In chipping sparrows specifically, one study certainly suggests that the birds will change their aggressive response to simulated intrusions based on the trill rate of the intruder. When presented with song that had an artificially-increased trill rate, males approached the source of the sound more closely, spent more time investigating the source of the sound, and later attacked a taxidermic chipping sparrow mount more (Goodwin and Podos 2014). Unfortunately, chipping sparrows appear to be a seldom-used model organism for studies of aggressive signaling in birds; most of the literature available on the topic covers a range of other species.

The swamp sparrow is one often-studied emberizid triller that is known to shift its vocal performance in different aggressive contexts. In a 2010 study by DuBois *et al.*, male swamp sparrows dramatically increased the rate of aggressive behaviors when presented with a high-quality vocal performance when compared with a low-performance control. The behavioral changes included both non-vocal displays such as wing-waving and attack flights, as well as the rate at which the target birds performed both regular and soft song. In particular, soft song has been connected with high levels of aggression in male songbirds (Akcay *et al.* 2011). Most notably, this differential response to vocal performance only occurred when the researchers presented target birds with vocal stimuli that were different on the between-bird, rather than within-bird, scale of variation. When the same population of sparrows was confronted with two separate playback rounds representing the high- and low-performance extremes within a single bird, there was no differential response in any of the measured behaviors. This indicates that male swamp sparrows are certainly able to distinguish performance differences on the between-bird scale (as were presented to the subjects in this study) and inclined to respond to those differences, but either cannot discriminate or will not respond to smaller-scale performance shifts.

A second study clarified the circumstances under which a territorial bird would be prompted to respond to a singing intruder. Swamp sparrows vary their response to intruders based not only on the vocal performance of the rival bird, but on the discrepancy in vocal ability between the two; the initial bird's aggressive behaviors were predicted by his own trill rate, but he was less inclined to behave aggressively toward low-performance playback (Mosely *et al.* 2013).

Just as plumage ornamentation and courtship behaviors vary widely across bird species, it is likely that the degree to which male birds are able or willing to discriminate and respond to differences in vocal performance may differ between taxa; the chiffchaff, a European wood warbler that produces a trill-like vocalization that can be measured using similar methods to the one in this study, is one example of a species in which the males do not respond to shifting playback performances whatsoever (Linhart *et al.* 2013). When presented with three sets of stimuli (control, slow syllable rate, and fast syllable rate), the experimental birds did not modulate their own syllable rate or change the rate of attack behaviors. However, the chiffchaffs did increase their own syllable rate and number of attacks significantly during playback when compared to before and after playback phases. In this species, it appears that the birds reserve their fast song for all aggressive contexts, regardless of the vocal abilities of the challenger. In the closely-related willow warbler, this trend is repeated with an added layer of complexity: the warblers respond more aggressively to intruders that have a much higher-pitched song (Linhart and Fuchs 2015). This is because low-pitched willow warbler song is indicative of large body size, a reliable predictor of the outcome of any head-to-head aggressive encounters. Similarly, male common nightingales will increase the proportion of trilled songs rather than whistled songs during a simulated intrusion, but these changes in song do not change in response to shifting intruder vocalizations; notably, this response was exaggerated in males that were already paired and defending a mate (Kunc *et al.* 2006).

In birds that modulate their song in response to different intruders, the direction in which performance shifts can also vary between species. While swamp sparrows increase their syllable rate when faced with a fast singer (DuBois *et al.* 2010), red-winged blackbirds appear to do the complete opposite (Cramer and Price 2007). Male blackbirds in that study responded much stronger to low-performance trills, which may suggest that they were more ready to expend the necessary energy to out-sing an intruder when that intruder did not pose a particularly great threat. There is also a third option for response preference in birds: responding more aggressively to either extreme or median vocal performance. This is seen in the banded wren (*Thryophilus pleurostictus*), which increased song matching when presented with median-performance playback; this song matching proved to predict approach behaviors, presumably to investigate the source of the vocalization and prepare for an attack (de Kort *et al.* 2009).

The existence of song matching itself has been considered to be excellent evidence for the ability of songbirds to discriminate vocalizations on the within-bird level when singing against an intruder (Krebs *et al.* 1891). Song matching is also hypothesized to be an aggressive signal that falls toward the bottom of the “hierarchy of aggressive communication”—that is to say, song matching does not directly predict top-tier aggressive attack behaviors, but instead precedes predictors of attack like soft song (Akcay *et al.* 2013). Among birds employing a repertoire for vocal performance, song matching is a common behavior used to initiate aggressive contact. This has been observed across numerous passerine genera (e.g. Cramer and Price 2007, Falls 1985, Lemon 1968, Shackleton and Ratcliffe 1994) and even in the song sparrow (Beecher *et al.* 2000), an emberizid closely related to the chipping sparrow.

If male chipping sparrows are indeed capable of discriminating vocal performance on a between-bird scale, they would certainly have been able to detect the difference present in the playback stimuli used in this study: the altered song pairs were engineered in such a way that they represented a wide enough range of trill rate and vocal deviation values that they fell far outside the range of possible values covered in the vocal performance of a single bird. Instead, the playback stimuli served to represent two entirely different birds, which should be intelligible to the sparrows if the established body of literature is to be believed. Unfortunately, a limited amount of research exists on the extent of vocal discrimination in birds in general, with even fewer studies on the vocal capabilities of the chipping sparrow in particular. It is currently unknown to what extent even females can clue into vocal performance, and it is possible that breeding-season males are too preoccupied trying to drive off all intruders regardless of song quality to change their behavior on this basis. Only further research can say with any certainty how well chipping sparrows are able to discriminate vocal performance within their species.

Other displays of aggression associated with song

Song is only one type of aggressive signal present in songbirds that can be employed in male-male encounters. After all, singing can only do so much to defend against intrusion if the invader is insistent on taking over a territory. The next logical step to singing bouts is to approach the intruder, after which birds may take part in visual display or proceed to attack. Song and attack displays are inextricable in male-male encounters: either song predicts attack, or a bird will attack in reaction to song.

In sparrows, warblers, and other songbirds, one common vocalization type emerges as a reliable predictor of attack: the “soft song”, or a low-amplitude version of one of the bird’s typical vocalizations. This phenomenon was first brought to light as an object of scientific interest by Dabelsteen *et al.* (1998) reviewing the widespread occurrence of quiet song in bird vocalizations. Since then, studies have been establishing the nature of the connection between attack and soft song. For example, 93% of black-throated blue warbler (*Setophaga caerulescens*) attacks on a taxidermic mount were predicted only by low-amplitude singing (Hof and Hazlett 2010). Low-amplitude song works in the opposite way as well; in addition to predicting attack in the singer, it can also incite aggression in the listener. Such is the case with the song sparrow, which approached closer to taxidermic mounts and performed more wing-wave displays when presented with soft song when compared to a mean-amplitude control (Templeton *et al.* 2012).

The wing-wave in emberizid sparrows has thus far been documented as an aggressive signal in the swamp sparrow and song sparrow (Anderson *et al.* 2012, Ballentine *et al.* 2008). Although this behavior has not been documented as occurring in the chipping sparrow, it is quite possible that these emberizids also use the wing-wave in male-male competitive interactions. In the swamp sparrow (*Spizella georgiana*), birds responded to a wing-waving robotic sparrow mount by approaching closer, waving their own wings, and singing more when compared to a non-waving sparrow robot (Anderson *et al.* 2013). If this behavior is frequently employed by chipping sparrows, it would be worth investigating the circumstances under which the wing-wave is employed and what connection it has with attack-oriented aggression and vocal performance.

The confounding effect of female listeners

A major confounding factor present in any study looking at the role of sexual display in male-male interaction is the fundamental fact that these behaviors evolved in connection with advertisement to females. Among the many reasons chipping sparrows may not modulate their song in response to changing playback circumstances, one major possibility is that their song performance is confounded by this other purpose. For example, a bird inclined to lower his vocal performance in the face of a low-quality intruder may not do so because of a stronger desire to impress local females and instead will always sing as well as he physically can.

Modulation of song performance is not limited to aggressive encounters with other birds; the twofold purpose of bird song as an aggressive signal and a sexual advertisement means that spontaneous song has plenty to reveal about a singing male. It can be difficult to assess *why* female birds of a given species are interested in good singers, but new studies are slowly emerging to begin addressing this subject (reviewed in Byers *et al.* 2010). To date, there have been no studies investigating female choice, pairing success, or territory quality in connection with vocal performance in the chipping sparrow. However, these types of study have been conducted on numerous other bird species and establish some key trends for understanding the role of bird song in determining which males will get to mate and raise young with a female.

One of the earliest and more central hypotheses for the reason females mate with males singing better song is that bird song fundamentally encodes important information about the genetic quality of the singing male. By choosing a male with good genes as a mate, the female is receiving no direct benefits that will help her in the short term; she is, however, receiving the indirect benefit of the increased chance of survival of her offspring, which would inherit some of the good genes of their father (Kirkpatrick and Ryan 1991). In the case of bird song, this typically comes in the form of females preferring to pair off with males that perform difficult songs well (Byers *et al.* 2010). Testing this long-held hypothesis requires that some key experimental challenges be surmounted, including defining vocal performance and establishing what connection, if any, it has with individual quality and mating success. That connection is still currently being characterized, but it would appear that better-singing birds tend to be larger and older individuals (e.g. Appleby and Redpath 1997, Ballentine 2009, Ballentijn and Ten Cate 1999, Cramer 2013, Vehrencamp *et al.* 2012), which might be large and long-lived because of high genetic quality.

Another aspect of male quality that females might detect in song is increased cognitive capacity. One obvious example of this is in the northern mockingbird (*Mimus polyglottos*), which will both copy and invent song phrases in order to expand its repertoire size. During the breeding season, males with larger repertoire sizes will have greater pairing success (Howard 1974). Sparrows that trill do not perform neurologically stressful vocalizations, however, and evolution has acted so that any given species will tend toward producing physically-demanding or neurologically-demanding song rather than a hybrid type (Cardoso and Hu 2011).

Whether females actually select for high vocal performance had not been tested with wild birds until a landmark study by Ballentine (2004) used the Podos (1997) method of quantifying vocal performance to test the prediction that high vocal performance elicited greater mating success for males. In a playback experiment with swamp sparrows, the females increased the rate of the copulation solicitation display (Searcy *et al.* 1985) when played high-performance song as opposed to the low-performance playback. A similar study on Lincoln sparrows (*Melospiza lincolnii*) demonstrated that females consistently prefer to approach songs that have high-performance trills than those that do not (Caro *et al.* 2010).

There could be some connection between the song that females prefer to solicit and the song that males prefer to use in competitive interaction or single out for attack. This interface between sexual selection and intraspecific competition has been the subject of few published studies, but what literature exists is promising. For example, male nightingales (*Luscinia megarhyncos*) will use occasional rapid trills as part of competitive singing with neighboring or intruding males, and the rate at which a given male incorporates these rapid trills into his vocalizations is predictive of later pairing success (Schmidt *et al.* 2008). This establishes a vital link between male bird competitive performance with later mating potential, with numerous explanations for the phenomenon available. While it is possible that females are eavesdropping on male-male competitive singing and then selecting the better singer of the two, it is also likely that the same birds capable of adding more rapid trills to their competitive song are also the same males able to defend a good territory and attract a mate.

This is an alternative hypothesis for the benefits that females receive via selection for good vocal display: that vocal performance somehow communicates or predicts territory quality or male parental care. This mode of selection persists because of the direct benefit offered to the female (Kirkpatrick and Ryan 1991): a male on a better territory will bring better food to the female as she incubates her eggs, and will later provide superior nutrition to the chicks, so there is plenty of motivation for a female bird to seek out a social mate on a high-quality territory. Like many North American songbirds, the blue-black grassquit (*Volatinia jacarina*) is a small Neotropical tanager that uses a combination of plumage ornamentation and vocal display to entice females. Manica *et al.* (2014) quantified territory quality by food availability and found that males sang more often and more consistently when defending a high-quality territory. Display using iridescent plumage ornamentation had no connection to territory quality, on the other hand. Because of the close relationship that seems to exist between grassquit vocal performance and the food availability on the territory of the singer, females would benefit from choosing vigorous singers as mates. Whether the territory or the song came first is anyone's guess; the most plausible explanation is that bigger, stronger birds simply have the energy required to find and defend the best territory possible and still have the drive to sing often and consistently to attract females. A female grassquit listening to the songs of nearby males could then simply listen for the bird singing well and often, and choose to mate with him due to the food offerings on his territory or the superior genetic material that he might pass onto their offspring. Either way, selection for this type of birdsong in connection with territory is conserved. This pattern also exists outside of the passerines, often considered to be the only true songbirds: the frequency of tawny owl hoots is constrained by body size, and those individuals that have a high-pitched hoot will be smaller and have a greater ectoparasize load than their low-hooting neighbors (Appleby and Redpath 1997), and though this particular study found no difference in pairing success by vocalization, it is possible that some information about male quality is picked up by the females listening to the male hoots. In European collared-doves, the number of song elements included in the coo vocalization is tightly connected with body size; smaller and weaker birds will often only produce a two-element coo, while larger birds will sing three-element coos with extended syllables (Ballentijn and Ten Cate 1999).

Unable or unwilling to change vocal performance?

Although chipping sparrows produce only one type of song in their adulthood, there will be some amount of variation inherent in the vocal performance beyond qualities such as song duration and performance timing. The chipping sparrows in this study certainly demonstrated considerable within-individual variability in song bandwidth, though shifts in bandwidth were not evoked by changing quality in playback stimuli. This could be partially due to the inherent error present in recording birdsong; depending on weather conditions, the direction the bird is facing, and the distance from the recorder to the bird, portions of the bandwidth can be blurred or removed entirely when viewed in a spectrogram. Because of this possibility, sonograms were screened carefully for quality before including them in the analyses. Trill rate, on the other hand, can still be reliably measured on even very unclear spectrograms because it merely requires that the researcher be able to distinguish one syllable from another without making any measurements beyond the length of the song. The remarkably high intra-class correlation coefficients for both bandwidth and trill rate do indicate that on the within-bird scale there is relatively little variation in vocal performance, especially when compared to the between-bird scale of variation. That being said, the 10% decrease in within-bird consistency for bandwidth over trill rate may not simply be a relic of experimental error; in this study, many of the recorded birds would occasionally shift the overall pitch and bandwidth audibly between songs (pers. observation). This occurred at different rates for different birds; for example, the male with the color band combination Red-black/Black-metal almost constantly sang with a wavering bandwidth, which gives the trill a more musical quality, while Green-black/Yellow-metal maintained a more consistent bandwidth in his drier trill.

Why, then, do chipping sparrows not modulate their song in an aggressive context, when it might benefit them to shift their vocal performance situationally? If singing a high-performance song is physiologically taxing or costly, an individual bird that has the ability to modulate his song significantly (in trill rate as well as bandwidth) according to context could benefit from this ability by reserving his high-performance song for bouts of advertisement (e.g. when a female is visibly present) or when telegraphing future aggression (provided that chipping sparrow song can predict aggressive behavior, which has not yet been established in this species). A population consisting entirely of birds that have the ability to constantly change their song, however, could corrupt the information content of bird song as an advertising signal altogether. Females listening in when a bird sang the most challenging song possible for his neurological capacity and syringeal morphology might respond differently to the male as opposed to when he produced an easier song. The inconsistency in vocal performance within an individual would disrupt the utility of trill performance limits as a sexual index signal; females would no longer select for it, and this type of song would eventually be phased out of existence. Alternatively, females might have to sample more songs per male to get sufficient information, as a low-quality male might be less able to sing a large number of high-performance songs in a single bout of advertising.

That situation is, of course, hypothetical; the present reality is that chipping sparrows do not appear to shift their vocal performance situationally, and that they tend to have a remarkably high level of within-bird consistency in trill rate and bandwidth both. For those birds that do possess higher variation in their song performance, are they simply not inclined to respond to a greater threat of a high-performance intruder in comparison with a sickly, weak singer? Dichotomizing the question of whether a bird is *unwilling* or *unable* to discriminate and respond to different vocal performance qualities may prove to be fallacy, however; a better view would be to accept unwillingness and inability as two factors acting on different timescales. On the short-term scale, the sparrows' reluctance to modulate their own vocal performance in response to intruders may be because a low-deviation performance is insufficient to drive off an intruder or because it is more easy and efficient to confront an intruder immediately using other aggressive behaviors like attack flights. The ultimate consequences for this may be an eventual "inability" to modulate vocal performance, which must evolve if this type of bird song is to be conserved as an informational signal (Searcy and Beecher 2009). In the chipping sparrow, whether the current inability to respond differentially to intruders could be either morphological (the bird simply cannot sing a better song in the face of a higher- or lower- performance singer) or neurological (the bird cannot detect differences in song or is not inclined to respond to such a change) has yet to be determined.

The question of honesty in animal signaling is a large and somewhat convoluted one, especially when the signal is behavioral and connected with pairing success. While such physically-rooted sexual signals as cervid antlers or the brilliant carotenoid-derived coloration of *Carpodacus* finches (Hall 1960) communicate reproductive fitness directly through a handicap or by showing the male's inherent quality, bird song presents a fundamental conundrum in that it is a signal that can feasibly be cheated by a male that is sufficiently motivated. In a species where females are directly selecting for decreased vocal deviation, it would benefit singing males to be performing the most difficult song possible while singing spontaneously. However, this is not the case with many species; the second function of song as an aggressive signal leads birds to shift their own vocalizations in aggressive contexts (e.g. Anderson *et al.* 2012, Ballentine *et al.* 2008, Burt *et al.* 2001, Hof and Hazlett 2010).

Conclusions and considerations

Chipping sparrows and other members of *Spizella* represent a neglected genus in the field of songbird vocal performance, despite high potential for research to be conducted in the species. This study began to characterize novel aspects of vocal performance in the chipping sparrow, including determining whether or not males of the species are able to modulate their song in different aggressive contexts depending on the vocal quality of a simulated intrusion. This is also the first study that attempts to characterize morphological variation in the rufous cap of male sparrows and correlate it with bill morphology and song performance, though the sample size of captured birds was too small for any conclusions to be drawn from these measurements.

Beyond sampling a larger group of birds, there are numerous avenues for future study in this species. The connection between female preference and increased male aggression toward different vocal performance levels has yet to be established and explored, and will provide considerable insight into the dual function of trilled song as an aggressive signal and an advertisement for potential mates. Additionally, the extent of aggressive response to different song qualities can be explored, as there might be a *Spizella* corollary to the *Melospiza* wing-wave that is employed during aggressive interactions with rival birds. Finally, the most significant part of the story yet to be unraveled is the role that females play in driving the evolution of bird song. This includes determining what other information about evolutionary fitness might be encoded in a trill, such as neurological or motor function, and how females perceive and respond to that information.

There is little research available on the vocal habits of any trilling *Spizella*, including both the chipping sparrow and the field sparrow. Considering the marked ontogenic differences in song between the *Spizella* and *Melospiza* genera, it would not be surprising if these birds also shared differences in their putative aggressive song and other attack behaviors. Due to the widespread distribution and ease of capture of these common backyard birds, it would be both wise and feasible to perform similar research on the chipping sparrow as has been done on the members of *Spizella.* Specific areas that merit research include (1) soft-song rates in response to simulated intrusion with taxidermic mount, (2) the various syllable types present in adult sparrow song and whether they have any relationship with female or male response to singing, (3) whether high-, median- and low-performance playback stimuli evoke different non-vocal responses, (4) the significance of "chip" call notes in aggressive contexts, (5) characterizing the relationship between morphology and vocal performance, and (6) investigating the significance of the rufous cap in aging and sexing birds, as well as its role, if any, in conveying a pairing advantage to males. Notably, all of these studies are feasible thesis projects in the Bates College Department of Biology if taken on by a motivated student knowledgeable in avian biology and willing to spend the field time required to learn safe bird handling and to make sufficient recordings.

Bird song is a product of sexual selection, a process fundamentally driven by females in songbirds, and uncovering the evolutionary pathway that this peculiar behavior took requires intimate knowledge of what females are selecting for in a potential mate. For being one of the most ubiquitous sounds in springtime, birdsong is surprisingly misunderstood, and further study of the entire Class Aves will continue to elucidate the balance that is struck between natural selection and sexual selection in the evolution of behavior.

Literature Cited

Akcay, C., Tom, M.E., Campbell, S.E. & Beecher, M.D. (2013) Song type matching is an honest early threat signal in a hierarchical animal communication system. *Proceedings of the Royal Society B*, **280**, 20122517–20122517.

Akçay, Ç., Tom, M.E., Holmes, D., Campbell, S.E. & Beecher, M.D. (2011) Sing softly and carry a big stick: signals of aggressive intent in the song sparrow. *Animal Behaviour*, **82**, 377–382.

Anderson, R.C., Searcy, W.A., Hughes, M., and S. Nowicki. (2012) The receiver-dependent cost of soft song: a signal of aggressive intent in songbirds. *Animal Behaviour*, **77**, 1443-1448.

Anderson, R.C., DuBois, A.L., Piech, D.K., Searcy, W.A. & Nowicki, S. (2013) Male response to an aggressive visual signal, the wing wave display, in swamp sparrows. *Behavioral Ecology and Sociobiology*, **67**, 593–600.

Andersson, M. (1994) *Sexual Selection.* Princeton University Press, New Jersey.

Appleby, B.M. & Redpath, S.M. (1997) Indicators of male quality in the hoots of tawny owls (*Strix aluco*). *Journal of Raptor Research*, **31**, 65-70.

Ballentine, B. (2004) Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology*, **15**, 163–168.

Ballentine, B. (2009) The ability to perform physically challenging songs predicts age and size in male swamp sparrows, Melospiza georgiana. *Animal Behaviour*, **77**, 973–978.

Ballentine, B., Searcy, W.A. & Nowicki, S. (2008) Reliable aggressive signalling in swamp sparrows. *Animal Behaviour*, **75**, 693–703.

Ballintijn, M.R. & Ten Cate, C. (1999) Variation in number of elements in the perch-coo vocalization of the collared dove (Streptopelia decaocto) and what it may tell about the sender. *Behaviour*, **136**, 847–864.

Baptista, L.F., and S.L.L Gaunt. (1997) Social interaction and vocal development in birds. In: S.T. Snowdon and M. Hausberger, eds. *Social Influence on Vocal Development*, pp. 23-40. Cambridge: Cambridge University Press.

Beecher, M.D. (2010) Birdsong and vocal learning during development. *Encyclopedia of Neuroscience*, **1**, 164-168.

Beecher, M.D., Campbell, S.E., Burt, J.M., Hill, C.E., and J.C. Nordby. (2000) Song type matching between neighboring song sparrows. *Animal Behaviour*, **59**, 21-27.

Buchanan, K.L., Leitner, S., Spencer, K.A., Goldsmith, A.R., and C.K. Catchpole. (2004) Developmental stress selectively affects the song control nucleus HVC in the zebra finch. *Proceedings of the Royal Society B*, **271**, 2381-2386.

Burt, J.M., Campbell, S.E. & Beecher, M.D. (2001) Song type matching as threat: a test using interactive playback. *Animal Behaviour*, **62**, 1163–1170.

Byers, B.E. & Kroodsma, D.E. (2009) Female mate choice and songbird song repertoires. *Animal Behaviour*, **77**, 13-22.

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

Cardoso, G.C. & Hu, Y. (2011) Birdsong Performance and the Evolution of Simple (Rather than Elaborate) Sexual Signals. *The American Naturalist*, **178**, 679–686.

Caro, S.P., Sewall, K.B., Salvante, K.G. & Sockman, K.W. (2010) Female Lincoln's sparrows modulate their behavior in response to variation in male song quality. *Behavioral Ecology*, **21**, 562–569.

Cramer, E.R.A. (2013) Physically challenging song traits, male quality, and reproductive success in house wrens. *PloS One*, **8**, e59208.

Cramer, E.R.A. & Jordan Price, J. (2007) Red-winged blackbirds Ageliaus phoeniceus respond differently to song types with different performance levels. *Journal of Avian Biology*, **38**, 122–127.

Cramer, E.R.A., Hall, M.L., de Kort, S.R., Lovette, I.J. & Vehrencamp, S.L. (2011) Infrequent Extra-Pair Paternity in the Banded Wren, a Synchronously Breeding Tropical Passerine. *The Condor*, **113**, 637–645.

Dabelsteen, T., McGregor, P.K., Lampe, H.M., Langmore, N.E., and J. Holland. (1998) Quiet song in birds: an overlooked phenomenon. *Bioacoustics*, **9**, 89-105.

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* London: J. Murray.

Dearborn, D.C., Anders, A.D. & Williams, J.B. (2005) Courtship display by great frigatebirds, Fregata minor: an energetically costly handicap signal? *Behavioral Ecology and Sociobiology*, **58**, 397–406.

DeLeon, S., Halitschke, R., Hames, R.S., Kessler, A., DeVoogd, T.J., and A.A. Dhondt. (2013) The effect of polychlorinated biphenyls on the song of two passerine species. *PLoS One*, **8**, e73471.

DeVoogd, T.J., Krebs, J.R., Healy, S.D., and A. Purvis. (1993) Relations between song repertoire size and the volume of brain nuclei related to song: comparative evolutionary analyses amongst oscine birds. *Proceedings of the Royal Society B*, **254**, 75-82.

DuBois, A.L., Nowicki, S. & Searcy, W.A. (2009) Swamp sparrows modulate vocal performance in an aggressive context. *Biology Letters*, **5**, 163–165.

DuBois, A.L., Nowicki, S. & Searcy, W.A. (2010) Discrimination of vocal performance by male swamp sparrows. *Behavioral Ecology and Sociobiology*, **65**, 717–726.

Eberhardt, L.S. (1994) Oxygen consumption during singing by male Carolina wrens (*Thryothorus ludovicianus*). *The Auk*, **111**, 124-130.

Falls, J.B. (1985) Song matching in western meadowlarks. *Canadian Journal of Zoology*, **63**, 2520-2524.

Gaunt, A.S. (1983) An hypothesis concerning the relationship of syringeal structure to vocal abilities. *The Auk*, **100**, 853–862.

Godard, R. (1991) Long-term memory of individual neighbors in a migratory songbird, *Nature*, **350**, 228-229.

Goller, F. (1998) Vocal gymnastics and the bird brain. *Nature*, **395**, 11–12.

Goodwin, S.E. & Podos, J. (2013) Shift of song frequencies in response to masking tones. *Animal Behaviour*, **85**, 435–440.

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

Grafen, A. (1990) Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.

Grant, B.R. & Grant, P.R. (1996) Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution*, **50**, 2471-2487.

Hill, G.E. (1990) Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Animal Behaviour*, **40**, 563-572.

Hoese, W.J., Podos, J., Boetticher, N.C. & Nowicki, S. (2000) Vocal tract function in birdsong production: experimental manipulation of beak movements. *The Journal of Experimental Biology*, **203**, 1845–1855.

Hof, D. & Hazlett, N. (2010) Low-amplitude song predicts attack in a North American wood warbler. *Animal Behaviour*, **80**, 821–828.

Howard, R.D. (1974) The Influence of Sexual Selection and Interspecific Competition on Mockingbird Song (Mimus polyglottos). *Evolution*, **28**, 428–438.

Huber, S.K. & Podos, J. (2006) Beak morphology and song features covary in a population of Darwin's finches (Geospiza fortis). *Biological Journal of the Linnean Society*, **88**, 489-498.

Illes, A.E., Hall, M.L. & Vehrencamp, S.L. (2006) Vocal performance influences male receiver response in the banded wren. *Proceedings. Biological sciences / The Royal Society*, **273**, 1907–1912.

Jackson, A.K, Evers, D.C., Etterson, M.A., Condon, A.M., Folsom, S.B., Detweiler, J., Schmerfeld, J., and D.A. Cristol. (2011) Mercury exposure affects the reproductive success of a free-living terrestrial songbird, the Carolina wren (*Thryothorus ludovicianus*). *The Auk*, **128**, 759-769.

Konishi, M. (1985) Birdsong: from behavior to neuron. *Annual Review of Neuroscience*, **8**, 125-70.

de Kort, S.R., Eldermire, E.R.B., Cramer, E.R.A., and S.L. Vehrencamp. (2008) The deterrent effect of bird song in territory defense. *Behavioral Ecology*, **20**, 200-206.

Kirkpatrick, M. and M.J. Ryan. (1991) The evolution of mating preferences and the paradox of the lek. *Nature*, **350**, 33-38.

Krebs, J.R., Ashcroft, R., and K. Van Orsdol. (1981) Song matching in the great tit *Parus major* L. *Animal Behaviour*, **29**, 918-923.

Kunc, H.P., Amrhein, V., and M. Naguib. (2006) Vocal interactions in nightingales, *Luscinia megarhyncos*: more aggressive males have higher pairing success. *Animal Behaviour*, **72**, 25-30.

Laidre, M.E. & Vehrencamp, S.L. (2007) Is bird song a reliable signal of aggressive intent? *Behavioral Ecology and Sociobiology*, **62**, 1207–1211.

Larsen, O.N. & Goller, F. (2002) Direct observation of syringeal muscle function in songbirds and a parrot. *The Journal of experimental biology*, **205**, 25–35.

Lemon, R.E. (1968) The displays and call notes of cardinals. *Canadian Journal of Zoology*, **46**, 141-151.

Lessels, C.M. and P.T. Boag. (1987) Unrepeatable repeatabilities: a common mistake. *The Auk*, **104**, 116-121.

Linhart, P. & Fuchs, R. (2015) Song pitch indicates body size and correlates with males' response to playback in a songbird. *Animal Behaviour*, **103**, 91–98.

Linhart, P., Jaška, P., Petrusková, T., Petrusek, A. & Fuchs, R. (2013) Being angry, singing fast? Signalling of aggressive motivation by syllable rate in a songbird with slow song. *Behavioural Processes*, **100**, 139–145.

Liu, W. & Kroodsma, D. (1999) Song development by chipping sparrows and field sparrows. *Animal Behaviour*, **57**, 1275–1286.

Liu, W.-C. & Nottebohm, F. (2007) A learning program that ensures prompt and versatile vocal imitation. *PNAS*, **104**, 20398–20403.

Madden, J.R., Dingle, C., Isden, J., Sparfeld, J., Goldizen, A.W., and J.A. Endler. (2012) Male spotted bowerbirds propagate fruit for use in their sexual display. *Current Biology*, **22**, 264-265.

Manica, L.T., Maia, R., Dias, A., Podos, J. & Macedo, R.H. (2014) Vocal output predicts territory quality in a Neotropical songbird. *Behavioural Processes*, **109**, 21–26.

Marler, P. and D. Isaac. (1960) Physical analysis of a simple bird song as exemplified by the chipping sparrow. *The Condor*, **62**, 124-135.

Martinez-Padilla, J., Mougeot, F., Perez-Rodriguez, L., and G.R. Bortolotti. (2007) Nematode parasites reduce carotenoid-based signaling in male red grouse. *Biology Letters*, **3**, 161-164.

McGraw, K.J., Safran, R.J., Evans, M.R., and K. Wakamatsu. (2004) European barn swallows use melanin pigments to color their feathers brown. *Behavioral Ecology*, **15**, 889-891.

Middleton, A.L. (1998) Chipping Sparrow (*Spizella passerina*). In: Poole, A. and F. Gill (eds.), *The Birds of North America*, No. 334. Academy of Natural Sciences, Philadelphia, and the American Ornithological Union, Washington, D.C.

Moseley, D.L., Lahti, D.C. & Podos, J. (2013) Responses to song playback vary with the vocal performance of both signal senders and receivers. *Proceedings of the Royal Society B*, **280**, 20131401–20131401.

Møller, A.P. (1988) Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature*, **332**, 640-642.

Mougeot, F., Irvine, J.R., Seivwright, L., Redpath, S.M., and S. Piertney. (2004) Testosterone, immunocopetence, and honest sexual signaling in male red grouse. *Behavioral Ecology*, **15**, 930-937.

Moore, S.D. (2013) Measuring vocal performance in song sparrows (*Melodia melospiza*), and its relationship to age, morphology, and song complexity. *University of Western Ontario – Thesis and Dissertation Repository*, Paper 1357.

Nowicki, S., Peters, S. & Podos, J. (1998) Song Learning, Early Nutrition and Sexual Selection in Songbirds. *American Zoologist*, **38**, 179–190.

Nowicki, S., Searcy, W.A., Hughes, M. & Podos, J. (2001) The evolution of bird song: male and female response to song innovation in swamp sparrows. *Animal Behaviour*, **62**, 1189–1195.

Nowicki, S., Searcy, W.A., and S. Peters. (2002) Brain development, song learning and mate choice in birds: a review and experimental test of the “nutritional stress hypothesis”. *Journal of Comparative Physiology*, **188**, 1003-1014.

Oberweger, K., and F. Goller. (2001) The metabolic cost of birdsong. *The Journal of Experimental Biology*, **204**, 3379-3388.

Pfaff, J.A., Zanette, L., MacDougall-Shackleton, S.A., and E.A. MacDougall-Shackleton. (2007) Song repertoire size varies with HVC volume and is indicative of male quality in song sparrows (*Melospiza melodia*). *Proceedings of the Royal Society B*, **274**, 2035-2040.

Podos, J. (1996) Motor constraints on vocal development in a songbird. *Animal Behaviour*, **51**, 1061–1070.

Podos, J. (1997) A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution*, **51**, 537–551.

Podos, J. (2001) Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature*, **409**, 185–188.

Prather, J.F., Peters, S., Mooney, R. & Nowicki, S. (2012) Sensory constraints on birdsong syntax: neural responses to swamp sparrow songs with accelerated trill rates. *Animal Behaviour*, **83**, 1411–1420.

Price, J.J., Earnshaw, S.M., and M.S. Webster. (2006) Montezuma oropendolas modify a component of song constrained by body size during vocal contests. *Animal Behaviour*, **71**, 799-807.

Ralph, C.L. (1969) The control of color in birds. *American Zoologist*, **9**, 521-530.

Reynolds, J.D. and M.R. Gross. (1990) Costs and benefits of female mate choice: is there a lek paradox? *The American Naturalist*, **136**, 230-243.

Schmidt, R., Kunc, H.J., Amrhein, V., and M. Naguib. (2008) Aggressive responses to broadband trills are related to subsequent pairing success in nightingales. *Behavioral Ecology*, **19**, 635-641.

Searcy, W.A. (1992) Measuring responses of female birds to male song. *In:* McGregor, P.K. (ed.), *Playback and Studies of Animal Communication*. Plenum, New York.

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

Searcy, W.A., Marler, P., and S.S. Peters. (1985) Songs of isolation-reared sparrows function in communication, but are significantly less effective than learned songs. *Behavioral Ecology and Sociobiology*, **17**, 223-229.

Searcy, W.A. & McArthur, P.D. Peters. S., and Marler, P. (1981) Response of male song and swamp sparrows to neighbor, stranger, and self songs. *Behaviour*, **77**, 152-163.

Searcy, W.A., Peters, S., Kipper, S. & Nowicki, S. (2010) Female response to song reflects male developmental history in swamp sparrows. *Behavioral Ecology and Sociobiology*, **64**, 1343–1349.

Sewall, K.B., Soha, J.A., Peters, S. & Nowicki, S. (2013) Potential trade-off between vocal ornamentation and spatial ability in a songbird. *Biology Letters*, **9**, 20130344–20130344.

Shackleton, S.A. and L. Ratcliffe. (1994) Matched counter-singing signals escalation of aggression in black-capped chickadees (*Parus atricapillus*). *Ethology*, **97**, 310-316.

Sherry, D.F., Jacobs, L.F., and S.J. Gaulin. (1992) Spatial memory and adaptive specialization of the hippocampus. *Trends in Neuroscience*, **15**, 298-303.

Smith, M.J. and D. Harper. (1995) Animal signals: models and terminology. *Journal of theoretical biology*, **177**, 305–311.

Smith, M.J. and D. Harper. (2004) *Animal Signals*. Oxford University Press, New York.

Spencer, K.A. and S.A. MacDougall-Shackleton. (2011) Indicators of development as sexually selected traits: the developmental stress hypothesis in context. *Behavioral Ecology*, **22**, 1-9.

Suthers, R.A., Vallet, E. & Kreutzer, M. (2012) Bilateral coordination and the motor basis of female preference for sexual signals in canary song. *The Journal of experimental biology*, **215**, 2950–2959.

Templeton, C.N., Akcay, C., Campbell, S.E., and M.D. Beecher. (2012) Soft song is a reliable signal of aggressive intent in song sparrows. *Behavioral and Ecological Sociobiology*, **66**, 1503-1509.

Vehrencamp, S.L., Yantachka, J., Hall, M.L. & de Kort, S.R. (2012) Trill performance components vary with age, season, and motivation in the banded wren. *Behavioral Ecology and Sociobiology*, **67**, 409–419.

Wilson, D.R., Bitton, P. P., Podos, J. & Mennill, D.J. (2014) Uneven Sampling and the Analysis of Vocal Performance Constraints. *The American Naturalist*, **183**, 214–228.

Weatherhead, P.J. and R.J. Robertson. (1979) Offspring quality and the polygyny threshold: “the sexy son hypothesis”. *The American Naturalist*, **113**, 201-208.

Westneat, M.W., Long, J.H., Hoese, W., and S. Nowicki (1993) Kinematics of birdsong: functional correlation of cranial movements and acoustic features in sparrows. *Journal of Experimental Biology*, **182**, 147-171.

Yasukawa, K., Blank, J.L., and C.B. Patterson. Song repertoires and sexual selection in the red-winged blackbird. *Behavioral Ecology and Sociobiology*, **7**, 233–238.

Zahavi, A. (1975) Mate selection-a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.

Zollinger, S.A., Podos, J., Nemeth, E., Goller, F. & Brumm, H. (2012) On the relationship between, and measurement of, amplitude and frequency in birdsong. *Animal Behaviour*, **84**, 1–9.

Appendix A: Tables

Table 1. Overview of songbirds in which a vocal performance trade-off has been characterized, with reference to sample papers in which to find more experimental information. This list is by no means exhaustive, and there are many other species that produce vocalizations that may be conducive to this sort of analysis. From Wilson *et al.* (2014).

Scientific name	**Common name**	**Reference**
Agelaius phoeniceus	Red-winged blackbird	Cramer and Price 2007
Aimophila ruficeps	Rufous-crowned sparrow	Podos 1997
Ammodramus humeralis	Grassland sparrow	Podos 1997
Amphispiza bilineata	Black-throated sparrow	Podos 1997
Amphispiza quinquestriata	Five-striped sparrow	Podos 1997
Artemisiospiza belli	Sage sparrow	Podos 1997
Calamospiza melanocorys	Lark bunting	Podos 1997
Camarhynchus parvulus	Small tree finch	Christensen *et al.* 2006
Cardinalis cardinalis	Northern cardinal	Podos 1997, Narango 2012
Cardinalis sinuatus	Pyrrhuloxia	Podos 1997
Chondestes grammacus	Lark sparrow	Podos 1997
Emberiza calandra	Corn bunting	Podos 1997
Emberiza schoeniclus	Reed bunting	Podos 1997
Geospiza fortis	Medium ground finch	Huber and Podos 2006
Geospiza scandens	Common cactus finch	Podos 1997
Junco hyemalis	Dark-eyed junco	Cardoso *et al.* 2007, Podos 1997
Junco phaeonotus	Yellow-eyed junco	Podos 1997
Lonchura oryzibora	Java sparrow	Kagawa and Soma 2013
Luscinia megarhyncos	Common nightingale	Schmidt *et al.* 2008
Melospiza georgiana	Swamp sparrow	e.g. Podos 1997, Ballentine *et al.* 2004, Ballentine 2006, Liu *et al.* 2008
Melospiza lincolnii	Lincoln's sparrow	Podos 1997, Sockman 2009
Melospiza melodi	Song sparrow	Podos 1997, Maddison *et al.* 2012
Melozone aberti	Abert's towhee	Podos 1997
Peucaea aestivalis	Bachman's sparrow	Podos 1997
Peucaea botteri	Botteri's sparrow	Podos 1997
Peucaea carpalis	Rufous-winged sparrow	Podos 1997
Peucaea cassinii	Cassin's sparrow	Podos 1997
Peucaea sumichrasti	Cinnamon-tailed sparrow	Podos 1997
Pipilo erythrophthalmus	Eastern towhee	Podos 1997
Pooecetes gramineus	Vesper sparrow	Podos 1997

Rhynchospiza strigiceps	Stripe-capped sparrow	Podos 1997
Serinus canaria	Island canary	Podos 1997, Draganoiu *et al.* 2002, Suthers *et al.* 2012
Setophaga petechia	Yellow warbler	Beebee 2004
Spizella passerina	Chipping sparrow	Podos 1997, Goodwin and Podos 2014
Thryophilus pleurostictus	Banded wren	Illes *et al.* 2006
Troglodytes aedon	House wren	Cramer 2013
Zonotrichia leucophrys	White-crowned sparrow	Podos 1997, Derryberry 2009

Table 2. Morphological summary for captured and banded chipping sparrows. Band combinations are read from top to bottom on the bird's left leg (before the slash) and then on the bird's right leg (after the slash). The lowest band on the bird's right leg is the metal (M) federal band, while the rest are plastic color bands in either red (R), black (K), orange (O), green (G), yellow (Y), blue (B), or white (W). Band combinations noted with an asterisk* indicate birds included in the playback experiment.

Band combination	*Wing length*	*Tarsus length*	*Culmen depth*	*Culmen width*	*Cap length*	*Rufous extent*	*Recordings?*
RK/KM*	71.5	16.5	6.7	4.4	13.1	20.1	Yes
OG/RM*	72.5	17.9	7.5	4.7	12.8	18.1	Yes
YG/YM	68.0	16.4	6.7	4.1	10.5	17.9	No
GW/BM*	66.5	17.1	7.3	4.2	11.9	21.0	Yes
WB/GM	69.0	16.9	7.6	4.2	13.4	19.3	No
GK/YM	64.5	15.4	7.4	4.1	14.5	19.6	Yes
KB/RM	67.0	16.0	8.1	4.1	12.3	18.2	No
BW/WM	66.5	16.9	7.6	3.9	11.8	18.6	No
KG/OM*	72.5	16.4	9.1	4.0	15.3	18.2	Yes

Table 3. Matrix of Pearson correlation coefficients (r) for measured morphological characters. Coefficients run between -1.0 (a perfect negative correlation) and 1.0 (a perfect positive correlation). Correlations that were marginally nonsignificant are denoted with a cross†.

	Tarsus length	*Wing length*	*Culmen depth*	*Culmen width*	*Cap length*	*Rufous extent*
Tarsus length		0.51†	-0.09	0.58†	-0.29	-0.03
Wing length	0.51†		0.24	0.55†	0.30	-0.29
Culmen depth	-0.09	0.24		-0.34	0.62†	-0.36
Culmen width	0.58†	0.55†	-0.34		-0.01	0.09
Cap length	-0.29	0.30	0.62†	-0.01		0.09
Rufous extent	-0.03	-0.29	-0.36	0.09	0.09	

Table 4. Playback experiment results for the two factors of playback quality (good or bad) and playback phase (during the playback or silence period after the playback) for all five vocal metrics tested. Statistical significance is denoted with an asterisk* and marginal nonsignificance is denoted with a cross†.

Metric	**Factor**	**MS**	**F (1,14)**	**p-value**
Trill rate	Quality	0.00175	3.632×10^{-5}	0.9953
	During/After	0.01688	2.452	0.1397†
	Interaction	0.00206	0.2998	0.5926
Frequency bandwidth	Quality	0.03892	0.03320	0.8580
	During/After	0.00066	0.06739	0.7990
	Interaction	0.00248	0.2514	0.6239
Vocal deviation	Quality	0.04026	0.1275	0.7264
	During/After	0.00141	0.1395	0.7144
	Interaction	0.00203	0.1999	0.6617
Song rate	Quality	3.445	0.09433	0.7633
	During/After	155.3	6.595	0.0223*
	Interaction	2.820	0.1197	0.7345
Deterioration	Quality	0.00022	0.03089	0.8634
	During/After	0.00555	1.081	0.3190
	Interaction	0.00025	0.0485	0.8294

Appendix B: Macaulay Library Accession Numbers

ML Audio 73955. Chipping Sparrow (*Spizella passerina*). 27 May 1992; United States, Indiana. Keller, G.A.

ML Audio 84754. Chipping Sparrow (*Spizella passerina*). 6 April 1997; United States, Maryland. Hershberger, W.L.

ML Audio 87491. Chipping sparrow (*Spizella passerina*). 5 May 1998; United States, New York. Medler, M.D.

ML Audio 15425. Chipping sparrow (*Spizella passerina*). 3 June 1951; United States, Maryland. Allen, A.A.