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CHOICE AND CONSEQUENCE IN AVIAN VOCAL LEARNING: SONG DEVELOPMENT AND TERRITORIAL BEHAVIOUR IN SAVANNAH SPARROWS

by

IAN PAUL CAMPBELL THOMAS

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Choice and consequence in avian vocal learning: song development and territorial behaviour in Savannah Sparrows

by

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December 5, 2019

Declaration of Co-Authorship

I hereby declare that this thesis incorporates material that is the result of joint research, as follows:

I am the sole author of chapters 1 and 4, and the principal author of chapters 2 and 3. Chapters 2 and 3 were conducted under the supervision of Dan Mennill (University of Windsor), who contributed to the design of the study, data analyses, and writing of the chapters, as well as financial and logistical support throughout the process of the research, in the field in New Brunswick and in the lab in Windsor. In all cases, the key ideas, primary contributions, experimental designs, data analyses and interpretations were performed by myself, with input from my co-author. In addition, Chapters 2 and 3 also benefited from ongoing collaboration between Dan Mennill and Ryan Norris (University of Guelph), Amy Newman (University of Guelph), and Stéphanie Doucet (University of Windsor) in their long-term studies of the Savannah Sparrow population on Kent Island, and these collaborators contributed intellectually to the development of the two data chapters.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contributions of other researchers to my thesis, and I have obtained written permission from my co-author to include the above materials in my thesis.

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Abstract

In this thesis I study the effect of acoustic similarity on song selection and territorial aggression in Savannah Sparrows (*Passerculus sandwichensis*). In my first data chapter I studied the phenomenon of overproduction and selective attrition in Savannah Sparrow song development. Four years of field data reveal that Savannah Sparrows routinely exhibit overproduction of their song repertoires; more than half of young males express more than one song type early on in their first breeding season, before undergoing attrition to a single song. I found that the attrition of song types is a selective process, with males retaining songs that were more similar to their territorial neighbours. In my second data chapter I examined whether birds whose songs were similar to their neighbours benefited from lower levels of territorial aggression. Males that sang songs that were dissimilar to their neighbours faced higher levels of territorial aggression as indicated by higher numbers of aggressive calls detected in their territories. I conclude that birds which learn songs dissimilar to their neighbours face elevated levels of territorial aggression at the onset of the breeding season. My results provide support for the theory that vocal learning in songbirds can allow males to produce a song type that matches local cultural traditions, providing a benefit in terms of territorial defence.

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Chapter 1: General Introduction

Introduction

Social learning is widespread among animals, having been documented in arachnids (Clark et al. 2015), insects (Sherry 2008), fish (Manassa et al. 2014), reptiles (Kis et al. 2018), mammals (Pongrácz et al. 2011), and birds (Picard et al. 2017). Social learning, defined as an organism's ability to acquire behaviours from conspecifics through observation, fulfills a wide variety of functions, enabling organisms to build tools (Hunt and Grat 2003), access food resources (Picard et al. 2017, Sherry 2008), identify predators (Manassa et al. 2014), and produce species-typical signals (Clark et al. 2015). Although the value of social learning in acquiring behaviours that facilitate feeding or predator avoidance may be self-evident, the importance of social learning in acquiring species-typical signals seems more opaque, especially when we consider that the majority of animals appear to function adequately with signal behaviours that are innate.

Vocal learning is an adaptation whereby the production of species-typical auditory social signals are acquired through learning and mimicry. Vocal learning is instrumental to the production of human speech and is used to varying degrees by songbirds, hummingbirds, parrots, cetaceans, and bats, and possibly by seals and elephants (Fitch et al. 2008, Jarvis et al. 2017, Stoeger and Manger 2014). Songbirds in particular have been the focus of a considerable volume of vocal learning research for over half a century (Catchpole and Slater 2008). The learned vocalisations of birds exhibit high variability in acoustic structure and complexity, and biologists have carried out an enormous volume of studies to understand the function of song in songbirds (Catchpole and Slater 2008). The most widely accepted explanation for singing behaviour in songbirds is known as the “dual purpose hypothesis” (Catchpole and Slater 2008) which proposes that learned songs are used to simultaneously facilitate courtship and territorial defense. Extensive research has demonstrated that song is highly relevant to both of those arenas, although the ways in which vocal learning itself is pivotal to the process remain cryptic (Beecher et al. 2017). Because of the richness and diversity of vocal learning in songbirds, they offer some of the best opportunities to explore the evolution and adaptive value of this behaviour.

Overproduction and attrition in songbirds

Among temperate-zone songbirds, singing behaviour is generally restricted to male birds who learn their songs from conspecific animals (Catchpole and Slater 2008). For the many species of songbird that are closed-ended learners (i.e. those whose vocalizations are learned early in development and are then fixed after maturity), there appear to be two time-windows of critical importance in their song learning. The first sensitive period lasts for approximately 50 days after hatching when young birds memorize the songs of neighbouring adult males. The second period is in the following year at the beginning of their first breeding season when young males are attempting to establish their first breeding territory (Marler 1994). In that second window, young songbirds go through a period of crystallization where the songs that they learned in infancy are practiced and refined; after crystallization, songs will be expressed relatively unchanged for the remainder of a bird’s life (Marler 1982, 1994, Nelson et al. 2009, Nordby et al. 2007). These two periods of plasticity reflect an important innovation for vocal-learning animals such as songbirds: the ability to adopt the vocal phenotype of their conspecifics irrespective of their genetic relatedness. In a closed-ended learner, the evolutionary significance of this complex behaviour can be localized to this period of acquisition and choice.

Many young songbirds demonstrate a process called “song overproduction” wherein they learn a larger repertoire of songs than they express in their mature, adult repertoire (Nordby et al. 2007, Peter et al. 2017). This has been demonstrated to be particularly relevant in songbird species whose adult repertoires consist of only a single song type such as Swamp Sparrows (*Melospiza georgiana*; Marler 1982), Field Sparrows (*Spizella pusilla*; Nelson et al. 1992), and White-crowned Sparrows (*Zonotrichia leucophrys*; Nelson et al. 2000). The process through which the repertoire is pared down to the single song that will be used for future courtship and territorial defence is known as “attrition”. Attrition is part of the general process of crystallization where the bird takes the raw vocal material learned in infancy and modifies it into the fully defined repertoire it will use in maturity. During the process of attrition, we see a clear potential for the expression of song preference. For bird species which are closed-ended learners, there is a temporal limit on their ability to learn new songs, and after a sensitive period of their development no new tutor information can be acquired (Marler 1994). In some species this process of attrition has been identified as selective attrition (Nelson et al. 1992, 2000) where the young birds express clear patterns in determining whether a song is retained or discarded, suggesting they have a set of criteria for identifying and retaining preferred song structures.

Research on attrition in several species of sparrow has suggested that this process allows birds to closely match their song-types to those of their territorial neighbours (Marler 1982, Nelson et al. 1992, 2000). Since a juvenile bird during its natal summer will not know who its territorial neighbours will be during the following spring, these songbirds appear to learn multiple songs in their natal summer, and then select the preferred song based on their acoustic environment the following spring (Bell et al. 1998, Nelson et al. 2009). In other words, the young males are said to “overproduce” the multiple songs they learned in their natal year, and then undergo a process of “selective attrition” to arrive at a final crystallized song based on their acoustic experience at the start of their first breeding season. It is assumed that closely matching a local dialect is advantageous to the reproductive fitness of birds, as it may help them navigate intra-specific conflict (Beecher et al. 1996, Sung et al. 2005) or better attract mates (Nelson et al. 2013) during their first breeding year. In Chapter 2 of my thesis, I test whether Savannah Sparrows preferentially crystallize songs that are similar to their territorial neighbours.

Mitigation of aggression through acoustic signalling

Aggressive interactions between conspecific animals are costly behaviours that can be taxing and dangerous (Burgess et al. 2013, Ros et al. 2006, Smith and Taylor 1993). In order to minimize aggressive interactions, many animals produce vocal signals that either intimidate or placate potential aggressors (Arrigo-Nelson et al. 2001, Blount 1985, Mizuguchi et al. 2016). In addition to signals presented in agonistic encounters, many species are able to consistently produce complex signals that deter conspecifics from initiating conflict through either intimidation or indication of group membership, minimizing aggression through a consistent advertisement of their identity or status. Male Iberian Rock Lizards (*Iberolacerta cyreni*) use scent-marking to reduce the frequency and duration of territorial conflict by identifying themselves as long-term territory holders (Lopez and Martin 2011). Paper wasps (*Olistes exclamans*) use facial stripes to advertise prowess which helps to avoid costly agonistics encounters (Tibbets and Sheehan 2011). Subordinate male greater sac-winged bats (*Saccopteryx bilineata*) use learned vocalizations to advertise group membership and appease older males (Knörnschild et al. 2012).

In songbirds there is widespread evidence for the dear enemy hypothesis which suggests that males are more aggressive to unfamiliar birds than to known neighbours (Ackay et al. 2010, Briefer et al. 2008, Moser-Purdy et al. 2016, Draganoiu et al. 2014). A number of studies suggest that non-local song types provoke aggressive behaviour from conspecific animals (Beecher et al. 1996, Sung et al. 2005, Williams et al. 2019), although some recent research disputes this (Parra et al. 2017). These studies of the role of learned vocalizations in territorial signalling usually rely on playback experiments where the researchers produce an artificial stimulus and document the immediate reaction of the focal individual, using such metrics as closeness of approach, number of flights over the speaker, and speed of approach as proxies for levels of aggression.

These experiments, although valuable and enlightening, cannot test the experience of a living individual with a non-local song, and how the acoustic phenotype of an individual influences the aggression it faces on a day-to-day basis. In Chapter 3 of my thesis I test if those patterns of increased arousal translate to a greater number of agonistic interactions in the lives of individuals expressing non-local song.

Study system

Savannah Sparrows (*Passerculus sandwichensis*) are an excellent candidate species for studying song learning because adult males sing just a single song type to navigate all of their territorial and courtship challenges (Wheelwright and Rising 20008, Wheelwright et al. 2008). Savannah Sparrows learn their songs by listening to and emulating the songs of adult conspecifics and they do not learn songs heard after their natal summer (Mennill et al. 2018). Because Savannah Sparrows express only a single crystallized song-type, we can effectively link their social behaviour to a single acoustic phenotype, allowing us to identify the downstream effects of song structure on intrasexual conflict later in life.

My study population is located at the Bowdoin Scientific Station on Kent Island, a small 200-hectare island in the Bay of Fundy in New Brunswick, Canada. This population has been the subject of a long-term study for over 30 years (Wheelwright et al. 1998). Every adult in the central area of the study population is banded with a unique combination of three colour bands and one aluminum band, and every bird has its nest located and monitored with nestlings being weighed, measured and having their blood taken for paternity analysis. The study site is a 10-hectare area of meadow on Kent Island with an annual population of 40-50 breeding pairs of Savannah Sparrows (Wheelwright et al. 1998). Philopatry for this population is exceptionally high; between 40 to 80% of adult birds on the study site in a given year have hatched from within the population (Wheelwright et al. 1998), making this an ideal study population for to study cultural evolution and song learning. Male Savannah Sparrows return to the study site in mid-April, and females arrive roughly three weeks later (Wheelwright and Rising 2008). Currently five principal investigators are studying these birds (R. Norris, A. Newman, D. Mennill, S. Doucet, H. Williams) generating a comprehensive annual data set of demography, population dynamics, reproductive success, and vocal behaviour. This population is comparable to a lab population given the high resolution and comprehensiveness of data for each member of the study population, but remains a completely free-living wild population with only minor modifications to natural behaviours.

Thesis goals

The aim of this thesis is to examine the selection of song types in the vocal learning of the Savannah Sparrow and the effect of these learned acoustic phenotypes on territorial aggression. In my first data chapter (Chapter 2), I use a four-year data set to test the hypothesis that Savannah Sparrows employ overproduction and selective attrition to crystalize a song that is most similar to their territorial neighbours. In my second data chapter (Chapter 3) I use a two-year data set to test the hypothesis that

Savannah Sparrows with songs that are similar to their territorial neighbours will experience less aggression from conspecifics than individuals whose songs are dissimilar to their neighbours.

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Chapter 2: Overproduction and attrition in avian vocal learning: Social influences on the ontogeny of song in Savannah Sparrows

Chapter summary

Vocal learning is a rare adaptation that underpins both human language and the songs of oscine birds. Learned vocalisations are believed to facilitate both territorial defence and mate attraction, but we have a poor understanding of the adaptive value of learned vocalizations over unlearned vocalisations. To better understand vocal learning, we tracked the development of song in young male songbirds during their first breeding period. We measured acoustic similarity between the songs of young birds and their territorial neighbours. We used focal and autonomous recordings to compile extensive libraries of the songs produced by young birds in a colour-banded population of Savannah Sparrows, as well as the songs of all their neighbours. We found that 56% of young males exhibit overproduction, where they produce multiple song variants for several weeks after their arrival on the breeding grounds, and then their vocal repertoires undergo attrition to the species-typical single song type. We collected detailed measurements of the acoustic structure of each song type produced by each young male, and then we compared the acoustic similarity between each song type and the songs of older territorial neighbours. We found that individuals often retain the songs that most closely resemble their territorial neighbours and reject songs that are dissimilar. The acoustic similarity of the entire song, as well as the middle segment of the song, appears to be important in predicting song retention. Our results contribute to a growing body of research suggesting that territorial neighbours influence the expression of learned acoustic phenotypes. This research suggests that conforming to

local acoustic phenotypes is important for songbirds, a function which may be relevant to the evolution and maintenance of vocal learning across the animal kingdom.

Introduction

Despite the versatility they offer, learned behaviours can be costly for animals. The ability to learn imposes costs on animals including developmental costs (Searcy et al. 2008), physiological costs (Dunlap and Stevens 2016), opportunity costs of lost time during the learning process (Muth et al. 2015), and the potential costs of learning maladaptive behaviours (Marler 1970). To minimize these costs, animals can limit their learning behaviours to temporal windows or environmental conditions where benefits are maximized. Bees (*Bombus impatiens*), for example, assess the nectar rewards offered by novel flowers before deciding whether to learn how to access them (Muth et al. 2015). Ravens (*Corvus corax*) go through a period of neophilia as juveniles when they are exposed to a wide variety of potential food items and when parental care reduces the opportunity costs of learning, becoming neophobic at maturity (Heinrich 1994). Given that animals appear to maximize the benefits of learned behaviours by expressing them within favorable environmental or temporal windows, these learning strategies shed light on what aspects of learning are most adaptive. Animals that selectively employ learning highlight the most essential elements for adaptation and evolution, making ideal models for understanding the adaptive value of learning across the animal kingdom.

Many oscine songbirds manage the costs associated with learning by employing a restricted period of vocal learning, where songs are only learned within brief temporal windows early in life (Marler 1994). After these learning periods, an individual’s song usually becomes as rigidly stereotyped as any innate characteristic (Marler 1994). Many birds exhibit a behaviour known as “overproduction” late in the learning process, when young birds exhibit a larger repertoire of songs than they express in adulthood (Nordby et al. 2007, Peters et al. 2017). Overproduction has been demonstrated to be particularly relevant in songbird species whose adult repertoires consist of only a single song type, such as Swamp Sparrows (*Melospiza georgiana*; Marler 1982), Field Sparrows (*Spizella pusilla*; Nelson et al. 1992), and White-crowned Sparrows (*Zonotrichia leucophrys*; Nelson et al. 2000). The process in which the repertoire is pared down to the single song that will be retained into adulthood for future courtship and territorial defence is known as “attrition”. Attrition is part of the general process of song crystallization, where a bird takes the raw vocal material learned in infancy and modifies it to become the song it will use in maturity (Nordby et al. 2007). In some species this process of attrition has been identified as “selective attrition” (Nelson et al. 1992, 2000) where young birds express clear patterns in determining whether a song is retained or discarded, suggesting they have a set of criteria for identifying and retaining particular song structures. Understanding the factors that guide avian song learning deepens our understanding of the unique advantages offered by social learning, and why social learning has evolved across the animal kingdom.

Research on overproduction and attrition in several species of sparrow has suggested that this process provides birds with the ability to closely match songs of their territorial neighbours (Marler 1982, Nelson et al. 1992, 2000). During their natal summer, when juveniles are memorizing songs produced by adults in their environment, young birds will not know who their territorial neighbours will be during the following spring. Young birds often learn multiple song types in their first summer, and then choose one particular song based on their acoustic environment the following year during their first breeding season (i.e. selective attrition; Bell et al. 1998, Nelson et al. 2009). It is assumed that closely matching a local dialect is advantageous to the birds because it helps them navigate territorial interactions with other males (Beecher et al. 1996, Sung et al. 2005) or to attract mates (Nelson et al. 2013). Young birds may experience less aggression if their song contains acoustic features familiar to their neighbours (Beecher et al. 1996). Some studies have suggested that atypical song types correlate with higher parasite loads (MacDougall-Shackleton 2002), and therefore singing local songs might be an honest indicator of male quality.

Recent research has revealed that the repertoires of Savannah Sparrows (*Passerculus sandwichensis*) are constrained by the song types they were exposed to in their first three months of life (Mennill et al. 2018). In an experimental study of song learning in wild birds, male Savannah Sparrows learned song types that they heard both during their natal summer and again at the outset of their first breeding season (Mennill et al. 2018). This suggests that the final, crystallized song of a bird may not represent the absolute ideal song structure for local conditions, but instead the best one available to the bird from a pre-existing set of songs developed during his natal summer. The process of overproduction and attrition has never been studied in Savannah Sparrows, but anecdotal observations by Mennill et al. (2018) suggest that it occurs: several birds were observed to produce multiple song types early in their first breeding season.

Overproduction might allow these birds to test multiple learned song types before they select the most effective song to retain into adulthood. This provides a young bird with a degree of flexibility they would not have if they crystallized their song repertoire earlier in their development. This may mean that Savannah Sparrows are able to limit the costs of song learning (Logue et al. 2008, Searcy et al. 2008) to their natal year, but retain some of the advantages of flexibility into their first breeding season.

In this study our goal was to document the development of song in young male Savannah Sparrows over a four-year field study. We tested the hypothesis that Savannah Sparrows exhibit overproduction, and then undergo selective attrition in order to express similar song types to their territorial neighbours. We evaluated two main predictions that stem from this hypothesis. First, based on evidence from other single-song repertoire species (Swamp Sparrow, Marler 1982; White-crowned Sparrow, Nelson et al. 1992, 2000), we predicted that Savannah Sparrows would exhibit overproduction, producing multiple songs early in life but retaining one song into adulthood. Second, based on evidence from those same overproducing species, we predicted that the process of attrition would be guided by song similarity with neighbours, where birds would retain the song that was most similar to those songs by neighbouring animals.

Methods

General methods

We conducted our research at the Bowdoin Scientific Station on Kent Island, New Brunswick, Canada (44°35’N 66°46’W). As part of a long-term investigation of this population of Savannah Sparrows, in June of each year we captured all adults in mist-nets and gave them a unique combination of colour-bands (Woodworth et al. 2016). In September, prior to migration, we captured young-of-the-year in mist nets and gave them unique combinations of colour-bands. Each spring we identified the age of all returning birds based on their colour band combinations. We assumed that unbanded birds arriving on the study site in spring were first-year birds due to the high territorial fidelity demonstrated by adult birds in this population (Wheelwright et al. 2008); we confirmed this assumption by assessing the plumage and molt characteristic of young birds when they were captured for banding and blood sampling. We differentiated males from females based on the production of song, and captured birds were sexed by the presence of either cloacal protuberance or brood patch. Sex identification was facilitated by the earlier arrival of males on the study site (Woodworth et al. 2016); during late April and early May, the population was exclusively made up of males. We observed the behaviour of each male upon arrival from migration to determine the extent of his territory. The study site is laid out in a grid of 50×50m squares, and we created detailed territory maps each day, reflecting a male’s position within a grid square and with reference to local landmarks including vegetation features.

We collected focal recordings of males when they arrived from migration and continued recording them throughout the breeding season. In all four years of the study, we collected in-person focal recordings using hand-held digital recorders (Marantz PMD661 digital recorder and a Sennheiser ME66/K6 microphone mounted in a Telinga parabola; 44.1 kHz sampling frequency; 16-bit accuracy; WAV format). Daily, we collected focal recordings of all singing males in the first four hours of the morning from male arrival (mid-April to mid-May) until the onset of nesting at the end of May. Using the focal recordings, we compiled a complete song library of all males on the study site, producing a comprehensive record of all acoustic phenotypes expressed in the population.

In addition to the focal recordings collected in all four years of this study, in 2018 we collected exhaustive sampling of the voices of young males using autonomous digital recorders (Wildlife Acoustics Song Meter SM2; 44.1 kHz sampling frequency; 16-bit accuracy; WAC format; see Mennill et al. 2012). We placed autonomous recorders at the centre of each focal male’s territory, close to the preferred singing perches we had observed during focal recording sessions. We placed autonomous recorders on each male from his arrival (mid-April to mid-May) until the onset of nesting at the end of the May. In some cases, male territory location changed subtly from day to day, usually in response to the arrival of other males on the island; we documented these changes during our focal-recording sessions, and moved the automated recorders as necessary, to ensure that the automated recorders remained near the centre of the territory of the intended animal. Given the small territory size of Savannah Sparrows, average 0.21 ha on our study site (Wheelwright and Rising 2008), and the broad recording range from our autonomous recorders (we could typically hear males with territories up to 100m away from the recorder), we are confident that these recordings are adequate for sampling all vocalizations from the target animals.

Song identification and classification

We identified song types by examining our field recordings as sound spectrograms using Syrinx-PC sound analysis software (J. Burt, Seattle WA). We define a song type as a series of notes with distinctive spectro-temporal qualities produced in a consistent order. Adult male Savannah Sparrows produce only one song type, with high consistency across their lives (Wheelwright et al. 2008), showing only small variations in the frequency and duration of certain song elements over time (Williams et al. 2013). (In less than 2% of animals, a male will produce two song types into adulthood, Williams et al. 2013, Mennill et al. 2018, but there are no such males in the current dataset.) For our study, each song type had to exhibit a syllable with unique spectro-temporal properties that was not exhibited in any other song types produced by that individual in order to be classified as a distinct song type (as in Williams et al. 2013). This meant that songs which only deleted or duplicated elements were not classified as distinct song types. Furthermore, each song type had to be sung at least twice by each male (because our focal recordings only captured a portion of each male' singing output, any song type recorded twice would likely have been expressed many more times throughout the day). In our focal recordings, different song variants were attributed to each of the young males by observing the male’s colour bands during the recording sessions.

In addition to the focal recordings, in 2018 we examined every song of each focal bird detected in autonomous recordings, by annotating all songs produced between 0600 to 0800 h in the first four days after arrival. We included all young birds in our study where the autonomous recorder captured 200 or more songs from each bird during this four-day period (n =17 males). We used our song library of all established (adult) males on the study site to identify songs that could not be attributed to another nearby male. To avoid falsely ascribing a novel song type to a focal bird, we would only ascribe a song type to a focal bird if it was expressed in a bout of already-documented song types from the focal bird at the same amplitude in both microphone channels as the current songs of the focal bird (suggesting a similar location as the focal bird) and without ever overlapping with the documented songs of the focal bird. These criteria allowed us to reliably assign newly documented song types to the target animal. If we did not detect any evidence of overproduction in the focal recordings or our scanning of the autonomous recordings we assume that this bird did not demonstrate overproduction.

Acoustic distance measurements

We measured the fine structural features of recorded songs using AviSoft sound analysis software (R. Sprecht, Berlin, Germany). We employed the automated parameter measurements feature of AviSoft to minimize any human subjectivity in quantifying differences between songs. We used a frequency threshold of -20 Hz relative to the maximum of each selection when collecting automated measurements. We categorized our measurements based on four segments of Savannah Sparrow song: the introduction, the middle segment, the buzz, and the terminal segment (terminology from Williams et al. 2013). For each of the four song segments we measured six features: the element rate, average pause length, average max frequency, average minimum frequency, average dominant frequency, and average note bandwidth (Figure 2.1). We also measured the pause length between the three song segments, the length and number of notes in the middle segment and buzz segment, as well as the duty cycle of the middle segment. We did not measure song length and number of notes for the introduction and terminal segments because of the high variability in segment length within a given male's expression of his song type (personal observation). We did not measure duty cycle for the buzz because it generally consists of a single note.

Based on these 32 spectro-temporal measurements, we plotted all songs in multi-dimensional space, and calculated the squared Euclidean distances between pairs of songs. This gave us a technique for assessing numerically the acoustic similarity between pairs of songs. We refer to this measurement as "acoustic distance" (as in Gordhino et al. 2015, Koetz et al. 2007, and Sung 2005) and we note that two songs with a low acoustic distance score are very similar, whereas two songs with a high acoustic distance score are very different. To calculate acoustic distances we used the clustering platform within JMP (v. 14; SAS Institute, Cary, NC), selecting hierarchical cluster analysis using the centroid (squared Euclidean distances) calculation method. This technique produces Euclidean distance measurements that are standardized, regardless of the units of the original measurements, by subtracting the column mean from each value and then dividing this number by the standard deviation of the column. From within the clustering platform in JMP, we selected the option to save the distance matrix which created a table outlining the squared Euclidean distances between all measured individual songs. Note: we did not conduct clustering analyses with this output, we used the platform only to produce pair-wise Euclidean distance measurements.

To ground-truth this approach for measuring acoustic similarity, we confirmed that our acoustic distance calculations produce reliable estimates of acoustic similarity by conducting several comparisons. We took a subset of established adult males whose songs were recorded in multiple years (44 individual song recordings from 12 different males) and compared repeated measurements of songs from the same bird recorded in the field in different years. In this dataset, birds had an average pair-wise acoustic distance measurement of 5.74±0.53 from different-year recordings of their own songs versus an average acoustic distance of 8.15±0.53 from the entire population in 2018 (paired t-test: $t=4.48$, $p<0.003$, $N=12$). From these analyses we calculated that songs had a 30% greater mean acoustic distance to other songs in the population than their own songs from previous years. The mean 5.74 distance between recordings of songs that are ostensibly the same appear to reflect consistent variation in a male's own singing performance, variation in the background noise of a given recording, and variations in the automated parameter measurement tool in AviSoft across different recording sessions. Despite these variations, our findings that two songs recorded from the same male have lower acoustic distance scores than two songs recorded from two different males makes us confident that these distance measurements capture biologically relevant relationships between songs. It is important to emphasize that this populations consists of many birds who have learned nearly identical songs from a common group of song tutors (Wheelwright et al. 2008, Mennill et al. 2019, Williams et al. 2015), which helps explain why birds have a relatively close mean similarity to the songs of the study population at large.

Previous studies of Savannah Sparrows, including the birds in our study population, reveal that that the middle segment of the song is particularly important for individual recognition (Wheelwright et al. 2008, Williams et al. 2013). Therefore, in addition to our comparisons of the entire song, we also compared the middle song segments of males to themselves in previous years and their mean middle segment similarity to the entire population. As in our whole-song analyses, we ground-truthed our analytical approach by comparing middle segments of songs collected from the same male in different years to songs from different males. These results showed the same pattern as our whole-song comparisons: male middle segments had a mean acoustic distance of 2.07±0.23 from themselves in other years, compared to mean distance of 4.25±0.23 to the entire population in 2018 (paired t-test: t=9.43, $p<0.001$, N=12).

Data analysis

Our dataset consists of 41 males that we recorded extensively over the four-year study, including 26 males that demonstrated overproduction (see Results). For 24 of the 26 birds that exhibited overproduction, we discerned which song was retained into adulthood by recording them repeatedly after nesting had begun. For two of the 26 birds, however, the male vanished in spring, before we were able to identify which song was retained into adulthood (we presume these two males were depredated). For males that exhibited overproduction and attrition, we compared songs that males retained to those that they discarded using two-tailed t-tests. All values are presented as mean ± standard error. We compared these songs using their mean acoustic distance to each male's territorial neighbours. Neighbours were defined as birds with established pre-existing territories in their second breeding year or older that had territorial boundaries less than 25 metres from the focal male's territory.

Results

Overproduction and attrition

Across four years of field studies focused on 41 young male Savannah Sparrows, we found 26 males that exhibited overproduction (i.e. 63% of males that we studied). Of these 26 overproducers, 18 (69%) exhibited two distinct song types, six (23%) exhibited three distinct song types, and two (8%) exhibited four distinct song types. Among the 26 overproducers, 24 survived into the first breeding season, and all 24 males underwent a process of attrition, whereby they winnowed their repertoire to a single song type within two weeks of arrival on the breeding grounds in their first year (Figure 2.2). All 24 males sang only a single song type for the remainder of their adult lives: in all cases, it was the song that survived after the phase of overproduction and attrition.

Selective attrition

For each male that exhibited overproduction and attrition, we compared the songs that males discarded to the songs they retained. Retained songs showed smaller acoustic distances in comparison to the average acoustic distance across all neighbours compared to discarded songs (Figure 2.4; paired t-test: t=2.32, p=0.03, n=24). Retained songs did not show any systematic differences in acoustic distance to each male's most-similar neighbour (Figure 2.4; paired t-test: t=1.2, p=0.24, n=24). In other words, males retained songs that sounded more similar in comparison to their group of neighbours, but did not appear to retain songs that sounded more similar to their most-similar sounding neighbour (Figure 2.3).

The middle segment of Savannah Sparrow song shows extensive variation, and is believed to be especially relevant for individual recognition (Chew 1981, Williams et al. 2013). Indeed, some Savannah Sparrow researchers define distinct song types based on the middle segment alone (Williams et 2013). Based on this previous research we believed the middle segment might be especially relevant to selective attrition and so we repeated our analyses by focusing on the middle segment rather than the entire song. The middle segments of retained songs showed lower mean acoustic distance in comparison to all neighbours when compared to discarded songs (Figure 2.4; paired t-test: t=3.03, P<0.006, N=24). The middle segments of retained songs also showed lower acoustic distances to the most-similar neighbour when compared to discarded songs (Figure 2.4; paired t-test: t=2.48, p=0.02, N=24). In other words, when focusing on the middle segment of songs, males retained songs that sounded more similar to their group of neighbours and to their most-similar neighbour.

Discussion

We found that overproduction, followed by attrition, is commonplace for Savannah Sparrows in their first breeding spring. Although their adult repertoire size is just one song type (Wheelwright et al. 2008, Williams et al. 2013), more than half of young Savannah Sparrows produced two, three, or four song types in the initial days upon their arrival to the breeding grounds. Within the first two weeks of the breeding season, the overproducing males then rejected all-but-one song type which they sang for the duration of the breeding season, and the duration of their adult lives. Overproduction was not observed in older males, which produced one song throughout their adult lives, a fact that has been documented in previous studies (Wheelwright et al. 2008; Williams et al. 2013; Mennill et al. 2018). For male Savannah Sparrows that exhibited overproduction and attrition, we compared both the songs they retained and the songs they discarded to the songs of other males in their neighbourhood, including comparisons of whole songs as well as the variable middle segments of songs. In our analysis of entire songs we showed that males retain songs that have higher acoustic similarity to all territorial neighbours, although their retained song was not more similar to their most-similar neighbour’s song than expected by chance. Our analysis of the middle segment shows that males retain songs that have higher mean middle-segment similarity to all territorial neighbours, as well as higher middle-segment similarity to the most-similar neighbour. Our results support the hypothesis that Savannah Sparrows exhibit overproduction, and then undergo selective attrition to express similar songs to their territorial neighbours.

Due to the logistical challenges of finding young males immediately upon their arrival on the study site and the limited time frame in which we were able to focally sample each male’s repertoires, we suspect that our results actually underestimate the prevalence of overproduction in the population. We feel it is probable that many males went through their process of overproduction and attrition before we were able to record their repertoire and we suspect that most if not all males do show some overproduction an attrition in their first breeding year.

In a recent review of research on overproduction and attrition in songbirds, Peters and Nowicki (2017) outlined five explanations for the adaptive value of overproduction. (1) Overproduction allows birds to discard poorly learned or accidentally acquired songs. (2) Overproduction allows males to retain songs that match their eventual territorial neighbours. (3) Overproduction allows males to retain songs that match their local dialect. (4) Overproduction allows males to retain songs that are preferred by females. (5) The learned repertoire of unexpressed songs might help males identify other examples of the local dialect and therefore recognize whether conspecifics are local or foreign birds. Our results do not offer support for explanation 1, because we observed many songs that appeared fully expressed but were eventually discarded. Our results are consistent with explanation 2 and 3, but our current research does not offer us the capacity to distinguish between them. Future research could examine whether the mean acoustic distance to the population is a better predictor of attrition and retention than mean acoustic distance to neighbours. Our results do not support explanation 4 because we observed selective attrition to be completed before females arrived in the colony. Finally, our results do not offer explicit support for explanation 5, although neither do they contradict this explanation. Further study could illuminate whether individual Savannah Sparrows show long term recognition of song types they themselves have learned and discarded

There has been some limited evidence that female behaviour can influence selective attrition in cowbirds (*Molothrus ater*) (Smith et al. 2000), and there is some evidence in Common Chaffinches (*Fringilla coelebs*) that selective attrition can be a mechanism for weeding heterospecific song out of the mature repertoire (Thorpe 1952); yet the overwhelming bulk of evidence suggests that male-male interactions shape selective attrition (Peters & Nowicki 2017). Our results on Savannah Sparrows are consistent with the idea that male-male interactions shape selective attrition. Our study joins the growing body of research (Marler 1982, Nelson et al. 1992, Nordby et al. 2001), that demonstrates the importance of overproduction in allowing males to produce similar songs to their territorial neighbours. For species that demonstrate clear regional dialects, such as White-crowned Sparrows, researchers have identified selective attrition as instrumental in maintaining local culture phenotypes despite consistent geneflow (Bell et al. 1998). In Song Sparrows, where individuals express multiple song types, selective attrition allows males to maintain multiple song types that are shared with individual neighbours (Nordby et al. 2007). Although Savannah Sparrows do show regional differences in song syllables, they do not appear to have defined regional dialects (Chew 1981) and therefore we suspect neighbourhood-based dynamics, as in Song Sparrows, are more likely drivers of attrition than population-wide cues. Our research is unique in that not only does it deal with the song as a complete structure, but also tests the importance of an individual song segment in the process of attrition. Previous work on White-crowned sparrows has demonstrated that different song segments appear to express different signals (Nelson & Poesel 2006), but to our knowledge we are the first to test the role of particular song segments in selective attrition. The selective retention of song types whose middle segments resemble territorial neighbours supports previous research on Savannah Sparrow song that emphasized the importance the middle segment in reflecting the identity of the signaller (Williams et al. 2013).

Our results reveal that overproduction is common during the early adult lives of Savannah Sparrows, and therefore overproduction is a worthwhile area of investigation for research on cultural evolution and tutor selection. Previous research in Savannah Sparrows operated under a premise that a male’s mature repertoire was reflective of the individual’s relationship with a specific tutor (Wheelwright et al. 2008). Our results suggest that the model of a single tutor is unlikely in Savannah Sparrows, and that the song development of single-repertoire songbirds may reflect a varied process of learning and selection extending from the natal summer into the following spring. We suggest that follow-up research on the role of tutors in song expression should incorporate not just the crystallized song of an adult male, but an individual's entire overproduced set of songs. An investigation that examined whether neighbouring males to an individual's natal territory were highly represented in his overproduced repertoire would allow us to determine whether song learning reflects the immediate natal area or a more dispersed sampling of the entire population. Similarly, previous research on the long-term cultural evolution of Savannah Sparrows documenting the development of song elements over multiple years (Williams et al. 2013), focused on song elements present in crystallized repertoires. This study suggested that certain song elements were under directional selection across generations. We feel that an analysis of song evolution that incorporated overproduction and attrition would provide a powerful test of this conclusion as we could test whether song elements assumed to be under selection were being actively retained or discarded during crystallization. Our results demonstrate that overproduction can be a prominent component of avian song learning and we believe it should be incorporated into future research on song ontogeny and cultural evolution.

Researchers have offered multiple hypothesis to explain the adaptive value of vocal learning in animals. One hypothesis is that organisms use vocal learning to create novel sexual signals which are more attractive to prospective mates than the more stereotyped songs produced without learning (Jarvis 2006). Another hypothesis is that animals use vocal learning to optimize the acoustic structure of their calls for maximum transmission in their immediate physical environment (Jarvis 2006). Yet another hypothesis is that the costs of learning represent honest signals of fitness and therefore organisms strive to learn more physiologically challenging songs in order to demonstrate their fitness (Podos 2017). Finally, there is the hypothesis that has grown out of multiple studies on selective attrition (Peters & Nowicki 2017): that vocal learning is instrumental in allowing animals to conform to local dialects and acquire successful phenotypes culturally rather than genetically (Marler 1982, Nelson et al. 1992, 2000). We used the phenomenon of selective attrition to explore this question, as this phenomenon offers a unique opportunity to see what aspects of their acoustic phenotype individuals retain. Our research demonstrates that vocal learning in Savannah Sparrows is a selective process where males retain songs that match the acoustic phenotype of their neighbours. Our work supports the hypothesis that vocal learning in animals facilitates the adoption of local acoustic phenotypes with the added nuance that different segments in a song may exert greater influence than others in achieving this objective.

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Figures

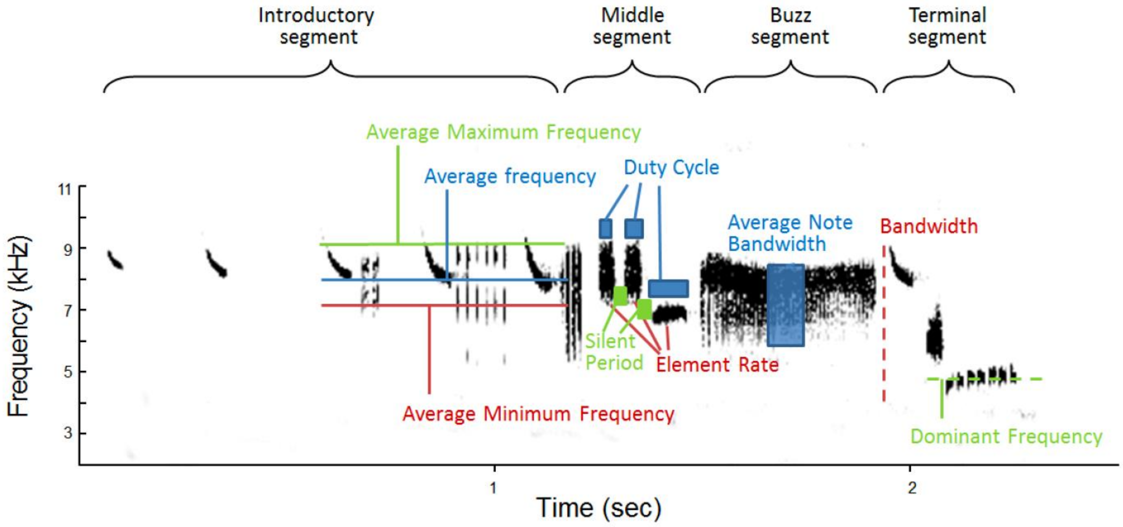

Figure 2.1. Sound spectrogram of a Savannah Sparrow song, showing the four segments of the song, and the measurements collected from each song.

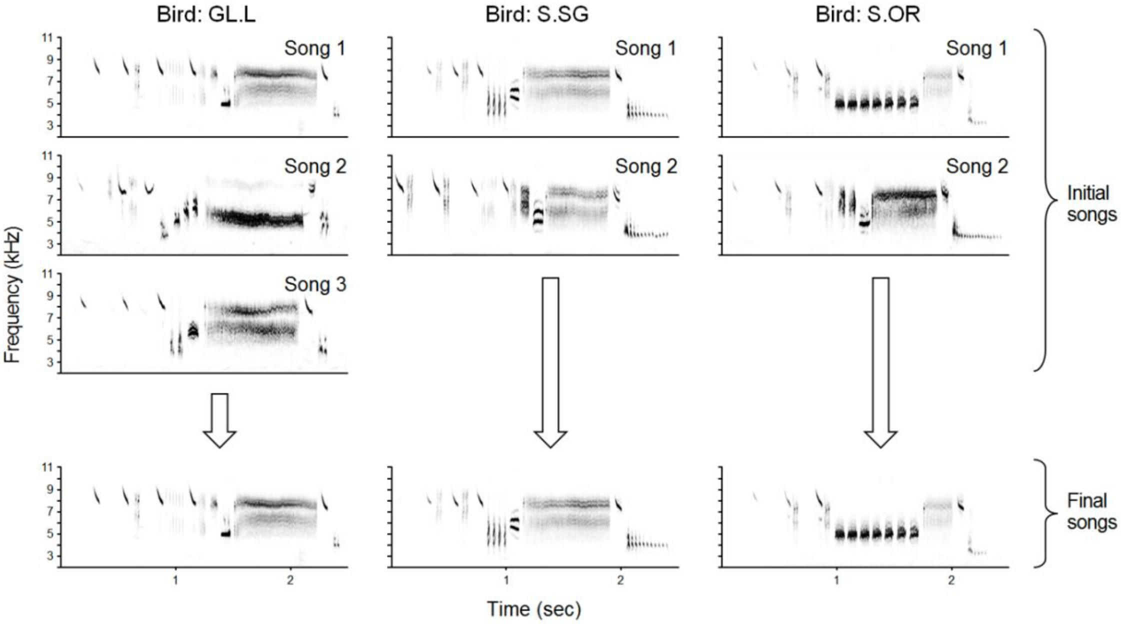

Figure 2.2. Sound spectrograms of the initial songs produced by three young males (GL.L, S.SG, S.OR; males are identified by the combination of coloured bands on their legs) during the initial weeks of their first breeding season (top) and the final songs males produced after undergoing repertoire attrition (bottom).

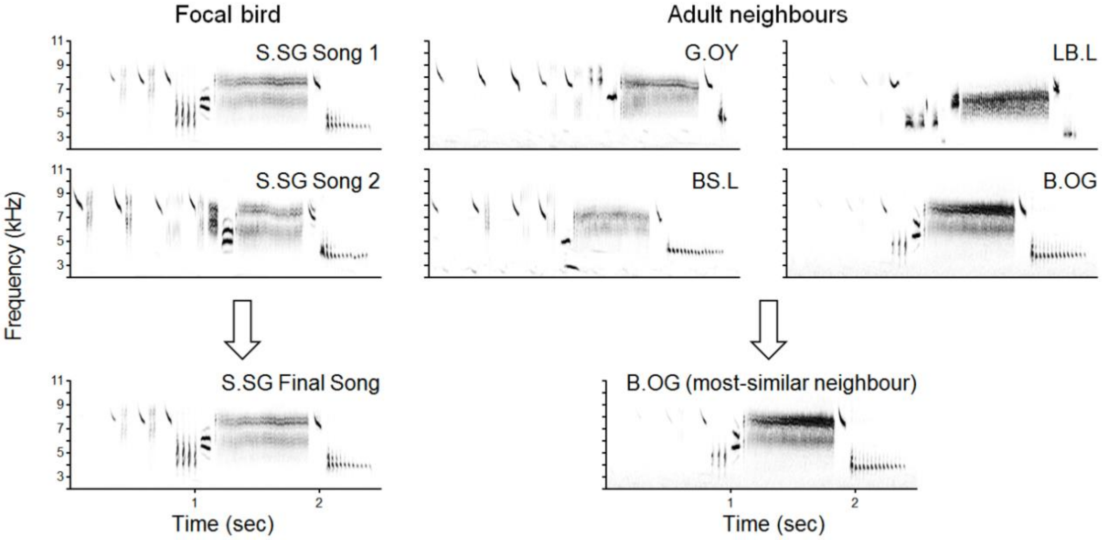

Figure 2.3. An example of the process of attrition, showing the two initial songs produced by young focal bird, S.SG (top left), and the final song that he sang after undergoing repertoire attrition (bottom left). For comparison, we show the songs from S.SG's four territorial neighbours (G.OY, LB.L, BS.L, B.OG; top right). The neighbour that was most acoustically similar was B.OG (bottom right).

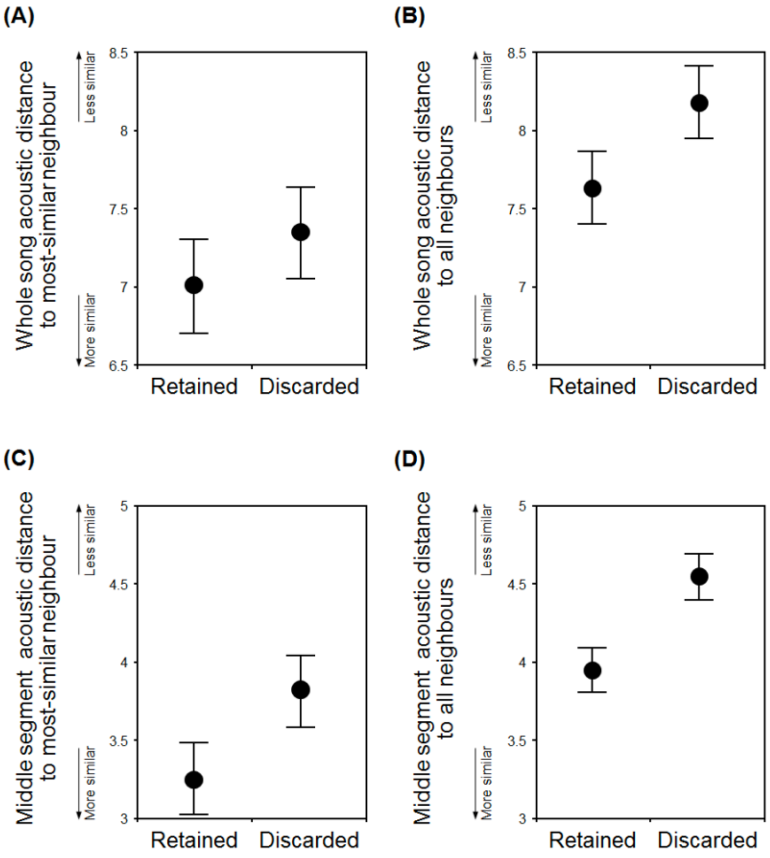

Figure 2.4. Acoustic distances of whole songs (top) and middle segments (bottom) to most similar neighbour (a and c) and mean distance to all neighbours (b and d) between discarded and retained songs in overproducing males.

Chapter 3: Avian vocal learning and intrasexual aggression: A field study of the structure of learned songs and aggressive interactions in Savannah Sparrows

Chapter summary

In eight groups of animals, young individuals learn their vocalizations by listening to adults, and those learned vocalizations come to play an important role in territory defence later in life. Vocal learning facilitates the evolution of complex forms of animal signals, and sophisticated forms of communicating aggression, particularly in the context of territoriality. Studying a population of Savannah Sparrows (*Passerculus sandwichensis*), we tested how differences in the structure of learned songs influence aggression between territorial males. We measured the acoustic characteristics of the songs of all males in an island-living population of sparrows in eastern Canada, and we used these measurements to calculate how closely the songs of first-year males resemble the songs of their older territorial neighbours. We then measured the intensity of territorial aggression faced by these young males by collecting day-long recordings during the period of territory establishment, quantifying the number of aggressive calls as a measure of conflict within the territory. We found that males whose songs were acoustically dissimilar to their neighbours' songs experienced higher levels of aggressive calls on their territories. From this we infer that birds which learn songs dissimilar to their neighbours face elevated levels of territorial aggression. Therefore, vocal learning has adaptive value in that it allows males to adapt to local vocal culture, thereby minimizing the frequency of hostile interactions with rivals. Our results provide support for the theory that vocal learning in songbirds is a mechanism that facilitates territorial defense.

Introduction

Vocal learning, the capacity of animals to imitate sounds they hear, is a rare adaptation reported in only eight animal lineages (Fitch et al. 2008, Jarvis et al. 2017, Stoeger and Manger 2014). The adaptive value of this behaviour is contentious (Nowicki & Peters 2017); why should learned vocalizations provide more benefits than genetically-inherited vocalizations. Animals use learned vocalisation to facilitate long distance communication (Stoeger and Manger 2014), social cohesion (Janik 2014), conflict reduction (Knörnschild et al. 2012), courtship (Catchpole and Slater 2008, Janik 2014) and inbreeding avoidance (Filatova et al. 2013). Vocal learning provides animals with the plasticity to adapt to the specific environmental or social conditions, allowing young individuals to produce an acoustic phenotype that is influenced by their social environment rather than their genetic lineage. Through vocal learning, individuals can acquire the phenotype of successful individuals without needing to be descended from them (Janik 2014, Knörnschild et al. 2012).

The potential adaptive benefit of vocal learning depends on different variants of the learned vocalizations having different fitness outcomes, but those benefits and costs are difficult to quantify and test. Songbirds are an enormously diverse sub-order of birds (Jetz et al. 2012) and their vocal learning behaviour has been intensively studied for over half a century (Catchpole and Slater 2008). Vocal learning has been demonstrated to be costly in birds, with proper phenotypic expression being vulnerable to physiological stress (Searcy et al. 2008, Schmidt et al. 2013) and the potential cost of failure to learn from species-typical models (Marler 1970). The adaptive benefit that presumably offsets those costs remains poorly understood (Beecher 2017).

Bird song is a complex phenomenon that operates simultaneously as an antagonistic signal of territorial defence and as a courtship mechanism (both an attractant and repellant depending on the sex of the receiver); this is known as the Dual Function Model of birdsong (Catchpole and Slater 2008). The dual function of bird song is clearly demonstrated in birds that sing multiple song types, such as in wood-warblers (family Parulidae) where there is a consistent separation between song-types that play a role in territory defence versus mate attraction (Spector 1991). Bird species that do not demonstrate such a clear separation between song types it is presumed that a single acoustic phenotype is used for both purposes, and that the information contained within is simultaneously relevant to rival males and prospective mates; this has been revealed to be true for the songs of chickadees (*Poecile atricapillus*)) and tits (*Parus major*) (Mennill et al. 2002, 2003, Otter et al. 1999).

Acoustic similarity with territorial neighbours has been demonstrated to influence song learning (Marler 1982, Nelson et al. 1992), suggesting that similarity to neighbours increases a song's effectiveness in either mate attraction or territorial defense. Previous investigations have revealed that male songbirds that produce songs which match local dialects can benefit from fewer costly territorial interactions with rivals (Beecher 1996). Male Song Sparrows (*Melospiza melodia*), for example, use locally shared song types to avoid the escalation of territorial conflict (Beecher et al. 1997). Many studies have suggested that songs which are acoustically dissimilar provoke a higher aggressive response than those of a local dialect (Akçay et al. 2010, Draganoiu et al. 2014, Briefer et al. 2008, Moser-Purdy et al. 2016, Williams et al. 2019). To our knowledge all previous studies on this topic have used playback experiments to gauge how birds respond to local versus foreign songs. It is assumed that heightened aggressive responses to playback of acoustically dissimilar songs is consistent with the idea that vocal learning allows animals to conform to local phenotypes and thereby benefit from the advantage of lessened territorial aggression.

To better understand the value of learned songs in territorial male-male aggression, we studied Savannah Sparrows (*Passerculus sandwichensis*), a species where each adult male produces only a single song type (Wheelwright et al. 2008). The simplicity of their repertoires makes Savannah Sparrows an interesting study species in which to examine how a single learned vocalization can be used to communicate information to territorial rivals and potential mates (Wheelwright et al. 2008; Mennill et al. 2018). Male Savannah Sparrows arrive on their breeding grounds in spring, and exhibit high song output during territorial interactions between rival males (Moran et al. 2019). Males arrive from migration several weeks before females (Woodworth et al. 2016), and for first-year males, each male settles upon the acoustic phenotype that he will express for the rest of his life during those first weeks of territorial interaction (Wheelwright et al. 2008; Chapter 2). Given that females are absent when young males crystallize their songs in the early weeks of their first breeding season, we recognize that intrasexual behaviour plays an especially important role in song learning for Savannah Sparrows.

Based on the widespread pattern that birds preferentially crystallize local song-types (Nelson et al. 1992, 2000), and the playback investigations that show foreign song types provoke heightened aggression during territorial interactions (Akçay et al. 2010, Draganoiu et al. 2014, Briefer et al. 2008, Williams et al. 2019), we examine the relationship between territorial aggression and the acoustic similarly between young males and their older neighbours. Our hypothesis is that acoustic similarity influences territorial aggression, where young males with songs that are dissimilar to their neighbours face higher levels of intrasexual aggression. This relationship may shape the widespread pattern of young birds adopting local dialects (Marler 1982, Nelson et al. 1992, 2000). We predicted that young male Savannah Sparrows with songs that are dissimilar from their older neighbours would experience a higher level of territorial aggression than young males whose songs are similar to their neighbours. We expected this trend would be evident in the number of aggressive calls exchanged between each young male and his neighbours, with a negative correlation between the distinctiveness of a young male's song and the number of aggressive calls recorded within his territory boundaries in early spring.

Methods

General field methods

We conducted our research at the Bowdoin Scientific Station on Kent Island, New Brunswick, Canada (44°35'N 66°46'W). As part of a long-term investigation of the population of Savannah Sparrows on this island, in June of each year we captured all adults in mist-nets and gave them a unique combination of colour-bands (Woodworth et al. 2016). In September, prior to migration, we captured young-of-the-year in mist nets and gave them unique combinations of colour-bands. Each spring we identified the age of all returning birds based on their colour band combinations. Due to the high territorial fidelity demonstrated by adult birds in this population, we assumed that unbanded birds arriving on the study site in spring were first-year birds (Wheelwright et al. 2008); we confirmed this assumption by assessing the plumage and molt characteristic of young birds when they were captured for banding and blood sampling. We differentiated between males and females based on the production of song, and we confirmed the sex of captured birds based on the presence of either cloacal protuberance or brood patch. Sex identification was facilitated by the earlier arrival of males on the study site (Woodworth et al. 2016); during late April and early May, the population was exclusively made up of males. We observed the behaviour of each male upon arrival from migration to determine the extent of his territory. The study site is laid out in a grid of 50×50m squares, and we created detailed territory maps each day based on our observations of birds' song posts and movement patterns, plotting each male's position within a grid square and with reference to local landmarks, including vegetation features.

We collected focal recordings of males when they arrived from migration, and continued recording them throughout the breeding season. In all four years of the study, we collected in-person focal recordings using hand-held digital recorders (Marantz PMD661 digital recorder and a Sennheiser ME62/K6 microphone mounted in a

Telinga parabola; 44.1 kHz sampling frequency; 16-bit accuracy; WAV format). Daily, we collected focal recordings of all singing males in the first four hours of the morning, starting with the arrival of males (mid-April to mid-May) until the onset of nesting at the end of May. Using these focal recordings, we compiled a complete song library of all males on the study site, providing a comprehensive record of all acoustic phenotypes expressed in the population.

In addition to the focal recordings collected in all four years of this study, in 2018 we collected exhaustive sampling of the voices of young males using autonomous digital recorders (Wildlife Acoustics Song Meter SM2; 44.1 kHz sampling frequency; 16-bit accuracy; WAC format; see Mennill et al. 2012). We placed autonomous recorders at the centre of each focal male's territory, close to the preferred singing perches we had observed during focal recording sessions. We placed autonomous recorders near each male from his arrival (mid-April to mid-May) until the onset of nesting at the end of the May. In some cases, male territory location changed subtly from day to day, usually in response to the arrival of other males on the island; we documented these changes during our focal-recording sessions, and moved the automated recorders as necessary, to ensure that the automated recorders remained near the centre of the territory of the target male. Given the small territory size of Savannah Sparrows (average: 0.21 ha on our study site; Wheelwright and Rising 2008), and the broad recording range of our autonomous recorders (we could detect recordings of the songs of males with territories up to 100m away from the recorder, although males that were closer to the focal animal were much more easy to detect), we are confident that these recordings were useful for sampling all vocalizations from the target animals.

Acoustic distance measurements

We measured the fine structural features of recorded songs using AviSoft sound analysis software (R. Sprecht, Berlin, Germany). We employed the automated parameter measurements feature of AviSoft to minimize any human subjectivity in quantifying differences between songs. We used a frequency threshold of -20 Hz relative to the maximum of each selection when collecting automated measurements. We categorized our measurements based on four segments of Savannah Sparrow song: the introduction segment, the middle segment, the buzz segment, and the terminal segment (terminology from Williams et al. 2013). For each of the four song segments we measured six features: the element rate, average pause length, average maximum frequency, average minimum frequency, average dominant frequency, and average note bandwidth (see Chapter 2, Figure 2.1). We also measured the three pause lengths between the four song segments, the length and number of notes in the middle segment and buzz segment, as well as the duty cycle of the middle segment. We did not measure song length and number of notes in the introduction and terminal segments because of the high variability in segment length within a given male’s expression of his song type (personal observation). We did not measure duty cycle for the buzz because it typically consists of a single note.

Based on these 32 spectro-temporal measurements, we plotted all songs in multi-dimensional space, and calculated the squared Euclidean distances between pairs of songs. This gave us a technique for assessing numerically the acoustic similarity between the songs of two different males. We refer to this measurement we as acoustic distance (as in Gordhino et al. 2015, Koetz et al. 2007, and Sung 2005) and we note that two songs with a low acoustic distance score are very similar, whereas two songs with a high acoustic distance score are very different (Fig. 3.1). To calculate acoustic distance measurements we used the clustering platform within JMP (v. 14; SAS Institute, Cary, NC), selecting the calculation method of hierarchical cluster analysis using the centroid (squared Euclidean distances). This technique produces Euclidean distance measurements that are standardized, regardless of the units of the original measurements, by subtracting the column mean from each value and then dividing this number by the standard deviation of the column. From within the clustering platform in JMP, we selected the option to save the distance matrix which created a table outlining the squared Euclidean distances between all measured individual songs. Note: we did not conduct clustering analyses with this output, we merely used the platform only to produce pair-wise Euclidean distance measurements. We previously ground-truthed this analytical approach of acoustic distance measurements (see Chapter 2). We compared these songs using their mean acoustic distance to each male’s territorial neighbours. Neighbours were defined as birds with established pre-existing territories in their second breeding year or older that had territorial boundaries less than 25 metres from the focal male’s territory.

Classification of aggressive calls

In addition to their musical song, Savannah Sparrows have multiple types of call that have been documented to be associated with agonistic encounters (Goibels 1967, Wheelwright and Rising 2008). We selected two call types that have a distinct acoustic structure readily identifiable on sound spectrograms. (1) The buzz call (Fig. 3.1) is a wide bandwidth note with a longer duration at high frequency, that has been variously identified as the aggressor note (Goibels 1967), and the subordination call (Wheelwright and Rising 2008); note: the buzz segment of the Savannah Sparrow song has nothing to do with the buzz call, but we use this nomenclature to remain consistent with previous studies. The buzz call has been identified as the definitive call note of aggressive interactions in Savannah Sparrows (Goibels 1967), and our field observations suggest that this call is commonplace during aggressive interactions in spring. (2) The decrescendo call (Fig. 3.1) is a descending string of notes (Fig. 3.1) that frequently accompanies the agonistic wing waving display of Savannah Sparrows (Goibels 1967, Wheelwright and Rising 2008, Moran et al. 2018); this call is identified elsewhere as the aggressive flight call (Moran et al. 2018, Wheelwright and Rising 2008) but we label it the decrescendo call to avoid tautology. Our field observations suggest that decrescendo calls occur often during territorial interactions, although they are not as common as buzz calls. To calculate a single measure of aggressive calls, we used a sum of the number of buzz calls and the number of decrescendo calls.

Using Syrinx-PC sound analysis software (J. Burt, Seattle WA) we examined the autonomous recording for each focal male and counted every occurrence of these aggressive call types within a defined time period (see below). We adjusted spectral gain to be as high as possible to allow us to view even quiet notes in the recording, adjusting the gain as needed when ambient noise fluctuated. The quantification of aggressive calls was made blindly relative to the identity of the territorial male, so that subjective bias could not give rise to spurious relationship.

Two periods of aggression measurements

We selected two time periods in the life of each young male in which to quantify the occurrence of aggressive calls, sampling aggressive interactions over a two-day interval for each period. (1) We sampled birds 10 days after a male arrived on the study site from spring migration. These recordings capture the behaviour of each male once he had just established a territory and settled on his final song type. Given that male arrival on the study island can range from mid-April to mid-May, these recordings fell at different times over this period (range: May 2 to May 21). Hereafter we refer to these recordings as the 10-days-after-arrival period. (2) To sample aggression at a time that was roughly simultaneous for all birds in the population, we examined automated recordings for every focal bird for two days between May 18 and May 22 (two-day periods with perfect overlap was not possible because some recorders had batteries changed during time period, and this window allowed an uninterrupted two-day period for each male as simultaneously as possible). These recordings allowed us to capture a synchronous catalogue of all aggressive interactions taking place on the study site at once, independent of of male arrival date. These records capture the behaviour of all males once female birds had arrived on the study site (Woodworth et al. 2016), and the population was going through courtship, mating, and the initiation of nesting. Hereafter we refer to these recordings as the late May period. In both the 10-days-after-arrival period and the late-May period, aggressive calls were counted over two consecutive days from 06:00-20:00 (i.e. the 10-days-after-arrival counts included counts over both the 10th and the 11th day after arrival).

In 2019, birds exhibited unusual behaviour in the early spring (i.e. during the 10-days-after-arrival period), which led us to exclude that recording period from our analyses, a decision we made before analyzing our field data. Although dates of arrival from migration were consistent in 2018 and 2019, there was a huge reduction in song output and territorial fidelity in late April and early May of 2019. This behaviour was unusual, and inconsistent with behaviour we have observed in this population during late-April and early May between 2014 and 2018. Given that our placement of autonomous recorders was based on our confidence in correctly identifying territorial boundaries, we did not feel confident that the birds had established a territory 10 days after arrival in 2019. To confirm our suspicion that bird behaviour was unusual in early May of 2019, we compared song output of males 10-days-after-arrival in 2018 and 2019, for all males recorded between May 1 and May 15. We found that total song output was greatly reduced in 2019 (220.3±27.9 songs per hour per male for n=10 males in 2018; 62.8±36.0 songs per hour per male for n=6 males in 2019; Mann Whitney U test: U=2.7, p<0.008, n=14), further justifying the exclusion of the 10-day-after-arrival assessment of aggression for 2019.

Analysis

We compared each male's acoustic distance score to his territorial neighbours versus the number of aggressive calls (the sum of all buzz calls and decrescendo calls expressed over a two day period) recorded on his territory for n=15 males from 2018 that were recorded 10-days after arrival, and with n=23 males from 2019 and 2019 that were recorded in late May. Based on previous research (Williams et al. 2013), and findings of a parallel investigation (Chapter 2), we recognized that the middle segment of Savannah Sparrow song is particularly variable between individuals, whereas the introductory segment is highly variable between successive songs from an individual, and the buzz segment and terminal segment are highly stereotyped across the population. Therefore, we repeated our comparison of acoustic similarity scores both for the entire song as well as for the middle segment. Counts of aggressive calls were log transformed to achieve normality.

We checked our data for outliers, which we defined as values that were more than three standard deviations beyond the mean, and found one bird in our dataset with an unusually low number of aggressive calls detected on his territory. This bird's territory sat at the edge of our study site, and had a unusually elongated shape around two buildings of the Bowdoin Scientific Station; this may have affected our ability to record his entire territory with the autonomous recorder. We excluded this bird from our analyses, given that the data associated with this bird was unusually low, most likely explained by the bird's calls not being adequately sampled by the recorder.

Results

We found a relationship between acoustic similarity between the songs of young male Savannah Sparrows and their older territorial neighbours versus the number of aggressive calls recorded on their territories; the more dissimilar a bird’s song to his neighbours, the greater the aggression he experienced. We found a positive relationship between similarity and aggression 10 days after a young male’s arrival from migration. We found that the number of aggressive calls tended to increase with the mean acoustic distance of entire songs (Fig 3.2a; r=0.41, p=0.13, n=15). When we focused on the middle segment of the song, a component of Savannah Sparrow song we identified as important in selective attrition (Chapter 2), we found that number aggressive calls increases with mean acoustic distance of the entire song (Fig 3.2c; r=0.55, p=0.03, n=15). We also found this positive tendency between similarity and aggression in late May, at a similar time of year for all of the recorded animals, further into the breeding season. We again found that the number of aggressive increased with the mean acoustic distance of entire songs (Fig 3.2b; r=0.41, p=0.06, n=21). When we focused on the middle segment of the song, we again found the same pattern (Fig 3.2d; r=0.36, p=0.10, n=21).

Discussion

Our results provide support for the hypothesis that acoustic similarity to neighbours influences an individual's exposure to territorial aggression. Previous research has found that the acoustic structure of the middle segment of the Savannah Sparrow's song is important in communicating individual identity (Williams et al. 2019), and a concurrent investigation to this one found that the middle segment is important during the process of song learning (Chapter 2). We conclude that the acoustic similarity between both the entire song and the middle segment of young male Savannah Sparrows' songs and songs of their neighbours, are associated with aggressive interactions.

The adaptive value of vocal learning in songbirds has been challenging to identify and define. The impetus to adapt to local dialects has been documented in many studies of different species of songbirds (Marler 1982, Nelson et al. 1992, 2000) and suggests that the capacity of an individual to match their acoustic phenotype to that of their neighbours represents an important facet of vocal learning. Researchers have suggested that adopting local dialects could be advantageous in both sexual selection (Nelson et al. 2013) and territorial defense (Beecher et al. 1996, Sung et al. 2005). Multiple experimental studies using playback have suggested that foreign songs elicit more aggressive response than local ones (Akçay et al. 2010, Draganoiu et al. 2014, Briefer et al. 2008, Williams et al. 2019). These results suggest that an individual expressing a local song will face less territorial aggression and be better able to hold their territory than an individual with a foreign song. Our results offer some further support to these findings, particularly for the middle section of Savannah Sparrow song. To our knowledge this is the first study to document this phenomenon outside of the context of playback simulation, capturing instead the actual interactions of individuals in the course of their normal territorial activities.

Our results suggest that not only do foreign songs illicit an aggressive response but that individuals who express them encounter higher rates of aggression on their territories. The role played by the middle segment in predicting aggression reinforces the findings of previous studies that the middle segment of this species song plays an important role in communication (Williams et al. 2013; Chapter 2). Taken together, the middle segment appears to play a role in song selection during song learning (Chapter 2) and exposure to aggression (current study). The heightened aggression faced by males with songs that are dissimilar from their neighbours may be the mechanism that drives selective attrition, because birds may discard songs that expose them to increased conflict. These conflicts should be expected to incur the well-documented costs associated with territorial challenges (Burgess et al. 2013, Ros et al. 2006, Smith and Taylor 1993), and thereby shape song development.

These results shed light on the evolution of song repertoires in songbirds. Under the widely accepted dual purpose model of birdsong, where song learning is believed to facilitate territorial defense and mate attraction (Catchpole and Slater 2008), it is intriguing that birds would evolve a single signal capable of satisfying both disparate purposes. The correspondence between the similarity of the middle segment of the song and aggressive interactions suggests that the acoustic phenotype of a single song might have components that serve different functions, with some parts (in this case, the middle segment of the song) being involved in territorial interaction, whereas other parts serving a role in courtship. Indeed, a very recent investigation suggests that the trilled section of Savannah Sparrow song appears to play a role in mate choice, whereas the middle section does not (Hacheol & Handford 2019). Our research suggests that studies of birdsong, and especially ones that attempt to identify their social function, would do well to consider the song not just as a coherent whole but as a collection of different components that may fulfil distinct functions at distinct times of year.

Conclusion

Our research reveals that first year Savannah Sparrows face increased aggression if their songs differ from their established neighbours. We found that the similarity of the entire song and the middle segment of Savannah Sparrow song shows a relationship with the number of aggressive calls. Our research is among the first to document how different song structures can influence the territorial interactions of birds over an extended period of time. We inferred that aggressive interactions carry fitness costs for territorial sparrows. Further research could quantify these costs by examining whether individuals who have distinct songs incur physiological or reproductive costs. We have identified the middle segment of the Savannah Sparrow song as being associated with territorial aggression, there are three other distinct components that presumably are also serving important signalling roles, testing their importance would help more fully understand the phenomenon of vocal learning. Lastly we have examined how vocal learning is relevant to intrasexual conflict. The other key tenet of the dual purpose model is that birdsong is a sexual signal. It is important to understand if the acoustic distance is also important in courtship, or if other acoustic qualities are preferred by females, which could result in disruptive selection.

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Figures

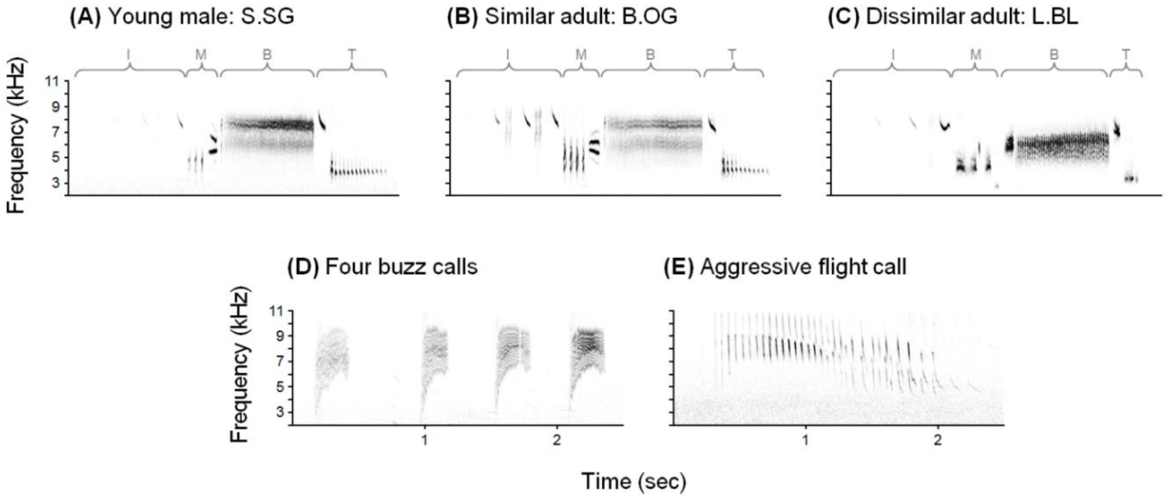
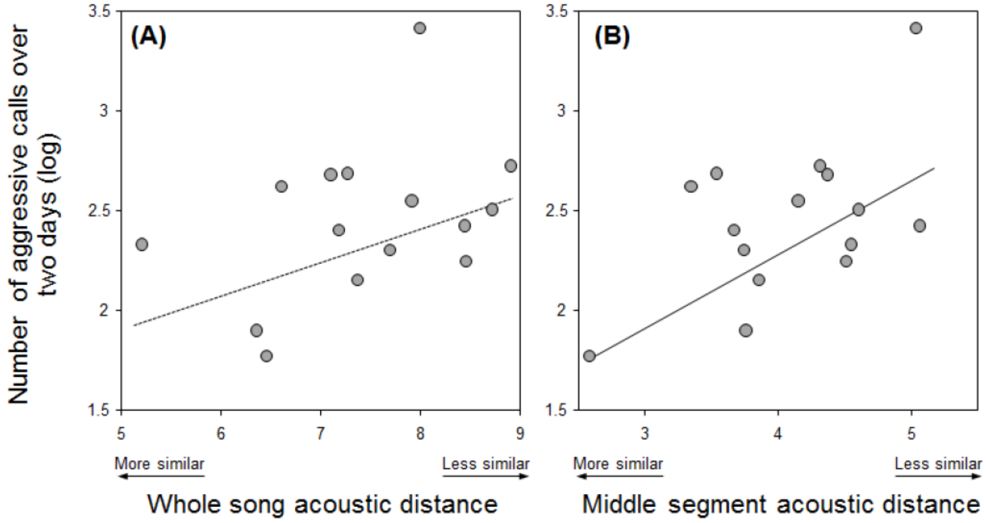


Figure 3.1: Sound spectrograms of the songs and aggressive calls studied in this investigation. Top: Songs from three Savannah Sparrows: (A) Song from first-year male S.SG (birds named for colour bands on their legs). (B) An acoustically similar song from neighbour B.OG. (C) An acoustically dissimilar song from a bird elsewhere in the population (L.BL). For all three songs, brackets indicate the Introductory segment (I), the middle segment (M), the buzz segment (B), and the terminal segment (T). Bottom: Aggressive calls of Savannah Sparrows: (D) Four buzz calls. (E) One decrescendo call.

10-days-after-arrival period



Late-May period

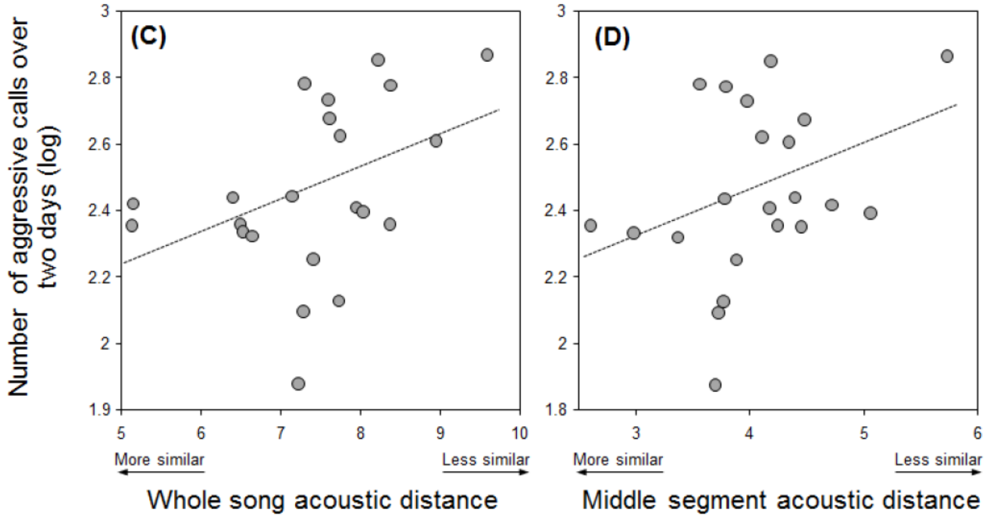


Figure 3.2. The relationship between the acoustic distance of Savannah Sparrow songs in comparison with their neighbours and the number of aggressive calls recorded on their territories over a two-day period, for both 10 days after the birds arrived from migration (top) and late May of the same year (bottom). We compared acoustic similarity for both whole songs (left) as well as the middle segment of songs (right). Lines of best fit are shown for all four scatterplots, with a solid line for relationships with a significance threshold of $p<0.05$ and a dashed line for a significance threshold of $p<0.10$.

Chapter 4: General Discussion

Summary

Over the course of these two data chapters I have attempted to shed light on the adaptive value of vocal learning in birds. I felt this question was best answered by examining the criteria that individual birds use in determining what acoustic phenotype to adopt and then once they exhibited their definitive signal, what were the downstream effects. I chose Savannah Sparrows (*Passerculus sandwichensis*) as my model species due to their relatively simple song, their well-studied vocal culture (Wheelwright et al. 2008), and the long-term dataset available for the Kent Island Savannah Sparrow study population (Wheelwright et al. 2008, Williams 2013).

In my first data chapter (Chapter 2) I explored the phenomenon of overproduction and attrition in Savannah Sparrows. I documented the extent of song overproduction in male Savannah Sparrows in their first breeding year. I observed over 50% of the population demonstrating overproduction. These results confirmed that overproduction is a common behaviour in Savannah Sparrow song ontogeny and that many individuals continue to exhibit vocal plasticity at the beginning of their first breeding season. The focus of my research was identifying whether attrition was selective, with some acoustic features being routinely selected for, or random in which there was no pattern reflecting which songs were retained or discarded. Based on existing research from related species that suggested birds preferentially retain songs that are structurally similar to local song-types (Marler and Peters 1982, Nelson et al. 1992, Nelson et al. 2000), I predicted that if attrition were selective, individuals would retain songs most similar to those of their territorial neighbours. My results supported this hypothesis; discarded songs had a lower acoustic similarity to both their most-similar territorial neighbour and to the entire neighbourhood overall. This pattern was particularly true for the middle segments of the song, which is the most variable component of Savannah Sparrow song. Taken together, these results demonstrated that conforming to local dialects drives song selection in Savannah Sparrows, and that the use of overproduction and selective attrition is the mechanism that facilitates this.

In my second data chapter (Chapter 3) I examined if a young male Savannah Sparrow's song similarity to his neighbours influences his exposure to territorial aggression. If selective attrition is a mechanism for birds to express songs that are similar to their neighbours, then individuals may incur a cost if they are less successful in achieving that similarity. There is widespread evidence from playback experiments that birds who sing local songs face less aggression than birds who sing foreign song type (Akçay et al. 2010, Briefer et al. 2008, Williams et al. 2019). I wanted to further explore this hypothesis by testing if individuals who sang foreign songs experienced more territorial aggression than males whose songs were similar to their neighbours. I found that acoustic similarity of the entire song and the middle segment was inversely related to the number of aggressive call notes for individuals both ten days after arrival and later on in the breeding season. My interpretation of these results is that young birds whose songs are more distinct from those of their older neighbours will face more territorial aggressionin the breeding season. This compliments my finding in chapter 2 that the acoustic distant to older neighbours of the entire song and the middle segment of the song are relevant to young males as they select which song to retain. I hypothesize then that this selective attrition is driven by aggressive interactions with older males.

Future directions for chapter 2

My findings on the importance of acoustic similarity to neighbours in the process of selective attrition are consistent with earlier studies of other overproducing songbird species (Marler 1982, Nelson et al. 1992, Nelson et al. 2000). I feel that my research sits comfortably with previous research on this phenomenon, but also adds new insights that invite further investigation. One interesting feature of my results is the suggestion that the acoustic distances are of varying relevance for different sections of the song. This suggests that different segments of a bird's song may be under different selection pressures and possibly serve as distinct signals (Nelson and Poesel 2007). This would make attrition a mechanism with multiple axis in which an individual would be potentially trying to incorporate a range of ideal signals into one acoustic phenotype. The introductory segment of the Savannah Sparrow song has notes (called click-trains) that appear to combine a rapid production with a high bandwidth (Williams et al. 2013), this has been suggested to be costly to produce and therefore may be an honest signal of male quality (Podos 2017). Indeed, research on Savannah Sparrow cultural evolution over multiple years has suggested that these high bandwidth click-trains may be under directional selection (Williams et al. 2013). If this is the case then we would expect individuals should select the song that includes the highest number of these costly notes that the individual can produce. My research leaves open the possibility that performance and neighbour matching mechanisms could be operating simultaneously on distinct components of the song. If this was supported in further research on this study system, it would help reconcile these two ideas.

A further refining of my research could examine if particular neighbours have a greater effect on selective attrition in young males. All older neighbours are treated as equally likely influences in my study, however different neighbours may interact more with a young bird depending on various environmental or individual factors. Gauging the level of interaction between the focal bird and each of its older neighbours might reveal that certain neighbours have an outsized effect on song ontogeny. One way to accomplish this would be to measure the number of examples of each neighbour's song near the focal bird's autonomous recorder. If one neighbour is overrepresented in a focal bird's territory, we could assume that he is interacting more with the focal bird and might have a greater influence. We then might predict that our focal bird's process of selective attrition could be less directed at the whole neighbourhood, but rather at this particularly influential neighbour.

Further research could also be done on the factors that constrain an individual's initial vocal repertoire. Previous research on this population compared the songs of young males to their fathers and territorial neighbours, and found little evidence that natal environments influence song crystallization (Wheelwright et al. 2008). Yet that study only examined each male's fully crystallized song without examining the bird's initial repertoire during the period of overproduction (indeed, the fact that Savannah

Sparrows exhibit overproduction was unknown at the time; Wheelwright et al. 2008). My dataset could be used to examine the degree to which the entire overproduced repertoire is influenced by an individual's natal acoustic environment. It would be worthwhile to examine an individual's natal territory and compare each overproduced song to the songs of all natal neighbours. We could then identify if natal territory placement constrains the song learning of Savannah Sparrows or if their overproduced repertoire represents a random sample of the entire population's repertoire.

Another area of interest are the birds that did not appear to demonstrate overproduction. My dataset and my methods could be used to examine what influences the expression of overproduction in the first place. It could be that individuals who exhibit a song that is already very similar to their neighbours may rapidly select it, discarding any other learned song types almost immediately. It might also be that natal conditions might influence a bird's capacity to overproduce. Arrival date may also be relevant, as individuals who arrive early or in less dense territories might delay crystallization until their territorial neighbourhood is more fully defined. My dataset could be used to compare numerous attributes of document overproduction with those who did not appear to express it.

Future directions for chapter 3

My results on chapter 3 open up many exciting questions regarding the adaptive value of learned song. My results suggest multiple studies on the potential costs of expressing locally distinct song types. My research suggests that males with songs that are dissimilar to their territorial neighbours may face higher rates of aggressive encounters with their neighbours. Other research could test if those males with dissimilar songs also show physiological signs of having experienced increased aggression. Based on my interpretation that young males with dissimilar songs face higher aggression, we would expect that these same males would have elevated levels of hormones such as corticosterone or testosterone during the initial 10 days of the breeding season (Deviche et al. 2016). Due to an apparent decrease in aggressive interactions, those higher stress levels might be expected to decline as the breeding season progresses. This test could further support my hypothesis that males with unusual songs are facing elevated levels of aggression, and demonstrate the way in which the ability to adopt local dialects can minimize physiological cost (Burgess et al. 2013, Smith and Taylor 1993).

My research has suggested that the process of selective attrition may be instrumental in minimizing aggression from territorial rivals. My data highlight a special importance of the middle segment of the Savannah Sparrow song in minimizing aggressive interactions. If further research is done on the selection process for other song segments, it would be valuable to also identify if those patterns of attrition and retention are also relevant for managing territorial aggression. If for instance, if the introductory segment of the song is associated with an honest signal of quality, we could use my methodology to asses if a higher performance introductory sections are also important in territorial defense.

An important avenue for future research in this area is to explore the relevance of Savannah Sparrow songs to the other half of the dual purpose hypothesis: mate attraction (Catchpole and Slater 2008). My results provide some support for the hypothesis that selective attrition allows individuals to adopt a song that influences their territory defence behaviour. However, I did not have the opportunity to explore whether these same signals are also effective in attracting females. It would be worthwhile to study the acoustic distances between the middle segments of territorial neighbours to see if this influences female choice. This might be best studied by looking at extra-pair copulations because these represent the purest expression of female preference. I feel that metrics associated with social mate choice could ultimately be a product of successful territorial defense, as males with desirable territories may be able to attract a social partner more easily. Although this would still suggest that song structure is important for mate selection, it does not adequately separate female choice from successful intrasexual defense. Because extrapair copulation is a pure genetic donation without any property or care provided, I think it serves as an unconfounded measure of attractiveness.

It is possible that the features of Savannah Sparrow song that help males manage intrasexual conflict, may not be identical to the features that help males attract mates. Different components of the song may have different target audiences, with the middle sections being directed at rival males whereas other song sections being relevant for females. The introductory segment of Savannah Sparrow song has already been identified as potentially being under performance related selection (Williams et al.

2013) and therefore we could test if the quality of the male's introductory segment was correlated with higher rates of extra-pair paternity. If males with high quality introductory segments were more successful in siring extra-pair young we would have found powerful support for the performance hypothesis and also demonstrated that multiple functions can be simultaneously expressed in one signal. If we did not find that song structure predicted reproductive success, we might find that other aspects of song production such as singing rate or song volume carried the relevant information females use to assess potential mates.

Conclusion

My research contributes to our understanding of learned song in oscines by offering further support for two hypotheses on song learning and function. I tested these hypotheses in novel ways and added additional clarity to how we understand birdsong. My research introduced a field methodology for monitoring bird behaviour and quantifying acoustic similarity that can be used to further explore the evolution and function of birdsong. I demonstrated that acoustic similarity is a driving force in selective attrition in Savannah Sparrows and that the middle segments of their songs appear to be loci for his effect. I also demonstrated that this metric of acoustic similarity is correlated with territorial aggression and therefore that individuals whose songs differ more from their neighbours experience higher rates of conflict. My thesis identifies the acoustic features that Savannah Sparrows use to inform their song development and the role of those same acoustic features in subsequent territorial defense.

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