TRILLED SONG TYPES ARE MORE SALIENT THAN NON-TRILLED SONG TYPES IN AGONISTIC INTERACTIONS BETWEEN MALE SONG SPARROWS (*MELOSPIZA MELODIA*)

A thesis presented to the faculty of Western Carolina University in partial fulfillment of the requirements for the degree of Master of Science in Biology

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ABSTRACT

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Most research on song complexity has mainly focused on repertoire size. However, the way various song structures within a repertoire function in male-male interactions is less well understood. In this study, I have explored the functional significance of songs containing a trilled syllable type shown to have a clear maximum physiological performance barrier versus songs that lack a trilled element. I performed playback experiments with 44 song sparrows on the campus of Western Carolina University in North Carolina. I found that males responded significantly more strongly to trilled than non-trilled songs, suggesting that song sparrows discriminate between song types within a repertoire. The results of this study suggest that male-male interactions may be important drivers for the evolution of complex repertoires in song sparrows. Future studies should focus on understanding how trilled and non-trilled songs function in male-male interactions.

INTRODUCTION

Understanding the evolution of the diversity of animal signals and how they function in communication is the subject of much research (Darwin 1872; Hauser 1996; Bradbury & Vehrencamp 1998). Signals can be simple index signals, which are intrinsically tied to the physiological aspects of the signaler such as size (Maynard Smith & Harper 1995; Davies and Halliday 1978; Riechert 1978) to more complex, multimodal ornaments. Complex signals arise because of qualities that are stimulating to the receiver (reviewed in Hebets and Papaj 2005). Complex signals have evolved in response to sexual selection (Andersson 1994), environmental properties (Endler 1992), risk of predation (Stoddard 1999), and social organization (Blumstein & Armitage 1997). Much research on signal complexity has focused on the effects of intersexual signaling and how mate choice leads to the evolution of elaborate ornaments (Basolo 1990; Andersson 1994; Endler & Basolo 1998) and complex vocalizations (Ryan 1998; Collins 1999). Large song repertoires in songbirds are a complex acoustic signal, and are a classic example of a sexually selected trait favored by intersexual selection (Searcy 1992; Andersson 1994). Yet, less is known about how male-male interactions influence the evolution of song repertoire complexity. In this study, I investigate how male-male interactions influence the evolution of song repertoire complexity.

Studies of song complexity have mainly focused on repertoire size, defined as the number of songs in the repertoire or number of syllable types (Catchpole & Slater 2003). Learned, multi-song repertoires are present in 75% of oscine species (MacDougall-Shackleton 1997). Repertoire size varies widely across species

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(Catchpole & Slater 2003). In general, females prefer males who sing large repertoires (Hasselquist et al. 1996; Searcy 1984, 1985,1992; Lampe & Saetre 1995; Reid et al. 2004). Within species, repertoire size correlates positively with the size of relevant parts of the brain (High Vocal Center (HVC)) (Pfaff et al. 2007) and post-hatching condition/phenotypic quality (Nowicki et al. 1998). Thus, repertoire size in many species functions as an honest signal of quality that is used by females to choose mates. While it is likely that female preference drives signal complexity for the most stimulating signal (Searcy 1992; Drăgănoiu et al. 2002; Cui et al. 2016), both male and female receivers respond preferentially to repertoire size and within-song syllable complexity (Leitão et al. 2006). Females who mate with males with large repertoires are benefitting because they are mating with genetically superior males. How intrasexual signaling drives signal complexity is less well understood than intersexual signaling. Because the same vocalizations that are associated with intersexual selection are used in intrasexual competition (Rand and Ryan 1981; Searcy et al. 2006; Beecher et al. 1996; Akçay et al. 2013), it is conceivable that competition could be an additional driver of signal complexity.

The use of song in birds that possess complex vocal repertoires provides an opportunity to investigate the evolution of repertoire complexity, but demonstrating selection for repertoire complexity requires evidence of its function. In many songbird species, males will use song competitively by attempting to match song types with competitors. In agonistic interactions, matching a song type is used to escalate aggressiveness while switching song types is used to de-escalate the interaction (Akçay et al. 2013). Within this song matching framework, song type is thought to be relevant

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only to the extent of whether song types match or not, and this functions as a conventional signal (Veherencamp 2001). Less research has been devoted to understanding whether songs within the repertoire might serve different functions in male-male interactions. Research on repertoire size has suggested that song types are interchangeable and that the primary function of differing song types is to increase stimulus diversity (Nottebohm 1972; Krebs et al. 1978; Searcy 1992), reduce habituation of the receiver (Hartshorne 1973), and/or to relieve stress on syringeal muscles (Lambrechts & Dhondt 1988). However, recent studies on several species suggest song types may serve individual functions (Weary et al. 1994; Beebee 2004; Trillo & Vehrencamp 2005).

Functional significance of individual song types has been described in wood warblers (Weary et al. 1994; Beebee 2004). Some male wood warblers have two acoustically distinct song type groups (Type I & II). Type I songs are sung slowly, early in the season during pre-mating, which suggests a mate attraction function. Type II songs tend to be faster with lower fundamental frequencies. Type II songs are sung near territorial boundaries (Spector 1991; Staicer 1996), suggesting a territorial defense function. Banded wrens (*Thryothorus pleurostictus*) use certain song types over others in specific contexts such as the dawn chorus, mate attraction, and agonistic communication (Trillo & Vehrencamp 2005). In this study, I test the functional significance of songs types within a repertoire in male-male interactions in song sparrows.

Song sparrows are an excellent species in which to test the functional significance of different song types within a repertoire. Song sparrows are a species

with complex, learned repertoires (Beecher et al. 2000). Song sparrows crystallize multi song-type repertoires of between 7-11 songs (Beecher et al. 2000) (Fig. 1). Females song sparrows show a preference for more song types (Searcy and MacArthur 1981). Males in some populations show a high degree of song type sharing which they use in male-male interactions (Beecher et al. 2000). Yet, no study has investigated whether song types in song sparrow repertoires vary in functional significance. That is, within a repertoire are some song types more salient than in others? In this study, I test whether males can discriminate between song types within a repertoire that vary in structure.

If songs within song sparrow repertoires differ in meaning based on structure in male-male competition, then receivers should respond more aggressively to certain song types over others. I tested my hypothesis by using song playback to territorial male song sparrows to see whether presence or absence of trilled elements in song affects the aggressive response of the receiver. Song types that contain trilled elements are physiologically demanding (Podos 1997). Females have been shown to prefer trills that are more difficult to produce (Vallet & Kreutzer 1995; Vallet et al. 1998; Ballentine et al. 2004). Thus, because trilled songs are physically demanding and are shown to be important in male-female interactions, they may be important in male-male interactions. If trilled song types are more functionally salient in aggressive interactions between male song sparrows, then I predict that trilled songs will cause focal males to approach the playback speaker more closely than non-trilled songs.
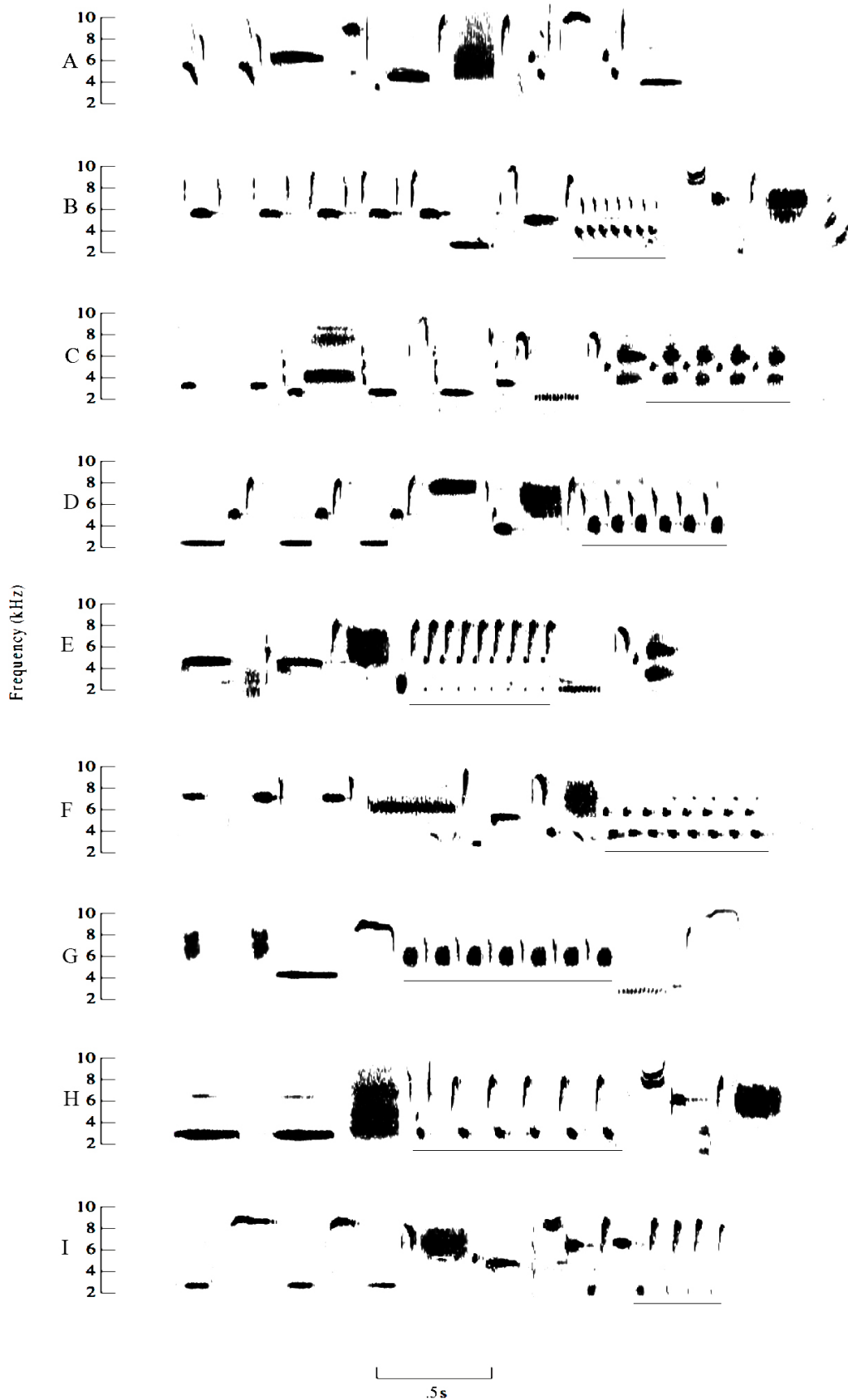
Frequency (kHz)

.5 s

Figure 1. An example of a full repertoire from an individual male from my study population. This is representative of a typical song sparrow repertoire that exhibits a high degree of variation between song types. Trilled elements (rapid oscillations between two or more notes) are common, but not present in all song types. Trilled elements in this repertoire have been underlined. Notice that song A lacks a trill while songs B-I contain trills.
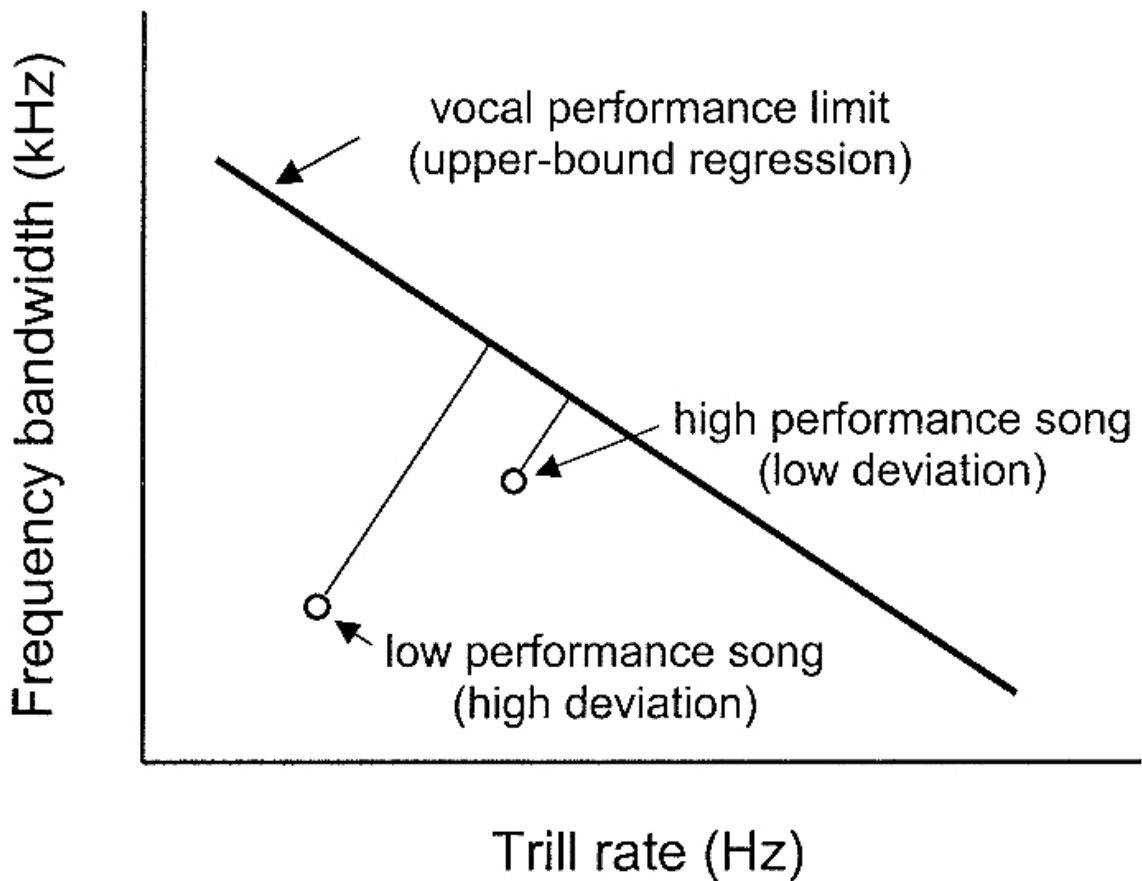
Figure 2. The function of trill rate as defined by bandwidth constrains song performances to a triangular distribution in acoustic space (Podos 1997). This creates a vocal performance limit which represents all values of highest possible performance song for an individual or species. Performance is quantified by the orthogonal distance from this vocal performance limit. High performance (low deviation) songs are songs that require a high degree of mandibular motion to produce. Low performance (high deviation) songs are characterized by both slow note repetition and low mandibular movement (Adapted from Ballentine et al. 2004).

METHODS

Study Area and Species

I conducted my study on a population of song sparrows located on the campus of Western Carolina University in Cullowhee, NC (35°18'N, 83°11'W, elevation 640 m). The habitat there consists of open lawns, parking lots, and buildings surrounded by ornamental shrubs, hedges, and trees. The study population of song sparrows is part of ongoing research in which territories are monitored regularly. Beginning in late January, males re-establish territories and increase territorial behavior. During this time, males will sing from distinct song posts at various locations within their territories (Arcese et al. 2002, Hyman, pers. comm.). Breeding occurs from early March through August, with some fledglings remaining present on their natal territories into September. I mapped territories of 49 males that I used for experiments (23 in experiment 1 and 26 in experiment 2). Most of the focal males had been marked with unique color band combinations. During this study, it was not necessary to band unmarked males used because male song sparrows rarely switch territories once the breeding season has begun (Scales et al. 2011).

Exemplar Songs

I created exemplar songs in three categories: trilled local, non-trilled local, and foreign control. I created these from full repertoire recordings made in Summer 2014 from the study population. I analyzed the songs in 'Raven Pro' (v.1.4. Bioacoustics Research Program, Cornell University, Ithaca, New York) and I identified examples from each repertoire as being "trilled" or "non-trilled". I defined a trill to be a syllable that contains

four or more repeated cycles of two or more notes at a rate of 4Hz or greater. The process for recording repertoires followed the methods of Searcy et al. 1985. For my foreign exemplars in experiment 1, I used recordings made in Summer of 2004 from Northwestern Pennsylvania. I then chose songs from each category (trilled, non-trilled, and foreign) to create exemplar files. I created and volume normalized all songs (to ensure that all exemplars were 90 dB at 1m) in Garageband (Apple, Inc. Cupertino, California). Trilled and non-trilled songs used in each exemplar were recorded from the same individual. Thus, any difference in response can be interpreted as a focal male perceiving differences of song type and not differences in males. Each focal bird in both experiments heard a unique set of songs, with the trilled and non-trilled local songs originating from the same singer to control for quality of the singer or atypical songs (Kroodsma 1986).

Study Site Division

To avoid the possibility of neighbor recognition (Fisher 1954, Stoddard et al. 1992, Temeles 1994, Hyman and Hughes 2006, Akçay et al. 2009), I grouped the study site into distinct geographic "neighborhoods". I separated these "neighborhoods" by distance (minimum 15m), campus buildings, or both. Neighborhood separation ensured that the exemplars were recorded at least five territories away from the focal male's territory. I avoided testing neighbors on the same day.

Aggression Assays

I assayed aggression of focal males in response to conspecific playback at the center of a bird's territory (Nowicki et al. 2002, Hyman et al. 2004, Hyman & Hughes 2006). I used average approach (m) to the speaker as a measure of aggressive

response. A lower average approach distance to the speaker characterizes the response as being more aggressive than a higher average approach distance (Hyman & Hughes 2006). Approach distance is a reliable metric of aggressive behavior (Searcy et al. 2006). I conducted assays from April to June during peak activity between 0600 and 1100 hours.

For each trial, I placed the playback speaker (SME-AFS, Saul Mineroff Electronics, Elkmont, New York) at the center of the focal male's territory. I standardized the playback volume to be 90 dB at 1m for all trials. Flags were placed at 0-1m, >1-4m, >4-8m, >8-16m, and >16m from the speaker. During the trial, I recorded distance the focal bird was to the speaker every 5 seconds. I calculated an average distance over the entire trial to use in subsequent analyses.

Experiment 1

In the first experiment (April-June 2015), each subject received three treatments: 1) Local trilled song, 2) Local non-trilled song, and 3) foreign song. Each exemplar set included trilled and non-trilled songs from the same individual. In this experiment, I used foreign song as a control to compare to the local songs. The purpose of including the foreign song treatment was to include a nonaggressive control. Song sparrows react more aggressively to local song over foreign song (Searcy et al. 1997; Wilson & Vehrencamp 2001). Including the foreign control allows me to determine if non-trilled songs are recognized as local, conspecific songs. The foreign exemplars were a mix of trilled and non-trilled songs from a site in Northwestern Pennsylvania. The playback files consisted of a single song type repeated six times. I broadcast song at a rate of one song every fifteen seconds for a total of two minutes. I followed this with five minutes of

silence. I recorded the focal male's distance for a total of seven minutes, two during playback and five afterward.

Experiment 2

A second experiment was conducted the following Spring to further explore the difference between trilled and non-trilled songs. In the second experiment (April-May 2016), each subject received two treatments: 1) local trilled song and 2) local non-trilled song. The playback files consisted of two different songs (i.e. two different trilled songs for trilled trials and two different non-trilled songs for non-trilled trials), each song repeated three times before switching to the next song. Song was broadcast at a rate of one song every fifteen seconds for a total of seven minutes. I recorded the focal male's distance for a total of seven minutes during playback.

Data Analysis

For experiment 1, I log-transformed the distance from the speaker and used repeated measures ANOVA to account for the within-subject experimental design. I used paired t-tests as post-hoc comparisons with Holm-Bonferroni adjustments to determine which treatments were significantly different from each other. For experiment 2, I log-transformed the average distance to the speaker. I analyzed distance data from experiment 2 by paired t-test. To determine if any responses were unusual, I calculated a Pearson's correlation coefficient for my entire experiment 2 dataset. I conducted all analysis in R (v3.3.0).

RESULTS

Experiment 1

In the aggression assays, I found a significant difference in average approach among the total trials when analyzed for the entire seven-minute treatment (repeated measures ANOVA, DF=44, F=6.465 P=0.00345). Post-hoc tests showed that there was a significantly more aggressive approach for the Trilled treatment (T) than the foreign control treatment (C) (Paired T test, P=0.028). Focal males responded more aggressively to the non-trilled treatment (NT) than the foreign control (C) (Paired T test, P=0.028). No significant difference was found between responses to T and NT (Paired T test, P=0.593) for the full seven-minute trial period (Figure 3).

However, when analyzed as the portion of the trial that includes the song playback (minutes 1-2) without the period of silence (minutes 3-7), different results were found. I found a significant difference in average approach overall (repeated measures ANOVA DF=44 F=6.058, P=0.00474). Post hoc tests revealed a more aggressive approach to T than NT (Paired T-test, P=0.03 adj.=holm) as well as a more aggressive approach to T than C (Paired T test, P=0.03 adj.=holm) (Figure 4).

Experiment 2

In the aggression assays for Experiment 2, I found a significant difference in average approach between the two trials, with focal males consistently approaching the speaker more closely in response to the trilled treatment than the non-trilled treatment (Paired T-test, t=1.8039, DF=25, P=0.042). In addition, aggressive response was consistent and repeatable within individual, showing that none of the responses were

unusually aggressive or nonaggressive for the individual (Pearson's product-moment

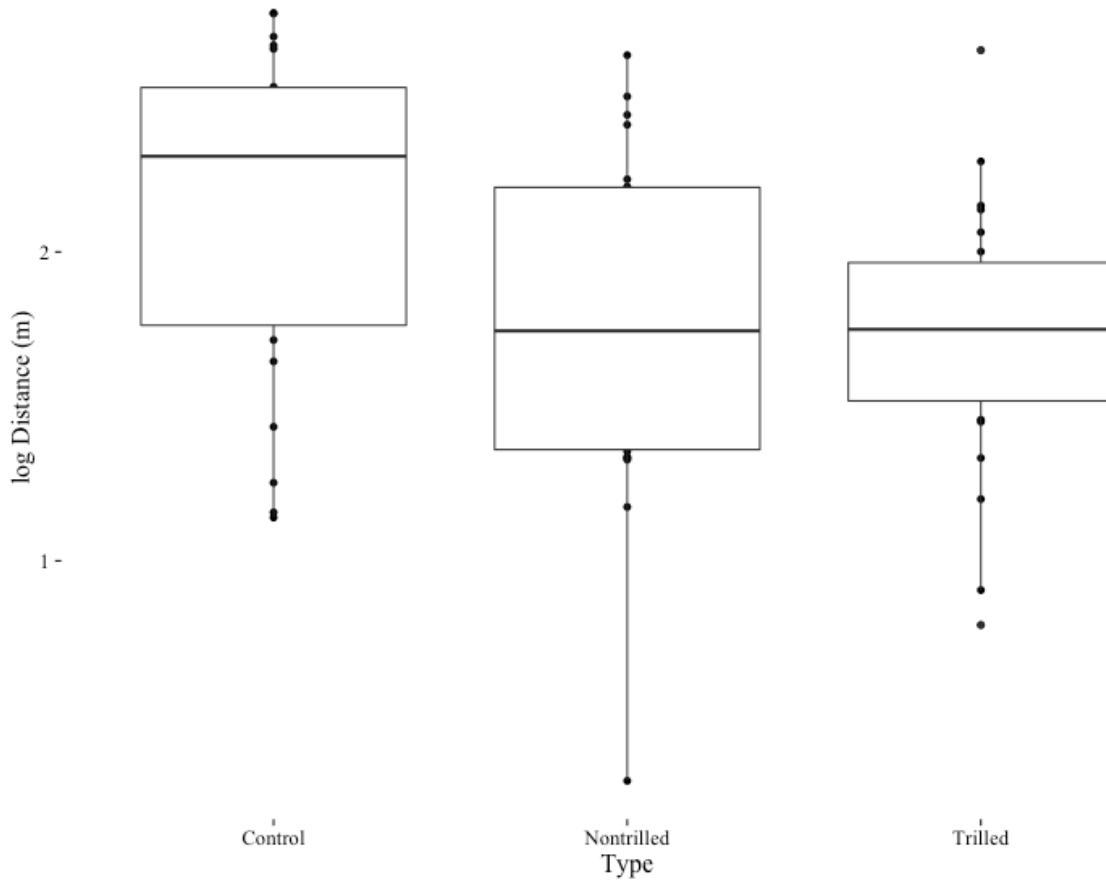correlation, adjusted r-squared=0.6086, p=<0.001) (Figure 5).

Figure 3. Mean approach distances for subjects to playback trials in response to trilled

song, non-trilled song, and foreign song for 23 male song sparrows over the course of

the whole trial (Repeated measures ANOVA, DF=44, F=6.465 P=0.00345). The C

songs elicited a much weaker aggressive response than T song (Paired T test, P=0.028) and NT song (Paired T test, P=0.028).
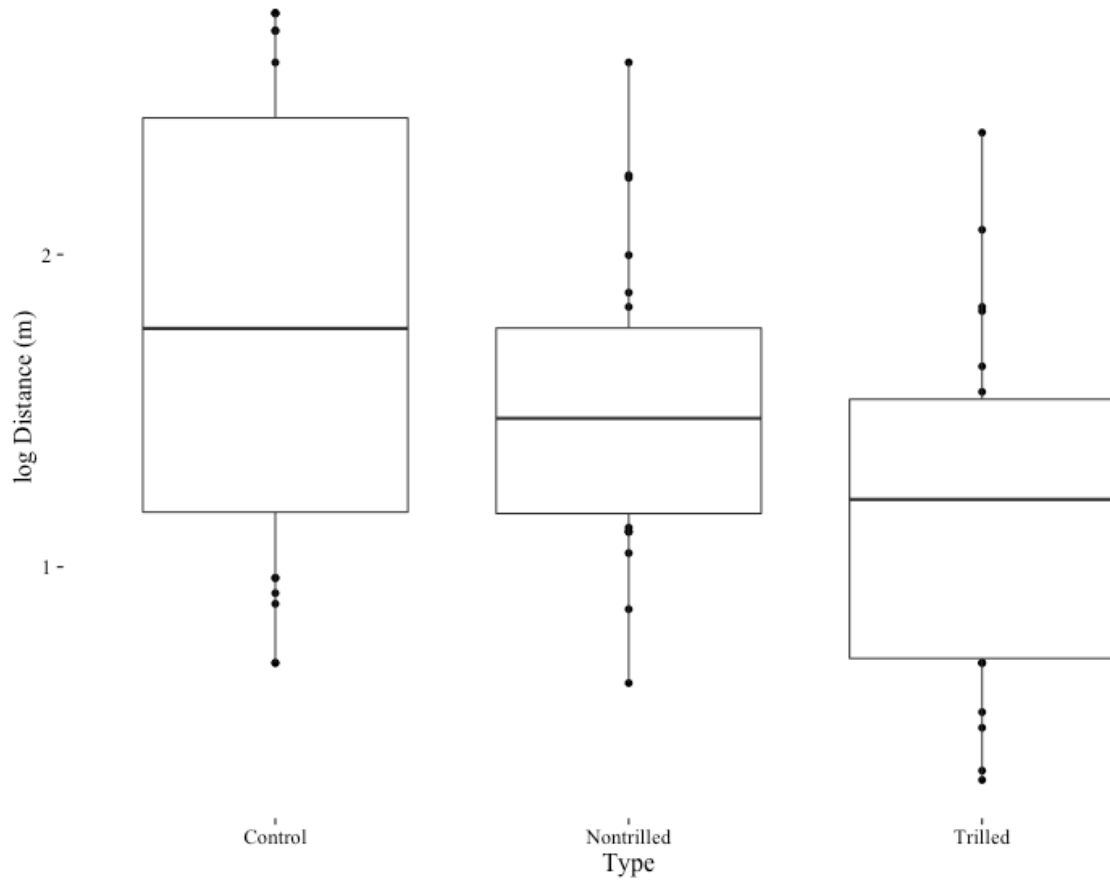

Figure 4. Mean approach distances during playback for all treatments during playback (Repeated Measures ANOVA DF=44 F=6.058, P=0.00474, N = 23). Post hoc tests reveal a difference between the T and C (Paired T test, P=0.03 adj.=holm) and T and NT (Paired T test, P=0.03 adj.=holm).

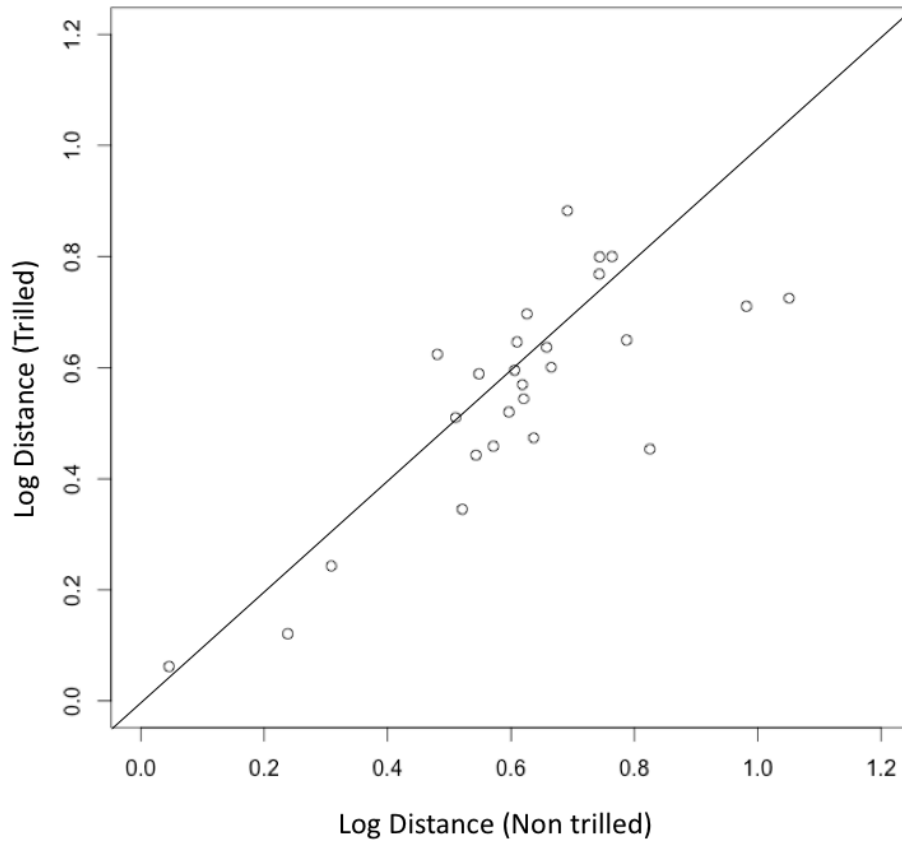Figure 5. Log approach distances for 26 male song sparrows in response to 7 minutes of trilled and non-trilled song. There was a statistically significant difference in approach distance within individual (Paired T-test, t=1.8039, DF=25, P=0.042). The distance of approach is positively correlated showing that responses are repeatable within individual (Pearson's product-moment correlation, adjusted r-squared=0.6086, p=<0.001).

DISCUSSION

My results show that male song sparrows discriminate between songs that are

from the same singer, but either contain or lack a trilled element. Across two similar,

within-male playback experiments, focal birds responded more strongly to trilled song

types than non-trilled song types from the same singer based on distance to the

speaker. In line with previous authors (Slater 1981; Leitão & Riebel 2003; Leitão et al.

2006), I interpret closer approach to the speaker (simulating a singing conspecific

intruder) as more aggressive response. Results of this study support the hypothesis that

trilled song types elicit stronger responses from male song sparrows than non-trilled

song types.

In experiment 1, I tested trilled songs against non-trilled songs. I used foreign

conspecific song as a control treatment. In this experiment, non-trilled songs received

more aggressive responses than foreign songs, while trilled and non-trilled songs did

not differ. The results of this experiment confirm that both the trilled and non-trilled local

songs are more aggressive signals than foreign songs in my study population. This

confirms previous findings that local song elicits a more aggressive response than

foreign song (Searcy et al. 1997; Wilson & Vehrencamp 2001). However, in the overall

analysis of experiment 1, I could not detect a difference in response between trilled and

non-trilled song. One reason for this finding could be that I used a short playback period

of only two minutes (six songs) followed by a long recovery period. It seemed likely that

such a long recovery period might obscure more subtle differences in responses of

males. Therefore, to understand whether there were differences in response of males

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during the playback, I analyzed responses of males just for the two-minute period that song was played. I found that responses between trilled and non-trilled local songs were significantly different. Although my original hypothesis predicted a difference in response to trilled and non-trilled song, the experiment as designed was unable to detect a difference. This suggested the need for a second, more powerful experiment to further examine the relationship between trilled and non-trilled song types. Experiment 2 was designed to feature a much longer playback period (seven minutes instead of two) and would not use foreign exemplar songs. The foreign exemplar was omitted because Experiment 1 provided sufficient evidence that both trilled and non-trilled song types were recognized as local song.

In Experiment 2, I found significant differences in aggressive response based on presence of a trilled element in the song. Corroborating the results of Experiment 1, focal males responded more aggressively to trilled songs than non-trilled songs. The difference in response indicates that the trilled song may be a more aggressive signal than the non-trilled song. My results also show that the responses are repeatable within individual, which is a similar finding to that of Hyman et al. (2004) (Fig. 4). Response repeatability shows that aggressive birds will respond aggressively to playback, while less aggressive birds respond less aggressively to playback. Individual variation in aggressiveness was controlled for by a within-subjects' experimental design. Despite the high degree of correlation between each focal male's responses to both exemplars, I still found a consistent difference in how they responded to songs with trills versus songs without trills. This is evidence that supports previous literature which suggests song types may be used selectively by singers (Weary et al. 1994; Beebee 2004;

Staicer 1996; Trillo & Vehrencamp 2005;). It also confirms findings that receivers are listening to and responding to song structure (Vallet & Kreutzer 1995; Vallet et al. 1998). Further, it may suggest that individual song function may be a driver of repertoire complexity.

My experiment provides support for the hypothesis that male-male interaction is an important driver of repertoire complexity. Across two experiments, I found evidence that suggests song types are not truly equivalent in repertoires. Complex song structures are shown to be significant in both intersexual and intrasexual interactions (Vallet & Kreutzer 1995; Vallet et al. 1998; Leitão et al. 2006), yet songs of varying structures and syllable complexities persist in song repertoires. Some song types may be more salient in male-male communication based on structure (Petrusková et al. 2014), and my experiment provides evidence for this hypothesis. Some studies have found that songs within repertoires differ in function, and are used in selective contexts (Weary et al. 1994; Beebee 2004; Trillo & Vehrencamp 2005). However, my study is one of the first to demonstrate that certain song types may be used preferentially in agonistic contexts in song sparrows, thus showing intrasexual signaling is a possible driver of repertoire complexity.

If both trilled and non-trilled song types were recognized as conspecific songs, why would individuals respond differently to them? One explanation is that the trill is used for performance comparison in counter-singing interactions. It is argued that the trill is an index signal of motor capability (DuBois et al. 2011), and thus song matching may allow birds to compare each other's trill performances by singing the same song. However, in eastern populations of song sparrows, such as my study population, whole-

song sharing is less common than in western populations (Hughes et al. 1998). Eastern populations seem to learn and recombine song elements, meaning that whole song-sharing is rare (Hughes et al. 1998). So, in eastern populations, whole song-matching may not be as important as song syllable matching. I did not test my hypothesis within the framework of song matching, however the increased aggressiveness in response to the trilled exemplars likely is informative when compared to the reduced aggressiveness in response to a song that lacks a trill. If a song with a trill reveals information about the singer (motor capability, post-hatching quality, current condition), it may be adaptive to not always reveal such information. Logue and Forstmeier (2008) published a model detailing song matching strategies and hypothesized that the need for subordinate males to possess non-aggressive songs. The non-trilled song and the reduced aggressiveness of responses to it may imply the non-trilled song is a conventional signal of reduced aggression. These songs may persist in most repertoires because the cost of possessing a non-aggressive song in even a dominant male's repertoire may be lower than a costly, avoidable fight. The differences in response that I found between these two general song type categories suggest that these songs perform separate functions within the repertoire.

Further study of the functional significance of trilled song types could examine the possibility that different trill types could elicit different responses. I could manipulate trills to be higher performance (faster while maintaining wide bandwidth) and lower performance (slower while maintaining wide bandwidth). There is evidence in similar species that receivers may be listening to the nuances of trill performance. In playback experiments, female swamp sparrows (Melospiza geogiana) give more copulation

solicitation postures to natural songs that were closer to the species' upper performance barrier (Ballentine et al. 2004). Playback experiments with male swamp sparrows show that focal birds approach higher performing songs more closely than lower performing songs (DuBois et al. 2011). Structure of the trill may also be significant. Trills vary in structure within repertoires. Some are composed of two oscillating notes, while some trills contain more notes. Conducting an experiment where performance is not directly manipulated, but where composition of the trill is an explanatory variable is a natural next step. There are precedents for the significance of trill structure within repertoires in the literature. Trillo & Vehrencamp (2005) found functional differences of bird song based on structure within repertoires, showing that song types seem to be intended for specific circumstances such as when the female mate is near or whether the singing is occurring during the dawn chorus. Functional significance of song has also been described in wood warblers (Weary et al. 1994; Beebee 2004). Similarly, studies of tree pipits (anthus trivialis) have found that louder, simpler trills are more significant in male-male interactions than softer, more complex trills (Petrusková et al. 2014).

In summary, song sparrows judge singers by the acoustic features of their songs, confirming both my hypothesis and models of song functional significance found in other species with complex repertoires. I tested the significance of song type in agonistic contexts by comparing trilled song sparrow songs with non-trilled songs to determine which elicited a stronger response from conspecific males. I found that the trilled songs elicited significantly more aggressive responses, indicating that songs within repertoires possess some functional significance from one another in this context. These results provide evidence for male-male competition as a potential driver of repertoire size.

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