



Microgeographical variation in birdsong: Savannah sparrows exhibit microdialects in an island population

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Social communication often involves vocal learning, whereby young animals learn their vocalizations early in life by imitating the sounds of adults. In animals that learn their vocalizations, it is common to find patterns of geographical variation known as 'vocal dialects', acoustic features shared within a cluster of animals that differ from the vocalizations of animals in nearby clusters. Dialects may form when animals learn their vocalizations early in life and then disperse short distances, or when they modify their vocalizations to match local vocal patterns after dispersal. Dialects are typically studied at a regional or continental scale, but they may also persist at smaller scales in so-called 'microgeographical song dialects' or 'microdialects'. Microdialects have received little research attention. In this study, we investigate microdialects and dispersal distance in song-learning Savannah sparrows, *Passerculus sandwichensis*, through a 4-year study of birds living on three islands in the Bay of Fundy, Canada. Our analyses yield evidence of microgeographical variation: birds showed higher acoustic similarity to their neighbours than to faraway individuals in the same population. When we classified songs on the basis of their highly variable middle sections, we found that particular song types formed spatial clusters of similar-sounding individuals. Therefore, acoustic variation in Savannah sparrow song appears to show dialects across small geographical distances. In an analysis of dispersal from natal sites to breeding sites, we found a median distance of 189 m, consistent with previous findings. Our results suggest that limited dispersal distances, combined with the social processes of vocal learning (overproduction and selective attrition), likely contribute to the presence of microdialects.

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Imitative vocal learning plays an important role in the complex social communication of diverse animals, including songbirds and humans (Beecher, 2017; Nottebohm, 1970). Many vocal learners have a specific period of learning that occurs early in life and is followed by dispersal from their natal location (Fitch et al., 2008; Jenkins et al., 2007). When dispersal distance is small, or when learning is not completed until after dispersal, vocal learners often exhibit dialects where groups of animals in a region produce similar sounds that are acoustically different from animals in other regions. Many groups of vocal learners show evidence of vocal dialects, including hummingbirds (Wiley, 1971), parrots (Wright & Wilkinson, 2001), bats (Prat et al., 2017), whales (Whitehead et al., 1998) and humans (Henry et al., 2015).

Vocal dialects are particularly common among oscine songbirds, a diverse group of more than 4000 species where individuals develop songs by imitating the vocalizations of others (Bradbury & Vehrencamp, 2011; Marler & Tamura, 1962; Planqué et al., 2014). Song dialects were first documented in a foundational study of white-crowned sparrows, *Zonotrichia leucophrys*, where individuals from different regions of California were found to exhibit distinctive and consistent acoustic differences (Marler & Tamura, 1962). Since then, evidence of dialects has been identified in diverse songbird species, and vocal dialects appear to be common whenever birds exhibit vocal learning followed by short dispersal distances (Briefer et al., 2011; Keighley et al., 2019; Liu et al., 2008; McGregor, 1980; Salinas-Melgoza & Wright, 2012).

The first song dialects described in California white-crowned sparrows were studied over a total distance of 1000 km with 10 different song dialects identified across this distance (Marler & Tamura, 1962), and most of the dialects documented in other species have spanned broad geographical scales (Bradbury &

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Vehrencamp, 2011). For example, in golden-crowned sparrows, *Zonotrichia atricapilla*, dialects span distances of 500–1700 km (Shizuka et al., 2016), in mourning warblers, *Oporornis philadelphia*, dialects span distances of 600–2000 km (Pitocchelli, 2011) and in red-faced cisticolas, *Cisticola erythrops*, dialects span distances over 6500 km (Benedict & Bowie, 2009). Although large-scale dialects may be a phenomenon arising from vocal learning and dispersal, dialects that span large geographical distances may also play a functional role in population recognition, allowing individuals to differentiate between local and nonlocal individuals (Marler & Tamura, 1962), which may have implications for mate selection and territory defence (MacDougall-Shackleton et al., 2002). Song segments that remain unchanged for decades are likely the song components that convey population-specific information, contributing to the formation and maintenance of macrogeographical song dialects (Chilton & Lein, 1996; Williams et al., 2019).

Although broad-scale dialects are well documented, dialects might also occur at smaller scales. Whereas most studies of geographical variation in animal sounds focus on distances of hundreds to thousands of kilometres, microgeographical song variation focuses upon local neighbourhoods of territorial birds whose breeding territories may all be located within hundreds of metres. These small-scale dialects are usually referred to as 'microgeographical song dialects' or 'microdialects' (Baker & Cunningham, 1985; Briefer et al., 2011; Payne, 1978). In their review of geographical variation in birdsong, Podos and Warren (2007), differentiated microgeographical dialects as those spanning less than 2 km or involving fewer than 100 individuals. Microdialects may provide a fitness advantage to birds that match the locally common song (Payne, 1982); when birds produce songs that match the songs of their neighbours, they may benefit from fewer costly territorial interactions with rivals (Beecher et al., 1996; Thomas et al., 2021). To date, several investigations of songbirds provide evidence of microdialects. For example, in European wrens, *Troglodytes troglodytes*, microdialects are present across distances as short as 200 m (Catchpole & Rowell, 1993). In Madagascar paradise flycatchers, *Terpsiphone mutata*, microdialects have been documented across 1 km distances (van Dongen & Mulder, 2006). It is an open question whether microdialects are widespread among song-learning birds, and whether microdialects can be explained by patterns of song-learning behaviour or dispersal, or a combination of these and other factors.

There are multiple forces that might contribute to the formation of microdialects, and these forces may mirror those that drive macrogeographical dialects. The presence of a small-scale natural barrier, such as a small water body or a patch of inhospitable habitat, might be an insignificant boundary against dispersal but might provide a communication barrier between nearby groups of animals, thereby giving rise to microdialects (Catchpole & Rowell, 1993; Kopuchian et al., 2004; Leader et al., 2000). Social forces may also influence the development of microdialects. If animals learn songs from neighbours and then disperse short distances and preferentially settle near animals that produce similar songs, this could give rise to microdialects. Alternatively, regardless of dispersal distance, if young animals modify their songs based on the sounds that they hear after dispersal, and if there is pressure to sound similar to neighbours (Liu & Nottebohm, 2007), this too could give rise to microdialects. The boundaries of microdialects may change over time with changes in dispersal patterns or changes in habitat (Chilton & Lein, 1996; Derryberry, 2009). By quantifying microdialects and studying dispersal patterns and song-learning behaviour, we will develop a deeper understanding of the forces that give rise to microdialects and the mechanisms that contribute to geographical song variation.

We studied microgeographical variation in a population of Savannah sparrows, *Passerculus sandwichensis*, living on islands in the Bay of Fundy, New Brunswick, Canada. Our past work on this population has shown that each male learns one individually distinctive song within the first year of his life, and that this song remains consistent through adulthood (Mennill et al., 2018). Savannah sparrow songs consist of four segments (Appendix, Fig. A1; Wheelwright et al., 2008; Williams et al., 2013; Williams et al., 2019). The most significant variation between individuals occurs in the middle and terminal segments of the song (Wheelwright et al., 2008; Williams, 2021; Williams et al., 2019). Previous studies show that Savannah sparrows exhibit vocal dialects across large geographical distances of hundreds of kilometres, such as across the maritime regions of eastern North America (Williams et al., 2019), the Californian coast (Bradley, 1994) and southwestern Ontario (Sung & Handford, 2006). However, as in most songbirds, it remains unknown whether Savannah sparrows exhibit microdialects.

In this study, we ask whether Savannah sparrows exhibit microdialects, and, if so, what factors contribute to the formation of these microdialects. We hypothesized that local song learning, combined with short dispersal distances, would give rise to microdialects where neighbouring animals have similar songs. This hypothesis would be relevant to any bird where song is learned by imitating tutors and is not crystallized before the beginning of the first breeding season. We recorded and measured the position of every male in our study population, then calculated pairwise acoustic similarity measurements between all pairs of males and quantified dispersal distances. With these data we evaluated several predictions following from our hypothesis. First, we predicted that male Savannah sparrows would show higher acoustic similarity to their neighbours compared to more distant animals within the population. Second, based on evidence from other investigations of microgeographical variation (e.g. European wrens: Catchpole & Rowell, 1993; Madagascar paradise flycatchers: van Dongen & Mulder, 2006), we predicted that, at a population scale, songs would exhibit a dialect-like pattern with clusters of animals singing similar songs. Finally, to determine whether shorter dispersal distances could contribute to the formation of microdialects, we predicted that males who dispersed shorter distances from their natal site would sound more similar to their neighbours than males who dispersed longer distances from their natal site.

METHODS

General Methods

We conducted our research on the three islands of the Bowdoin Scientific Station in the Bay of Fundy, New Brunswick, Canada (44°35'N, 66°46'W): Kent Island, 2.8 × 0.7 km (80 ha); Hay Island, 0.7 × 0.4 km (30 ha); Sheep Island, 0.7 × 0.2 km (17 ha; Fig. 1). Some central portions of Hay and Kent Islands are forest habitat and are not occupied by Savannah sparrows (dark green regions in Fig. 1). In the springs of 2016 through 2019, 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 et al., 2012). In late May and early June of each year, we placed autonomous recorders in a grid formation of 50 × 50 m squares in the grassy habitat of all three islands. Recorders were left in place for 48 h at each location, but if wind or rain interrupted the recordings, they were left in place for longer to ensure there was a clear, good-quality recording. Savannah sparrows have small territory sizes (average: 0.21 ha; Wheelwright & Rising, 2008), and so



Figure 1. Map of Bowdoin Scientific Station in the Bay of Fundy, New Brunswick, Canada (44°35'N, 66°46'W). Light green areas represent Savannah sparrow habitat. Dark green areas represent forested areas of the islands, which are not inhabited by Savannah sparrows. Black dots depict locations of autonomous recorders, which were placed throughout each regional boundary of the study site and left to record for 24–48 h.

each recorder was within recording range of many male territories. Given 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 the 50 × 50 m grid positioning of our recordings allowed us to sample songs from all Savannah sparrows on the three islands. Indeed, we routinely detected the same males in two or more nearby recording locations.

Trained researchers differentiated between male Savannah sparrows by examining field recordings as sound spectrograms using Syrinx-PC sound analysis software (J. Burt, Seattle, WA, U.S.A.). Each adult male Savannah sparrow produces only one song type (less than 1% of males produce two song types). Male songs have individually distinctive components, with the middle and trill sections of their songs being particularly variable. Songs remain consistent throughout a male's adult life, showing only small variations in the frequency and duration of certain song elements over time (Thomas et al., 2021; Wheelwright et al., 2008; Williams et al., 2013). Consequently, we could identify individuals based on the structural details of their songs in the recordings. Within our long recordings, we focused on annotating songs from 0400 to 0800 hours and 1800 to 2000 hours in each recording; these are times when Savannah sparrows are particularly vocally active (Moran et al., 2019). From each recording, we saved a sound

spectrogram for each unique individual. We mapped all individuals, placing a sound spectrogram on a satellite photograph of the study site at a point nearest to the automated recorders where each bird's voice was sampled. When the same male's songs were recorded by multiple nearby recorders (this was true for most birds), we placed a single good example of that song at a position closest to the recorder at which they were the loudest.

Acoustic Distance Measurements

After isolating the recording with the best signal-to-noise ratio and the smallest amount of overlapping background noise for each individual, we measured the fine structural features of each male's song using Avisoft SAS-Lab Pro software (R. Sprecht, Berlin, Germany). We used automated parameter measurements in Avisoft to reduce human subjectivity in quantifying acoustic features of songs. Because Savannah sparrows produce a consistent song with little variability over their lives, only one song per male was measured (Thomas et al., 2021; Wheelwright et al., 2008). We categorized measurements based on the four segments of Savannah sparrow song (Appendix, Fig. A1; terminology from Williams, 2021; Williams et al., 2013). For each of the four song segments, we measured six features: the element rate, the average pause length between segments, the average maximum frequency, the average minimum frequency, the average dominant frequency and the average note bandwidth. We also measured the three interior pause lengths between the four song segments, the length and number of notes in the middle and buzz segments and the duty cycle of the middle segment (i.e. the length of the segment minus the intersyllable silent intervals). We did not quantify song length and number of notes in the introduction and terminal segments due to variation in segment length within individuals (males often drop or add notes from the beginning of the introductory segment and the end of the terminal segment between subsequent songs). Additionally, we did not quantify the duty cycle for the buzz segment because this segment generally consists of only one note. In total, we used 32 spectrotemporal measurements for our analyses.

Based on these 32 spectrotemporal measurements, we plotted all songs in multidimensional space and calculated the squared Euclidean distances between each pair of individuals. We call this measurement 'acoustic distance'. Following an approach developed by Thomas et al. (2021), we calculated acoustic distance between songs using the clustering analysis platform within JMP (v.14; SAS Institute, Cary, NC, U.S.A.), selecting the hierarchical cluster analysis using the centroid, squared Euclidean distances calculation method. We saved the distance matrix produced from the clustering platform in JMP to create a table that outlines the squared Euclidean distances between all measured individual songs. Two songs that are highly similar will have a low acoustic distance score; two songs that are very different will have a high acoustic distance score.

We determined the average acoustic distance score of each male and all his territorial neighbours to determine acoustic similarity within a neighbourhood. Immediate territorial neighbours were defined as males whose song was recorded loudest at an adjacent recorder or the same recorder as the focal male. We compared the average acoustic distance score for each male to his neighbours against the average acoustic distance score for each male to randomly chosen individuals with territories at least 1 km away. For each comparison, we matched the number of randomly chosen distant males to the number of immediate neighbours for each male (e.g. males that had two immediate neighbours were compared to two randomly chosen distant

males). Previous research has shown that the middle segment of the Savannah sparrow song is particularly variable between individuals and may be especially important in communicating individual identity (Williams et al., 2013). We therefore conducted a comparison of acoustic similarity scores both for the entire song as well as just the middle segment. This allowed us to explore whether the middle segment was a driving factor in microdialects in this population. Comparisons of the acoustic similarity for the whole song and middle segment between neighbours and distant birds were repeated for each individual in all 4 years of the study. We compared the acoustic distances for whole-song data using paired *t* tests (whole-song differences were normally distributed: Kolmogorov–Smirnov test for normality: $K = 1.28$, $P = 0.08$; skewness: -0.16 ; kurtosis: 1.84) and for middle-section data using Wilcoxon tests (middle-section differences were not normally distributed: $K = 1.42$, $P = 0.03$; skewness: -0.36 ; kurtosis: 4.17).

In 2013–2018 we conducted a playback experiment to study vocal learning in this population (see Mennill et al., 2018, 2019). In that experiment, we used loudspeakers to simulate vocal tutors broadcasting novel stimuli and found that 34 birds learned songs from our playback-simulated tutors (30 birds learned the novel songs directly from the simulated tutors; 4 learned the novel songs from other birds on the island; Mennill et al., 2018). To ensure that the current study of dialects was not influenced by this playback experiment, we repeated all analyses excluding male songs that exhibited characteristics matching the playback stimulus from the simulated tutors; we found the same patterns whether or not we included the birds that were also part of the experiment described by Mennill et al. (2018, 2019; see Appendix, Table A3), and therefore we continued our analyses using our full data set.

Natal Dispersal Distance

The Kent Island Savannah sparrow population at Bowdoin Scientific Station is well known for its high natal site philopatry (Mauck & Wheelwright, 1998; Mitchell et al., 2012). We measured the natal dispersal distance of male Savannah sparrows that hatched in the central 10 ha study area where nesting data were collected. We measured natal dispersal distance as the distance between each bird's natal nest and the centre of his territory the next year, following a similar approach used by Wheelwright and Mauck (1998) in a previous analysis of this population. The centre of each territory was determined using the mapped territory outline compiled each year by the field research team. Our dispersal data set included data from 39 males born from 2014 to 2018 who returned to establish their first breeding territory in the years 2015–2019. We measured the linear distance between each individual's natal nest and the centre of his territory during his first breeding season.

Ethical 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 checking mist nets frequently (typically, nets were observed by the banders and birds were extracted as soon as they hit the net). We held the birds for the minimum amount of time possible (typically, less than 15 min) keeping them in a cloth bag until they were measured, banded and released.

RESULTS

Acoustic Similarity

Male Savannah sparrows sounded more similar to their neighbours than to distant birds in the population. Songs showed smaller acoustic distances in pairwise comparisons between neighbours (average acoustic distance: 7.31) than between birds at least 1 km away (average acoustic distance: 7.67; paired *t* test: $t = 6.7$, $P < 0.0001$, $N = 988$ birds across 4 years; comparisons for each year are shown in the Appendix, Table A1); both comparison groups showed substantial variation in acoustic similarity in each of the 4 years (Fig. 2). When we repeated this analysis using the acoustic features of only the middle section of the song instead of the entire song, we found the same pattern across the 4 years of the study (average acoustic distance to neighbours: 4.09; average acoustic distance to distant birds: 4.26; Wilcoxon signed-rank test: $W = 41496$, $P < 0.0001$, $N = 1002$), although in our analyses of variation in middle sections within individual years, we found strong evidence for this pattern in only 1 year and moderate or weak evidence in the remaining 3 years (Appendix, Table A2).

To understand patterns of song clustering, we inspected sound spectrograms and applied a classification scheme used by Williams (2021). The middle section of all songs conformed to six population level song types (Fig. 3; this analysis excluded the experimental birds from the song tutoring experiment in Mennill et al., 2018, 2019): (1) middle sections comprising two 'ch' notes; (2) middle sections comprising two 'ch' notes and a dash; (3) middle sections comprising two to four short notes and a single dash; (4) middle sections comprising more than two 'ch' notes (known as 'stutter songs'); (5) middle sections comprising a single 'ch' note followed by a dash; (6) middle sections comprising a single dash. The remaining segments (the introduction, buzz and terminal segments) had similar characteristics among most males. When we categorized songs into the six types on the basis of their middle section, clusters of males with similar middle segments tended to group together geographically across the three islands (Fig. 3, Appendix, Figs A2–A5). Clusters of neighbouring birds with the same middle segments ranged in size from two neighbours to 10 or

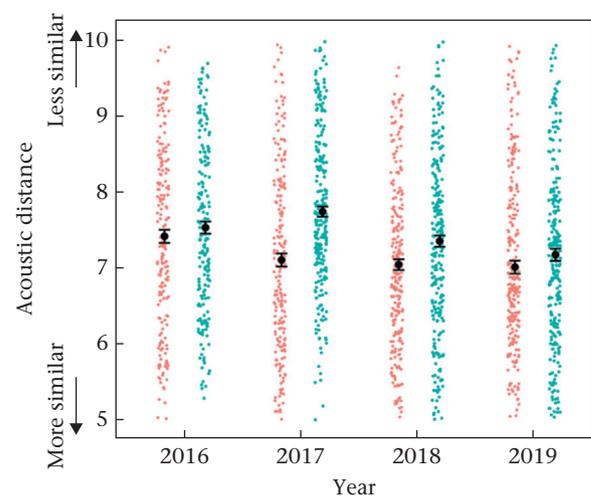


Figure 2. Plots depicting the average acoustic distance between birds and their neighbours (pink) versus randomly selected distant birds at least 1 km away (blue) for 2016, 2017, 2018 and 2019. For each group, the mean is shown as a black circle with standard error bars, and the coloured dots show the full range of data. Acoustic distances were determined with a hierarchical cluster analysis using centroid, squared Euclidean distances (see Methods).

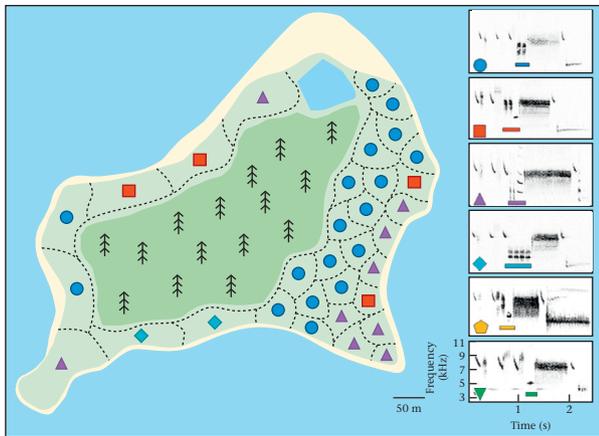


Figure 3. Map of Hay Island (2017, $N = 33$) illustrating geographical song variation. There are six song types present within the population, distinguished based on the middle section of the song: dark blue circles denote two 'ch' notes, red squares denote two 'ch' notes and a dash, purple triangles denote short notes and a dash, blue diamonds denote multiple 'ch' notes, yellow pentagons denote one 'ch' note and a dash, and green upside-down triangles denote a single dash (terminology from Williams et al., 2013). Songs with a single dash and songs with one 'ch' note and a dash occur elsewhere in the study population but are not present on this island. Dotted lines represent approximate territories boundaries for each male. See Appendix (Figs A2–A5) for full maps of all three islands in each of the 4 years of the study.

more adjacent birds. All six middle-section types were spread across the study islands in all 4 years of the study, intermixed with other middle-section song types. The six middle-section song types were present in a similar ratio across each of the 4 years of the study (Appendix, Table A4).

Dispersal Distance

Among 34 males, we calculated a median natal dispersal distance of 189 m (range 42–550 m; Table 1). To evaluate whether males who disperse smaller distances sound more similar to their neighbours than do males who disperse greater distances, we conducted a correlation analysis between dispersal distance and each bird's average acoustic distance to his territorial neighbours in his first breeding year. We found that male natal dispersal distance was not correlated with acoustic similarity between a male and his territorial neighbours (Pearson's correlation: $r_{32} = 0.19$, $P = 0.29$; Fig. 4).

DISCUSSION

Our analyses of small-scale acoustic variation in an island population of Savannah sparrows provide evidence of a microdialect pattern, where neighbouring animals share similar song characteristics. Patterns of geographical variation in Savannah sparrow

Table 1

Natal dispersal distance (distance between the natal nest and the centre of the territory during the first breeding year) for the study population of male Savannah sparrows

Hatch year	Natal dispersal distance (m)			N
	Median	Minimum	Maximum	
2015	382	236	550	4
2016	147	77	430	16
2017	212	42	540	8
2018	275	135	415	6
All years combined	189	42	550	34

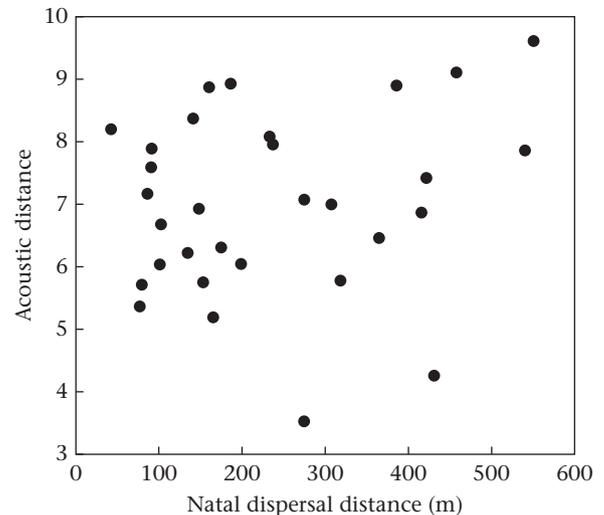


Figure 4. Plot demonstrating the relationship between natal dispersal distance and acoustic distance between focal males and territorial neighbours in their first breeding season.

song were previously described across large distances of hundreds of kilometres (Bradley, 1994; Sung & Handford, 2006; Williams et al., 2019). The current investigation provides the first description of microgeographical variation for Savannah sparrows at the scale of hundreds of metres. Small-scale geographical variation was evident when we analysed the entire songs of Savannah sparrows and also when we focused on the highly variable middle section of songs. When we categorized the variable middle section of the song, we identified six population level song types, which we found in clusters of acoustically similar territorial males, with local sharing of population-wide song types that recurred elsewhere in the population. Our analyses of natal dispersal demonstrated low dispersal distances, where males settle within 189 m of their natal site. However, variation in male dispersal distance showed no relationship with acoustic similarity to neighbours.

Vocal dialects have been described in diverse animals at a variety of scales. In their review of vocal dialects in 42 species of birds and mammals, Podos and Warren (2007) categorized vocal dialects into spatial scales of <2 km ('microdialects'), 2–10 km ('small dialects'), 10–100 km ('medium dialects') and >100 km ('large dialects'). Six species (14%) of animals in their review showed dialects on the scale of microdialects: little hermits, *Phaethornis longuemareus*; indigo buntings, *Passerina cyanea*; Smith's longspurs, *Calcarius pictus*; house wrens, *Troglodytes troglodytes*; saddlebacks, *Creadion carunculatus*; orange-tufted sunbirds, *Nectarinia osea* (Podos & Warren, 2007). Additional investigators have reported microdialect level variation since Podos and Warren's review. For example, skylarks, *Alauda arvensis*, share song syllable sequences between neighbours, but show little sharing between patches 2 km apart (Briefer et al., 2008); black redstarts, *Phoenicurus ochruros*, share song types within regions but rarely across regions separated by 0.2–2.4 km (Draganoiu et al., 2014); and grey-browed brushfinches, *Arremon assimilis*, share songs between neighbours but not across regions 2 km apart (Rodríguez-Fuentes et al., 2022). Therefore, microdialects are recognized in diverse bird species, including temperate and tropical birds and migratory and nonmigratory birds.

One possible mechanism for the formation of microdialects may be short dispersal distances. Past research conducted in our study population examined the dispersal patterns of juvenile Savannah sparrows between 1987 and 1995 (Wheelwright & Mauck, 1998).

Savannah sparrows showed high natal site philopatry, often returning to the same field where they had hatched the year before, with a median male natal dispersal distance of 203 m (Wheelwright & Mauck, 1998). Our data, from 2014 to 2019, showed the same patterns: males routinely returned to the same field where they were born and had a median dispersal distance of 189 m between their natal nest and their first breeding territory. One possible mechanism that could generate microdialects would be for birds to learn songs in their natal year and later establish their first breeding territory near their natal site, a pattern which holds true in Savannah sparrows (Mennill et al., 2018) and many song-learning birds (e.g. white-crowned sparrow: Morton, 1992; great tit, *Parus major*: Rivera-Gutierrez et al., 2010; yellow-naped Amazon, *Amazona auropalliata*: Salinas-Melgoza & Wright, 2012). However, when we examined the relationship between dispersal distances and acoustic similarity to territorial neighbours, we found that males who dispersed shorter distances did not sound more similar to their neighbours than males who dispersed greater distances. Therefore, while short dispersal distances may play a role, they are not likely to be the sole contributing factor to the formation of microdialects in this study population.

The ontogeny of vocal learning behaviour in songbirds may further contribute to the formation of microdialects. As in other songbirds, Savannah sparrows learn songs during a brief period of time early in life, and once this learning process is complete, male song becomes fixed for the duration of each male's adult life (Marler & Nelson, 1994; Mennill et al., 2018). Many song-learning birds exhibit behaviours known as overproduction and attrition. These behaviours occur when birds express a larger repertoire of songs when they are juveniles than when they are adults (overproduction), and then reject some songs before settling on their final adult repertoire (attrition; Nelson, 1992, 2000; Nordby et al., 2007; Peters & Nowicki, 2017). The process of overproduction and attrition may provide birds with the opportunity to closely match the songs of their territorial neighbours (Marler & Peters, 1982; Nelson, 1992, 2000). When young birds learn songs from nearby adults during their natal summer, they do not know the identity of their eventual territorial neighbours during their first breeding season the following spring (Bell et al., 1998). Juvenile males may therefore benefit from learning multiple song types during their natal summer and then selecting a single song that matches their eventual territorial neighbours (Baptista & Morton, 1982; Bell et al., 1998; Nelson & Poesel, 2009). Our previous research focusing on overproduction and attrition in Savannah sparrows demonstrated that males routinely overproduce songs and then retain songs that are similar to those of their territorial neighbours during their first breeding season (Thomas et al., 2021). This phenomenon may play an important part in explaining the formation of microdialects in Savannah sparrows that we have described here; if a juvenile male learns multiple songs, then there is a high likelihood that one of those songs will match those of his territorial neighbours during his first breeding season, and this will give rise to clusters of similar-sounding males.

In addition to the ideas that short dispersal distances could contribute to the formation of microdialects, and that patterns of overproduction and postdispersal song attrition could contribute to the formation of microdialects, a third possible explanation exists. If birds learn songs after dispersal, from nearby animals in their breeding area, this too could give rise to microdialects. We know that this possibility does not apply to Savannah sparrows, because previous research shows that males learn multiple songs in their natal year (Mennill et al., 2018) and undergo selective attrition in their first breeding year (Thomas et al., 2021). We have no evidence of any Savannah sparrow learning songs after their natal year, in spite of a song-learning playback experiment designed to test for

this type of learning (Mennill et al., 2018, 2019). Yet this third possible explanation could apply to any species where vocal learning occurs in the postdispersal period.

What does it mean for birds to live in a world where microdialects exist? There may be important implications for both female choice and aggression between neighbouring territorial males. Research examining song preference in female song sparrows, *Melospiza melodia*, demonstrated that females prefer the songs of mates and neighbours compared to the songs of strangers from their own population (O'Loughlen & Beecher, 1999). Furthermore, females prefer the songs of strangers that resemble the songs of their mates compared to songs of strangers that do not (O'Loughlen & Beecher, 1999). Therefore, female choice may promote acoustic similarity among nearby males, and males will be more likely to disperse short distances and adopt the song type of their male neighbours, further contributing to the maintenance of microdialects. A second implication of living in a population structured by microdialects is reduced aggression between neighbours. When neighbouring territorial males produce similar songs, they exhibit decreased aggressive interactions (Thomas et al., 2021), demonstrating another advantage for conforming to local microdialects. In the future, these implications could be explored through more in-depth studies of territorial aggression and mate choice.

In conclusion, we have demonstrated that Savannah sparrows exhibit microdialect patterns where there is higher acoustic similarity between neighbouring individuals compared to distant animals. Our research provides evidence that dialect patterns, well known at large geographical scales, are also expressed on local scales. Future research might consider exploring the influence of the process of overproduction and attrition in the development of microdialects, and whether certain components of birdsong are more influential to the formation of microdialects to better our understanding of the formation and maintenance of this phenomenon.

Author Contributions

A.L.J.H. and D.J.M. conceived of the study and wrote the manuscript; A.L.J.H., S.L.D. and D.J.M. conducted the sound analyses with assistance from the scientists listed in the acknowledgments; S.M.D., D.R.N., A.E.M.N., H.W. and D.J.M. collected field data; all authors shared in discussing, editing and revising the manuscript.

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Appendix

Table A1

Summary of paired *t* tests comparing acoustic distance scores of whole songs of males to neighbours and distant birds, across 4 years of data

	Mean	SE	<i>t</i>	<i>P</i>	<i>N</i>
All data					
Neighbours	7.31	0.05	6.7	<0.0001	988
Distant birds	7.67				
2016					
Neighbours	7.61	0.09	2.1	0.04	213
Distant birds	7.80				
2017					
Neighbours	7.29	0.12	4.8	<0.0001	251
Distant birds	7.89				
2018					
Neighbours	7.18	0.11	3.7	0.0002	260
Distant birds	7.59				
2019					
Neighbours	7.23	0.12	2.2	0.03	264
Distant birds	7.44				

Means and standard errors are reported for acoustic similarity between male neighbours and between randomly chosen distant males > 1 km away; *N* = total number of males studied in each year.

Table A2

Summary of Wilcoxon signed-rank tests comparing acoustic distance scores of the middle section of songs of males to neighbours and distant birds, across 4 years of data

	Mean	SE	<i>W</i>	<i>P</i>	<i>N</i>
All data					
Neighbours	4.09	0.04	41496	<0.0001	1002
Distant birds	4.25				
2016					
Neighbours	4.28	0.08	1311	0.15	213
Distant birds	4.42				
2017					
Neighbours	3.99	0.11	5153	<0.0001	250
Distant birds	4.26				
2018					
Neighbours	4.07	0.06	1277	0.33	275
Distant birds	4.14				
2019					
Neighbours	4.06	0.08	1971	0.11	264
Distant birds	4.23				

Means and standard errors are reported for acoustic similarity between male neighbours and between randomly chosen distant males > 1 km away; *N* = total number of males studied in each year.

Table A3

Summary of *t* tests comparing acoustic distance scores of whole songs of males to neighbours and distant birds, excluding birds with songs that matched experimental stimuli, across 4 years of data

	Mean	SE	<i>t</i>	<i>P</i>	<i>N</i>
All data					
Neighbours	7.22	0.05	6.9	<0.0001	962
Distant birds	7.60				
2016					
Neighbours	7.58	0.09	1.9	0.06	209
Distant birds	7.75				
2017					
Neighbours	7.18	0.12	4.1	<0.0001	244
Distant birds	7.66				
2018					
Neighbours	7.18	0.11	3.7	0.0002	260
Distant birds	7.59				
2019					
Neighbours	7.01	0.11	3.8	0.0002	249
Distant birds	7.41				

Means and standard errors are reported for acoustic similarity between male neighbours and between randomly chosen distant males > 1 km away; *N* = total number of males studied in each year.

Table A4

Relative frequency of each of the six population level song types in each of the 4 years of the study

Year	Song type 1	Song type 2	Song type 3	Song type 4	Song type 5	Song type 6	Other
All data	45.9%	28.8%	9.6%	5.8%	2.1%	0.7%	7.1%
2016	47.6%	29.2%	9.0%	4.2%	2.4%	0.5%	7.1%
2017	49.4%	26.7%	11.6%	5.6%	2.8%	0.4%	3.6%
2018	42.9%	28.9%	9.9%	6.6%	2.2%	0.4%	9.2%
2019	44.3%	30.3%	8.0%	6.4%	1.1%	1.5%	8.3%

See Fig. 3 and Appendix Figs A2–A5 for island maps and spectrograms of the song types classified on the basis of the middle section of the song. Variation between years is expected to arise on the basis of settlement of new birds recruited to the population each year and is the focus of an ongoing study of cultural evolution in this population.

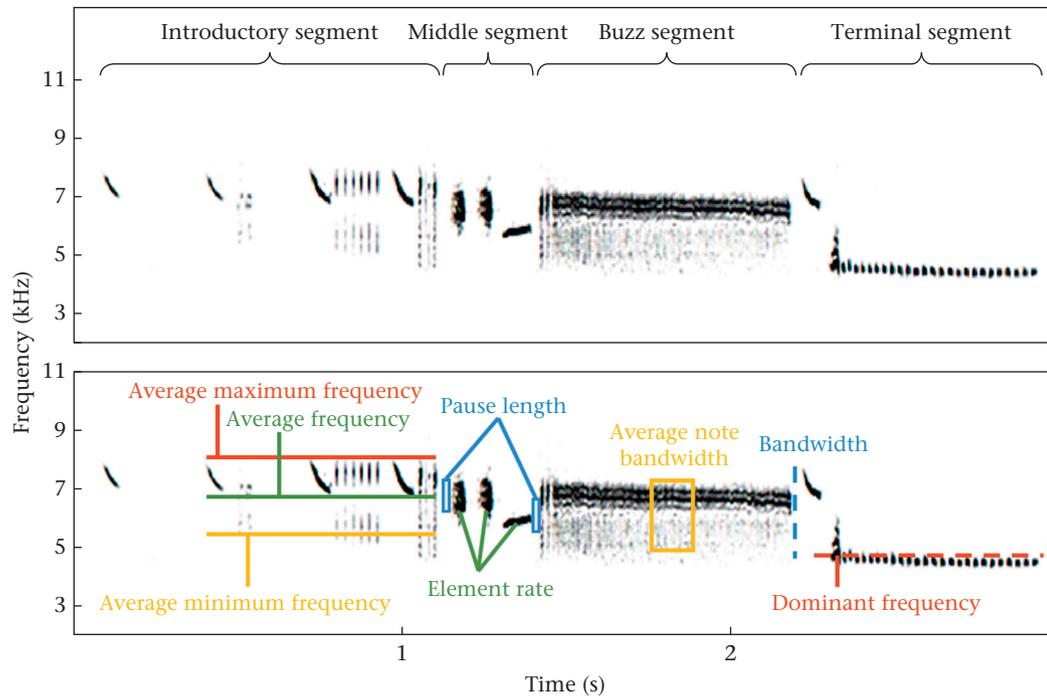


Figure A1. Sound spectrograms of the song segments and spectrotemporal characteristics of a typical Savannah sparrow song. Top: sound spectrogram identifying the four segments of Savannah sparrow song. Bottom: the same song depicted to show the fine structural features measured to calculate acoustic similarity. For reasons of clarity, only a subset of measurements are illustrated for each song segment; all measurements were collected from all of the distinct notes in all four song segments (see [Methods](#) for details).

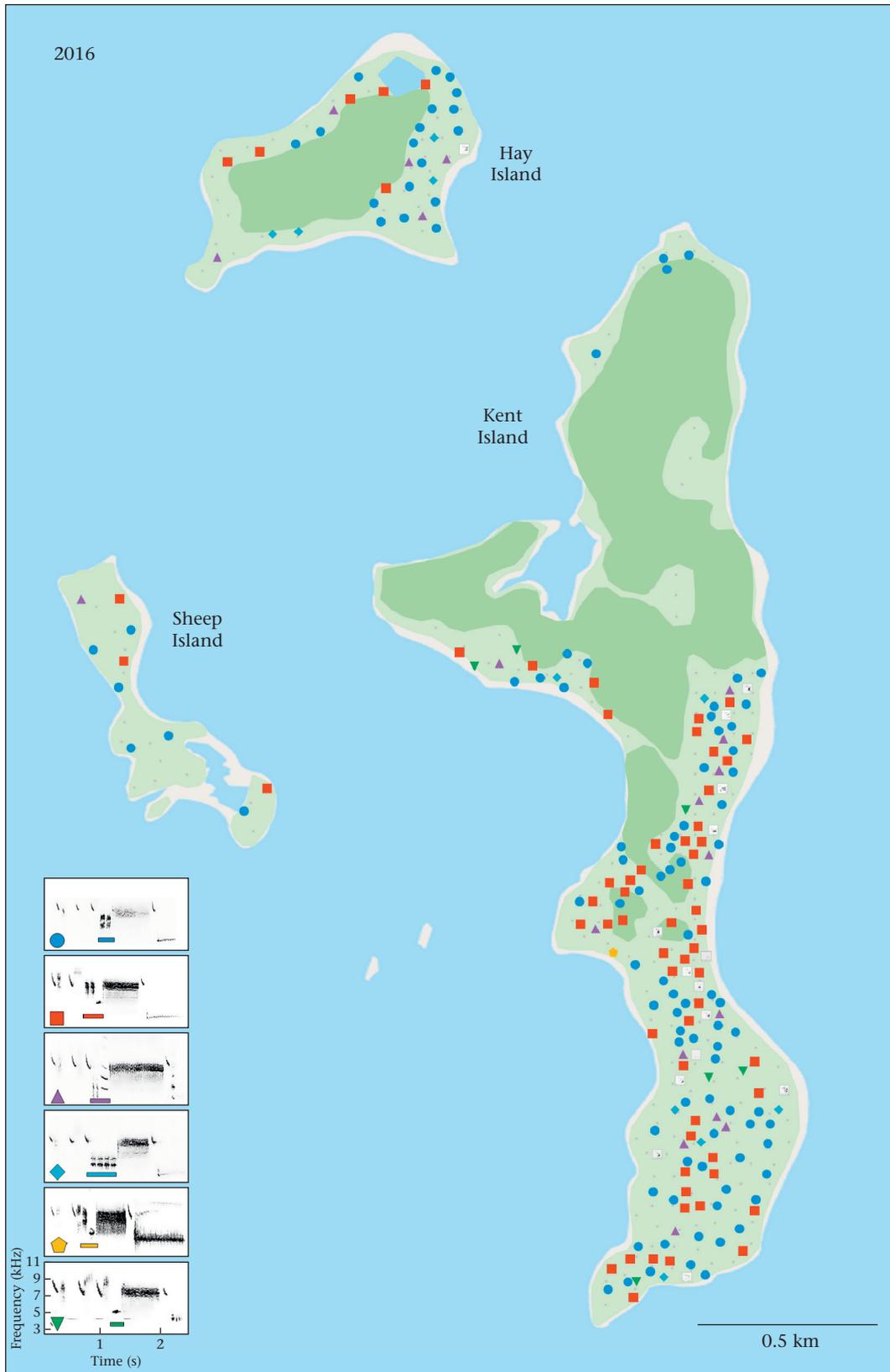


Figure A2. Map of all male Savannah sparrows detected in the year 2016, colour-coded by the six different types of middle sections of their songs as shown in the lower left (also see Fig. 3 text legend for a description of each song type). Grey boxes indicate songs with middle sections that matched experimental playback songs from Menniil et al. (2018, 2019).



Figure A3. Map of all male Savannah sparrows detected in the year 2017, colour-coded by the six different types of middle sections of their songs as shown in the lower left (also see Fig. 3 text legend for a description of each song type). Grey boxes indicate songs with middle sections that matched experimental playback songs from Mennill et al. (2018, 2019).

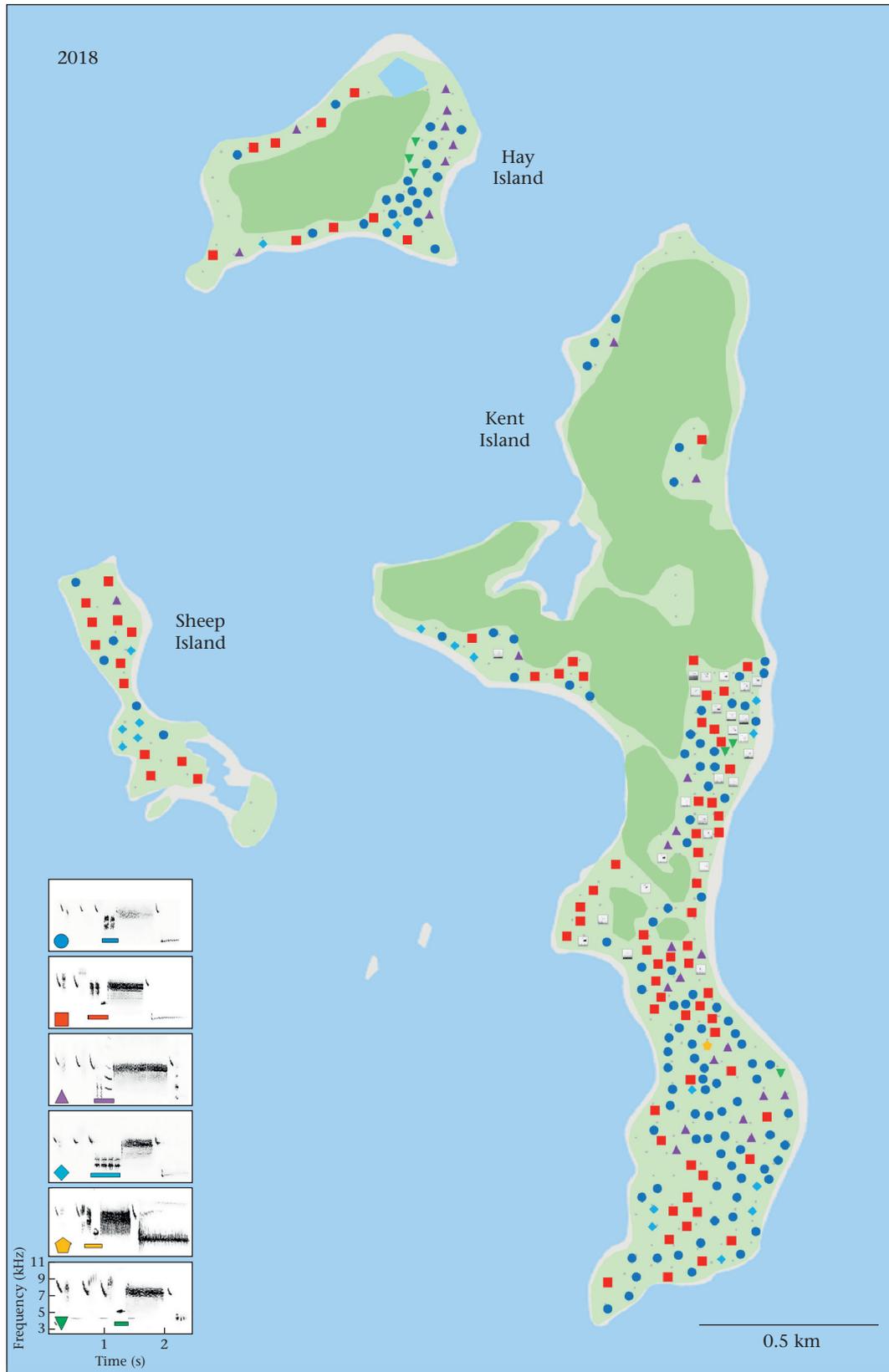


Figure A4. Map of all male Savannah sparrows detected in the year 2018, colour-coded by the six different types of middle sections of their songs as shown in the lower left (also see Fig. 3 text legend for a description of each song type). Grey boxes indicate songs with middle sections that matched experimental playback songs from Mennill et al. (2018, 2019).

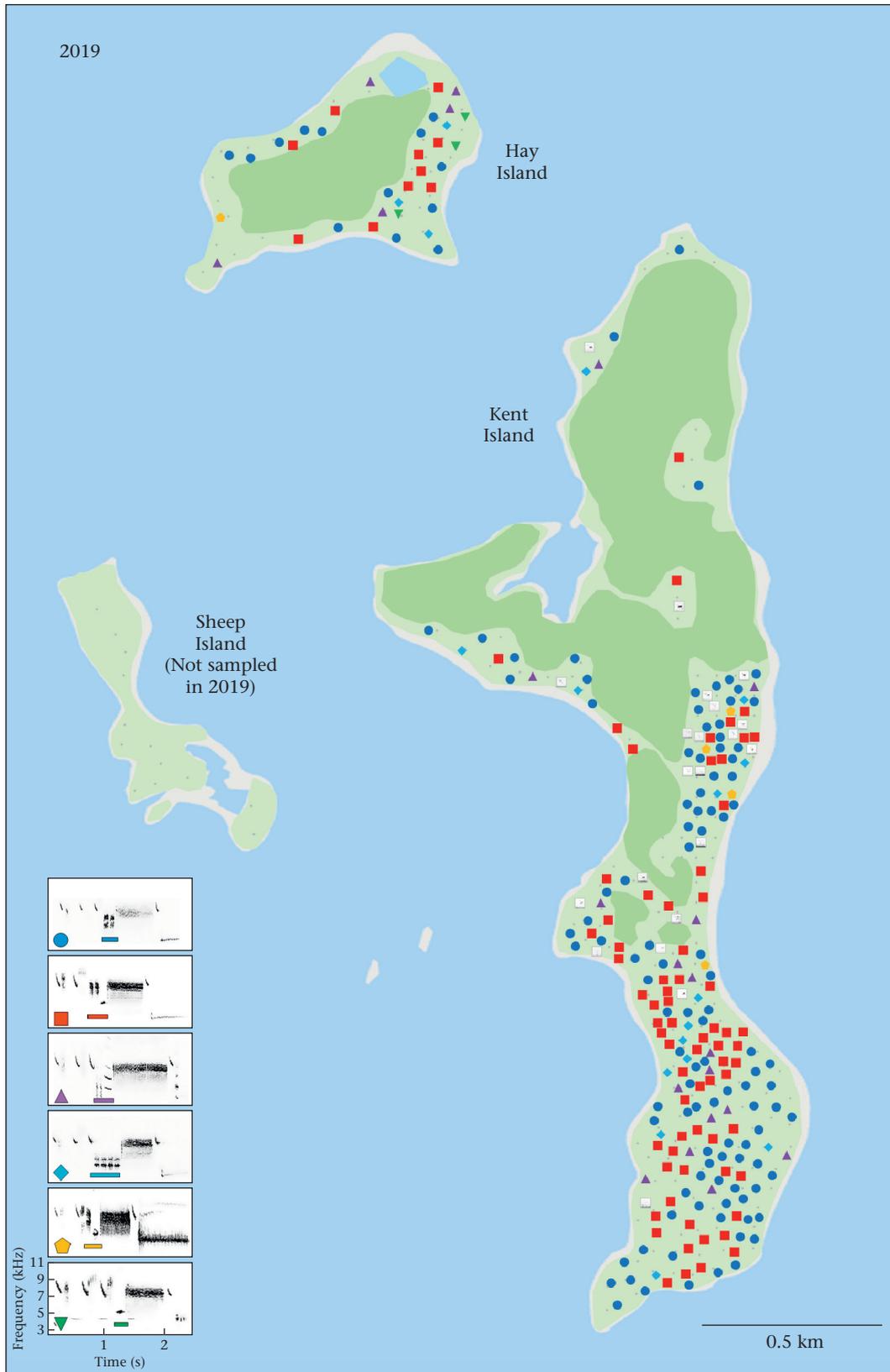


Figure A5. Map of all male Savannah sparrows detected in the year 2019, colour-coded by the six different types of middle sections of their songs as shown in the lower left (also see Fig. 3 text legend for a description of each song type). Grey boxes indicate songs with middle sections that matched experimental playback songs from Mennill et al. (2018, 2019).