

**VOCAL BEHAVIOUR OF SONG AND SWAMP SPARROWS UPON ARRIVAL ON
SHARED BREEDING GROUNDS**

By

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Abstract

Closely related species interact often, typically competitively, aggressively, and asymmetrically, with a consistent dominance hierarchy among species. Competition for resources appears to be a rate-limiting step in diversification, but beyond this, we know little about the ecological role of aggression in facilitating or constraining the coexistence of species due to the difficulty in observing natural interactions. To examine how closely related species in a dominance hierarchy aggressively interact, and how those interactions may facilitate coexistence, we documented vocalizations of Song (*Melospiza melodia*) and Swamp (*M. georgiana*) sparrows during natural and simulated territory settlement to answer the question: How does vocal behaviour of a dominant species change when first faced with a subordinate competitor on shared breeding territory? Though sample sizes were too low for statistical testing, we saw slightly increased rates of “Swamp Sparrow-like” songs sung by Song Sparrows in relation to Swamp Sparrow presence, as well as trill syllable lengths of Song Sparrow songs approaching average lengths of Swamp Sparrow trill syllables. These trends may suggest syllable sharing or vocal shifts in Song Sparrows as a response to Swamp Sparrow competitors – this vocal convergence may be beneficial in mediating conflicts over shared resources. We also provide novel descriptions of Swamp Sparrow behaviour during settlement on territories overlapping Song Sparrows. Further descriptions of vocal interactions can inform how closely related species interact aggressively, and will contribute to our understanding of how aggression might relate to coexistence on shared territories.

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Glossary

Note – each individual sound within a song (Berwick et al. 2011)

Syllable – repeated patterns or clusters of notes (Marler and Peters 1977)

Phrase – non-repeated groups of syllables within each song (Berwick et al. 2011)

Song Type – distinct singing pattern comprised of notes, syllables, and phrases sung by a male.

Individuals can sing many different song types. There is less variation within a song type than between – song types can be grouped distinctively (Beecher and Brenowitz 2005)

Song Category – binned song types based on attributes. Each song category (A, B, C) incorporates many song types.

Repertoire – number of song types sung by an individual male. Variable between individuals.

SOSP – standardized alpha code for Song Sparrow (*Melospiza melodia*)

SWSP – standardized alpha code for Swamp Sparrow (*Melospiza georgiana*)

TRES – standardized alpha code for Tree Swallow (*Tachycineta bicolor*)

Chapter 1 - Introduction

1.1 Coexistence and Biodiversity

Rates of diversification appear to be limited by the ability of closely related species to coexist (Price et al. 2014); whether closely related species can coexist, in turn, is often determined by their ecological interactions (Peiman and Robinson 2010). These ecological interactions are typically competitive, aggressive, and asymmetric, with a consistent dominance hierarchy among species (Martin et al. 2017). Competition in closely related species with a high degree of overlap in resource use can decrease fitness, with higher costs for behavioural subordinates who are excluded from priority resources (Morse 1974, Martin and Martin 2001a, Amarasekare 2002, Weber and Strauss 2016). Yet, aggression may serve as an adaptive form of communication that can limit fitness detriments related to overt competition and help partition resources successfully (Cody 1969, Grether et al. 2013). Ultimately, how these competitive, aggressive interactions facilitate or constrain species coexistence is poorly known, in part due to the difficulty in observing them naturally. In order to maintain stable coexistence, and more broadly, local biodiversity, closely related species must limit the costs of interspecific competition (MacArthur and Levins 1967, Chesson 2000, Price et al. 2014). Understanding how biodiversity is maintained is critical to provide insight into the broader scope of how ecosystems function, which is inherently important for the health of ecological communities.

Interactions between species are pivotal factors in the coexistence of closely related or ecologically similar species (MacArthur and Levins 1967, Chesson 2000). Heterospecific aggression (behavioural responses such as aggressive vocalizations, assertive approaches, or physical attacks directed towards competitors; Drury et al. 2015) is common, but was historically

thought to serve primarily as a preventative measure against hybridization (Orians and Willson 1964), and has been attributed to accidental or misdirected aggression in species that look similar (Murray 1971, 1976). However, closely related species commonly coexist and aggressively interact, and currently, interspecific aggression is believed to be an adaptive response to heterospecific pressure that plays a large role in minimizing the costs of interference competition (Grether et al. 2013, Freeman et al. 2016). Aggression between closely related species often reflects a consistent dominance hierarchy, with the behaviourally dominant species in the pair winning the majority of fights for resources (Martin et al. 2017). Despite potential fitness impacts, dominance hierarchies are consistent and ubiquitous in nature, suggesting ecological stability. It is important to understand the role of interspecific aggression within these hierarchies, as behavioural dominance can influence resource use (for example, nest sites, range limits, foraging sites; Alatalo et al. 1987, Martin and Martin 2001b, Duckworth and Badyaev 2007, Freshwater et al. 2014), when and where species live, and more broadly, patterns of biodiversity.

Often, closely related species in dominance hierarchies that directly compete for resources in sympatry fare much better in the absence of the other. When a dominant species is removed, the subordinate species tends to shift their behaviour or resource use, suggesting that subordinate species are left with suboptimal habitat. For example, Orange-crowned (*Oreothlypis celata*) and Virginia's (*O. virginiae*) warblers that live in overlapping habitats in Arizona experience higher fitness when the other species has been removed (Martin and Martin 2001a). When the dominant Orange-crowned Warbler is removed from an area, the subordinate Virginia's Warbler moves into higher quality nest sites and is able to access more food (Martin and Martin 2001a). In addition, both species experience less nest predation in the absence of the

other, leading to increased fledging rates, demonstrating that coexistence inflicts high fitness costs (Martin and Martin 2001a). Here, aggression between Orange-crowned and Virginia's warblers is suggested to be an adaptive strategy that mediates the fitness costs of density dependent predation (Martin and Martin 2001a). The subordinate is often excluded from preferred nest sites, thus reducing nest density, but is still able to coexist and utilize overlapping territory and foraging locations. Similarly, tits will undergo a foraging niche shift (Alatalo et al. 1985); when larger (likely competitively dominant) tit species are removed, the smaller ones move into those previously occupied foraging niches. Dominance hierarchies in coexisting species are a widespread pattern, suggesting that there are underlying mechanisms that allow closely related competing species to stably coexist. Understanding how closely-related species in a dominance hierarchy can coexist provides insight into how local species diversity is maintained, and what factors prevent dominant species from excluding subordinates altogether.

Such asymmetric competition has implications for trait evolution among species that share resources (Freshwater et al. 2014). In theory, due to the high cost of defending space and resources, interspecific aggression should be selected against and thus competing species should diverge to limit detrimental interactions (Orians and Willson 1964, Grether et al. 2009, Losin et al. 2016), especially in dominance relationships where there is a consistent winner gaining access to higher quality resources (Morse 1974, Freshwater et al. 2014). Indeed, interspecific competition has been observed to drive trait divergence; for example, Darwin's finches diverged in beak morphology to lessen competition for food (Darwin 1859, Lack 1947). Additionally, because of asymmetric competition, subordinate species show consistent differences in migration distance and traits such as foraging behaviour or nest site usage as compared to dominant heterospecifics (Freshwater et al. 2014). These patterns of trait divergence are usually seen and

expected in traits associated with resource use, but divergence in signal traits, especially those that mediate conflict, may be just as common (Drury 2015).

Less intuitively, interspecific interactions can also lead to trait convergence when selection favours shared signals among interacting species (Cody 1969, Grether et al. 2013). Recent work provides evidence suggesting that interspecific aggression is not simply a negative consequence of coexistence and competition for shared resources, but is likely an adaptive response that permits species to coexist while reducing fitness costs (Peiman and Robinson 2010, Losin et al. 2016). Convergence in traits involved in character recognition (for example, song or appearance) may be adaptive, allowing interspecific aggressive interactions to be more effective due to better recognition and communication between species (Cody 1969, Grether et al. 2009, Reif et al. 2015).

Therefore, in the absence of stronger factors, traits that assist in mediating interspecific competition and conflict should be selected for in dominance hierarchies (Martin and Martin 2001a, 2001b, Freshwater et al. 2014). Aggressive communication, such as vocalizations and threatening approaches, can be used as warning signals, without having to expend the energy required for physical conflict (Losin et al. 2016). Vocal behaviour is an excellent tool to study interspecific interactions as much work has been done on bird song as a context-specific signalling behaviour, allowing for interpretable interactions between individuals (e.g. Catchpole and Slater 2008, Searcy and Beecher 2009, Searcy et al. 2014), which can help inform how aggressive interactions are shaping ecology, evolution and biodiversity.

1.2 Aggression and Song

Interspecific interference competition is common in sympatry, usually indicated by behavioural aggression (Losin et al. 2016, Grether et al. 2017). In birds, song is a communicative

signal that can reduce the frequency of costly fights. Songbirds provide an excellent platform to study interspecific aggression because their interactions have an easily traceable soundtrack. Other than mate attraction, male bird song functions primarily as an aggressive signal used to repel competitors from their territory (Kroodsma and Byers 1991, Catchpole and Slater 2008). Male song alone (no decoy or physical bird present) can reduce territory invasions compared to territories with no song (Kroodsma and Byers 1991). Muting experiments also indicate that song and other vocalizations are crucial in interactions between conspecific males (Peek 1972, Westcott 1992).

Additionally, in aggressive disputes, birds exhibit the “dear enemy effect”, showing less aggression to known neighbours than to unfamiliar intruders (Fisher 1954, Temeles 1994, Searcy et al. 2014), demonstrating an ability to recognize and distinguish individuals based on song and repertoire alone. Several studies illustrate the ability of birds to recognize and respond specifically to each other’s vocalizations, providing support that song recognition is an adaptive behaviour, and heterospecific-directed aggression is not a result of misidentification (e.g. Rice 1978b, Baker 1991, Martin et al. 1996).

In many species, individual song recognition is important for mediating interactions. Western Song Sparrows (*Melospiza melodia*) demonstrate both song-type matching and repertoire matching when in contact with conspecific neighbours (Stoddard et al. 1992, Beecher et al. 2000, Beecher and Campbell 2005). Song matching is an aggressive signal in birds, and Song Sparrows have demonstrated more prevalent song-type matching earlier in the breeding season when territorial aggression is at its highest, while later in the season, repertoire matching is more common (Stoddard et al. 1992). Song Sparrows are more likely to respond aggressively when type-matched, and de-escalate conflict when threatened by switching to unmatched songs

(Burt et al. 2001). Additionally, when communicating with a neighbour, no unshared songs are used, implying that Song Sparrows use context-dependent vocalizations (Beecher et al. 2000). Many species of warblers also exhibit context-dependent singing behaviour, often using a specific song type in territorial interactions, whether it be inter- or intraspecific (Morse 1966). Male Yellow Warblers (*Setophaga petechia*) sing two distinct song types in different contexts. Yellow Warblers seem to preferentially use one song type when interacting with Chestnut-sided Warblers (*S. pensylvanica*) along territory boundaries, while using the other song type to interact with conspecific males (Morse 1966). Kroodsma (1973) noted that House Wren (*Troglodytes aedon*) males occasionally sang Bewick's Wren (*Thryomanes bewickii*) songs in interspecific interactions, where Bewick's Wrens would countersing, matching the song that the House Wren copied. Singing similar songs thus appears to convey some information about territoriality, which can be important for intra- and interspecific communication. These examples demonstrate that, in addition to identifying conspecific individuals, several bird species are also able to reliably distinguish heterospecific competitors and respond aggressively to them, likely preventing interspecific matings, helping to maintain territory boundaries, and reducing costs of coexistence and competition (e.g., Baker 1991, Martin and Martin 2001b, Sedláček et al. 2006). Along an elevational gradient, interspecific aggression lessens away from the zone of contact, (Jankowski et al. 2010, Freeman et al. 2016), and interspecific differences in song diminish within hybrid zones (Secondi et al. 2003), suggesting that aggression is indeed an adaptive response in sympatric related species and heterospecific song learning and recognition plays a major role in these interactions.

This evidence suggests that vocal behaviour can be used to mediate conflict - simply by switching song types, signals can be targeted to heterospecifics and costly physical aggression

can be avoided. Indeed, song sharing or vocal resemblance has been suggested to reduce aggressive physical interactions between neighbours. For example, Red-eyed (*Vireo olivaceus*) and Philadelphia (*V. philadelphicus*) vireos are ecologically similar, yet maintain distinct territories through interspecific aggression (Rice 1978a, 1978b). Furthermore, they respond aggressively to playback of each other's songs, and show evidence of stable coexistence due to the presence of interspecific territoriality (Rice 1978a, 1978b). Although these two species are phenotypically and ecologically similar, the maintenance of separate territories seems to be enough to allow coexistence (Rice 1978a, 1978b). In order to maintain distinct territories, Philadelphia Vireos, which are considerably smaller and socially subordinate to Red-eyed Vireos, sing nearly identical songs to the Red-eyed Vireos. Philadelphia Vireos respond less aggressively to Red-eyed Vireos than conspecifics, while Red-eyed Vireos respond equally aggressively to heterospecific and conspecific playback, likely due to their competitive dominance (Rice 1978a, 1978b). Philadelphia Vireos have seemingly evolved such a similar repertoire in order to communicate effectively with their dominant heterospecifics while minimizing fitness costs associated with fighting. Song type matching signals aggressive intent, but switching songs may de-escalate aggression, as in Song Sparrows (Burt et al. 2001). If Philadelphia Vireos do not explicitly type-match Red-eyed Vireos, but sing similar songs, then these convergent vocalizations may be an adaptive response that advertises territory boundaries while reducing the occurrence of costly physical interactions. While the maintenance of completely exclusive territories is rare in birds, here, spatial partitioning seems possible due to territoriality facilitated by vocal mimicry.

Mimetic singing is the phenomenon in which one species of bird exactly copies the song or call of another species, for the purpose of deceit or misidentification by the receiver of the

vocalization (Baptista and Catchpole 1989, Dalziell et al. 2015). Mimicry in songbirds is common among birds that exhibit song learning (Catchpole and Slater 2008, Dalziell et al. 2015). In eastern Ontario, Blue Jays (*Cyanocitta cristata*) mimic the calls of Red-shouldered Hawks (*Buteo lineatus*) almost indistinguishably (Smith et al. 2013). This strategy of mimicking species that are larger or dominant seems advantageous; if the mimic is good enough, it may be able to deceive a listener, which can potentially avoid conflict or predation (Dalziell et al. 2015). However, we also see many examples of dominant birds mimicking subordinate birds (e.g., Great Tits (*Parus major*) mimic Blue Tits (*Cyanistes caeruleus*) (Gorissen et al. 2006)). This, along with little good evidence that mimicry is truly deceptive, challenges the classical definition of mimicry as a signal for deceit (Dalziell et al. 2015). In this case, the term heterospecific vocal resemblance (or heterospecific song matching) may be more accurate, as song matching still confers an advantage without requiring deception of the receiver.

Heterospecific song matching, where one species shares the song of another species, has been documented in several closely related species. For example, Great Tits are dominant to Blue Tits, and preferentially use shared songs in heterospecific interactions (Gorissen et al. 2006). Heterospecific vocal resemblance is also seen in species such as the Thrush Nightingale (*Luscinia luscinia*) (Sorjonen 1986, Reif et al. 2015) where heterospecific songs make up a large proportion of their repertoire (“mixed singing”). Thrush Nightingales are dominant to Common Nightingales (*L. megarhynchos*), and incorporate many Common Nightingale songs into their repertoire. Mixed singing in Thrush Nightingales has been suggested not to be a strategy of deceit (as this would not be beneficial if the Common Nightingale already recognizes the Thrush Nightingale as dominant), but could be vocal convergence in order to mediate interactions in sympatry (Reif et al. 2015). As has been suggested in Philadelphia and Red-eyed Vireos, singing

similar songs may increase vocal aggression, but facilitate resource partitioning, potentially reducing the intensity of interspecific competition (Rice 1978b, Reif et al. 2015). Cody (1969, 1973) argued that convergence in vocalizations is beneficial in defending territory interspecifically – if song matching is aggressive, then vocal convergence increases interspecific song matching and aggression, which may increase territoriality, lessening the competition for resources within an individual’s space.

Evidence to date suggests that heterospecific vocal convergence may be an adaptive response that increases the efficacy of communication between closely-related species (Cody 1973, Secondi et al. 2003, Grether et al. 2013, Reif et al. 2015). Using specific songs in interspecific interactions can more efficiently mediate interspecific territoriality and aggression, which can reduce costly interactions that arise due to coexistence. We see several accounts of interspecific convergence and recognition of alarm calls that allows for interspecies communication (Magrath et al. 2015a, 2015b), however, how frequently this occurs in song is poorly known. Much of the literature on vocal resemblance has been either conflicting or inconclusive, or else focused mainly on intra- instead of interspecific effects. Understanding the use and prevalence of heterospecific vocal resemblance and recognition in sympatry is an important step towards figuring out how closely related species in dominance relationships are able to coexist and mediate interactions, which has wide-reaching implications for our understanding of the maintenance of biodiversity as a whole.

1.3 Scope of Thesis

For my Masters’ thesis, I was interested in how two closely related species interact when they first come into contact on overlapping breeding territories, and how their interactions might facilitate coexistence. I chose Song Sparrows (*Melospiza melodia*) and Swamp Sparrows (*M.*

georgiana) as my study species because they are common, well-studied songbirds with an established dominance hierarchy, making them an excellent study system to help answer my question.

1.3.1 Study Species

Song and Swamp sparrows are closely related species that have similar ecological preferences and share many resources. In my study locations, Song Sparrow and Swamp Sparrow breeding habitat overlaps in marshes. Asymmetric, aggressive interactions between these two species suggest that the larger (~19 g) Song Sparrows have a competitive advantage (Grant 1966, Willson 1972, Greenberg 1988), yet the smaller (~15 g) Swamp Sparrows still nest successfully on overlapping territories (Willson 1972, Greenberg 1988). This well-studied dominance hierarchy, and the species' overlap in breeding territory and resources, make sparrows an excellent system to study interspecific aggression. In addition, like other songbirds, sparrow interactions have a soundtrack, creating the opportunity to record interactions through vocalizations.

Since Song and Swamp sparrows are found in sympatry with overlapping territories, they must learn to distinguish between each others' songs (Peters et al. 1980). Male Song Sparrows have a large repertoire (~6-12 songs on average) of complex song types (Nordby et al. 1999), consisting of two or more phrases (Marler and Peters 1977). Song Sparrows sing bouts of one song type before switching to another (Nordby et al. 1999). Song repertoires in the Song Sparrow are completed by their first year, and songs are learned from neighbouring males (Nordby et al. 1999). Conversely, Swamp Sparrow repertoires consist of an average of three song types (Marler and Sherman 1985), all variations on a single trill composed of three or four notes. Swamp Sparrows exhibit much more specificity when learning songs as a juvenile,

contributing to the low variability of song within the species (Kazuo and Dooling 1990). There is no evidence suggesting Song and Swamp sparrows learn to sing each others' songs in the wild (Marler and Peters 1977, Peters et al. 1980); in fact, both species selectively learn their own species-specific songs even when raised in isolation (Marler and Peters 1977).

Both Song and Swamp sparrows vary in how each individual structures the syllables within their songs (Marler and Peters 1977). Swamp Sparrow-like songs consist of a trill (single phrase) of identical syllables at a steady rate (Marler and Peters 1977). The key difference between Song and Swamp sparrow songs is the presence of more than one phrase in a Song Sparrow song (Peters et al. 1980). Song Sparrows learned both Song and Swamp sparrow syllables while Swamp Sparrows learned only their own syllables in a tutoring experiment by Peters et al. (1980). However, territorial Song Sparrow males (>1 year old) are able to distinguish conspecific from heterospecific songs, suggesting that song recognition improves over time (Peters et al. 1980). Syllable type is also important to adult male Song Sparrows for song recognition. Swamp Sparrows use syllable structure and not temporal arrangement when distinguishing between songs (Peters et al. 1980, Kazuo and Dooling 1990). Since Swamp Sparrows hold smaller territories, usually within or largely overlapping a Song Sparrow territory, Swamp Sparrows are likely to be more prone to hearing Song Sparrow song in their critical learning period, making it beneficial to have a more selective song learning ability (Peters et al. 1980).

Both species use syllable structure to identify species-specific songs, therefore, the presence of trill syllables (2+ repeated notes) in Song Sparrow songs must be important for interspecific recognition, as Swamp Sparrow songs only consist of a trill. If Song Sparrows display heterospecific vocal resemblance for the purpose of interspecific recognition and conflict

mediation as a response to Swamp Sparrows, I expect to see a shift in vocal behaviour in Song Sparrows after the Swamp Sparrows arrive, as seen by the use of songs which have a trill phrase in them that is most similar to a Swamp Sparrow trill.

1.3.2 Thesis Objectives and Predictions

I used a combination of natural observations and playback experiments to answer the question: How does vocal behaviour of a dominant species change when first faced with a subordinate competitor on shared breeding territory? I predicted that upon arrival of Swamp Sparrows, Song Sparrows would change their vocal behaviour to use songs that sound more similar to Swamp Sparrow songs in order to mediate conflict. I expected to see a shift in Song Sparrow vocalizations after arrival of Swamp Sparrows in three ways: a) an increase in the proportion of Swamp-Sparrow-like songs (hereafter “Category C songs”, see Methods), b) an increase in Trill Score (a score based on song profiles for each day, see Methods), and c) a shift to song types with trill syllable lengths more similar to Swamp Sparrows (~0.169 seconds, see Results). I also provide previously undocumented information on the nature of interactions between Song and Swamp sparrows during territory settlement.

Though much literature exists on the ability of Song and Swamp sparrows to recognize and distinguish the others’ vocalizations, characterizations of their behavioural interactions upon arrival at their breeding grounds have never been described, particularly during moments of initial contact during settlement. To date, territorial aggression between Song and Swamp sparrows has never been investigated by classifying and comparing vocalizations before and after the natural arrival of an interspecific competitor. My study begins to fill this gap in knowledge by providing detailed auditory observations of interactions during natural habitat colonization, as well as playback experiments of simulated territory invasion.

Chapter 2 – Methods

2.1 Natural Arrival

We collected all data from the Queen's University Biological Station, Elgin, Ontario, Canada. Dr. Paul Martin initially used the following methods to collect data in April 2015, which I have used to supplement my own data collected in April of 2017 and 2018. Target sites were marshes where Song and Swamp sparrows had both been observed nesting in past years. We searched for Song Sparrow breeding territories in early April and deployed two continuous, automated Wildlife Acoustics Song Meter SM2 recording devices (Wildlife Acoustics, Inc., Maynard, MA, USA) in the middle of their breeding territories. In order to properly survey the entire territory, each recorder was equipped with two microphones, one attached to the recorder, and another 10 metres away attached to a wire, for a total of two recorders with four microphones per site. Array set-up occurred after a Song Sparrow male had been observed to have established territory, but before a Swamp Sparrow arrived to the area, in order to record the exact moment in which a competing Swamp Sparrow arrived on the territory of a Song Sparrow. Recordings ran continuously, with a 10 second break in recording per hour to compile and save the audio. Recordings ran until a Swamp Sparrow was observed on territory and stayed for 48 hours.

I used Audacity 2.1.3 to analyze recorded audio and categorize territorial songs from Song Sparrows into different song types. I transcribed audio for a 72-hour period: the day a Swamp Sparrow was first heard on territory, the day before, and the day after. I did this visually using sonograms of the recordings, sorting songs into types and documenting how many songs of each type were sung on each of the three days. Swamp Sparrow songs were also transcribed. While automated song classification software exists, it varies widely in accuracy, and no

software has consistently reached the level of accuracy of a trained human (Swiston and Mennill 2009, Wolfgang and Haines 2016, Thompson et al. 2017), especially when identifying songbirds with widely varying repertoires such as the Song Sparrow.

I further binned Song Sparrow songs into three categories related to presence or absence of a trill phrase, as a means of measuring similarity to a Swamp Sparrow song. Here, I define a trill as a series of oscillating notes with at least two notes per syllable, and at least two syllable repetitions. Swamp Sparrow trills have three to four notes per syllable. Song Sparrow song categories include: (A) songs with no trill phrase, (B) songs with a trill phrase with two notes per syllable, and (C) songs with a trill phrase with three or more notes per syllable (see figure A1). This measurement represents similarity of the Song Sparrow song to a Swamp Sparrow song, a song with a trill (B or C) being more similar to a Swamp Sparrow song than a song with no trill (A), and a trill with three to four notes per syllable (C) being more similar to a Swamp Sparrow song than one with two notes per syllable (B).

I calculated a trill score by assigning Category A a score of 0, Category B a score of 1, and Category C a score of 2. These scores represent the perceived quality of the trill components and similarity to Swamp Sparrow songs. I then multiplied the number of songs in each category by their trill score and divided by the total number of songs to get an average trill score for each day at each site, allowing for comparison of song quality between days.

For each song type within the categories, I randomly selected 10 songs and measured the length of one syllable (oscillation) within a trill (seconds, N/A for Category A). I repeated this categorization for Swamp Sparrow songs from each site. I then took the mean of these measurements to calculate the average characteristics of each song, and used weighted averages (based on the number of each song type sung) to calculate the average characteristics of each

Category (See Tables A1 and A2). I used these categorical measurements, as well as song frequency data (Table A1), to describe natural arrival using vocalizations of the Song and Swamp sparrows at each site.

2.2 Playback Experiments

In April 2018, I conducted a playback experiment using song recordings of Song Sparrows (positive control), Swamp Sparrows (experimental), and Tree Swallows (*Tachycineta bicolor*; negative control). I chose Tree Swallows as a control species because they commonly overlap Song Sparrow territories during the breeding season at my study sites, and arrive at a similar time to Swamp Sparrows. In contrast to Swamp Sparrows, Tree Swallows are aerial insectivores and cavity nesters (Winkler et al. 2011) and are therefore unlikely to compete for resources with Song Sparrows. Aggressive interactions between Tree Swallows and Song Sparrows have never been reported (Arcese et al. 2002, Winkler et al. 2011); therefore, I expected that Song Sparrows should recognize Tree Swallows as non-threatening neighbours at my study sites. For the Song Sparrow and Swamp Sparrow playback recordings, I chose recordings from non-neighbouring individuals in order to observe the reactions of how Song Sparrows respond to unfamiliar conspecifics as compared to unfamiliar heterospecifics. This prevented confounding results due to the dear enemy effect, as birds tend to react less aggressively to familiar neighbours than to strangers (Fisher 1954).

I first searched for Song Sparrow males and watched them for 30 minutes to observe the limits of each territory. I did this for six different individual Song Sparrow males. I ran the experiment over the course of three days at each site, in blocks of three different times of playback. Each day, I used one recording of one species and played it three times, at 6:00 AM, 8:00 AM, and 10:00 AM. These times encompass the hours in which Song Sparrows are most

actively singing and defending territory (sunrise to mid-morning). I did not play more than one species' song per day in order to prevent carry-over effects. The order in which species' song was played was block-randomized to reduce any potential effect of stimulus order.

I used a repeat of six songs from each species and filtered out the lowest 1000 Hz to minimize background noise. I then looped the six songs for six minutes at the average natural singing rate for each species, as calculated using local recordings of each of these three species. For Tree Swallows, average natural song rate was 120 songs per minute; Song Sparrows sing four songs per minute, and Swamp Sparrows sing three songs per minute. I used Audacity to standardize amplification levels between all recordings.

I used no recordings of soft songs, only territorial broadcast songs sung by males. To minimize the possibility that each of the songs used in the playback recordings may represent a different quality, stage, or status, I kept the treatments as independent as possible, recognizing that the songs may differ in message between each trial. I used different recordings (individuals) for each site in order to maintain independence between trials.

I used two constantly recording Wildlife Acoustics Song Meter SM2 recorders in each male's territory, and a FoxPro Scorpion X1B speaker (FOXPRO Inc., Lewistown, PA, USA) in the middle of the two recorders to broadcast the playback. I controlled the speakers using a remote control, and set them to play at 80 dB (the natural singing volume of broadcast song) (Anderson et al. 2008). To mitigate battery issues (dying overnight, draining due to cold temperatures, water damage), I put in charged batteries and turned the speakers on between 10-60 minutes before the first 6:00 AM playback, depending on when I arrived at each site. For each playback track, I used Audacity to insert silence before the playback so that the playback track began at 6:00 AM (i.e., each site was 10 minutes apart, and I deployed at 5:00, 5:10, 5:20, 5:30,

5:40 and 5:50; each respective playback track had 60, 50, 40, 30, 20, and 10 minutes of silence before the stimulus began so all speakers played at the same time). Once the speakers were turned on, I left the site so as not to bias the focal birds' responses.

Using Audacity, I transcribed the target Song Sparrow's songs for an 18-minute period for each playback session (54 minutes/day) – the six minutes that the playback was running, the six minutes before, and the six minutes after, in order to determine changes in vocal behaviour in response to the playback. I used the same transcription and analysis technique as outlined in section 2.1. I used these singing behaviours to infer how male Song Sparrows react to simulated territorial invasions, and how behaviours differ when confronted with different species.

I encountered many weather-related and technological challenges while doing these experiments. From April 12-16 2018, eastern Ontario experienced a heavy rain and ice storm, which postponed my experiment. In addition, due to cold overnight temperatures, speaker and recording equipment did not always function properly (i.e., did not turn on, water got into equipment, batteries died prematurely). Furthermore, at one of the sites, an animal chewed through the wire on one of the microphones, therefore stopping all recordings on one of the recorders. To prevent this in the future, weather-proof equipment or water-proofing of equipment used is recommended, as well as using additional posts to suspend microphone wires to prevent tampering from animals.

Sample sizes in this project are low due to the difficulties I experienced in performing these experiments. Because of this, traditional statistical testing was not appropriate for these data, as we were interested in population-level patterns, but only attained a few individuals in which to analyze. Differences or patterns referred to in the results section do not reflect statistical support or significant differences.

Chapter 3 – Results

3.1 Characterization of Natural Arrival

At all sites, the first signal of a Swamp Sparrow’s arrival was a territorial song. Calls were not common at any site. Overall, Swamp Sparrows began singing between 5:25-6:05 AM on their first day, singing a small bout of songs (between 4-11) over the course of the morning (Table 1). Most Swamp Sparrows did not sing past 7:00 AM, with the exception of Telephone Bay’s male, who sang until 10:30 AM the morning of arrival. On the Day After arrival, all Swamp Sparrows sang more songs than on the Day Of arrival, with the exception of the male at Curtis Marsh, who sang half the number of songs than on the Day Of arrival. A second male showed up at Telephone Bay on the Day After the first male’s arrival, contributing to an extreme spike in Swamp Sparrow songs at the site; regardless, the original male sang almost non-stop for the entire day, an unusual behaviour as compared to the other male Swamp Sparrows. On the Day Of arrival, Swamp Sparrow singing stopped at Telephone Bay at 20:07:13, at LeRoy around 5:43:02, Curtis around 5:21:34, and Bedford around 10:52:59. The male at Cow Island sang until 10:34:16, and then started singing a second bout between 17:40:30 and 20:07:12.

Table 1: Date and time of arrival of Swamp Sparrows at each site (n = 5), and song frequency of Swamp Sparrow songs for Day Of arrival and Day After arrival. All sites had one male Swamp Sparrow singing except Telephone Bay, which had a second male arrive on the Day After, contributing to a high number of Swamp Sparrow songs at the site.

Site	Year	Date of Arrival (Day Of)	Time of First Song on Day Of	Number of Songs on Day Of	Time of First Song on Day After	Number of Songs on Day After
Bedford Swamp	2017	April 11	5:40:49	5	5:49:24	43
Cow Island	2017	April 10	6:04:21	8	5:50:31	126
Curtis Marsh	2015	April 30	5:26:23	11	5:17:15	5
LeRoy Marsh	2018	April 23	5:26:35	4	4:49:08	24
Telephone Bay	2017	April 12	6:01:19	6	5:46:00	1052

Following the arrival of Swamp Sparrows, four out of five male Song Sparrows demonstrated a peak in the proportion of Category C songs sung on the Day Of Swamp Sparrow arrival, with a decrease on the Day After. Males at two of the sites (Telephone Bay, LeRoy Marsh) showed a decrease in proportion of Category C songs on the Day After to less than the proportion sung on the Day Before. Males at one site (Cow Island) sang increasingly higher proportions of Category C songs each day (Figure 1).

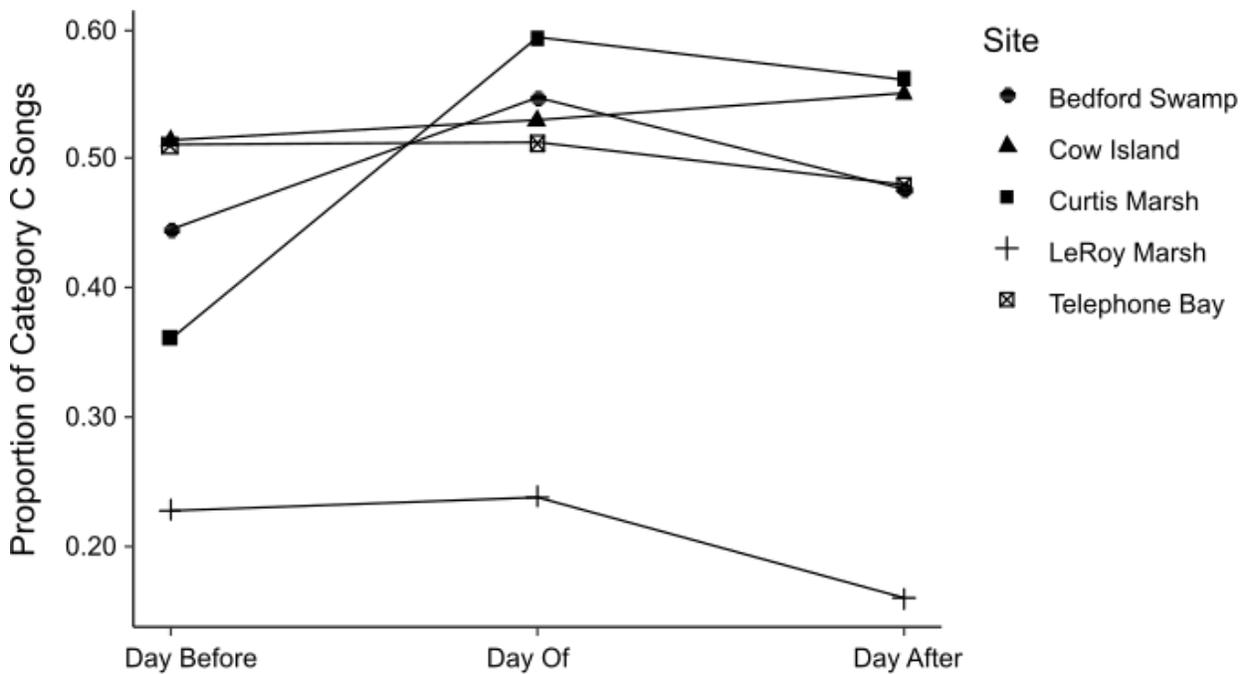


Figure 1: The daily proportion of Category C songs sung by male Song Sparrows at each site of natural arrival. For four out of five males, the proportion of Category C songs peaked on the Day Of arrival, with the exception of Cow Island, which showed an overall increasing trend.

Average daily trill score peaked on the Day Of for three of the sites (Bedford Swamp, Curtis Marsh, and Telephone Bay). One of the sites showed an overall increasing trend (Cow Island) and one showed an overall decreasing trend (LeRoy Marsh) (Figure 2).

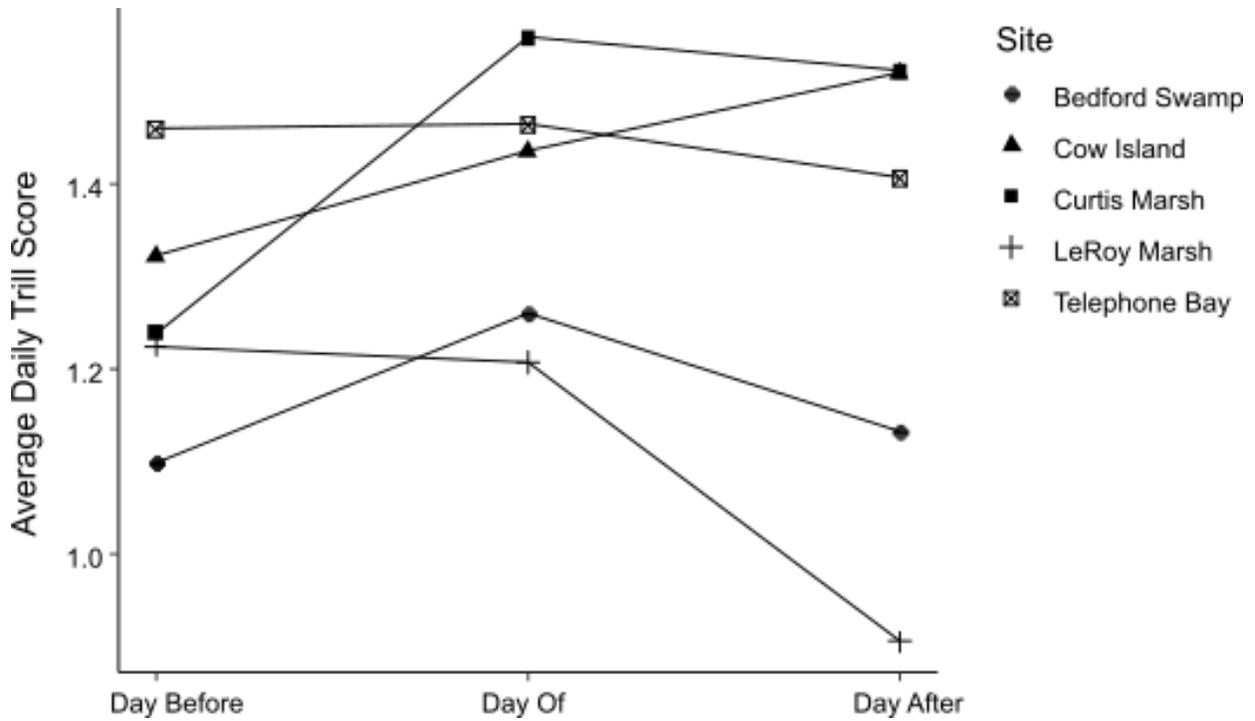


Figure 2: Average daily trill score. An increasing score represents an increase in the proportion of songs with a trill (Category B & C) sung by Song Sparrow males on that day.

Four out of five Song Sparrow males sang longer trill syllables in Category B songs on the Day After as opposed to the Day Before (Figure 3). Average trill syllable length for all Swamp Sparrows observed ($n = 5$) is 0.169 seconds, as indicated by dotted lines in Figures 3, 4, 9, and 10.

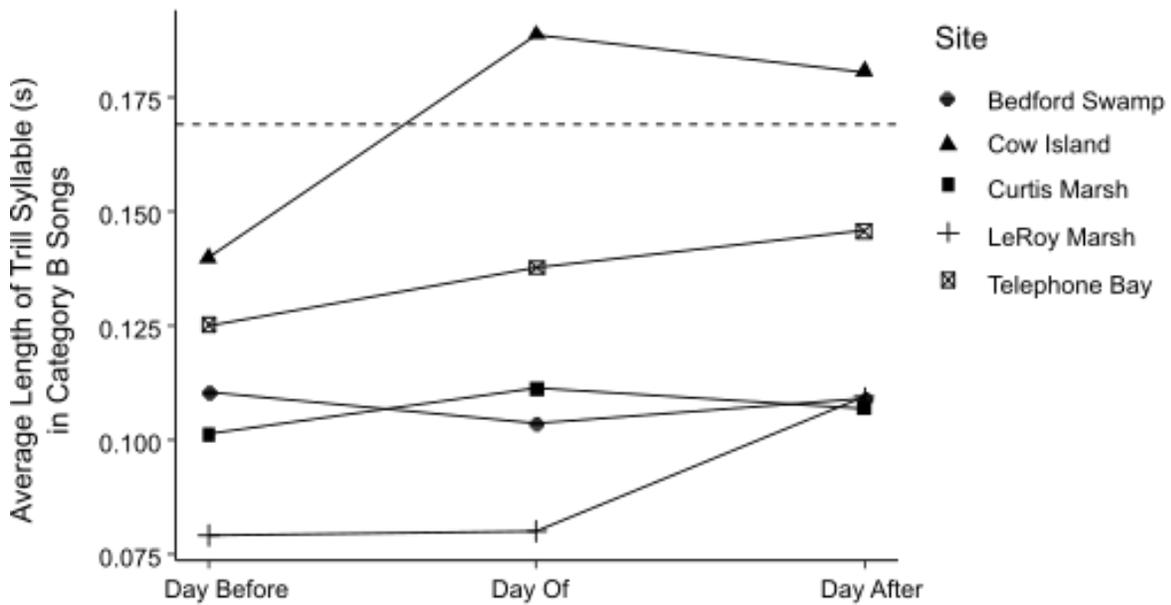


Figure 3: Weighted average length in seconds of trill syllable in Category B songs sung by Song Sparrow males. The dotted line represents a global (averaged over all sites) average trill syllable length for Swamp Sparrows (0.169 s).

Conversely to Category B songs, no trend was observed in the change in trill syllable in Category C songs. Males at one site (Curtis Marsh) showed a decrease in trill syllable length on the Day Of arrival, with an increase on the Day After to similar length as the Day Before. Males at all other sites did not demonstrate a change in the average trill syllable length between days.

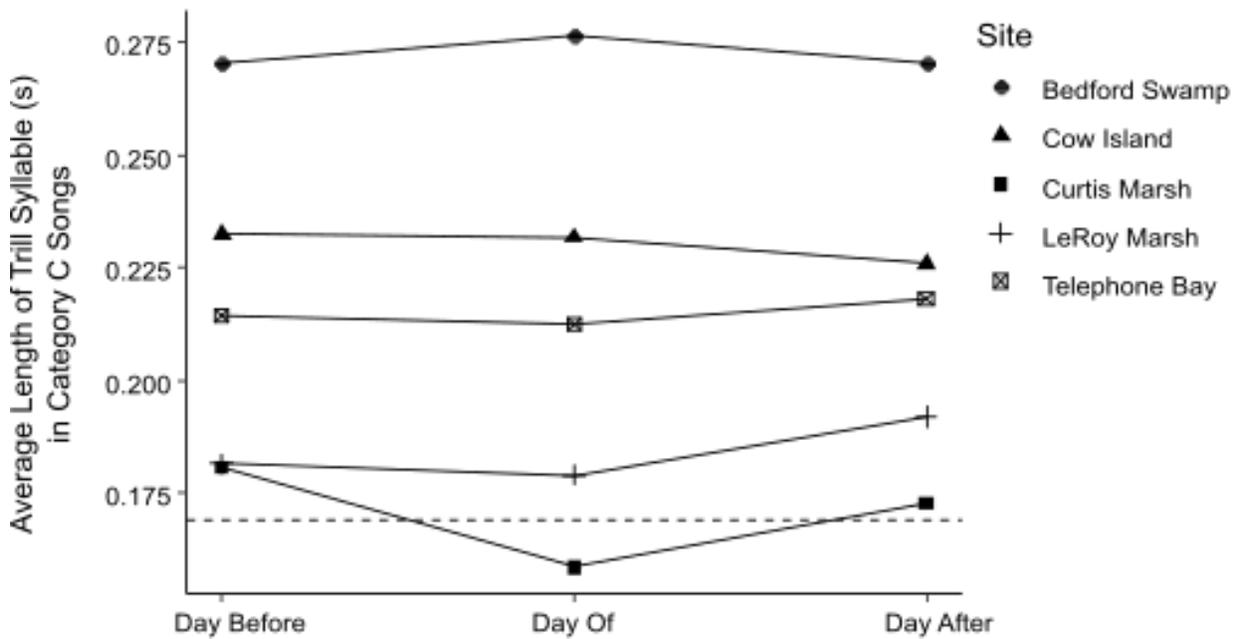


Figure 4: Weighted average length in seconds of trill syllable in Category C songs sung by Song Sparrow males. The dotted line represents a global (averaged over all sites) average trill syllable length for Swamp Sparrows (0.169 s).

3.2 Playback Experiments

Generally, song rate in male Song Sparrows increased following playback stimuli, with highest rates after the playback of songs. Highest rates of singing from target males overall were observed in relation to Song Sparrow playback stimuli. The male at Cow Island did not sing any songs for the entirety of the Tree Swallow playback trial (Figure 5).

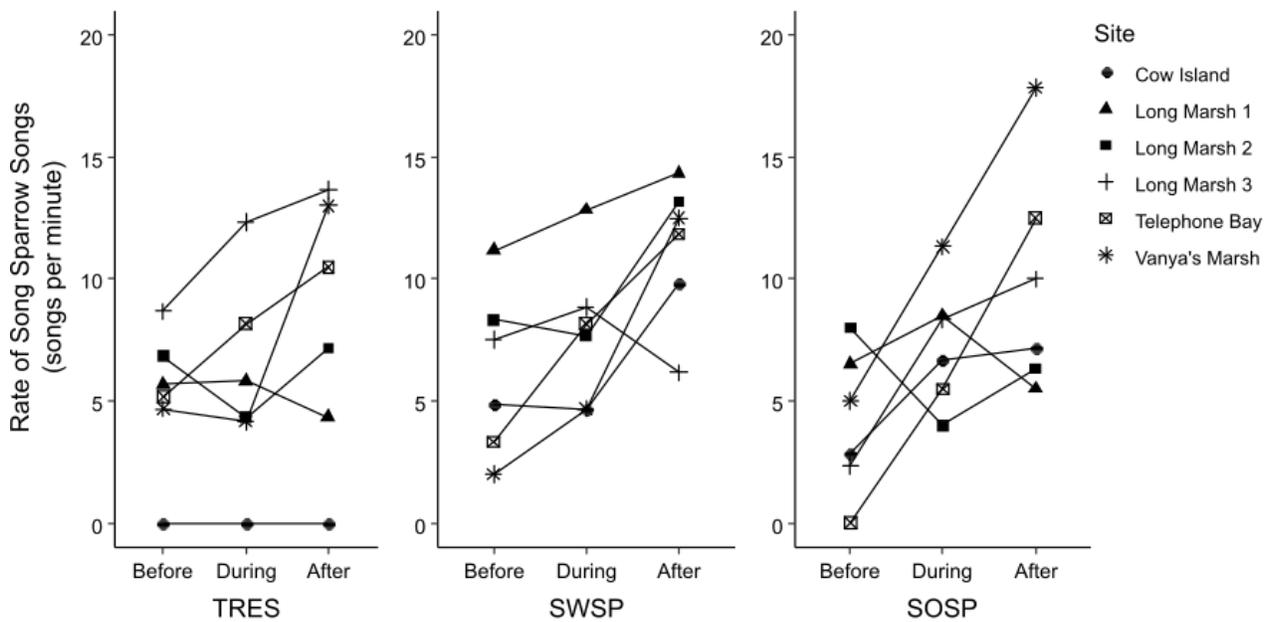


Figure 5: Rate of Song Sparrow songs sung in relation to playback. Total values are combined for all time trials (6:00, 8:00, 10:00) for each period. Before, During, and After correspond to the periods of six minutes before, during, and after the playback. Rates were calculated for each 18-minute period (six minutes for each time trial).

In general, Song Sparrow males sang more songs during the playback than before the playback, and the most songs after the playback as compared to before or during. The largest increase in song rate was observed in relation to the Song Sparrow playback, followed by the Swamp Sparrow, then Tree Swallow stimuli (Figure 6).

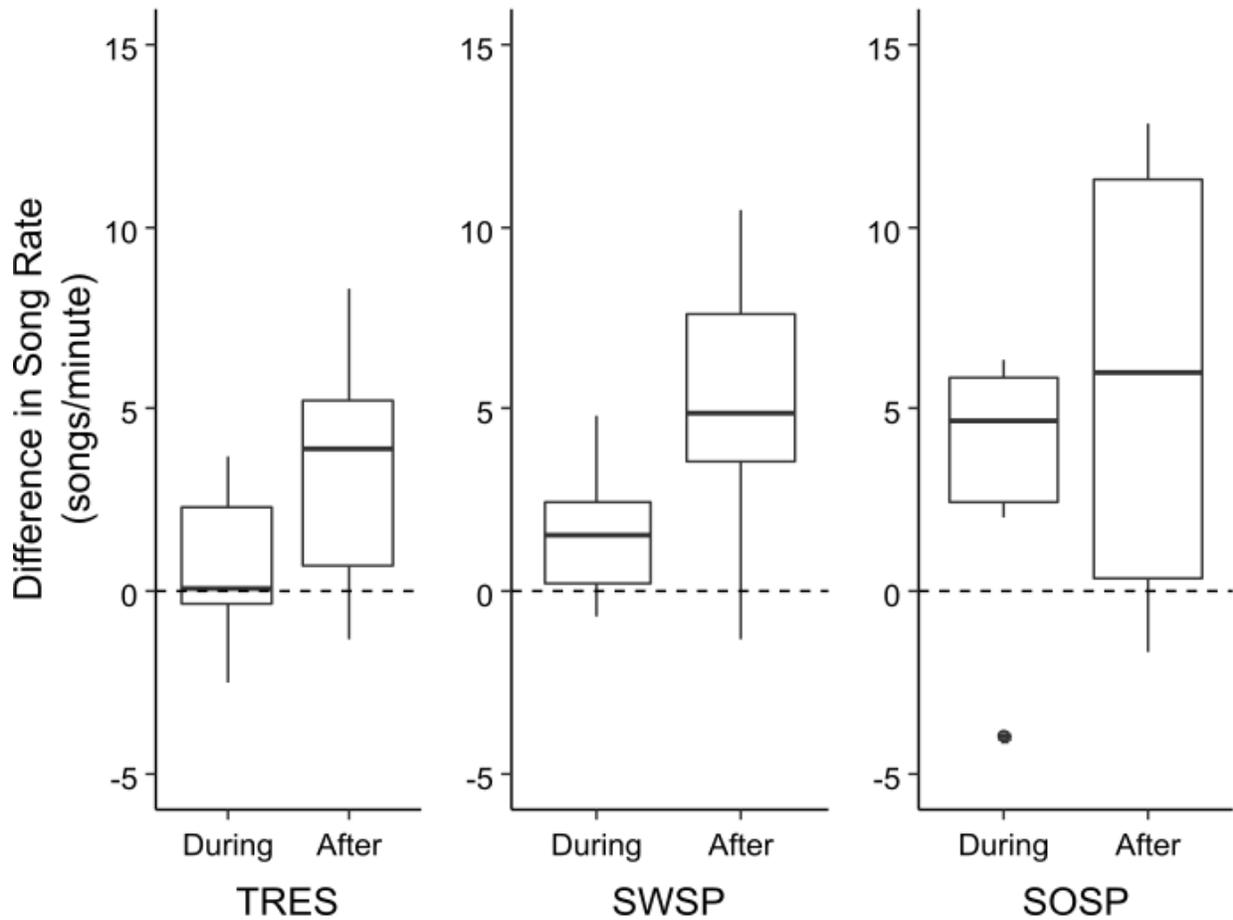


Figure 6: Difference in song rate of target Song Sparrow males ($n = 6$) in relation to playback, as compared to the 6-minute period before playback. Songs were combined for all time trials (6:00, 8:00, 10:00) for each period. Rates were calculated for each 18-minute period (six minutes for each time trial).

Each stimulus elicited a difference in the proportion of Category C songs sung before, during, and after the playback. Following Tree Swallow playback, male Song Sparrows seemed to decrease the proportion of Category C songs sung, or remain fairly consistent in the proportion (Figure 7, left panel). In relation to Swamp Sparrow stimuli, four target males greatly increased the proportion of Category C songs they sang (Cow Island, Long Marsh 2, Long Marsh 3, Vanya's Marsh) while the other two males decreased (Long Marsh 1, Telephone Bay) (Figure 7, middle panel). When Song Sparrow songs were played, the responses of the target males varied widely. The male at Long Marsh 3 decreased the proportion of Category C songs sung, while the males at Long Marsh 2 and Telephone Bay increased. Males at Cow Island and Vanya's Marsh peaked in proportion during the playback; Long Marsh 1 sang the lowest proportion of Category C songs during playback (Figure 7, right panel).

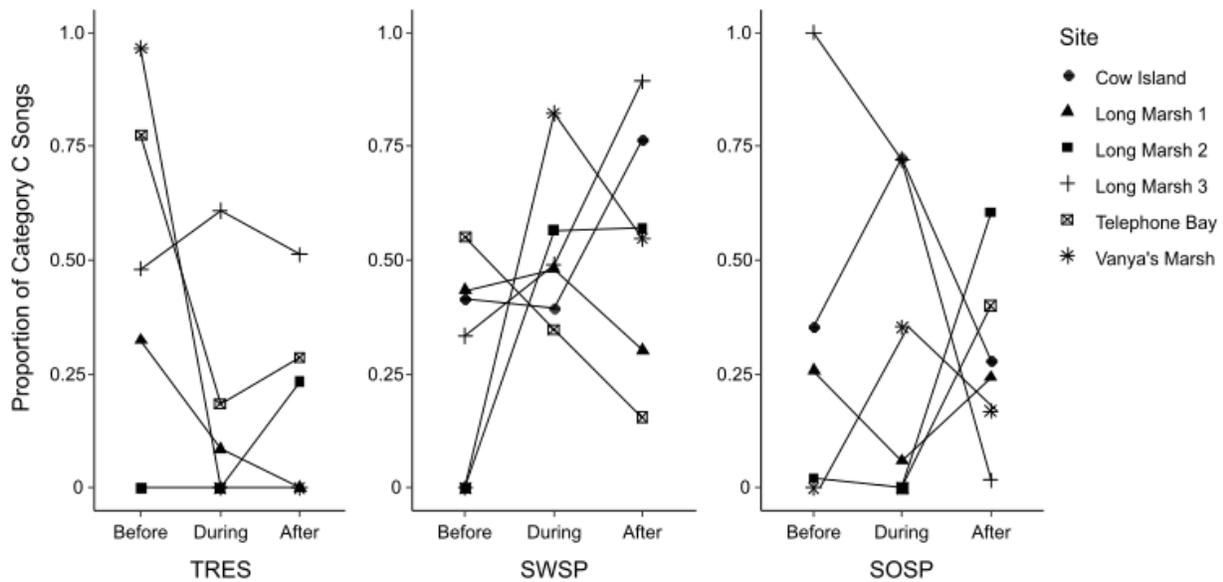


Figure 7: The daily proportion of Category C songs sung by male Song Sparrows in relation to playback. Songs were totaled for all time trials (6:00, 8:00, 10:00) for each period. Before, During, and After correspond to the periods of six minutes before, during, and after the playback. Proportions were calculated for each 18-minute period (six minutes per time trial). Missing data points represent instances where no songs were sung for the entirety of the 18-minute period.

During the Tree Swallow trials, three of the males (Long Marsh 1, Telephone Bay, Vanya's Marsh) demonstrated a decrease in average trill score from before to after the stimulus. Two of the males (Long Marsh 2 and 3) showed a slight increase, with the male at Long Marsh 2 peaking during the playback. The male at Cow Island sang no songs for the entire duration of each of the three Tree Swallow trials (Figure 8, left panel).

All males except one (Telephone Bay) demonstrated a higher trill score after the Swamp Sparrow playback stimulus as compared to before the stimulus. The male at Vanya's Marsh peaked in trill score during the playback, while the male at Cow Island had the lowest trill score during the playback (Figure 8, middle panel).

The change in trill score as a response to Song Sparrow stimuli varied between males (Figure 8, right panel). At Cow Island, trill score peaked during the playback, and decreased afterwards to less than what it was before the playback. A similar trend was seen at Vanya's Marsh, where the male's trill score peaked during the playback, then decreased to a similar level as before the playback. The male at Long Marsh 1 showed the opposite trend, decreasing during the playback then increasing trill score after the playback to a higher score than before. The male at Long Marsh 2 showed no change in trill score during the playback, then displayed an increased trill score after the playback. The male at Long Marsh 3 showed an overall increasing trend in trill score, while the male at Telephone Bay did not sing before the playback, but showed an increase in trill score after the playback as compared to during the playback.

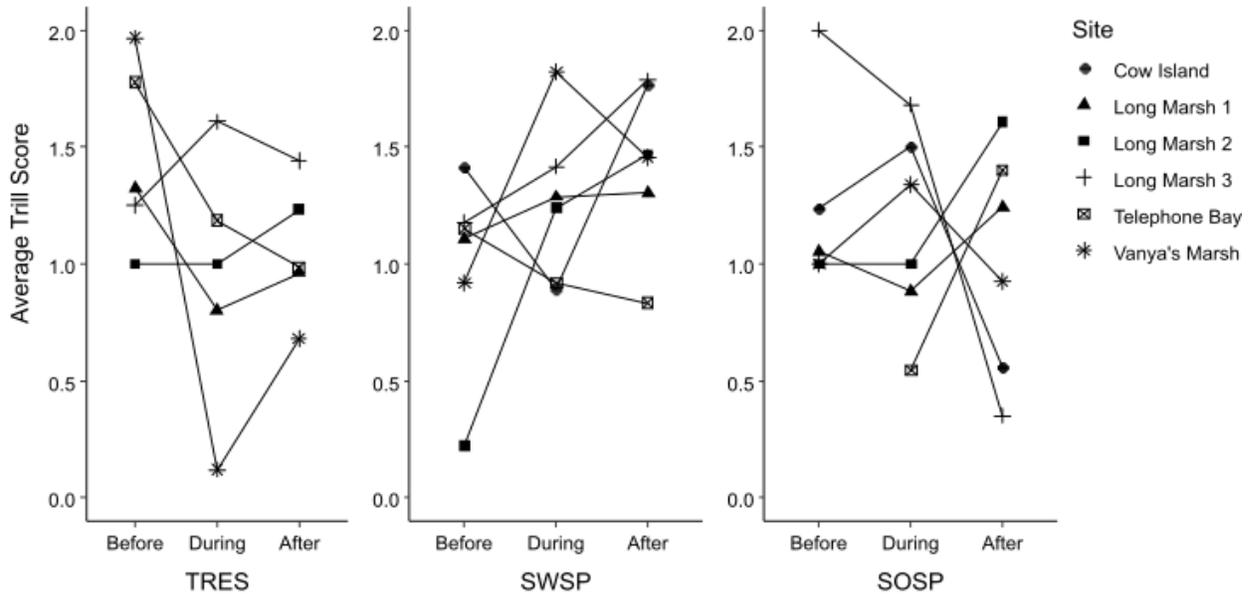


Figure 8: Average daily trill score. An increasing score represents an increase in the proportion of songs with a trill (Category B & C) sung by Song Sparrow males on that day. All three daily trials are totaled for each site to provide one value per site per day (6:00, 8:00, 10:00). Missing data points represent instances where no songs were sung for the entirety of the 18-minute period.

Following the Tree Swallow stimulus, the average length of trill syllable in Category B songs decreased slightly in all sites except Long Marsh 1, where the trill syllable length did not change throughout any of the trials (no response to any stimulus). The male at Cow Island did not sing at all during the Tree Swallow trial. When Swamp Sparrow songs were played, trill syllable length decreased during the playback, but increased after to longer than the average length before the playback. This pattern was observed in the males at Long Marsh 2 and Vanya's Marsh, while no pattern was observed for the male at Cow Island or Long Marsh 1. The male at Long Marsh 3 sang a longer average trill syllable during the Swamp Sparrow playback, but did not sing any Category B songs after the playback.

Regarding the Song Sparrow stimuli, target males either sang songs with longer trill syllables or showed no change. Males at Long Marsh 1, Long Marsh 2, and Telephone Bay

showed no change in trill score, while males at Cow Island, Vanya’s Marsh and Long Marsh 3 showed an overall increasing trend in the length of trill syllable. The male at Cow Island sang no Category B songs after the playback, while the males at Vanya’s Marsh and Long Marsh 3 did not sing any Category B songs before the playback (Figure 9).

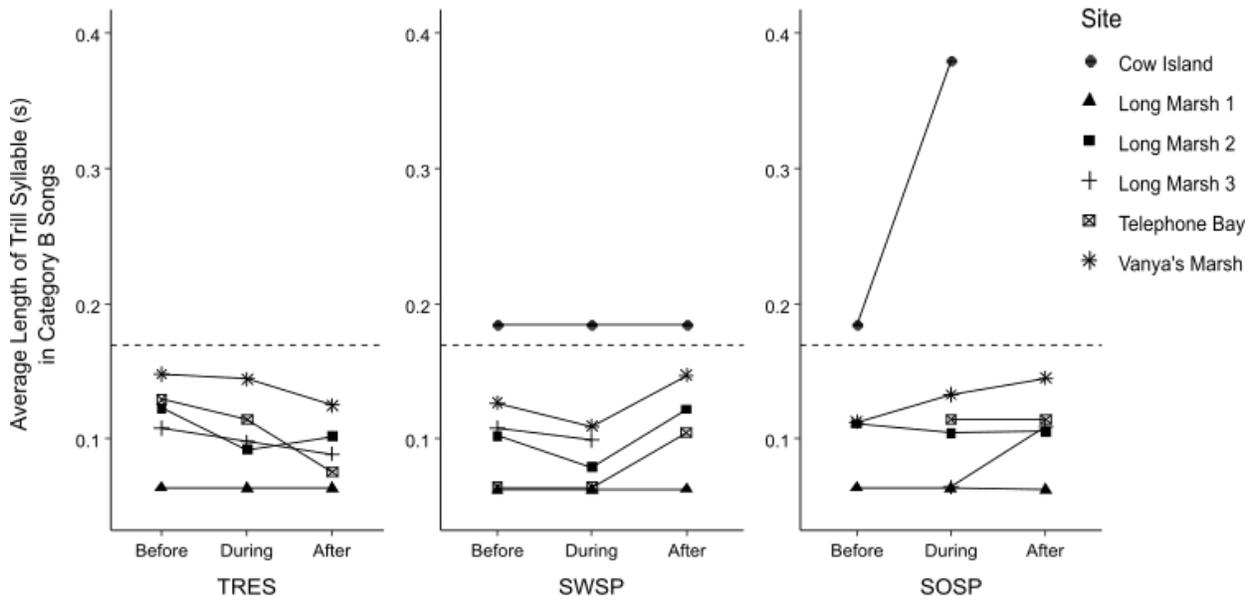


Figure 9: Weighted average length in seconds of trill syllable in Category B songs. The dotted line represents a global average trill syllable length for Swamp Sparrows (0.169 s). Missing data points represent instances where no Category B songs were sung for the entirety of the 18-minute period.

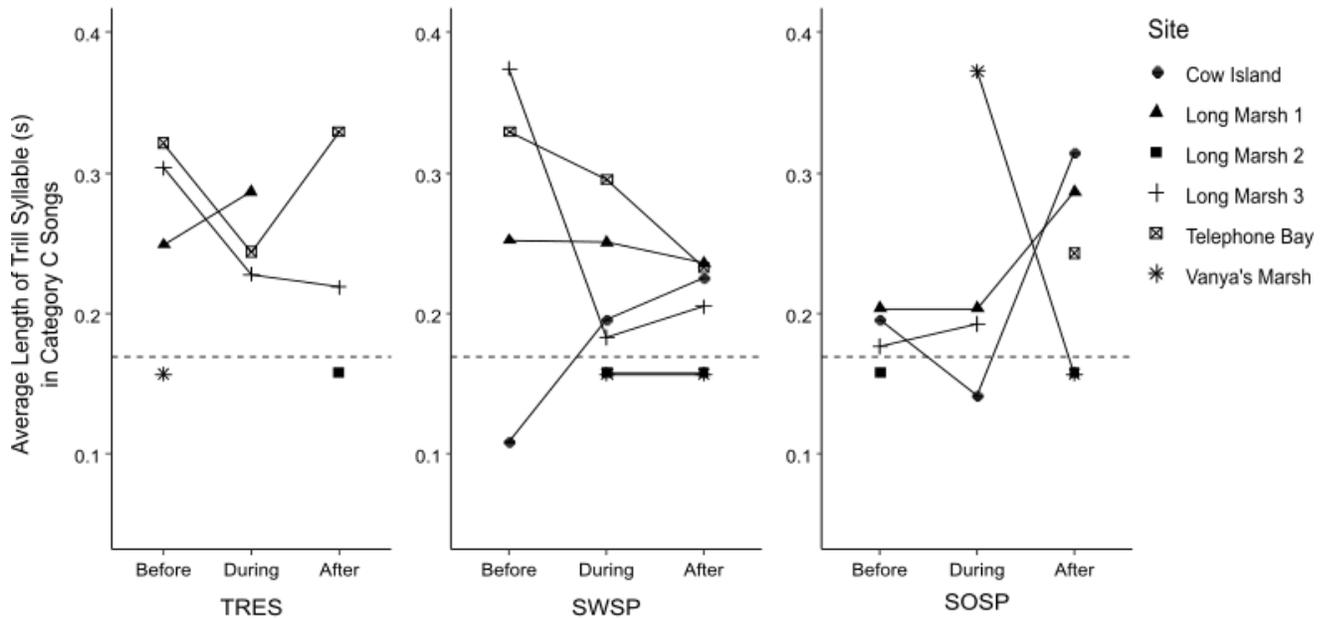


Figure 10: Weighted average length in seconds of trill syllable in Category C songs. The dotted line represents a global average trill syllable length for Swamp Sparrows (0.169 s). Missing data points represent instances where no Category C songs were sung for the entirety of the 18-minute period.

Target male's change in Category C trill syllable length was more variable than the change in Category B trill syllable length. Following the Tree Swallow trial, all six males showed a different pattern (Figure 10, left panel). The male at Cow Island sang no songs at all, the male at Vanya's Marsh sang Category C songs only during the period before the playback, while the male at Long Marsh 2 only sang Category C songs after the Tree Swallow playback. The male at Long Marsh 1 did not sing Category C songs after the playback, but showed an increase in length of trill syllable during the playback in comparison to before. The male at Long Marsh 3 showed an overall decreasing trend in syllable length, while the male at Telephone Bay sang the shortest syllables during the playback, returning to lengths after the playback that were similar to his average syllable length before the playback.

Interestingly, after the Swamp Sparrow playback, four of the six target males sang a very similar average trill syllable length, all around ~0.22 seconds long. The other two males (Long Marsh 2, Vanya's Marsh) showed no change in syllable length, and did not sing Category C songs before the playback. The males at Telephone Bay and Long Marsh 1 showed an overall decreasing trend, the male at Cow Island showed an increasing trend, and the male at Long Marsh 3 sang the shortest average syllable length during the playback, increasing after the playback (Figure 10, middle panel).

After being exposed to Song Sparrow playback, males at Cow Island, Long Marsh 1, and Long Marsh 3 demonstrated an increasing trend, though the male at Cow Island sang the shortest syllables during the playback, and the male at Long Marsh 3 did not sing Category C songs after the playback. The male at Vanya's Marsh did not sing before the playback, and decreased syllable length after the playback in comparison to during the playback. The male at Long Marsh 2 sang the same length of syllable before and after the playback, but sang no Category C songs during the playback (Figure 10, right panel).

Chapter 4 – Discussion

Vocal signals are thought to play an important role in aggressive, competitive interactions among closely related species of birds; song-matching may help to direct signals towards specific species. We evaluated heterospecific-directed aggression of Song Sparrows by documenting their vocal behaviour in response to their subordinate competitor, Swamp Sparrows. We hypothesized that Song Sparrows, in response to Swamp Sparrow presence, would alter their singing behaviour in three ways that collectively made their songs more similar to Swamp Sparrow songs: a) an increase in the proportion of Category C songs, b) an increase in Trill Score, and c) a shift to song types with trill syllable lengths more similar to Swamp Sparrows. Due to the limited sample size, we did not evaluate hypotheses using statistical tests; however, we observed some interesting preliminary trends in these data.

4.1 Discussion of Findings

4.1.1 *Natural Arrival of Swamp Sparrows*

Swamp Sparrows only sang a few songs in the morning of when they first arrived, and sang more the day after. Since song typically is used either to attract a mate or advertise territory boundaries (Kroodsma and Byers 1991, Catchpole and Slater 2008), broadcasting song upon arrival likely is a way to determine if other Swamp Sparrows are in the area. At Telephone Bay, on the day after the first Swamp Sparrow's arrival, a second male Swamp Sparrow was present, and the two males sang almost continuously the entire day. At all other sites, Swamp Sparrows stopped singing after only a few songs. It is possible, therefore, that Swamp Sparrow vocal behaviour upon arrival may be most highly influenced by the presence of conspecific males, although a larger sample size is required to draw conclusions. Swamp Sparrows, with their limited repertoire, use the same song types in multiple ways (Searcy et al. 1982), but seem to

modulate trill speed and frequency bandwidth in aggressive interactions (Dubois et al. 2009).

Due to a single male Swamp Sparrow being present at all other sites, we are unable to decipher potential conspecific aggressive trends within their songs. However, overall, the presence of other Swamp Sparrows seems to be the main factor influencing Swamp Sparrow singing behaviour.

4.1.2 Proportion of Category C Songs and Trill Score

Category C songs peaked on the Day Of arrival, suggesting that Song Sparrows may initially modulate their vocal behaviour in response to the arrival of Swamp Sparrows. During playback, an increasing trend in Category C songs during Swamp Sparrow trials was the most consistent trend throughout the whole experiment, with four out of six males increasing Category C song proportion. Trill score during natural arrival also peaked on the Day Of arrival, decreasing on the Day After; after Swamp Sparrow playback, generally, there was an overall increasing trend. Differences in response levels between Song Sparrows experiencing natural arrival versus those responding to playback calls are likely due to a few reasons: during natural arrival, the presence of a physical bird could affect the strength of response, while during playback, no decoy was present. In addition, during natural arrival, more than one Song Sparrow and their territories were recorded at each site, as it was unknown which territory the Swamp Sparrow would sing from upon arrival. During playback experiments, only a single male was targeted. Therefore, depending on the location where the Swamp Sparrow arrived, strength of aggressive response in Song Sparrow males during natural arrival may be dependent on proximity to their territory, potentially resulting in a weaker trend.

4.1.3 Trill Syllable Length

During natural arrival, males did not alter the average length of the trill phrase in their Category C songs, but we observed a trend towards longer trill syllables in Category B songs. These longer Category B songs approached the length of Swamp Sparrow trill syllables. Since Category C songs are already the most “Swamp Sparrow-like” due to syllable similarity, it is possible that male Song Sparrows modulate their frequency of use of other trill-containing songs in their repertoire, using song types that have a longer trill syllable in order to sound more similar to Swamp Sparrow songs.

During playback, responses were more variable, but half of the target males showed a similar trend of increased average syllable length in Category B songs in response to Swamp Sparrow playback, approaching natural Swamp Sparrow syllable lengths. Conversely to natural arrival, target males demonstrated a change in syllable length in Category C songs, approaching Swamp Sparrow syllable lengths. These patterns were not observed in Tree Swallow or Song Sparrow trials, suggesting that Song Sparrow males may specifically adjust their singing behaviour to use songs with similar syllable lengths to Swamp Sparrows.

4.2 Song and Evolution

4.2.1 Convergence in Sparrows

Eastern Song Sparrows do not often share entire songs with one another, and therefore do not repertoire-match like the western population (Dubois et al. 2015). However, eastern Song Sparrows do match partial songs, or song syllables (Anderson et al. 2005). Song Sparrows have the ability to learn Swamp Sparrow syllables (Peters et al. 1980), and if they do so in the wild, it is possible that they might use songs with those syllables preferentially in interactions with

Swamp Sparrows. In this way, Song Sparrows could syllable-match interspecifically in addition to intraspecifically, indicating aggressive intent.

Several species have been observed to modulate vocal behaviour when interacting with a heterospecific competitor (e.g., Morse 1966, Kroodsma et al. 1989, Gorissen et al. 2006). Song similarity may be due to convergent signal evolution, or through the use of flexible signaling, where a species has a large repertoire of songs, and preferentially uses similar ones in interspecific interactions. Different degrees of vocal similarity may be based on dominant and subordinate relationships: dominant Great Tits and Thrush Nightingales seem to use flexible signaling (Sorjonen 1986, Gorissen et al. 2006, Reif et al. 2015), sharing only a few songs with subordinates; in subordinate Philadelphia Vireos, the repertoire as a whole is quite similar to the dominant Red-eyed Vireo (Rice 1978b), suggesting convergent evolution in song. If vocal similarity is involved in the relationship between Song and Swamp sparrows, then the preliminary patterns are similar to patterns seen in tits and nightingales: dominant birds shifting to preferentially use shared songs (or in the case of Song Sparrows, potentially shared syllables), which can be classified as flexible signaling.

Whether competing species undergo convergent evolution in song or use flexible signal convergence likely depends on the nature of their ecological interactions. Song Sparrows do not always overlap territories with Swamp Sparrows, as Song Sparrows use a wider variety of breeding habitats (Willson 1972, Greenberg 1988, Mowbray 1997, Arcese et al. 2002). Therefore, complete evolutionary convergence in song is not beneficial to all Song Sparrows within a population. Here, flexible singing may be adaptive: Song Sparrows can modulate vocal behaviour based on the presence or absence of Swamp Sparrows. In these sparrows, this flexible

vocal convergence may facilitate coexistence by improving competitor recognition and advertising territory boundaries.

Amongst sparrows, there have been other recorded examples of interspecific aggression while using heterospecific song. Song Sparrows have been observed to use White-crowned Sparrow (*Zonotrichia leucophrys*) song in their repertoire in areas where they often interact (Catchpole and Baptista 1988), and Lincoln Sparrows (*Melospiza lincolnii*) have similarly been seen to mimic neighbouring White-crowned Sparrows (Baptista et al. 1981). Our preliminary results coupled with evidence that sparrows are able to learn heterospecific syllables or songs and mimic other species may indicate that flexible vocal convergence is a part of how Song and Swamp sparrows are able to closely coexist.

4.2.2 Selective Pressures on Song

Many factors influence the development of song, including habitat, community composition, song learning ability and morphology. However, since the main functions of song are territory defense and mate acquisition, those two selective pressures are likely to be the most influential, and so a balance in the efficacy of these two signals is likely. This trade-off between intra- and interspecific communication poses an issue for signal evolution (Tobias and Seddon 2009). Divergence between species is often expected in signals used in intraspecific contexts, but that can become problematic for heterospecific recognition (Tobias and Seddon 2009). However, if interspecific interactions are common, signals may converge between species.

Birds must distinguish between con- and heterospecific song in order to prevent costly hybridization. Signal convergence has been suggested to cause issues and mistakes in conspecific versus heterospecific recognition, but asymmetric aggression and the ability to respond differently to familiar and unfamiliar birds is part of a growing body of evidence that

provides support for Cody's (1969, 1973) character convergence hypothesis, refuting Murray's claims of misdirected aggression (1971, 1976). For example, Banded Wrens (*Thryophilus pleurostictus*) rely much more heavily on vocal cues than physical (plumage) ones in distinguishing between heterospecifics, indicating high specificity in vocal recognition (Hick et al. 2016). Many other species can reliably distinguish not only between heterospecifics and conspecifics, but between individuals as well. In addition, convergence in territorial songs, while simultaneous divergence in nonterritorial signals (including other vocalizations and visual signals) has been observed in other species, including Peruvian and Yellow-breasted Warbling-antbirds (*Hypocnemis peruviana* and *H. subflava*), indicating that signal convergence can be limited to only a portion of a vocal repertoire (Tobias and Seddon 2009).

Such context-specific vocalizations are a relatively widespread pattern in songbirds, as many species have several song types within their repertoire which can be used in different contexts. This is further evidence that birds are able to distinguish reliably between conspecific and heterospecific individuals. Great Reed Warblers (*Acrocephalus arundinaceus*) use two types of songs: a short song in territory defense, and a longer one when advertising to a potential mate (Catchpole 1983). Blackburnian (*Setophaga fusca*) and Black-throated Green (*S. virens*) warblers use one song for attracting females and another for inter- and intraspecific territorial conflicts (Morse 1967). Cuban Grassquits (*Tiaris canorus*) similarly sing different songs to male and female conspecifics (Baptista 1978). Though identification seems not to pose issues, songbirds still must balance the efficacy of song in territorial contexts and song that is attractive to a potential mate. However, these requirements are not necessarily in conflict. Yellow Warblers use one song type in intraspecific territorial disputes, and the other in interspecific territorial

disputes; the song type used to ward off intrusive Chestnut-sided Warblers is the same song type used to attract a mate (Morse 1966).

Context-dependent vocalizations have also been widely observed in Song Sparrows, indicating that male Song Sparrows do not sing randomly. Song complexity (the number of syllables within a repertoire) is positively related with syllable sharing within a population of Song Sparrows (MacDougall-Shackleton et al. 2009). This suggests that a Song Sparrow song can convey information about the song learning ability of that male, and therefore, singing behaviour can advertise male quality. Females from many species of songbirds show preference for large song repertoires (Searcy 1992), which is beneficial for females if song repertoire reflects higher quality males (those that are older, and/or hold larger territories) (Catchpole and Slater 2008). Female songbirds also tend to prefer songs that are more complex, and males that have higher song output (MacDougall-Shackleton et al. 2009). Captive female Song Sparrows solicit more in response to larger repertoires (Searcy and Marler 1981, Searcy 1984), and larger repertoire has been linked to higher fitness in Song Sparrows (Reid et al. 2005b, 2005a, Pfaff et al. 2007). Males with larger repertoires and higher song complexity may be better able to modulate vocal behaviour, as they have more song options available to use. Song switching also prevents habituation by females, increasing interest in potential mates (Catchpole and Slater 2008). Therefore, it is possible that male Song Sparrows could switch to song types that can convey territorial information to heterospecifics via syllable matching, while at the same time, advertising quality to potential mates. A larger repertoire may not only be beneficial in using context-specific songs in aggressive interactions, but also confers an advantage in mate attraction. Here, selective pressures acting on song align, which may be a driving factor of flexible vocal convergence in Song and Swamp sparrows.

However, some costs may be associated with song convergence; for example, increased similarity in song may increase occurrence of hybridization. Pied Flycatchers (*Ficedula hypoleuca*) often incorporate Collared Flycatcher (*F. albicollis*) songs into their repertoire, and can attract females of the opposite species when singing mixed song types (Qvarnström et al. 2006). Additionally, female songbirds use song-learning ability of males to assess quality – if a male Song Sparrow incorporates Swamp Sparrow syllables into his repertoire, that may indicate poor song-learning specificity, which could decrease his attractiveness to a mate (Nowicki et al. 2002). Female Song Sparrows also exhibit preference for song types from their mate’s repertoire (O’Loghlen and Beecher 1997), indicating that song type is important for female choice. Therefore, interspecific song or syllable sharing by Song Sparrow may influence female sexual preferences, which could prove to be a cost to fitness. An abundance of selective pressures influence bird song, and the efficacy of territory defense (within and among species) and mate attraction must be balanced.

4.3 Recommendations and Conclusions

Overall, without larger sample sizes, we cannot make any conclusions regarding the vocal responses of Song Sparrows to co-occurring Swamp Sparrows. Future studies could add to ours to produce a larger sample size with more playback experiments to bolster results. Time permitting, several rounds of playback experiments would be beneficial, as would increasing the number of sites to observe natural arrival of Swamp Sparrows. All three characteristics measured showed changes in relation to arrival of Swamp Sparrows from natural arrival or playback, and would benefit from a larger sample size to be able to solidify trends seen in this project with statistical results. A measurement of overall daily song quality that is calculated differently from Trill Score may be useful, as there are multiple ways to calculate each Trill Score (a score of 1

could mean 100% Category B songs, or 50% Category A and 50% Category C songs). Slowing down Tree Swallow playback may also prove useful, as due to the rapid song rate of Tree Swallows, the control playback included many more songs than the experimental sparrow tracks. If time is a limiting factor in the future, concentrating on the differences in song categories may be most beneficial, as the strongest trends were seen as a change in song category proportion. Within-song variation of Song Sparrows may also prove interesting if no significant change in song Category is revealed, as individual songs can differ in note or syllable repetition within song types (Nowicki et al. 1999). If syllable matching is prevalent, testing response strength in relation to Song Sparrow repertoire size may shed light on the potential trade-off between territorial and mate attraction vocalizations. This study would also benefit from an expansion to include other species pairs with different phenologies: in eastern Ontario, Red-eyed Vireos exhibit dominance and similar vocalizations to the sympatric Warbling Vireos (*Vireo gilvus*) (Freshwater et al. 2014), but arrive on territory later than their subordinates, opposite to Song and Swamp sparrows. Conducting similar experiments using vireos may unveil differences based on arrival timing that cannot be revealed by examining a single species pair.

Our preliminary study uncovers some potentially important behavioural shifts in Song Sparrow vocalizations associated with a heterospecific competitor. Here, if behavioural convergence in signals via syllable sharing is occurring, Song and Swamp Sparrows are able to communicate better, mediating potentially costly fights. Females maintain species-specific recognition, reducing the risk of detrimental hybridization with species.

Convergence in signal traits may arise from similar ecological pressures driving similar trait production (Laiolo 2012). However, song convergence in sympatry seems most related to social conditions, not environmental, as seen by more aggression in sympatry versus allopatry

(Secondi et al. 2003, Tobias and Seddon 2009, Laiolo 2012). Sympatric convergence in territorial signals likely plays a role in mediating interactions (Secondi et al. 2003, Tobias and Seddon 2009). For example, where Crested (*Galerida cristata*) and Thekla (*G. theklae*) larks overlap in sympatry, they have converged in territorial signals, which elicit more aggressive responses in than in allopatry (Laiolo 2012).

Such aggression is ubiquitous in nature, and may be mediated by convergence in song. We now understand that birds have more sophisticated recognition abilities than was once implied by Murray (1971, 1976), and that vocal convergence poses little threat of accidental hybridization, but can advertise aggressive and territorial intent without physical altercations. As aggression is the most prevalent form of interspecific competition, understanding its implications for trait evolution, as well as its function in ecological interactions between coexisting related species, is critical (Grether et al. 2013). Future work on ecological interactions between closely related species will inform if aggressive vocal behaviours serve as an adaptive strategy to reduce fitness costs of coexistence, as has been suggested in other avian species (Martin et al. 1996, Martin and Martin 2001b). Dominance relationships and the interspecific, aggressive interactions that they encompass play a role in speciation and diversification (Price et al. 2014), and therefore, identifying the processes and interactions that allow species to coexist can inform how we perceive and preserve biodiversity.

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Appendix

Table A1: Frequencies of Song Sparrow and Swamp Sparrow songs sung during natural arrival.

Site	Day	# Category A Songs	# Category B Songs	# Category C Songs	Total # Songs	# Swamp Sparrow Songs
Bedford Swamp	Before	610	803	1132	2545	0
	Of	331	458	953	1742	5
	After	554	608	1058	2220	43
Cow Island	Before	1365	2092	3658	7115	0
	Of	399	1595	2246	4240	24
	After	42	561	740	1343	178
Curtis Marsh	Before	45	192	134	371	0
	Of	15	152	244	411	11
	After	30	291	412	733	5
LeRoy Marsh	Before	4	1257	372	1633	0
	Of	15	356	116	487	4
	After	27	63	17	107	24
Telephone Bay	Before	270	2263	2645	5178	0
	Of	152	1371	1600	3123	6
	After	201	1215	1306	2722	1052

Table A2: Values for figures 1-4 representing quality of song sung by Song Sparrow males during natural arrival.

Site	Day	Proportion of Category C Songs Sung	Daily Trill Score	Average Length of Trill Syllable in Category B Songs (s)	Average Length of Trill Syllable in Category C Songs (s)
Bedford Swamp	Before	0.445	1.099	0.111	0.270
	Of	0.547	1.260	0.104	0.276
	After	0.477	1.133	0.109	0.271
Cow Island	Before	0.514	1.322	0.140	0.233
	Of	0.530	1.436	0.189	0.232
	After	0.551	1.520	0.181	0.226
Curtis Marsh	Before	0.361	1.240	0.101	0.181
	Of	0.594	1.557	0.111	0.159
	After	0.562	1.521	0.107	0.173
LeRoy Marsh	Before	0.228	1.225	0.079	0.182
	Of	0.238	1.207	0.080	0.179
	After	0.159	0.907	0.109	0.192
Telephone Bay	Before	0.511	1.459	0.125	0.214
	Of	0.512	1.464	0.138	0.212
	After	0.480	1.406	0.146	0.218

Table A3: Values represented in figures 5-6 representing songs sung by Song Sparrow males during playback experiments. Song frequencies are combined across time trials and represent an 18-minute period.

Site	Day	Period	Stimulus	Total # Songs	Song Rate (songs/min)	# Category A Songs	# Category B Songs	# Category C Songs
Cow Island	1	Before	TRES	0	0	0	0	0
		During		0	0	0	0	0
		After		0	0	0	0	0
	2	Before	SOSP	17	2.833	2	9	6
		During		40	6.667	9	2	29
		After		43	7.167	31	0	12
	3	Before	SWSP	29	4.833	0	17	12
		During		28	4.667	14	3	11
	Long Marsh 1	1	Before	SWSP	67	11.167	22	16
During			77		12.833	15	25	37
After			86		14.333	0	60	26
2		Before	TRES	34	5.667	0	23	11
		During		35	5.833	10	22	3
		After		26	4.333	1	25	0
3		Before	SOSP	39	6.500	8	21	10
		During		51	8.500	9	39	3
Long Marsh 2		1	Before	SWSP	50	8.333	39	11
	During		46		7.667	15	5	26
	After		79		13.167	8	26	45
	2	Before	SOSP	48	8.000	1	46	1
		During		24	4.000	0	24	0
		After		38	6.333	0	15	23
	3	Before	TRES	41	6.833	0	41	0
		During		26	4.333	0	26	0
	Long Marsh 3	1	Before	TRES	52	8.667	12	15
During			74		12.333	0	29	45
After			82		13.667	6	34	42

		Before		45	7.5	7	23	15
	2	During	SWSP	53	8.833	4	23	26
		After		37	6.167	4	0	33
		Before		14	2.333	0	0	14
	3	During	SOSP	50	8.333	2	12	36
		After		60	10.0	40	19	1
		Before		0	0	0	0	0
	1	During	SOSP	33	5.5	15	18	0
		After		75	12.5	0	45	30
Telephone		Before		20	3.333	8	1	11
Bay	2	During	SWSP	49	8.167	21	11	17
		After		71	11.833	23	37	11
		Before		31	5.167	0	7	24
	3	During	TRES	49	8.167	0	40	9
		After		63	10.5	19	26	18
		Before		30	5.0	0	30	0
	1	During	SOSP	68	11.333	1	43	24
		After		107	17.833	26	63	18
Vanya's		Before		28	4.667	0	1	27
Marsh	2	During	TRES	25	4.167	22	3	0
		After		78	13.0	25	53	0
		Before		12	2.0	1	11	0
	3	During	SWSP	28	4.667	0	5	23
		After		75	12.5	7	27	41

Table A4: Values represented in figures 7-10 representing songs sung by Song Sparrow males during playback experiments. Songs were combined across time trials and represent an 18-minute period.

Site	Day	Period	Stimulus	Proportion of Category C Songs Sung	Trill Score	Average Length of Trill Syllable in Category B Songs (s)	Average Length of Trill Syllable in Category C Songs (s)
Cow Island	1	Before	TRES	N/A	N/A	N/A	N/A
		During		N/A	N/A	N/A	N/A
		After		N/A	N/A	N/A	N/A
	2	Before	SOSP	0.353	1.235	0.184	0.196
		During		0.725	1.500	0.380	0.142
		After		0.279	0.558	N/A	0.314
	3	Before	SWSP	0.414	1.414	0.184	0.108
		During		0.393	0.893	0.184	0.196
		After		0.763	1.763	0.184	0.225
Long Marsh 1	1	Before	SWSP	0.433	1.105	0.062	0.252
		During		0.481	1.286	0.062	0.251
		After		0.302	1.302	0.063	0.236
	2	Before	TRES	0.324	1.324	0.064	0.249
		During		0.086	0.800	0.063	0.287
		After		0	0.962	0.063	N/A
	3	Before	SOSP	0.256	1.051	0.064	0.204
		During		0.059	0.882	0.063	0.204
		After		0.242	1.242	0.063	0.287
Long Marsh 2	1	Before	SWSP	0	0.220	0.102	N/A
		During		0.565	1.239	0.079	0.158
		After		0.570	1.468	0.122	0.158
	2	Before	SOSP	0.021	1.000	0.111	0.158
		During		0	1.000	0.104	N/A
		After		0.605	1.605	0.105	0.158
	3	Before	TRES	0	1.000	0.123	N/A
		During		0	1.000	0.092	N/A
		After		0.233	1.232	0.102	0.158
Long Marsh 3	1	Before	TRES	0.481	1.250	0.108	0.303
		During		0.608	1.608	0.098	0.228
		After		0.512	1.439	0.089	0.219

		Before		0.333	1.178	0.108	0.374
	2	During	SWSP	0.491	1.415	0.099	0.183
		After		0.892	1.784	N/A	0.205
		Before		1.000	2.000	N/A	0.177
	3	During	SOSP	0.720	1.680	0.065	0.193
		After		0.017	0.350	0.109	0.425
		Before		N/A	N/A	N/A	N/A
	1	During	SOSP	0	0.545	0.114	N/A
		After		0.400	1.400	0.114	0.243
Telephone Bay		Before		0.550	1.150	0.064	0.329
	2	During	SWSP	0.347	0.918	0.064	0.295
		After		0.155	0.831	0.105	0.233
		Before		0.774	1.774	0.129	0.321
	3	During	TRES	0.184	1.184	0.114	0.244
		After		0.286	0.984	0.076	0.329
		Before		0	1.000	0.113	N/A
	1	During	SOSP	0.353	1.338	0.133	0.373
		After		0.168	0.925	0.145	0.157
Vanya's Marsh		Before		0.964	1.964	0.148	0.157
	2	During	TRES	0	0.120	0.144	N/A
		After		0	0.680	0.125	N/A
		Before		0	0.917	0.127	N/A
	3	During	SWSP	0.821	1.821	0.109	0.157
		After		0.547	1.453	0.147	0.157

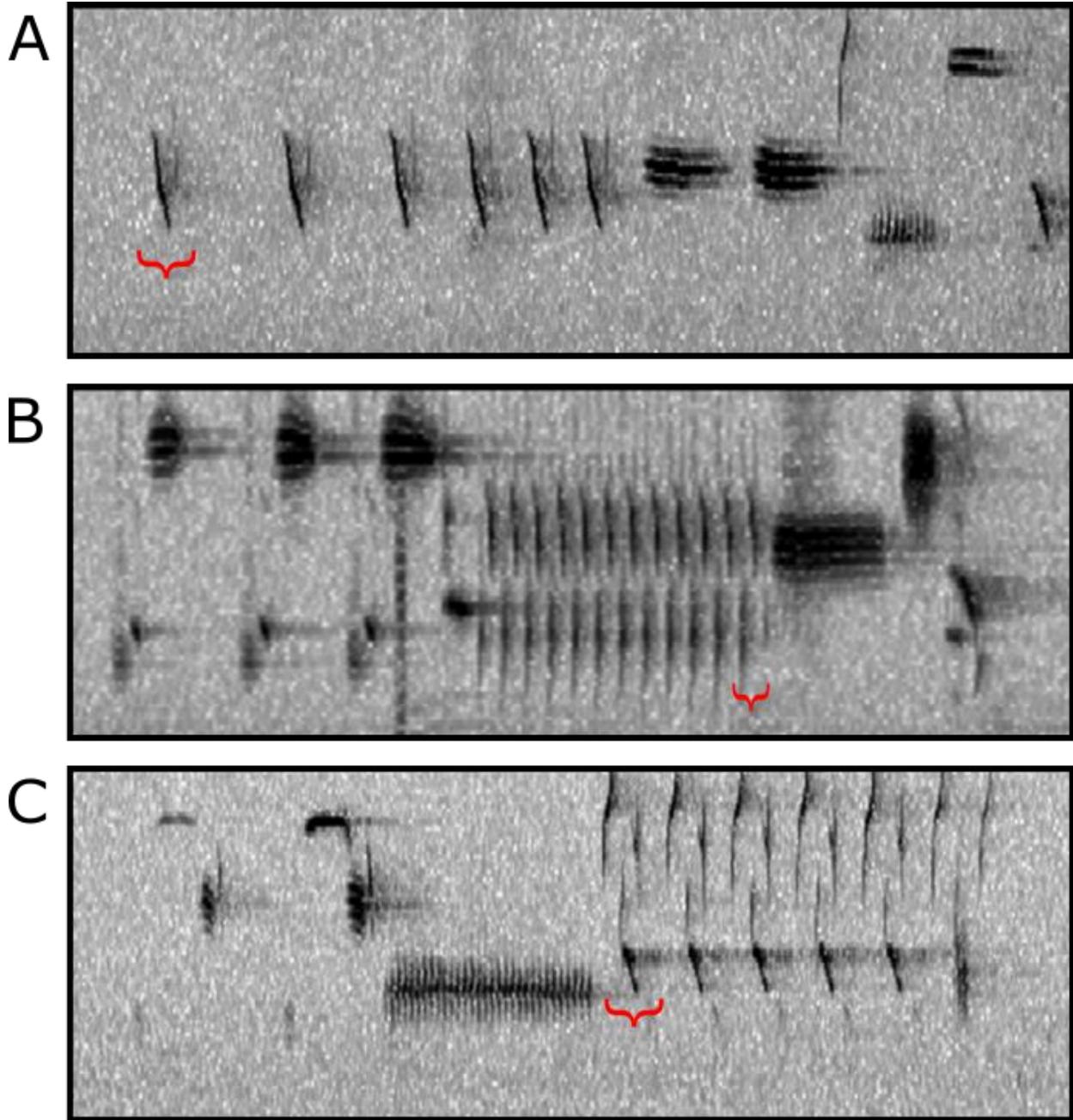


Figure A1: Song Sparrow sonograms representative of Categories A, B, C. Category A songs have one note per syllable (Panel A), Category B songs have two notes per syllable (Panel B), and Category C songs have three or more notes per syllable (Panel C), as illustrated by red brackets. Syllable length corresponds to the length (seconds) of each syllable outlined by the red bracket.

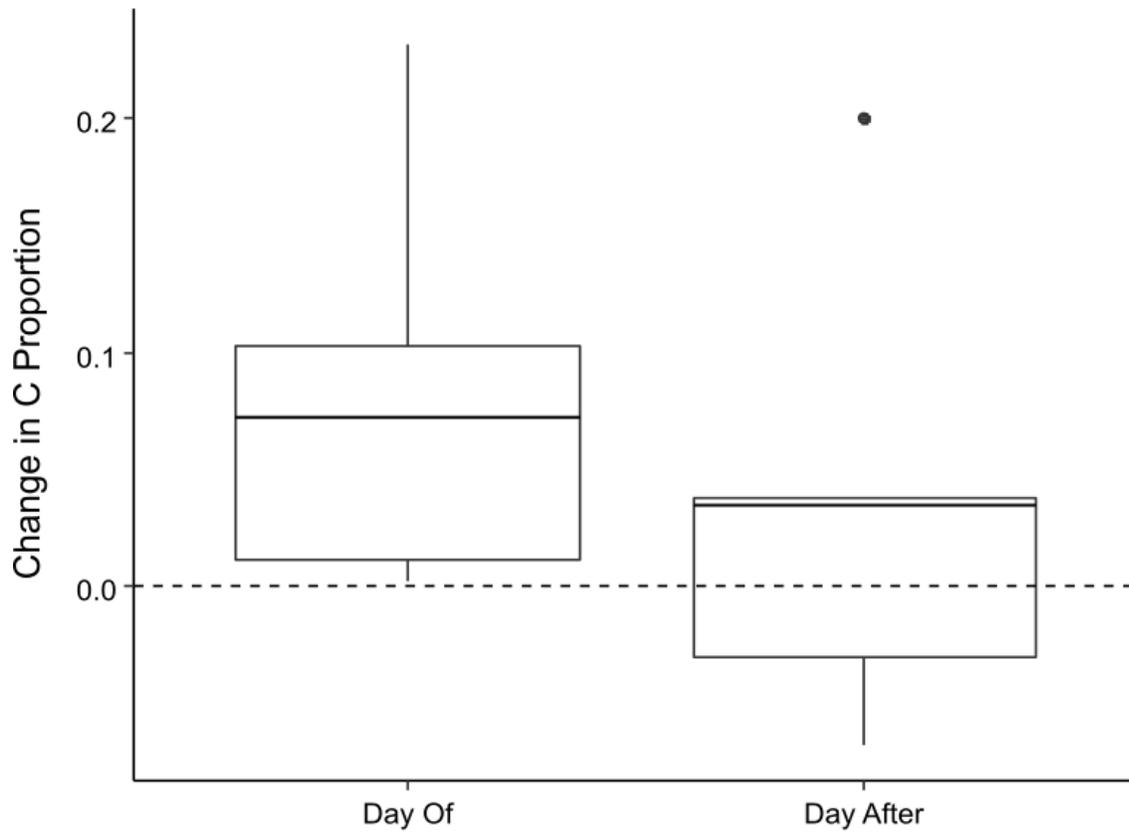


Figure A2: Change in the proportion of Category C songs sung by Song Sparrow males in comparison to the day before natural arrival of Swamp Sparrows ($n = 5$). The central black lines represent the median, box boundaries represent the 25th to 75th percentiles, and whiskers represent 1.5 times the interquartile range. Outliers are represented as black dots.

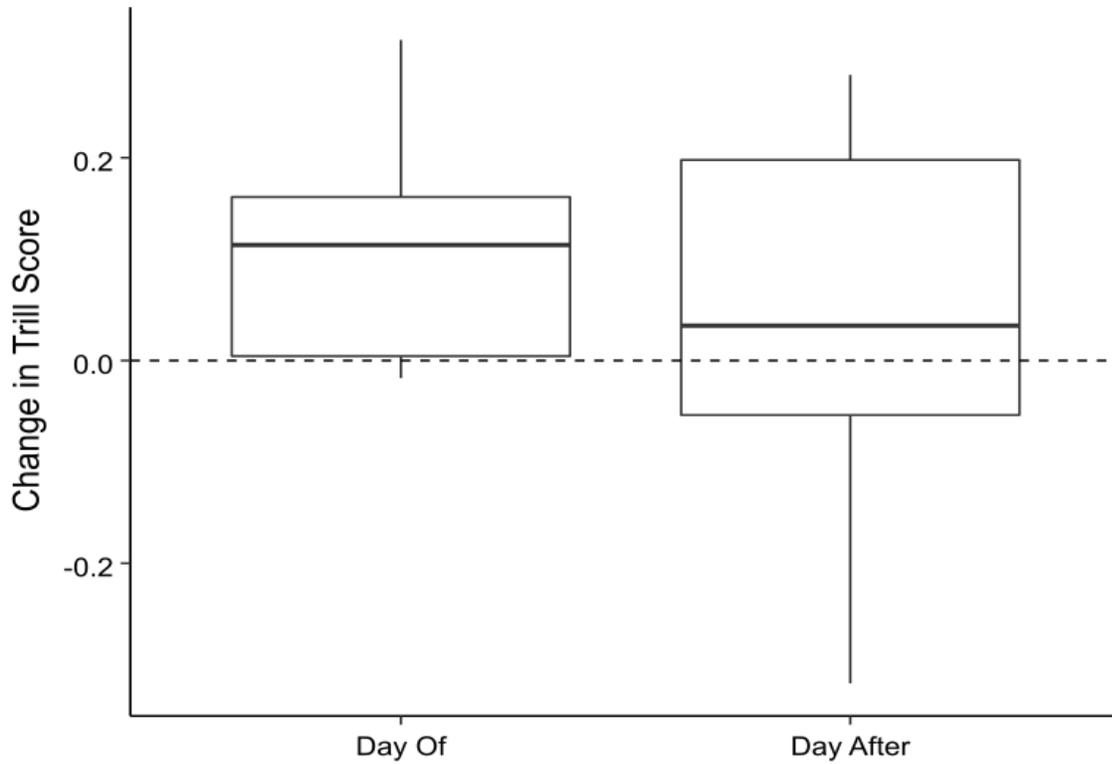


Figure A3: Change in Song Sparrow trill score in comparison to the day before natural arrival of Swamp Sparrows ($n = 5$). The central black lines represent the median, box boundaries represent the 25th to 75th percentiles, and whiskers represent 1.5 times the interquartile range. Outliers are represented as black dots.

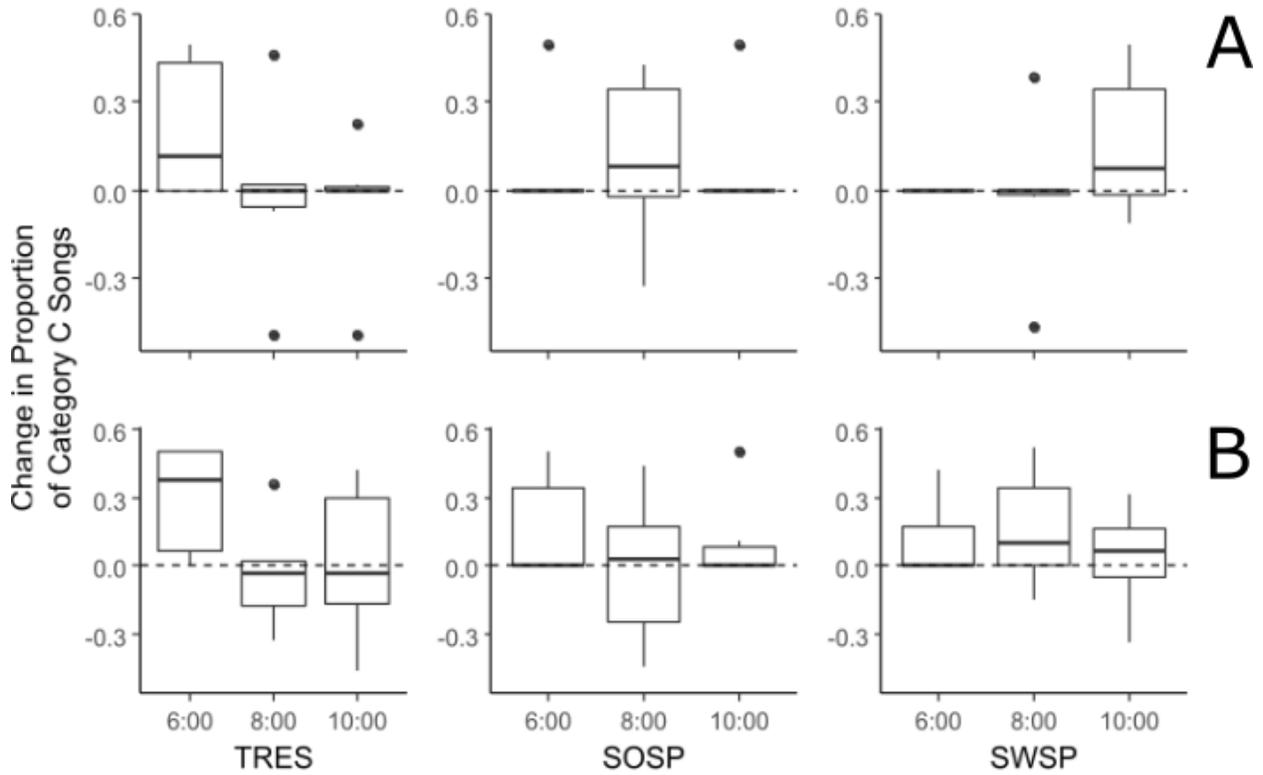


Figure A4: Change in the proportion of Category C songs sung by Song Sparrow males in response to playback stimuli ($n = 6$). Panel A represents the change from Before to During the playback, and panel B represents the change from Before to After the playback. The central black lines represent the median, box boundaries represent the 25th to 75th percentiles, and whiskers represent 1.5 times the interquartile range. Outliers are represented as black dots.

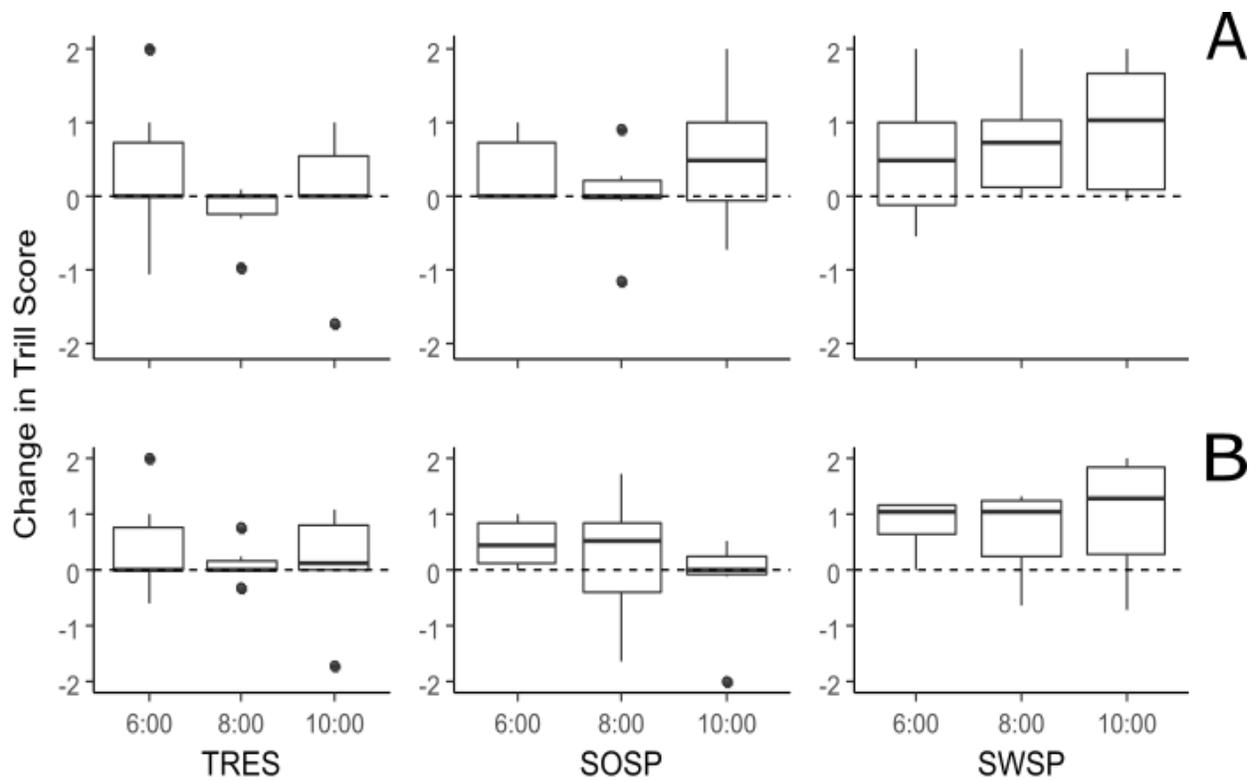


Figure A5: Change in Song Sparrow trill score in response to playback stimuli (n = 6). Panel A represents the change from Before to During the playback, and panel B represents the change from Before to After the playback. The central black lines represent the median, box boundaries represent the 25th to 75th percentiles, and whiskers represent 1.5 times the interquartile range. Outliers are represented as black dots.