

Vocal learning in Savannah sparrows: acoustic similarity to neighbours shapes song development and territorial aggression

Ian P. Thomas ^a, Stéphanie M. Doucet ^a, D. Ryan Norris ^b, Amy E. M. Newman ^b, Heather Williams ^c, Daniel J. Mennill ^{a,*}

^a Department of Integrative Biology, University of Windsor, Windsor, ON, Canada

^b Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

^c Biology Department, Williams College, Williamstown, MD, U.S.A.

ARTICLE INFO

Article history:

Received 25 September 2020

Initial acceptance 16 November 2020

Final acceptance 15 February 2021

MS. number: A20-00718

Keywords:

aggression
birdsong
learned song
overproduction
selective attrition
song learning
vocal learning

Vocal learning is a biologically rare adaptation that underpins both human language and the songs of songbirds. The adaptive value of vocal learning in birds is still poorly understood, but a growing body of literature suggests that vocal learning allows songbirds to gain a fitness advantage by adopting songs that are structurally similar to the songs of individuals in neighbouring breeding territories. In this study, we investigate patterns of song development, acoustic similarity, and territorial aggression in Savannah sparrows, *Passerculus sandwichensis*. Four years of field data reveal that Savannah sparrows routinely overproduce songs during development; more than half of young males sang more than one song type early in their first breeding season, before their repertoire underwent attrition to a single song that males maintained throughout the remainder of their lives. We also found that the attrition of song types is a selective process, with males retaining songs that are similar to the songs of their territorial neighbours. Males that sang songs that were more similar to their neighbours may have faced lower levels of territorial aggression, as indicated by lower numbers of aggressive calls. Our results provide support for the hypothesis that vocal learning in songbirds allows animals to produce songs that match territorial neighbours, possibly providing a benefit in terms of decreased aggression during territorial defence.

© 2021 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Social learning, defined as an animal's ability to acquire behaviours from conspecific animals through observation, fulfills a wide variety of functions. For example, social learning enables animals to build tools (Hunt & Gray, 2003), access food resources (Morales Picard et al., 2017; Sherry, 2008), identify predators (Manassa, McCormick, Dixson, Ferrari, & Chivers, 2014) and produce species-typical signals (Mates, Tarter, Ha, Clark, & McGowan, 2015). Vocal learning is a form of social learning where the development of auditory social signals involves the imitation of the sounds of others. 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, Schusterman, Reichmuth, Spasikova, & Mitchen, 2008; Jarvis, 2004; Stoeger & Manger, 2014). The complex songs of songbirds have been a major focus of vocal learning research for over half a century (Catchpole & Slater, 2008). The most widely accepted explanation for the function of complex

songs is known as the 'dual purpose hypothesis', which proposes that learned songs are used to simultaneously facilitate courtship and territorial defence (Catchpole & Slater, 2008). Extensive research has demonstrated that birdsong is highly relevant in both of those arenas, although the ways in which vocal learning provides an advantage remains cryptic (Beecher, 2017).

The ability to learn imposes costs on animals, including developmental costs (Searcy & Nowicki, 2008), physiological costs (Dunlap & Stephens, 2016), opportunity costs of lost time during the learning process (Muth, Keasar, & Dornhaus, 2015) and the potential costs of learning maladaptive behaviours (Marler, 1970). Some species of oscine songbirds manage the costs associated with learning by using a restricted period of vocal learning, where songs are only learnt within brief temporal windows early in life (Marler, 1994). For species that exhibit this closed-ended learning strategy, an individual's song usually becomes rigidly stereotyped after the learning period is complete (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 (Nelson, 1992, 2000; Nordby, Cully, Campbell,

* Corresponding author.

E-mail address: dmennill@uwindsor.ca (D. J. Mennill).

& Beecher, 2007; Peters & Nowicki, 2017). The process whereby the repertoire is pared down to the single song that will be retained into adulthood is known as 'attrition'. In some species, the process of attrition has been identified as 'selective attrition' (Nelson, 1992, 2000), whereby young birds express clear patterns in determining whether a song is retained or discarded. Research on overproduction, attrition and selective attrition has suggested that this process provides birds with the ability to closely match the songs of their territorial neighbours (Marler & Peters, 1982; Nelson, 1992, 2000). During their natal summer, when juveniles learn songs from nearby adults (Mennill et al., 2018), young birds do not know the identity of their future territorial neighbours the following spring, especially in migratory species or species that do not defend territories year-round. Therefore, young birds may benefit from learning multiple song types in their natal summer, and then choosing one particular song based on their acoustic environment in the following spring during their first breeding season (i.e. selective attrition; Bell, Trail, & Baptista, 1998; Liu & Nottebohm, 2007; Nelson & Poesel, 2009). However, we have a limited understanding about why birds overproduce songs and why particular songs are retained during the process of attrition.

Previous investigations have revealed that when songbirds produce songs that match local dialects, they benefit from fewer costly territorial interactions with rivals (Beecher, Stoddard, Campbell, & Horning, 1996). Song sparrows, *Melospiza melodia*, for example, use locally shared song types to avoid the escalation of territorial conflict (Beecher et al., 1997). Although studies comparing responses to foreign and local dialects most often report stronger aggressive responses to local dialects (Nelson, 1998; Williams et al., 2019), birds also discriminate among songs of local individuals, responding more aggressively to strangers than to neighbours (Falls, 1982; Moser-Purdy, MacDougall-Shackleton, & Mennill, 2017; Stoddard, Beecher, Horning, & Willis, 1990). The basis for this discrimination can be either familiarity with individual neighbours (Moser-Purdy & Mennill, 2016) or the presence of unfamiliar song elements in the strangers' songs (Briefer, Aubin, Lehongre, & Rybak, 2008). Many studies of this topic have used playback experiments to gauge how birds respond to neighbours' and strangers' songs. Heightened aggressive responses to playback of strangers' songs, which are often less similar to the bird's own song, are consistent with the idea that vocal learning allows animals to conform to local phenotypes and thereby benefit from the advantage of lower intensities of territorial aggression. Males whose songs conform to a local song type may also gain a fitness advantage from female choice of genetic partners (Nelson & Poesel, 2013), although our focus in this investigation is on male–male territorial aggression.

Recent research has revealed that song learning in Savannah sparrows, *Passerculus sandwichensis*, is guided by the song types that males hear in their first 3 months of life; experimental evidence shows that Savannah sparrow males preferentially learn song types that they hear during their natal summer and then hear again at the outset of their first breeding season (Mennill et al., 2018). Intriguingly, anecdotal observations by Mennill et al. (2018) suggest that overproduction and attrition occur in this species: several birds were observed to overproduce multiple song types early in their first breeding season. Overproduction might allow these birds to evaluate multiple learned song types before they select the most effective song to retain into adulthood. This strategy would provide young birds with a degree of flexibility they would not have if they crystallized their song repertoire earlier in development. Savannah sparrows might thereby limit the costs of song learning (Logue & Forstmeier, 2008; Searcy & Nowicki, 2008) to their natal year but retain some of the advantages of acoustic flexibility at the outset of their first breeding season.

In this study, we sought to document the development of song in young male Savannah sparrows and then study the implications for territorial aggression. We had two goals. First, we sought to determine whether Savannah sparrows exhibit overproduction and then undergo selective attrition in order to express similar song types to those of their territorial neighbours. We predicted that overproducing individuals would retain songs with acoustic features that most closely resembled their territorial neighbours' songs during their first breeding season. Second, we sought to determine whether Savannah sparrows singing songs similar to their neighbours' songs would experience different levels of territorial aggression. We expected that birds whose retained songs were more similar to their neighbours' songs would face lower levels of territorial aggression. Specifically, we predicted a negative correlation in a comparison of the similarity between a young male's song and those of his territorial neighbours and the number of aggressive calls recorded within his territory boundaries in early spring.

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 each a unique combination of coloured leg bands (Woodworth, Wheelwright, Newman, & Norris, 2017). In September, prior to autumn migration, we captured and banded many young-of-the-year birds in mist nets. Each spring we identified the age of returning birds based on their band combinations; when we observed unbanded birds arriving on the study site in spring, we assumed they were first-year birds due to the high territorial fidelity demonstrated by adult birds in this population (Wheelwright et al., 2008). For unbanded birds, we confirmed this assumption by assessing the plumage and moult characteristics of young birds when they were captured for banding and blood sampling. We differentiated males from females based on the production of song, and we confirmed the sex of captured birds by the presence of a cloacal protuberance or brood patch. Sex identification was further 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. Each year, we observed the behaviour of each male upon arrival from spring migration to determine the extent of his territory. The study site is laid out in a grid of 50 × 50 m 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 gridlines and vegetation features.

We collected focal audio recordings of males when they arrived from spring migration and continued recording them throughout the breeding season. In all 4 years of this study, we collected in-person focal recordings using hand-held digital recorders (Marantz PMD661 digital recorder; 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 4 h of the morning beginning with male arrival (mid-April to mid-May) and concluding with the onset of nesting (late May to early June). 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 4 years of this study, in 2018 we conducted extensive sampling of the

vocalizations of young males using autonomous digital recorders (Wildlife Acoustics Song Meter SM2; 44.1 kHz sampling frequency; 16-bit accuracy; WAC format; see Mennill, Battiston, Wilson, Foote, & Doucet, 2012). Beginning with the arrival of males and lasting until the onset of nesting, we placed autonomous recorders in the centre of each male's territory, close to the preferred singing perches we had observed during focal recording sessions. 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. Given the small territory size of Savannah sparrows (average: 0.21 ha; Wheelwright & Rising, 2008) and the broad recording range from our autonomous recorders (we could readily detect males with territories up to 100 m away from the recorder), we are confident that these recordings sampled 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, U.S.A.). We define a song type as a series of notes with distinctive spectrotemporal qualities produced in a consistent order. Each adult male Savannah sparrow produces only one song type, with high consistency across its life (Wheelwright et al., 2008), showing only small variations in the frequency and duration of certain song elements over time (Williams, Levin, Norris, Newman, & Wheelwright, 2013). Less than 2% of males produce two song types into adulthood (Mennill et al., 2018; Williams et al., 2013), but there are no such males in the current data set. For our study, we considered songs to be different song types when they contained at least one syllable with unique spectrotemporal properties that were not present in other song types produced by that individual (as in Williams et al., 2013). This meant that songs with 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's singing output, any song type recorded twice would likely have been sung 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.

For recordings collected with autonomous recorders in 2018 ($N = 17$ first-year males), we annotated all songs produced between 0600 to 0800 hours in the first 4 days after a male's arrival from migration. We used our song library of all established males on the study site to identify songs of nearby males. 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 occurred within a bout of already-documented song types from the focal bird at the same amplitude in both microphone channels (suggesting a similar location as the focal bird) and without ever overlapping with the documented songs of the focal bird. Most overproduced songs (79%) were detected during both the automated recording sessions and the in-person focal recording sessions, and the remaining overproduced songs were detected only in the automated recordings. If we did not detect any evidence of overproduction in the focal recordings or autonomous recordings, we assumed that the bird did not demonstrate overproduction.

Acoustic Distance Measurements

To assess the similarity of songs produced by different males, we collected fine structural measurements of recorded songs using AviSoft sound analysis software (R. Sprech, Berlin, Germany). We employed the automated parameter measurements feature of AviSoft to minimize human subjectivity in quantifying song features. 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 recognized segments of Savannah sparrow song: the introductory, 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: element rate, average pause length, average maximum frequency, average minimum frequency, average dominant frequency and average note bandwidth (Fig. 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

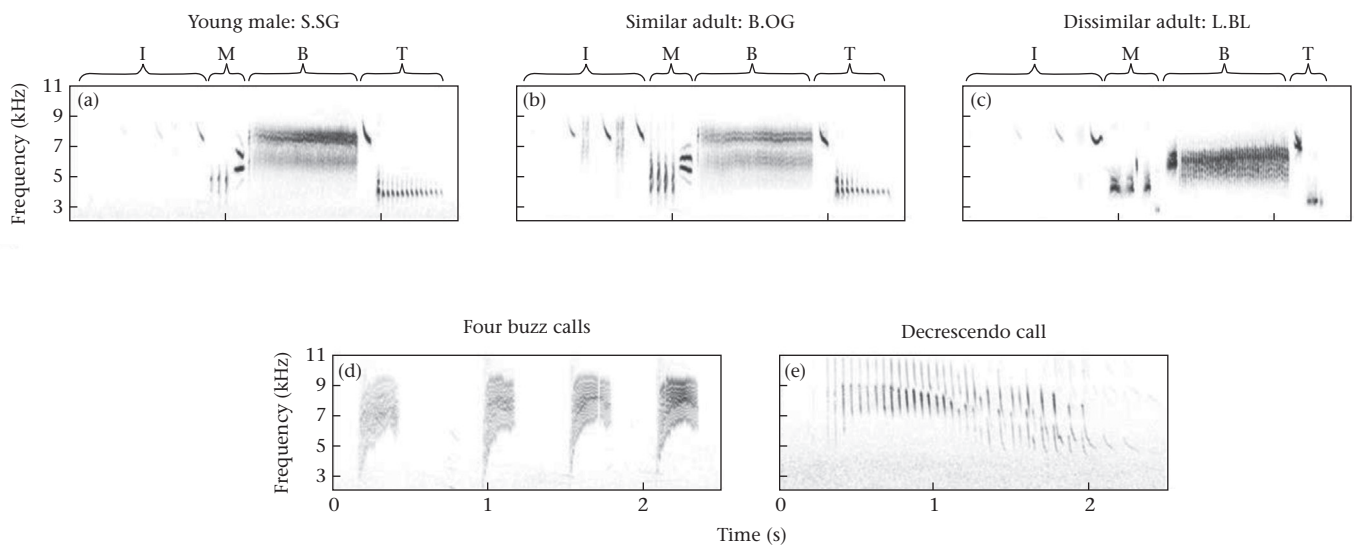


Figure 1. Sound spectrograms of three Savannah sparrow songs (top row) and two types of aggressive Savannah sparrow call (bottom row). (a) Song from first-year male S.SG (birds are named for colour bands on their legs). (b) An acoustically similar song from neighbour B.OG. (c) An acoustically dissimilar 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). (d) Four buzz calls. (e) One decrescendo call.

the duty cycle of the middle segment. We did not measure song length and number of notes for the introductory and terminal segments because of the high variability in segment length within a given male's expression of his song type (males routinely add and drop notes from the beginning of the introductory segment and the end of the terminal segment). We did not measure duty cycle for the buzz because it generally consists of a single note.

Based on 32 spectrotemporal measurements, we plotted all songs in multidimensional space and calculated the squared Euclidean distances between pairs of songs as a technique for numerical assessment of acoustic similarity. We refer to this measurement as 'acoustic distance' (as in [de Oliveira Gordinho, Matheu, Hasselquist, & Neto, 2015](#); [Koetz, Westcott, & Congdon, 2007](#); [Sung, 2005](#)); 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, U.S.A.), selecting hierarchical cluster analysis using the centroid (squared Euclidean distances) calculation method. This technique produced Euclidean distance measurements that were 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 saved the distance matrix containing 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 calculate pairwise Euclidean distance measurements.)

To ground-truth this approach for measuring acoustic similarity, we confirmed that our acoustic distance calculations produced reliable estimates of acoustic similarity by conducting several comparisons. We used 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 data set, birds had an average (\pm SE) acoustic distance measurement of 5.74 ± 0.53 from different-year recordings of their own songs versus an average acoustic distance measurement of 8.15 ± 0.53 to all other males in the population (paired t test: $t_{11} = 4.48$, $N = 12$, $P < 0.003$). From these analyses, we calculated that songs had a 30% greater mean acoustic distance to songs from other males in the population compared to their own songs from previous years. The mean distance score of 5.74 for repeated recordings of the song of the same adult male reflects variation in a male's own singing performance and the background noise across different recordings. Despite these variations, our finding that songs from the same adult male in different years had 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 population consists of many birds who have learnt very similar songs from a common group of song tutors ([Mennill et al., 2019](#); [Wheelwright et al., 2008](#); [Williams et al., 2013](#)), which helps explain why birds show high similarity to the songs of birds in the rest of the population.

Previous studies of Savannah sparrows, including the birds in our study population, reveal that the middle segment of the song is particularly variable and appears to be 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 segments of male songs to their own version in previous years and their mean middle segment similarity to the entire population. These results showed the same pattern as our comparisons of whole songs: male middle segments had a mean (\pm SE) acoustic distance measurement of 2.07 ± 0.23 from

different-year recordings of their own songs versus an average acoustic distance measurement of 4.25 ± 0.23 to all other males in the population in 2018 (paired t test: $t_{11} = 9.43$, $N = 12$, $P < 0.001$).

In a concurrent experimental study of vocal learning, we used loudspeakers to simulate vocal tutors that broadcast population-atypical songs (see [Mennill et al., 2018, 2019](#)). Seven of the 41 young males in the current study produced the experimental stimuli during the overproduction stage, four rejected experimental stimuli and retained population-typical stimuli and three retained experimental stimuli into adulthood. It is noteworthy that the loudspeakers producing looped playback were not capable of engaging in interactions with the subjects of the current study. We operated on the assumption that the playback experiment described in [Mennill et al. \(2018, 2019\)](#) did not alter the process of overproduction of males in the current study. Our recordings suggest that the increased diversity of tutors from that experiment did not increase overproduction: the percentage of birds that exhibited overproduction in 2019 (when the playback experiment described in [Mennill et al., 2018, 2019](#) was complete) was 67% ($N = 18$ birds sampled) and the percentage of birds that exhibited overproduction in 2016–2018 (when the playback experiment was ongoing) was 65% ($N = 23$ birds sampled).

Attrition Analysis

Our data set comprised 41 young (i.e. second-year) males that we recorded extensively over the 4-year study, of which 26 young males demonstrated overproduction. For 24 of the 26 overproducing males, we determined which song was retained into adulthood by recording them repeatedly after nesting had begun. Two of the 26 birds, however, vanished in the spring before we were able to identify which song was retained into adulthood (we presume these two males were depredated). For 18 of the 24 overproducing males who survived into the breeding period, we had extensive recordings during the process of attrition with multihour recordings (many hundreds of songs) collected over multiple days.

For males that overproduced and then eliminated songs, we used paired t tests to compare the acoustic similarity of their songs to those of their territorial neighbours, both for the songs that males retained versus the songs that they discarded. For males that overproduced more than two song types, we calculated an average for their discarded songs. All values are presented as means \pm SE. We compared retained versus discarded songs using their mean acoustic distance between the retained or discarded songs and each of the male's adult territorial neighbours. Neighbours were defined as birds with established territories in their second breeding year or older that had territorial boundaries abutting the focal male's territory or boundaries less than 25 m from the focal male's territory.

Classification of Aggressive Calls

In addition to their complex song, Savannah sparrows have multiple types of calls, including calls associated with agonistic encounters ([Gobeil, 1970](#); [Wheelwright & Rising, 2008](#)). We selected two call types that have a distinct acoustic structure readily identifiable on sound spectrograms: the buzz call and the decrescendo call. The buzz call ([Fig. 1](#)) is a broadband note with ascending frequency that has been variously identified as 'the aggressor note' ([Gobeil, 1970](#)) and 'the subordination call' ([Wheelwright & 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 ([Gobeil, 1970](#)), and our field observations also suggest that this call is commonplace

during aggressive interactions in spring. The decrescendo call (Fig. 1) is a string of notes that descends in pitch and decreases in amplitude; it frequently accompanies the agonistic wing waving display of Savannah sparrows (Goibeil, 1970; Moran, Doucet, Newman, Ryan Norris, & Mennill, 2018; Wheelwright & Rising, 2008). It is identified elsewhere as 'the aggressive flight call' (Moran et al., 2018; Wheelwright & Rising, 2008), but we label it 'the decrescendo call' to avoid ascribing a function to the call. 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 decrescendo calls. Although both sexes produce these two types of call, our observations in early spring suggest that the majority are produced by males. Given that our aggression scores were calculated from automated recordings, we do not know whether the aggressive calls were produced by the territorial male, his partner or his immediate neighbours, and therefore we treat our aggression score as a measure of the aggressive interactions taking place on the territory around the autonomous recorder.

Using Syrinx-PC sound analysis software (J. Burt, Seattle, WA, U.S.A.), we examined the autonomous recording for each focal male and counted every occurrence of these aggressive calls within a defined time period (see below). We adjusted spectral gain to maximize contrast and allow us to view even quiet notes in our recordings, adjusting the gain as needed when ambient noise fluctuated. To avoid subjective bias in our aggression measurements, the quantification of aggressive calls was made blind relative to the identity of the territorial male.

Two Periods of Aggression Measurements

Based on recordings from 2018 and 2019, we selected two time periods in the life of each young male during which to quantify aggressive calls, sampling aggressive interactions over a 2-day interval for each period. (1) We sampled birds beginning 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, typically, settled on his final song type (see Results). Given that male arrival on our study site can range from mid-April to mid-May, these recordings fell at different times over this period (range 2–21 May). Hereafter we refer to these recordings as the '10 days postarrival 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 2 days between 18 May and 22 May (2-day periods with perfect overlap was not possible because some recorders had batteries changed during that time period, leading to small gaps in their recording on 1 day). These records capture the behaviour of all males once female birds had arrived on the study site (Woodworth et al., 2016). Hereafter we refer to these recordings as the 'late May period'. For both the 10 days postarrival period and the late May period, we counted aggressive calls over two consecutive days from 0600 to 2000 hours (i.e. the 10 days postarrival 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 postarrival period), which led us to exclude that recording period from our analyses prior to analysing any of the field data. Although arrival dates in 2019 were similar to those in 2018, there was unusually cold weather in 2019 and, based on field recordings from the same time period during 2014–2018, we found an unusual reduction in song output and territorial fidelity in late April and early May of 2019. Given that our placement of autonomous recorders was based on correctly identifying territorial boundaries, we did not feel confident that the birds had

established territories 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 postarrival in 2018 and 2019, for all males recorded between 1 May and 15 May. We found that total song output was greatly reduced in 2019 (2018: 220 ± 28 songs per hour, $N = 10$ males; 2019: 63 ± 36 songs per hour, $N = 6$ males; Mann–Whitney U test: $U = 2.7$, $P < 0.008$).

Aggression Analysis

We counted the number of aggressive calls recorded on the territories of 15 young males from 2018 that were recorded during the 10 days postarrival period and of 23 males from 2018 and 2019 that were recorded in the late May period. Using a correlation analysis, we assessed the relationship between each male's acoustic distance score to his territorial neighbours versus the number of aggressive calls. We conducted this analysis for the average acoustic distance to all territory neighbours, and we also conducted a separate analysis for the most similar territorial neighbour. Based on previous research (Williams et al., 2013), 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. Therefore, we repeated our comparison of acoustic similarity scores both for the entire song as well as for the middle segment alone. The aggression scores were non-normal, so we analysed those data with Spearman's rank correlations.

Before running analyses, we checked all data for outliers, which we defined as values that were more than three standard deviations away from the mean; we excluded one bird in our data set 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 an unusually elongated shape around two buildings of the Bowdoin Scientific Station, which may have affected our ability to record this male's entire territory with the autonomous recorder.

Animal Welfare Note

This research was approved by the University of Windsor Animal Care Committee (AUPP 13–15). All bird banding was conducted by experienced bird banders with required permits from the Canadian Wildlife Service. We attempted to minimize stress during capture and handling by holding birds for the minimum amount of time possible.

RESULTS

Overproduction and Attrition

Of the 41 young male Savannah sparrows recorded during the prebreeding period of their first spring, 26 (63%) exhibited overproduction by singing two or more distinct song types. Of the 26 overproducers, 18 (69%) sang two distinct song types, six (23%) sang three distinct song types and two (8%) sang four distinct song types. Twenty-four of the 26 overproducers survived beyond the first weeks of the breeding season; all 24 males underwent a process of attrition, reducing their initial repertoire to a single song type (Fig. 2). After the process of attrition, all 24 males sang only one song type thereafter, including in subsequent years. In all cases, males retained the song that survived the process of attrition in their first breeding season, including males that were sampled for one, two or three subsequent breeding seasons.

Overproduction and attrition were evident only for first-year breeding males. We never found evidence of overproduction in males who were in their second breeding year or beyond ($N = 44$

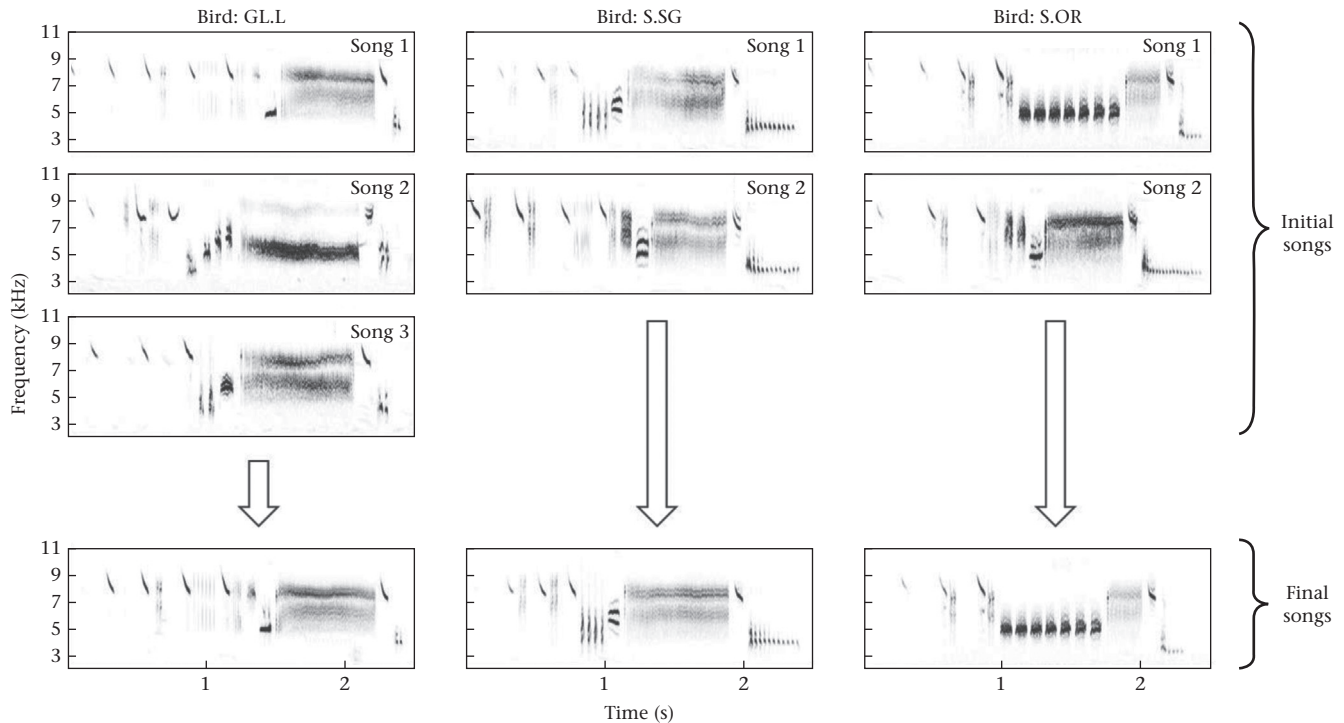


Figure 2. Sound spectrograms of the songs produced by three young males: GLL (left column), S.SG (middle column) and S.OR (right column); birds are named for the combination of coloured bands on their legs. Upper spectrograms show the initial songs recorded from the three males during the first weeks of their first breeding season. Bottom spectrograms show the final songs the three males produced after undergoing repertoire attrition.

older males that were recorded repeatedly in the early spring of 2017–2019).

There was considerable variation between individuals in the timescale of overproduction and attrition, ranging from 4 to 21 days between a male's arrival on the breeding grounds and the date of the last recording containing multiple song types (median 12 days; $N = 18$ males where we collected comprehensive recordings of overproduction). During the early part of the period of overproduction, males produced the song type they ultimately retained and the song type(s) that they ultimately discarded in similar proportions, but later in the period of overproduction, they favoured the retained song (Fig. 3). As the period of overproduction progressed, 16 males (89%) increased the frequency of production of the song they would ultimately retain. Two males, however, showed a different pattern, producing only one song type throughout the first week, then adding an alternative song that eventually became the crystallized song.

The timing of attrition completion was highly variable: the date on which males first committed to a single song ranged from 1 May to 31 May (median: 12 May; $N = 18$). Female Savannah sparrows arrive on the breeding grounds 2–3 weeks later than males (median male arrival: 26 April; median female arrival: 10 May; Woodworth et al., 2016). Some males had completed the process of attrition before the arrival of females, while other males were still overproducing when females arrived from migration. For 24 males that survived to breed, attrition was complete before egg laying in all 24 cases (and before pairing in many cases).

Selective Attrition

For each male that exhibited overproduction and attrition, we compared both the songs that males discarded and the songs they retained to the songs of their neighbours. Retained songs had a smaller mean acoustic distance to all neighbours' songs than did

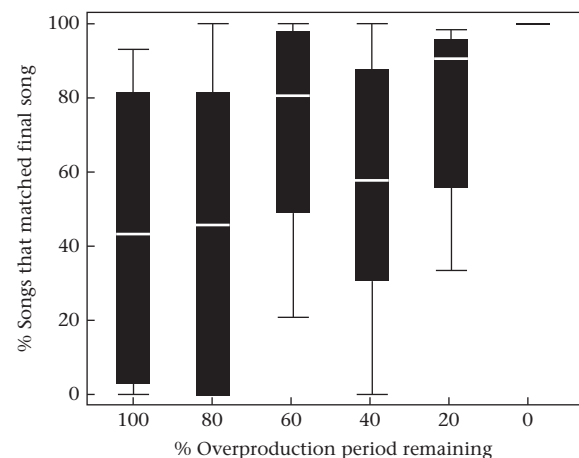


Figure 3. During the period of overproduction in early spring, male Savannah sparrows sang both their final crystallized songs as well as one or more additional songs that they discarded and never sang again after crystallization. The time period between arrival on the breeding grounds and the end of the period of overproduction is shown on the X axis, expressed as a percentage of the period of overproduction remaining until crystallization (the length of this period varied between males). Data are from repeated recordings of 18 males for which we had extensive recordings; 10 males sang two song types, 7 males sang three song types and 1 male sang four song types during the overproduction stage.

discarded songs (paired t test: $t_{23} = 2.3$, $N = 24$, $P = 0.03$; Fig. 4). Retained and discarded songs did not show clear differences in acoustic distance to the most-similar songs from neighbouring males (paired t test: $t_{23} = 1.2$, $N = 24$, $P = 0.25$; Fig. 4). In other words, males retained songs that sounded similar, on average, to that of all of their neighbours, but did not usually retain songs that were more similar to the most-similar songs from neighbouring males (Fig. 5).

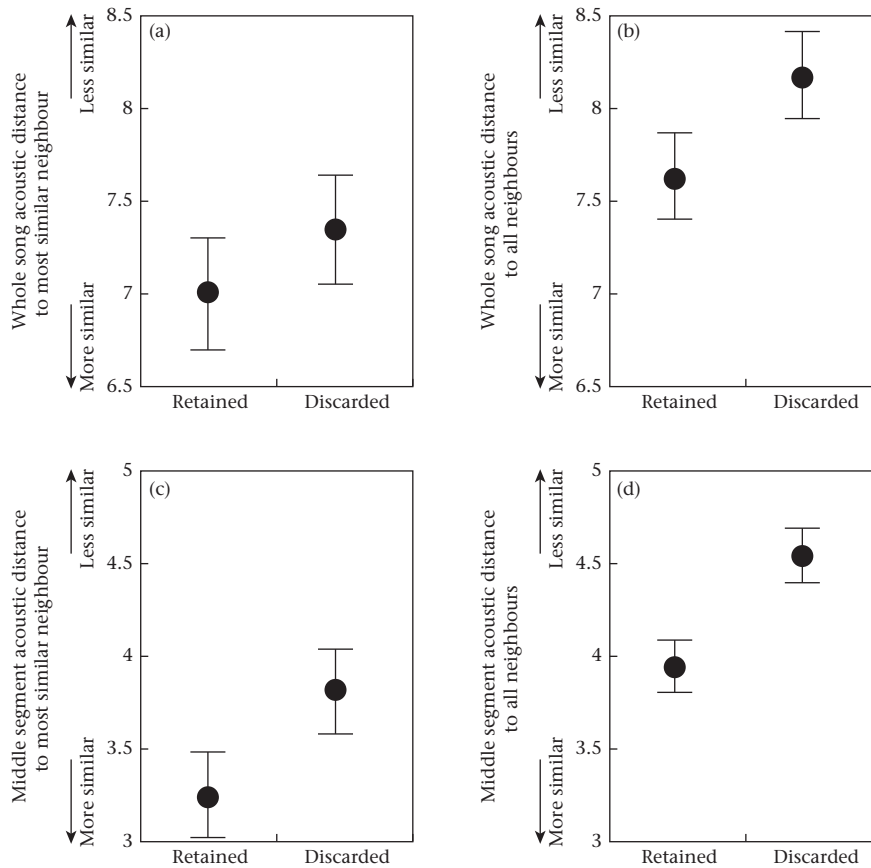


Figure 4. Acoustic distances of whole songs and middle segments, respectively, to the most similar neighbour (a, c) and to the mean distance to all neighbours (b, d) between discarded and retained songs recorded from overproducing young Savannah sparrows. Data show means and standard errors. Males retained songs that were more similar to the songs of their neighbours.

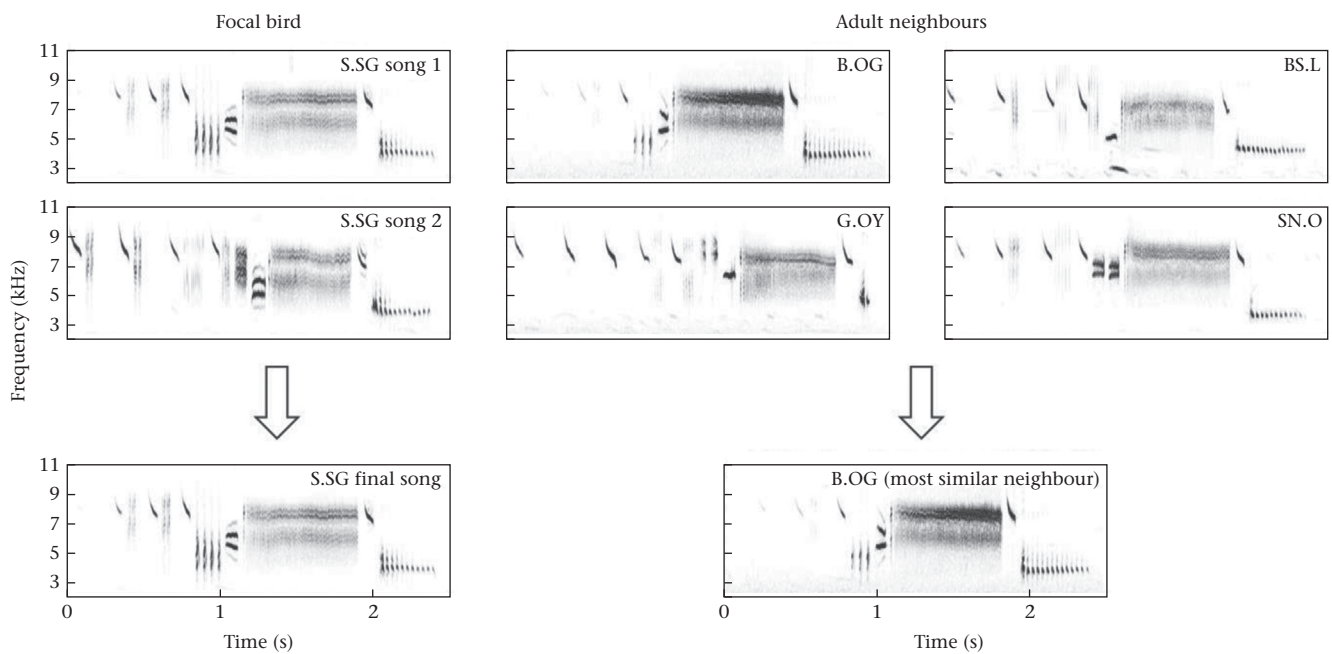


Figure 5. An example of the process of attrition, showing the two initial songs produced by a young focal bird, S.S.G (top left; birds are named after the colour bands on their legs), and the final song that he sang after undergoing repertoire attrition (bottom left). For comparison, we show the songs from S.S.G's four territorial neighbours: B.O.G, B.S.L, G.O.Y, S.N.O (top right). The acoustic similarity scores between S.S.G song 1 and these four neighbours was, respectively, 2.6, 6.3, 6.9, 5.4. The acoustic similarity between S.S.G song 2 and these four neighbours was, respectively, 6.1, 7.0, 5.4, 4.3. The final song crystallized by S.S.G showed the closest match to B.O.G (i.e. an acoustic similarity score of 2.6).

In our analysis of the middle segment of songs, a segment with extensive variation, we found the same pattern as for whole songs: middle segments of retained songs had smaller acoustic distances to all neighbours' songs in comparison to discarded songs (paired t test: $t_{23} = 3.0$, $N = 24$, $P = 0.006$; Fig. 4d). The middle segments of retained songs also had smaller acoustic distances to the most similar neighbour's song in comparison to discarded songs (paired t test: $t_{23} = 2.5$, $N = 24$, $P = 0.02$; Fig. 4). In other words, when focusing on the middle segment of songs, males retained songs that sounded more similar to the songs of their group of neighbours and also more similar to the songs of their most similar-sounding neighbour.

Aggression

The acoustic distance between the songs of young male Savannah sparrows and that of their older territorial neighbours showed a positive correspondence with the number of aggressive calls recorded on the young males' territories. At 10 days after a young male's arrival from migration, the number of aggressive calls did not show a strong positive relationship with the mean acoustic distance of entire songs (Spearman's rank correlation: $r_s = 0.40$, $N = 15$, $P = 0.16$; Fig. 6a). The same was true when we focused on the middle section of the song ($r_s = 0.30$, $N = 15$, $P = 0.32$; Fig. 6b). In late May,

however, the number of aggressive calls increased with the mean acoustic distance to neighbours' entire songs ($r_s = 0.40$, $P = 0.05$, $N = 21$; Fig. 6c) and to the middle segments of those songs ($r_s = 0.50$, $N = 21$, $P = 0.04$; Fig. 6d); a larger number of aggressive calls were recorded on the territories of young males whose songs were less similar to the songs of their neighbours. The first two relationships are unclear but suggestive of a positive association between acoustic distance and territorial aggression, although the sample sizes are small; the latter two relationships are suggestive of a positive association between acoustic distance and territorial aggression.

DISCUSSION

Overproduction, followed by attrition, is commonplace during the development of song for young male Savannah sparrows in their first breeding spring. Although their adult repertoire size is just one song type (Mennill et al., 2018; Wheelwright et al., 2008; Williams et al., 2013), more than half of young Savannah sparrows exhibited overproduction, producing two to four song types during the first weeks of their first breeding season. Savannah sparrows' small repertoires underwent attrition within the first 21 days of arrival on the breeding grounds, as males rejected all but one song type, which they sang for the duration of the first breeding season and in later

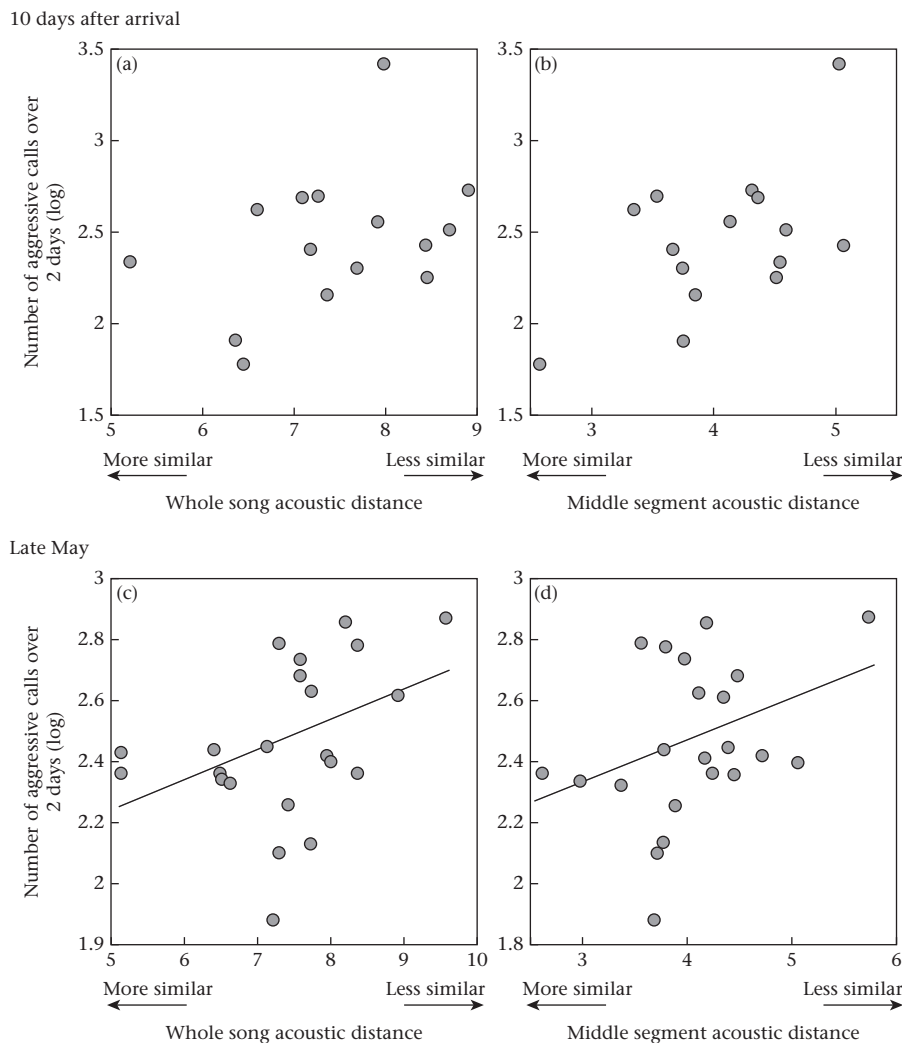


Figure 6. The relationship between the acoustic distance of Savannah sparrow songs in comparison with their neighbours and the number of aggressive calls recorded on their territories over two 2-day periods: 10 days after the birds arrived from migration (a, b) and in late May of the same year (c, d). We compared acoustic similarity for both whole songs (left) as well as the middle segment of songs (right). Lines of best fit in (c) and (d) show positive relationships between acoustic distance and number of aggressive calls.

years. Overproduction was not observed in older males. For males that exhibited overproduction and attrition, we found evidence that individuals preferentially retained songs that maximized the average acoustic similarity to the songs of their territorial neighbours. Therefore, our results demonstrate that young male Savannah sparrows exhibit overproduction and then undergo selective attrition to crystallize songs that are similar to the songs of their neighbours.

Our 4-year field study of free-living Savannah sparrows confirms that, as in other songbirds, the song-learning process involves overproduction followed by attrition. Chaffinches, *Fringilla coelebs*, use selective attrition as a mechanism for weeding heterospecific song out of their mature repertoire (Thorpe, 1958). Male brown-headed cowbirds, *Molothrus ater*, rely on female behaviour to guide their process of attrition, retaining song components that elicit sexual behaviour from female observers (Smith, King, & West, 2000). In New World sparrows (Passerellidae), multiple species show patterns of overproduction and attrition similar to the ones we documented in Savannah sparrows (Liu & Nottebohm, 2007; Marler & Peters, 1982; Nelson, 1992). White-crowned sparrows, *Zonotrichia leucophrys*, retain locally common songs that match the dialect of their breeding site (Nelson, 2000). Song sparrows, *M. melodia*, sing an average of 10.2 songs in their overproduced repertoires and undergo attrition to an average of 9.3 song types, retaining songs similar to the songs of their territorial neighbours (Nordby et al., 2007). Field sparrows, *Spizella pusilla*, also retain songs that most closely resemble a territorial neighbour (Nelson, 1992). Swamp sparrows retain songs that best advertise their performance capabilities (Podos et al., 2004), although the bulk of evidence suggests that male–male interactions shape selective attrition (Peters & Nowicki, 2017). Therefore, overproduction and attrition are taxonomically widespread behaviours and, within the New World sparrows, they are important behaviours that allow young males to develop an adult phenotype that matches the common song types in their breeding population.

In a recent review, five explanations were presented for the adaptive value of overproduction and attrition (Peters & Nowicki, 2017). (1) Overproduction allows birds to discard poorly learned or accidentally acquired songs. (2) Overproduction allows males to retain songs that match those of 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. In the case of Savannah sparrows, our results do not offer support for explanation 1, because we observed many songs that appeared stereotyped and well formed but were eventually discarded. Our results are consistent with explanations 2 and 3, but we are currently unable to distinguish between them. Our results do not support explanation 4 because, in many cases, we found that selective attrition was complete before females arrived at the breeding site. Finally, our results neither support nor refute explanation 5. Further study could illuminate whether individual Savannah sparrows show long-term recognition of song types that they themselves have learnt and discarded.

The variability in the timescale and patterns of attrition reveals considerable plasticity in Savannah sparrow song development. Sixteen of the 18 sparrows that overproduced songs early in the season winnowed their repertoire down to just one song type over a period of 4–21 days after arrival on the breeding grounds. Two individuals, however, sang one song exclusively for their first week before switching to a different song thereafter. In both cases, these shifts coincided with the arrival of older males in adjacent territories, and we observed a high level of aggressive behaviours

directed at the younger bird by the older neighbour. These observations suggest that young birds can rapidly discard a song that is detrimental to their territorial defence and switch to a more effective song throughout the early breeding season, potentially in response to territorial aggression. It might be advantageous, then, for young males to continue singing multiple song types into the start of their first breeding season, so that they have alternative songs if their acoustic neighbourhood changes over time. Because of 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 underestimate the prevalence of overproduction. It is possible that all males went through overproduction and attrition before we were able to record their repertoire.

Our results suggest that individuals who express songs that do not closely resemble their neighbours encounter higher rates of aggression on their territories. The middle segment appears to play a role both in song selection during song learning and in exposure to aggression after crystallization. The heightened aggression faced by males with songs that are dissimilar from those of their neighbours may be the mechanism that drives selective attrition, causing birds to discard songs that expose them to increased conflict. These territorial conflicts should be expected to impose the well-documented costs associated with territorial challenges (Burgess, Brown, & Lanyon, 2013; Smith & Taylor, 1993), and thereby shape song development because of the advantage of reducing such costs. Female choice of genetic partners may also contribute to male song conformity to local cultural traditions if males producing local songs gain a fitness advantage from female choice (Nelson & Poesel, 2013), although the current investigation focuses on male–male territorial aggression rather than female choice.

The adaptive value of vocal learning in songbirds has been challenging to identify (Beecher et al., 2017). The impetus to adapt to local dialects has been documented in many studies of different species of songbirds (Beecher, Campbell, & Stoddard, 1994; Marler & Peters, 1982; Nelson, 1992, 2000) and suggests that the capacity of an individual to match its acoustic phenotype to that of its neighbours represents an important facet of vocal learning. Researchers have suggested that adopting local dialects could be advantageous in territorial defence (Beecher et al., 1996; Sung & Park, 2005). Our results suggest that expressing similar songs to those of their neighbours translates to less territorial aggression, particularly for the middle section of Savannah sparrow song. Our methodology for documenting aggression provides a valuable approach for gathering noninvasive, biologically relevant behavioural data. The increased use of autonomous recorders to study social interactions could add valuable insight into how animals interact in a population over long timescales, something that cannot be tested, only inferred, from directed experiments using artificial stimuli.

Acknowledgments

We thank the Natural Sciences and Engineering Research Council of Canada (NSERC) for grants to S.M.D., A.E.M.N., D.R.N. and D.J.M. We thank Bowdoin Scientific Station for logistical support; this is contribution No. 279 from Bowdoin Scientific Station. We thank J. Burant, M. Elza, C. Macfarlane, K. McGuire, M. Meron and I. Moran for field assistance. We thank A. Bailey, H. Begin-Dyck, J. Bodner, K. Cavanaugh, A. Hensel, K. Laroia, K. McGuire, Z. Merheb, R. Ouellette, A. Saeed, F. Serhan, K. Tracey and A. Wilder for assistance with sound analysis.

References

- Beecher, M. D. (2017). Birdsong learning as a social process. *Animal Behaviour*, *124*, 233–246.

- Beecher, M. D., Campbell, S. E., & Stoddard, P. K. (1994). Correlation of song learning and territory establishment strategies in the song sparrow. *Proceedings of the National Academy of Sciences of the United States of America*, *91*(4), 1450–1454.
- Beecher, M. D., Nordby, J. C., Campbell, S. E., Burt, J. M., Hill, C. E., & O'Loughlin, A. L. (1997). What is the function of song learning in songbirds? *Perspectives in Ethology*, *12*, 77–97.
- Beecher, M. D., Stoddard, P. K., Campbell, S. E., & Horning, C. L. (1996). Repertoire matching between neighbouring song sparrows. *Animal Behaviour*, *51*, 917–923.
- Bell, D. A., Trail, P. W., & Baptista, L. F. (1998). Song learning and vocal tradition in Nuttall's white-crowned sparrows. *Animal Behaviour*, *55*, 939–956.
- Briefer, E., Aubin, T., Lehongre, K., & Rybak, F. (2008). How to identify dear enemies: the group signature in the complex song of the skylark *Alauda Arvensis*. *Journal of Experimental Biology*, *211*, 317–326.
- Burgess, E. A., Brown, J. L., & Lanyon, J. M. (2013). Sex, scarring, and stress: Understanding seasonal costs in a cryptic marine mammal. *Conservation Physiology*, *1*(1), Article cot014.
- Catchpole, C., & Slater, P. J. B. (2008). *Bird song: Biological themes and variations*. Cambridge, U.K.: Cambridge University Press.
- Dunlap, A. S., & Stephens, D. W. (2016). Reliability, uncertainty, and costs in the evolution of animal learning. *Current Opinion in Behavioral Sciences*, *12*, 73–79.
- Falls, J. B. (1982). Individual recognition by sound in birds. In D. E. Kroodsmas, & E. H. Miller (Eds.), *Acoustic communication in birds* (Vol. 2, pp. 237–278). New York, NY: Academic Press.
- Fitch, W. T., Schusterman, R. J., Reichmuth, C., Spasikova, M., & Mietchen, D. (2008). Vocal learning in pinnipeds: A model system for human speech evolution. *Journal of the Acoustical Society of America*, *123*, 3507–3507.
- Gobeil, R. E. (1970). Vocalizations of the Savannah sparrow. *Bird-Banding*, *41*, 18–21.
- Hunt, G. R., & Gray, R. D. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society B: Biological Sciences*, *270*, 867–874.
- Jarvis, E. (2004). Learned birdsong and the neurobiology of human language. *Annals of the New York Academy of Sciences*, *1024*, 749–777.
- Koetz, A. H., Westcott, D. A., & Congdon, B. C. (2007). Geographical variation in song frequency and structure: The effects of vicariant isolation, habitat type and body size. *Animal Behaviour*, *74*, 1573–1583.
- Liu, W.-C., & Nottebohm, F. (2007). A learning program that ensures prompt and versatile vocal imitation. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(51), 20398–20403.
- Logue, D. M., & Forstmeier, W. (2008). Constrained performance in a communication network: Implications for the function of song-type matching and for the evolution of multiple ornaments. *American Naturalist*, *172*, 34–41.
- Manassa, R. P., McCormick, M. I., Dixon, D. L., Ferrari, M. C. O., & Chivers, D. P. (2014). Social learning of predators by coral reef fish: Does observer number influence acquisition of information? *Behavioral Ecology and Sociobiology*, *68*, 1237–1244.
- Marler, P. (1970). A comparative approach to vocal learning: Song development in white-crowned sparrows. *Journal of Comparative and Physiological Psychology*, *71*(2), 1–25.
- Marler, P., & Nelson, D. A. (1994). Selection-based learning in bird song development. *Proceedings of the National Academy of Sciences of the United States of America*, *91*(22), 10498–10501.
- Marler, P., & Peters, S. (1982). Structural changes in song ontogeny in the swamp sparrow *Melospiza georgiana*. *Auk*, *99*, 446–458.
- Mates, E. A., Tarter, R. R., Ha, J. C., Clark, A. B., & McGowan, K. J. (2015). Acoustic profiling in a complex social species, the American crow: Caws encode information on caller sex, identity and behavioural context. *Bioacoustics*, *24*(1), 63–80.
- Mennill, D. J., Battiston, M., Wilson, D. R., Foote, J. R., & Doucet, S. M. (2012). Field test of an affordable, portable, wireless microphone array for spatial monitoring of animal ecology and behaviour. *Methods in Ecology and Evolution*, *3*, 704–712.
- Mennill, D. J., Doucet, S. M., Newman, A. E. M., Williams, H., Moran, I. G., Thomas, I. P., et al. (2018). Wild birds learn songs from experimental vocal tutors. *Current Biology*, *28*(20), 3273–3278. e4.
- Mennill, D. J., Doucet, S. M., Newman, A. E. M., Williams, H., Moran, I. G., Thomas, I. P., et al. (2019). Eavesdropping on adult vocal interactions does not enhance juvenile song learning: An experiment with wild songbirds. *Animal Behaviour*, *155*, 67–75.
- Morales Picard, A., Hogan, L., Lambert, M. L., Wilkinson, A., Seed, A. M., & Slocombe, K. E. (2017). Diffusion of novel foraging behaviour in Amazon parrots through social learning. *Animal Cognition*, *20*(2), 285–298.
- Moran, I. G., Doucet, S. M., Newman, A. E. M., Ryan Norris, D., & Mennill, D. J. (2018). Quiet violence: Savannah sparrows respond to playback-simulated rivals using low-amplitude songs as aggressive signals. *Ethology*, *124*(10), 724–732.
- Moser-Purdy, C., MacDougall-Shackleton, E. A., & Mennill, D. J. (2017). Enemies are not always dear: Male song sparrows adjust dear enemy effect expression in response to female fertility. *Animal Behaviour*, *126*, 17–22.
- Moser-Purdy, C., & Mennill, D. J. (2016). Large vocal repertoires do not constrain the dear enemy effect: A playback experiment and comparative study of songbirds. *Animal Behaviour*, *118*, 55–64.
- Muth, F., Keasar, T., & Dornhaus, A. (2015). Trading off short-term costs for long-term gains: How do bumblebees decide to learn morphologically complex flowers? *Animal Behaviour*, *101*, 191–199.
- Nelson, D. A. (1992). Song overproduction and selective attrition lead to song sharing in the field sparrow (*Spizella pusilla*). *Behavioral Ecology and Sociobiology*, *30*, 415–424.
- Nelson, D. A. (1998). Geographic variation in song of Gambel's white-crowned sparrow. *Behaviour*, *135*, 321–342.
- Nelson, D. A. (2000). Song overproduction, selective attrition and song dialects in the white-crowned sparrow. *Animal Behaviour*, *60*, 887–898.
- Nelson, D. A., & Poesel, A. (2009). Does learning produce song conformity or novelty in white-crowned sparrows, *Zonotrichia leucophrys*? *Animal Behaviour*, *78*, 433–440.
- Nelson, D. A., & Poesel, A. (2013). Song sharing correlates with lifetime social pairing success but not territory tenure in the Puget Sound white-crowned sparrow. *Behavioral Ecology and Sociobiology*, *67*, 993–1000.
- Nordby, C. J., Cully, J., Campbell, S. E., & Beecher, M. D. (2007). Selective attrition and individual song repertoire development in song sparrows. *Animal Behaviour*, *74*, 1413–1418.
- de Oliveira Gordinho, L., Matheu, E., Hasselquist, D., & Neto, J. M. (2015). Song divergence between subspecies of reed bunting is more pronounced in singing styles under sexual selection. *Animal Behaviour*, *107*, 221–231.
- Peters, S., & Nowicki, S. (2017). Overproduction and attrition: The fates of songs memorized during song learning in songbirds. *Animal Behaviour*, *124*, 255–261.
- Podos, J., Huber, S. K., & Taft, B. (2004). Bird song: The interface of evolution and mechanism. *Annual Review of Ecology, Evolution and Systematics*, *35*, 55–33.
- Searcy, W. A., & Nowicki, S. (2008). Bird song and the problem of honest communication. *American Scientist*, *96*, 114–121.
- Sherry, D. F. (2008). Social learning: Nectar robbing spreads socially in bumble bees. *Current Biology*, *18*, R608–R610.
- Smith, V. A., King, A. P., & West, M. J. (2000). A role of her own: Female cowbirds, *Molothrus ater*, influence the development and outcome of song learning. *Animal Behaviour*, *60*, 599–609.
- Smith, I. P., & Taylor, A. C. (1993). The energetic cost of agonistic behaviour in the velvet swimming crab, *Necora (= Liocarcinus) puber* (L.). *Animal Behaviour*, *45*, 375–391.
- Stoddard, P. K., Beecher, M. D., Horning, C. L., & Willis, M. S. (1990). Strong neighbor–stranger discrimination in song sparrows. *Condor*, *92*, 1051–1056.
- Stoeger, A. S., & Manger, P. (2014). Vocal learning in elephants: Neural bases and adaptive context. *Current Opinion in Neurobiology*, *28*, 101–107.
- Sung, H.-C. (2005). *Song variation and male reproductive success in the Savannah sparrow songs*, *Passerculus sandwichensis* (Ph.D. thesis). London, ON, Canada: The University of Western Ontario.
- Sung, H.-C., & Park, S.-R. (2005). Explaining avian vocalizations: A review of song learning and song communication in male–male interactions. *Integrative Biosciences*, *9*, 47–55.
- Thorpe, W. H. (1958). The learning of song patterns by birds, with especial reference to the song of the chaffinch *Fringilla coelebs*. *Ibis*, *100*(4), 535–570.
- Wheelwright, N. T., & Rising, J. D. (2008). Savannah sparrow (*Passerculus sandwichensis*). In P. G. Rodewald (Ed.), *The birds of North America*. Ithaca, New York: Cornell Lab of Ornithology version 2.0. .
- Wheelwright, N. T., Swett, M. B., Levin, I. I., Kroodsmas, D. E., Freeman-Gallant, C. R., & Williams, H. (2008). The influence of different tutor types on song learning in a natural bird population. *Animal Behaviour*, *75*, 1479–1493.
- Williams, H., Levin, I. I., Norris, D. R., Newman, A. E. M., & Wheelwright, N. T. (2013). Three decades of cultural evolution in Savannah sparrow songs. *Animal Behaviour*, *85*, 213–223.
- Williams, H., Robins, C. W., Norris, D. R., Newman, A. E. M., Freeman-Gallant, C. R., Wheelwright, N. T., et al. (2019). The buzz segment of Savannah sparrow song is a population marker. *Journal of Ornithology*, *160*, 217–227.
- Woodworth, B. K., Newman, A. E. M., Turbek, S. P., Dossman, B. C., Hobson, K. A., Wassenaar, L. I., et al. (2016). Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. *Oecologia*, *181*, 413–422.
- Woodworth, B. K., Wheelwright, N. T., Newman, A. E. M., & Norris, D. R. (2017). Winter temperatures limit population growth rate of a migratory songbird. *Nature Communications*, *8*, 14812.