

Familiarity and homogeneity affect the discrimination of a song dialect

Heather Williams^{a, *}, Sarah L. Dobney^b, Clint W. Robins^{a, c}, D. Ryan Norris^d,
Stéphanie M. Doucet^b, Daniel J. Mennill^b

^a Biology Department, Williams College, Williamstown, MA, U.S.A.

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

^c School of Environmental and Forest Sciences, University of Washington, Seattle, WA, U.S.A.

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

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Male songbirds of many species sing local song dialects that are restricted to defined geographical areas. In most tests of responses to local versus foreign dialects, males respond more aggressively to songs from their own dialect, presumably because local males represent more of a threat to their success. We asked how hearing foreign songs during development and territory establishment affects discrimination of the local dialect in wild Savannah sparrows, *Passerculus sandwichensis*. After foreign songs had been heard from loudspeakers in the study area in at least two consecutive breeding seasons, males reduced the intensity of their responses to the local version of the population-specific buzz segment of the song. Four years after the foreign songs were last broadcast on the study area, males again responded more aggressively to the local version of the buzz. As for the basis of these responses, we found no evidence that birds discriminated among dialects by comparing them to their own songs. However, auditory experience with a foreign song, whether during song development (from speaker-simulated song tutors) or during the current breeding season (from neighbours' songs), reduced the intensity of birds' responses to the local buzz type. Both familiarity, in the form of auditory experience with a song type, and homogeneity, when a song type is sung by all or nearly all of the population, appear to contribute to heightened aggressive responses to a local song dialect.

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Many birds learn to sing components of song that are shared with the other males in their geographical area, forming vocal dialects (Marler & Tamura, 1962; Podos & Warren, 2007; Wright & Dahlin, 2017). Specific song segments, such as the trill segment of white-crowned sparrow, *Zonotrichia leucophrys*, song (Nelson et al., 2004; Nelson & Poesel, 2007) or the buzz segment of Savannah sparrow, *Passerculus sandwichensis*, song (Williams et al., 2019), are common to populations and remain stable over time. Song sharing among neighbours can be facilitated by philopatry, when birds breed near the location where they hatched (Handley & Nelson, 2005; Marler, 1981; Yoon et al., 2013), or by social learning, when a young bird settles near an older conspecific and copies song features from that neighbour, or retains a song similar to the neighbour's while dropping other songs (Liu & Kroodsma, 2006; Nelson, 1992; Thomas et al.,

2021). In this way, learned song features that define dialects can be said to be both geographically and socially structured, and their expression can result in geographical song dialects.

Males respond more aggressively to the local dialect than to other dialects in nearly all of the species for which responses to different song dialects have been tested (for reviews, see Nelson, 1998; Parker et al., 2018). Although females' approach or solicitation responses often favour the local dialect (Baker, 1983; MacDougall-Shackleton et al., 2001; O'Loughlen & Beecher, 1999; Searcy et al., 2002), female preference for the local dialect is not universal (McGregor et al., 1988; Nelson & Soha, 2004; Poesel et al., 2012). A number of explanations have been advanced for why males might respond more aggressively to the local dialect. Perhaps the most compelling suggestion is that birds singing the local dialect represent a greater threat to a male's success (Rothstein & Fleischer, 2014) because they are more likely to establish and hold a territory in the local environment, or they are more likely to attract local females as mates. This 'threat hypothesis' is supported

* Corresponding author.

E-mail address: hwilliams@williams.edu (H. Williams).

by the finding that responses to a familiar neighbour's song are stronger when stakes are high, as when a mate is fertile (Koetz-Trowse et al., 2012; Moser-Purdy et al., 2017; Temeles, 1994).

The rule of stronger male responses to singers of the local dialect is not universal. A few studies have found an asymmetry of responses, with birds in one population responding more aggressively to the local dialect, while those in another population do not discriminate between dialects in their responses (Fernández-Gómez et al., 2021). In such cases, there may also be an asymmetry of auditory experience. For example, when territory-holding birds in a southern population of black-throated blue warblers, *Setophaga caerulescens*, were exposed to the songs of migrating birds from a northern population in early spring, they responded strongly to both northern and southern song types (Colbeck et al., 2010). In contrast, northern birds that only heard northern songs on their territories responded more aggressively to their own (northern) song type. Such findings suggest that familiarity with a different dialect plays a role in whether birds respond more strongly to local songs.

Recognition of the local dialect appears to arise after fledging (Hudson et al., 2019; Soha & Whaling, 2002; Whaling et al., 1997). Fledglings of philopatric species may hear and memorize the local dialect songs of nearby males as well as those of their social father, who feeds them, early in life (Wheelwright et al., 2008). These songs are stored as memories and serve as models for songs that the young birds will later learn to produce (Marler, 1970; Soha, 2020). Like white-crowned sparrows (Nelson, 1992) and chipping sparrows, *Spizella passerina* (Liu & Kroodsma, 2006), male Savannah sparrows learn song heard early in life and complete song learning as they establish territories in their first breeding season (Thomas et al., 2021). Early in that first breeding season, a male has the opportunity to hear the songs of males in the local population, including those of his immediate neighbours, determine which features these songs have in common and settle on a single, crystallized song that matches the local dialect. Although Savannah sparrows do not change their songs after their first year (Wheelwright et al., 2008), a male may nevertheless hear the songs of a different set of neighbours in subsequent years, or there can be systematic changes in the entire population's songs (Williams et al., 2013, 2022), which in turn might change some of the acoustic characteristics of the local dialect. In this way, auditory familiarity with the local song environment, both during song learning and in later years, could form the basis for an individual's recognition of the consistent acoustic features of their local dialect (Hamao, 2016; Vehrencamp et al., 2003). In contrast to this 'auditory familiarity hypothesis', another possibility is that males compare the songs they hear to their own songs. Auditory mirror neurons in the song system respond not only to the song a bird sings but also to songs that reflect the bird's auditory experience during development (Prather et al., 2008, 2009, 2010). These results are the basis for the hypothesis that heightened aggressive responses to the home dialect are based on similarity to the bird's own song, or the 'acoustic similarity hypothesis'.

A recent experiment with a wild population of Savannah sparrows has made it possible to test the basis for heightened responses to the local dialect and to test predictions about mechanisms for how birds learn to recognize the local dialect. From 2013 to 2018, a breeding population heard foreign songs from loudspeakers, broadcast on a natural singing schedule, and many young males copied those foreign songs (Mennill et al., 2018). As a consequence, song features that did not correspond to the local dialect were heard from speakers and from territory-holding males, and were a ubiquitous part of the acoustic environment experienced by all Savannah sparrows on the study site during those 6 years. After 2018, some birds continued to sing copied foreign songs, exposing their neighbours to those songs. In the current study, we used

playback experiments to compare males' responses to the population-specific buzz segment of Savannah sparrow song at three time periods: (1) before foreign songs were introduced, in 2012; (2) while experimental foreign songs were being broadcast on the study area, in 2016 and 2017; and (3) 4 years after the last speaker broadcasts of foreign songs, in 2022.

This playback experiment allowed us to assess the effects of the acoustic environment as well as the effects of a bird's singing and auditory experience on its responses to local versus foreign songs. To test the hypothesis that males assess the threat represented by another song by comparing it to their own song, we asked whether the acoustic similarity of the bird's own buzz to the stimulus buzz was correlated with the bird's response. We also compared the responses of birds that had different auditory experiences of foreign song. If memories of auditory experience during song development are the basis for discriminating local dialect singers from strangers, then males that differed in exposure to foreign song during song development (their first year) should respond differently to foreign songs. If males assess the songs sung by local males each year and adjust their aggressive responses accordingly, we predicted that the current version of the dialect would elicit the strongest responses. Taken together, the results of our playback studies allowed us to test the relative importance of three factors for generating the intensity of males' responses to conspecific songs: (1) homogeneity within the song dialect (whether more than 90% of the birds sing the local song dialect), (2) familiarity with that dialect as a territory-holding breeding male and (3) auditory experience with the dialect during development.

METHODS

Subjects

We studied Savannah sparrow breeding populations on three islands in the Grand Manan Archipelago (New Brunswick, Canada): Kent Island (44°34'54"N, 66°45'17"W), where a long-term study has followed birds for several decades at the Bowdoin Scientific Station and the nearby islands of Grand Manan (44°43'24"N, 66°45'10"W) and White Head (44°37'53"N, 66°42'57"W). The males in this archipelago sing the same song dialect (H. Williams, personal observation). On Kent Island, data on Savannah sparrows breeding on the main study area were gathered each year as part of a long-term study: adults were colour-banded, their territories were mapped, nests were located, nestlings were banded and males' songs were recorded (Hensel et al., 2022; Wheelwright et al., 2008; Wheelwright & Mauck, 1998; Woodworth et al., 2017). In addition, many juveniles from areas outside the main study site were banded in late summer, before migration (Woodworth et al., 2016). The population is philopatric and individuals return to breed within a few hundred metres of the nest where they hatched and usually return to the same territory in subsequent breeding years (Hensel et al., 2022; Wheelwright & Mauck, 1998). Song learning begins in the summer of the first year and is completed early the following spring when males return to breed for the first time (Mennill et al., 2018; Thomas et al., 2021). The numbers of birds that were subjects of playback presentation, their song types and the distribution of song types recorded at each location and in each year are shown in Table 1.

Song Recordings

The songs of subjects for this study were recorded using a Marantz digital recorder (PMD670 or PMD660) and a Sennheiser ME-66 directional microphone; our digital recordings used a 44 kHz rate and a 16-bit depth. We also used some songs recorded

Table 1
Playback subjects, their songs and the prevalence of foreign (Western) songs at sites and years used for the study

Year	Location	Subjects	Subjects recorded	Subjects singing foreign songs	Subjects hearing foreign songs	Total males recorded on study site	Total males singing foreign songs on study site
2012	Kent Island	16	16	0	0	46	0 (0%)
2016	Grand Manan	16	14	0	0	24	0 (0%)
2016	Kent Island	14	14	4	14	34	5 (15%)
2017	Kent Island	17	17	6	17	57	14 (25%)
2022	Kent Island	18	18	1	5	42	3 (7%)

Birds with any song element copied from the Western (speaker) songs were considered to sing foreign songs (see Mennill et al., 2018). Birds were considered to have heard foreign songs if speakers were playing Western songs that year or if their territory neighboured that of a male singing a copied Western song. Dialects were considered to be completely homogeneous if all of the recorded birds sang the same buzz type (Kent Island in 2012, Grand Manan in 2016) and nearly homogeneous if more than 90% of the recorded birds sang the same buzz type (Kent Island in 2022). None of the 2016–2017 subjects were tested in 2012, and none of the 2022 subjects were tested in previous years.

between 1993 and 2011 to characterize Kent Island variant buzzes and generate stimuli for buzz playbacks (see Wheelwright et al., 2008 for details on methods for those recordings). We digitized songs originally recorded on tape using SoundEdit Pro (Macromedia; 44 kHz and 16 bits).

Characterizing Buzz Types

Figure 1a shows an example of a song from the Grand Manan archipelago, including the buzz that is a geographical marker for this population. Figure 1b shows four categories of buzzes from Kent Island and elsewhere. In previous work, we found that buzzes could be characterized by two acoustic variables: the pulse period (interval between amplitude peaks within the buzz) and the mean frequency of the buzz, measured using SoundAnalysisPro (Tchernichovski et al., 1999; <http://soundanalysispro.com>). The Kent Island standard buzz segment, with a short pulse period (mean \pm SD = 10.57 \pm 0.54 ms, N = 432) and a high mean frequency (7847 \pm 234 Hz) is common to nearly all songs sung in the Grand Manan archipelago, including all of the study populations. Between 1980 and 2012, variant buzzes were sung by 38 of 457 birds recorded on Kent Island (Williams et al., 2019). All of these variant buzzes had a lower frequency (5578 \pm 651 Hz) and half (N = 19) had longer pulse periods (29.54 \pm 7.35 ms) than the standard version of the Kent Island buzz; we used buzzes with long pulse periods as 'Kent Island variant' stimuli. Songs from a population in Williamstown, Massachusetts, U.S.A. (42°41'6"N, 73°13'17"W), 550 km west-southwest of Kent Island, have a standard buzz segment with a pulse period longer than that of the Kent Island standard buzz (16.95 \pm 0.84 ms, N = 92) and a lower frequency (6842 \pm 607 Hz).

The fourth type of buzz derives from songs broadcast from speakers in the main Kent Island study area from 2013 to 2018 (Mennill et al., 2018). These songs were part of a field-based song learning experiment that asked whether and when young wild Savannah sparrows might learn these foreign speaker-presented songs during their first year. The songs played through the speakers were edited versions of foreign Savannah sparrow songs recorded from western North America and were chosen so that features of each song segment could be distinguished from the local dialect; hereafter we refer to these as 'Western (speaker)' songs and buzzes.

These Western (speaker) songs were played on a schedule and at a rate at the higher end of the natural range of territory-holding males. From 2013 through 2018, speakers were placed in fixed locations such that all birds on the study site heard the songs daily during the breeding season (details in Mennill et al., 2018). At the time of the playback experiments testing birds' responses to buzz types (late June – early July), we did not observe any of the males

holding territories near the long-term speakers directing aggressive behaviours at those speakers, or even appearing to attend to them.

A total of 30 birds copied Western (speaker) songs, either directly, from the speaker, or indirectly, by copying the songs of males that had originally copied the songs heard from the speakers (Mennill et al., 2018). As did males singing the Kent Island dialect, males singing copies of the Western (speaker) songs took up territories distributed across the Kent Island study site, successfully attracted females and fledged offspring and then returned to their territories in subsequent years.

The buzzes in the Western (speaker) songs heard on Kent Island from 2013 through 2018 varied, with mean pulse periods of 12.02 \pm 5.74 ms and mean frequencies of 6149 \pm 880 Hz. The Western (speaker) songs copied by males included buzzes with a range of characteristics similar to those of the songs broadcast through speakers (pulse period: 11.82 \pm 4.71 ms; mean frequency: 5694 \pm 833 Hz). Although the ranges of both measurements were considerably wider than those of Kent Island standard and Williamstown standard buzzes (Fig. 2a), the pulse periods of both the buzzes of Western songs played from the speakers and the buzzes of the birds that copied those Western (speaker) songs were on average similar to those of the Kent Island standard buzz, while the mean frequencies were lower. To maximize the distinctiveness of stimuli, we used buzzes from the lower part of the frequency range of the Western (speaker) songs in our playback study.

Playback Stimuli

To test birds' responses to different types of buzzes, we performed a playback study. We presented only buzzes, without the context of full song; previous research has shown that Savannah sparrows respond aggressively to buzzes presented alone, without the other elements of the song (Williams et al., 2019). This method allowed us to evaluate responses to buzzes without needing to consider any possible effects of other song segments. Sound stimuli were prepared using SoundEdit Pro (Macromedia) and Audacity (<https://www.audacityteam.org>) by extracting buzzes from high-quality song recordings. Each sound stimulus file consisted of a buzz embedded within a 12 s silence; repeating that file during playback yielded a rate of five buzz stimuli/min (Williams et al., 2019). We prepared a total of eight stimulus sets drawn from the songs of birds no longer present on the study site, with each set consisting of one Kent Island standard buzz, one Williamstown standard buzz, one Kent Island variant buzz and one Western (speaker) buzz that had been broadcast on the study area (Fig. 2b). For the Western (speaker) buzz stimuli, we chose to use only buzzes with pulse periods within the range of the standard Kent Island buzz and with mean frequencies lower than the Kent Island

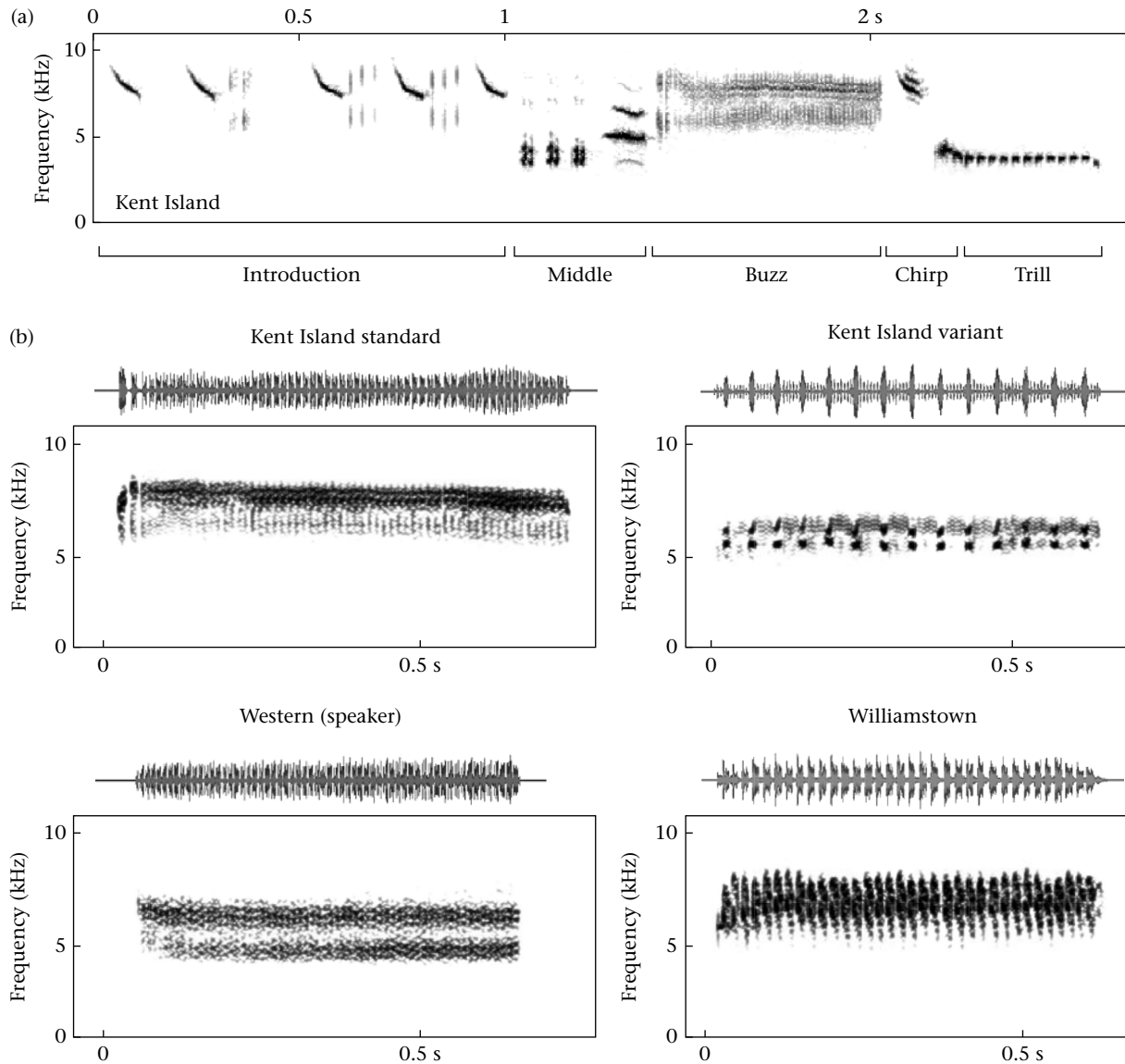


Figure 1. Savannah sparrow song segments and buzz types. (a) A typical Savannah sparrow song has five segments. The structure of the buzz segment is consistent across years within a population (Williams et al., 2019). (b) Waveforms and sound spectrograms for the four categories of buzzes used as stimuli in the playback study. Kent Island standard buzzes, with short pulse periods and high peak frequencies, were sung on Kent Island and on neighbouring islands, including Grand Manan and White Head, in all years. Western (speaker) songs were broadcast from speakers on the study site between 2013 and 2018 and varied in structure; many had short pulses and low peak frequencies. The Kent Island variant buzzes had long pulse periods and low peak frequencies. Williamstown standard buzzes, recorded more than 500 km from Kent Island, had intermediate peak frequencies and pulse periods.

buzzes. The four buzzes in each stimulus set were normalized to the same peak amplitude and edited to be within 5 ms of the same duration (sets varied in length; mean \pm SD = 0.59 \pm 0.07 s). Adjustments of buzz length were done in Audacity, either by deleting pulses from the middle of the original buzz or by copying and adding pulses from the original buzz into the middle of that buzz (the silent interval preceding each pulse was considered to be part of the pulse). The time–amplitude plot and the sound spectrogram of the resulting buzzes were carefully checked by eye to confirm that no evidence of editing was present, and the edited buzzes were also checked by ear to ensure that the editing had not introduced acoustic anomalies.

We also prepared a ‘primer stimulus’, a Kent Island song (recorded in 2003) in which the buzz had been replaced by silence. The primer stimulus was used to initially direct the subject’s attention to the playback. The primer stimulus and the buzz stimuli were stored on an iPod and presented through either a Realistic

Minimus 0.6 speaker (2012, 2016–2017) or an Anker SoundCore 2 speaker (2022) at an intensity of 70 dB as measured 2 m from the speaker with a BK 732A sound meter (fast response and A weighting).

Playback Protocol

Playback sessions were conducted in late June and early July between the hours of 0730 and 1430, in 2012, 2016, 2017 and 2022. To avoid attracting neighbours to contested boundaries, the playback speaker was placed within a male’s territory. The playback speaker’s location was also at least 25 m from any of the broadcast speakers used in the experiment described in Mennill et al. (2018); territories average approximately 50 m in diameter. Kent Island males were colour-banded and the territory boundaries were ascertained by repeated visual observation of each male’s movements. Subjects on Grand Manan Island and White Head Island

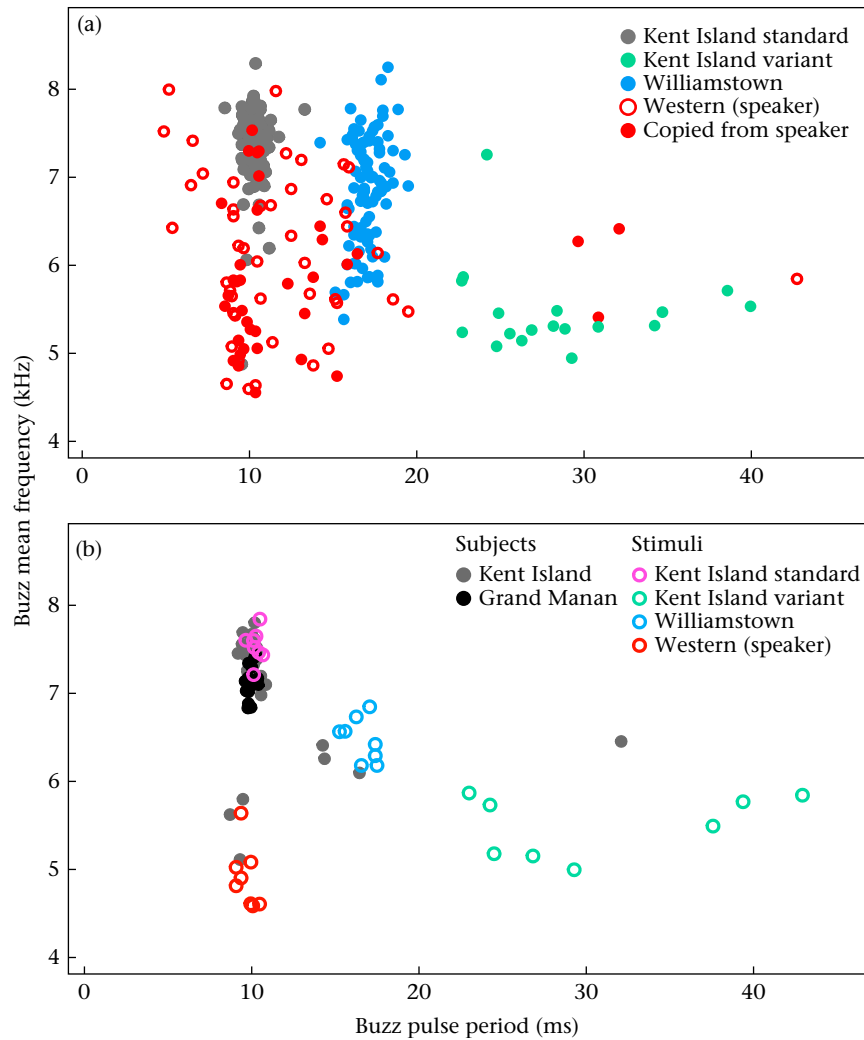


Figure 2. Acoustic features of Savannah sparrow song buzzes. (a) Kent Island standard buzzes have high mean frequencies and short pulse periods, while Williamstown standard buzzes have longer pulse lengths and a broader range of frequencies. The Kent Island variant buzz (sung between 1993 and 2009) had long pulse periods and low frequencies. The Western (speaker) songs broadcast on the study site between 2013 and 2018 had buzzes with a broad range of frequencies and pulse periods; many of the birds that copied those songs sang buzzes with low frequencies and short pulse periods. (b) The characteristics of the buzzes used as playback stimuli (open circles, eight of each type) and, when the song had been recorded, the buzzes sung by subjects of the playbacks on Kent Island (31 of 31 in 2016–2017) and Grand Manan (14 of 16 in 2016). Some of the Kent Island subjects had copied their buzzes from Western (speaker) songs broadcast on the study site, and so sang nonstandard buzzes.

(which we grouped as ‘Grand Manan’, since neither island experienced songs broadcast through speakers) were unbanded; we observed their movements prior to playback in order to determine their territory boundaries, and their songs were recorded whenever possible.

We followed a playback protocol that we established in previous work (Williams et al., 2019). The primer stimulus was played first to attract the male’s attention. The primer continued for 2 min after a male first responded by either approaching the speaker, performing a flutter flight or wing flutters (Wheelwright & Rising, 2008), or singing a soft song (Akçay et al., 2015; Moran et al., 2018). After the primer playback ended, aggressive displays usually persisted. We defined ‘disengagement’ as the first occasion when the subject either (1) sang a full, loud song, (2) began to forage, (3) began to preen or (4) flew more than 30 m from the speaker. A 2 min silent interval followed disengagement from the primer stimulus. The first buzz stimulus was then played for 2 min. We observed and characterized the response to that stimulus. After disengagement from the buzz stimulus, a 2 min silent interval followed, and then the next buzz stimulus was

played for 2 min. This sequence was repeated until a bird heard all three (2012) or four (2016–2017 and 2022) of the buzz stimulus types. The stimulus types were played in a varied, balanced order across playback trials. We used the 2 min interval between the end of one response and the beginning of the next stimulus to minimize any effect of variation in the motivational state of the bird across stimulus presentations. Playback sessions were not initiated on neighbouring territories on the same day. If a session failed because of disruptions on a bird’s territory (for example, an intrusion by a neighbouring bird or a gull landing nearby, or on Grand Manan and White Head islands, an occasional human on a recreational vehicle), at least 2 days passed before a second session was attempted. Apart from these considerations, territories on the study site were chosen at random on each given day from those that had not yet experienced a successful playback session, with the exception that, in 2022, an effort was made to include subjects of different ages and different current auditory experience of copied Western (speaker) songs.

In 2012, before the song learning experiment of Mennill et al. (2018) had begun and no speakers broadcasting songs were

present, we used three types of buzz stimuli: Kent Island standard, Williamstown standard and the Kent Island variant (in 2012, we had 15 stimulus sets, each with three stimuli; results for this year were originally reported in Williams et al., 2019). In 2016 and 2017, when speakers were broadcasting songs on Kent Island, and in 2022, 4 years after the speakers were last used, we added the Western (speaker) stimulus type to the playback study. There were eight stimulus sets in those years, and each subject was tested with all four buzz stimulus types. None of the 2016–2017 subjects were tested in 2012, and none of the 2022 subjects were tested in previous years.

We measured response duration (seconds from the end of the stimulus to the end of the response, or disengagement, see Fig. 3). We also scored a number of other variables (including approaching the speaker, flights, flutter flights, wing flutters and soft songs; Moran et al., 2018), but, as we have noted previously, individual birds vary in the aggressive behaviours they use in their responses. Response duration (time between the end of the stimulus playback and disengagement time) has previously been shown to be the most useful measurement for comparisons across Savannah sparrows with different behavioural profiles (Williams et al., 2019), and so we used that as our metric for analysis.

Statistical Analysis

We did not include in the analysis any playback trials in which an intruder disrupted the subject's behaviour during a playback session or when multiple males responded to the playback stimulus. In addition, trials within a playback session that followed an intrusion by a human or neighbouring sparrow were eliminated from the analysis. Only those subjects that completed at least two valid trials within a session were included in the analysis. In 2012, we completed 16 playback sessions, each with three stimulus types, on Kent Island (two of the stimulus trials were eliminated from the analysis because of intrusions by a neighbouring male, leaving a total of 46 stimulus playbacks). All 2012 Kent Island subjects had their songs recorded. In 2016, we completed 16 playback sessions, each with four stimulus types, on Grand Manan and White Head islands; 14 of the subjects also had their songs recorded. Also in 2016–2017, we completed 31 sessions, each with four stimulus types, on Kent Island (all of these birds were recorded). In 2022, we completed 18 playback sessions, again with four stimulus types each, on Kent Island (all subjects' songs were recorded); four stimulus playbacks (of 72) were eliminated from analysis because of intrusions by neighbouring males or because only the female from the territory responded.

We evaluated the effect of stimulus type upon response duration using mixed-effects linear models implemented within the lme4 package in R (Bates et al., 2015; R Core Team, 2017). These models also included trial number and subject identity as random variables. The overall model's significance was assessed using an ANOVA test (Satterthwaite's method) and the emmeans package was used for post hoc tests for differences between groups using the Kenward–Roger method (Lenth, 2022). Data were visualized using ggplot2 (Wickham, 2016) and sciplot (Morales, 2020).

All birds in this study were mated males. Breeding status, date and time of day were not included in the analysis because these factors did not affect responses in pilot studies (H. Williams, personal observation). We asked whether female presence and behaviour (responding to the playback or not) affected male response in this study; it did not ($F_{2,185} = 1.04$, $P = 0.36$). We also asked whether responses varied systematically across the different sets of stimuli that were matched for duration and amplitude (see Playback Stimuli above); they did not ($F_{7,180} = 1.36$, $P = 0.22$). Therefore female presence and stimulus set were not included in the model. To test the effects of interactions between variables and the responses to different stimulus types, a null model without the interaction was compared to the full model with the interaction and reported as a chi-square statistic.

To assess the possibility that birds on Kent Island in 2016–2017 had habituated to songs heard from long-term speakers and so were less responsive to playback overall, we compared their responses to successive stimuli within a playback session to the responses of birds from Grand Manan in 2016 (which had not heard songs from long-term speakers). We first removed the responses to stimulus types familiar to Grand Manan and White Head island birds (Kent Island buzzes) and to Kent Island birds (both Kent Island and Western buzzes) from the data set for those 2 years. We then used a GLMM to evaluate the effect of trial number, location and their interaction on response duration (subject identity was included as a random variable).

To test the effect of auditory experience with Western (speaker) buzzes on response duration, we analysed the 2022 data using two generalized linear models. The first included a variable denoting whether a bird had exposure to Western (speaker) buzzes in the same year as the playback (including both subjects that sang a copied version of the Western buzz and those with territories neighbouring that of a bird singing a copied Western buzz). The second model included a variable denoting whether a subject had extensive daily exposure to nonstandard buzzes during the song learning period. This allowed us to compare the responses of birds that hatched between 2014 and 2018 and so heard the Western songs broadcast

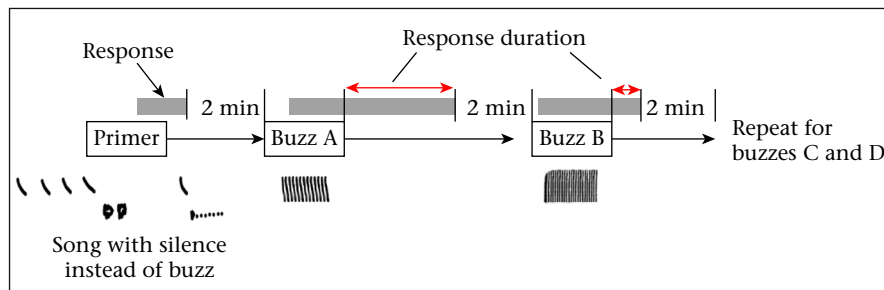


Figure 3. Schematic of the playback experiment protocol. The playback protocol was designed to minimize variation in behavioural state at the beginning of each trial (Williams et al., 2019). A 'primer' stimulus (a standard Savannah sparrow song with its buzz replaced by silence) was played for 2–5 min to attract the attention of the territory holder; the stimulus stopped 2 min after the bird's first approach (trials were not continued if there was no approach at the end of 5 min). When the bird ceased responding (sang a full, loud song, began foraging or preening, or flew more than 30 m away from the speaker), a 2 min silent period followed. At the end of that interval, the first buzz stimulus was played for 2 min. The responses of the bird were noted and the duration of the response was scored as the period during which the bird continued responding after the buzz playback stopped. To standardize behavioural state at the beginning of each stimulus, the playback of each stimulus was always begun 2 min after the bird stopped responding to the previous stimulus.

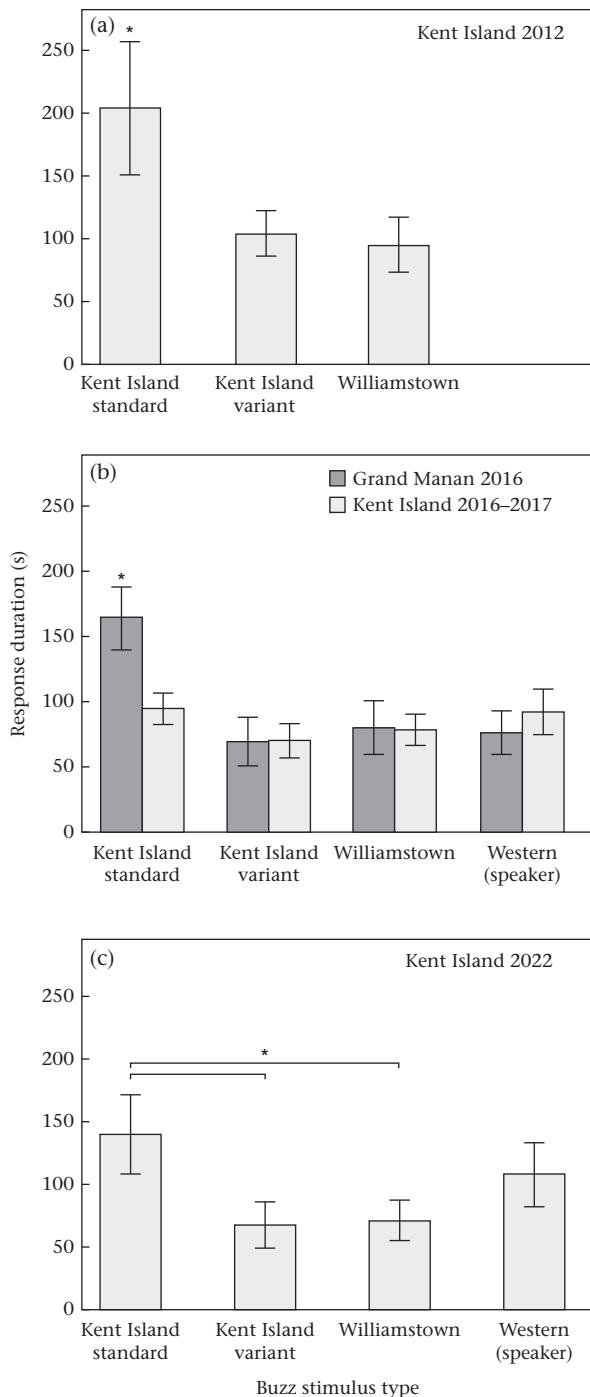


Figure 4. Duration of responses to different buzz types across 10 years and two sets of islands. Longer response durations represent stronger aggressive responses. (a) Responses of Kent Island birds in 2012, prior to the broadcast of Western (speaker) buzzes, to Kent Island standard buzzes, variant Kent Island buzzes and Williamstown standard buzzes. (b) Responses of Kent Island and Grand Manan birds in 2016–2017 to the same three buzz types as well as to Western (speaker) buzzes; during this period Western songs were broadcast through speakers on Kent Island. (c) Responses of Kent Island birds in 2022 to the four different buzz types, 4 years after speaker broadcast of Western songs ended. Error bars represent 95% confidence intervals. Asterisks denote responses that were significantly longer than all other responses in (a) and (b), $P < 0.05$. In (c), the asterisk and associated lines denote groups that were significantly different in response time ($P < 0.05$).

from speakers while developing their own songs to those of birds that hatched later and could only have heard the Western songs from adult males that had previously copied such songs.

Ethical Note

All applicable international, national and institutional guidelines for the care and use of animals were followed. Procedures were carefully reviewed by the Williams College Institutional Animal Care and Use Committee (WH-D), the Bowdoin College Research and Oversight Committee (2009–18), the University of Guelph Animal Care Committee (08R601) and the University of Windsor Animal Care Committee (AUPP-20-09) and were carried out as specified by the Canadian Wildlife Service (banding permit 10789D). All experiments complied with the current laws of the U.S. and Canada. Birds were captured for banding using mist nets and were immediately removed from the net and processed (colour bands were placed on the legs and body measurements were taken) before being released at the capture location. No birds were kept in captivity for this study.

RESULTS

Responses to Buzz Stimuli Were Affected by Exposure to Broadcast Western Songs

In 2012, Kent Island males' response duration varied with stimulus type ($F_{2,44} = 3.28$, $P = 0.05$ for the generalized linear model; Fig. 4a). Responses to buzzes from the local dialect (Kent Island standard) lasted longer (i.e. were more aggressive) than responses to the two other buzz types, including the Kent Island variant buzz ($t_{27} = 2.14$, $P = 0.04$) or the Williamstown standard buzz ($t_{28} = 2.28$, $P = 0.03$). The song learning experiment had not yet begun in 2012 and therefore no Western (speaker) buzz stimuli were presented. Similarly, Grand Manan males tested in 2016 (which had not heard songs broadcast on their breeding sites) discriminated between buzz types ($F_{4,60} = 10.89$, $P < 0.0001$ for the model; Fig. 4b), responding more aggressively (with a longer response duration) to buzzes from their own dialect (Kent Island standard) than to buzzes of the Kent Island variant ($t_{44} = 5.14$, $P < 0.0001$), the Williamstown standard buzz ($t_{44} = 4.47$, $P < 0.0001$) or the Western (speaker) buzz ($t_{44} = 4.14$, $P < 0.0002$).

In contrast, on Kent Island in 2016 and 2017, when the Western songs were being broadcast from speakers on the study site (and had been heard each breeding season since 2013), Kent Island males' responses did not differ across buzz types ($F_{4,120} = 0.81$, $P = 0.49$; Fig. 4b). Instead, the duration of the response to the Kent Island standard buzzes fell to the same level as for the other buzz types, with no significant differences in comparison to the Kent Island variant ($t_{97} = 1.41$, $P = 0.16$), the Williamstown standard ($t_{97} = 0.90$, $P = 0.37$) or the Western (speaker) buzzes ($t_{97} = 0.27$, $P = 0.79$). The stronger response to the local dialect buzz type was no longer present.

Because the 2016–2017 Kent Island birds had been exposed to songs from speakers during the breeding season, they might have become habituated to stimuli from speakers and consequently either had lower response intensities to all stimuli played through speakers than did birds without such exposure, or responded similarly (and relatively briefly) to all types of stimuli once they had determined that the source was a speaker. We tested these possibilities by (1) comparing overall response durations of Kent Island birds to those of Grand Manan birds, who did not hear songs from speakers, and (2) comparing the longest responses from birds on Kent Island (exposed to speakers playing Western songs throughout the breeding season) and those on Grand Manan (the control group). There was no difference in average response times at the two sites in 2016–2017 ($F_{1,186} = 1.20$, $P = 0.28$), and Kent Island birds continued to respond for an average of 83.8 s after the speaker stopped playing the stimulus. A total of 35 (of 188)

responses to stimuli continued for 3 min or more after the end of the playback trial: 15 responses (56% of which were to the Kent Island dialect) by eight different Grand Manan birds and 20 responses (21% of which were to the Kent Island dialect) by 15 different Kent Island birds. Finally, in a model testing the interaction of location and trial number on responses to unfamiliar stimulus types, there was a clear overall habituation effect (trial number: $F_{1,107} = 10.97$, $P < 0.01$) but no difference in the habituation of Grand Manan and Kent Island birds (interaction: $F_{1,107} = 1.26$, $P = 0.26$) or in their overall response durations ($F_{1,107} = 1.06$, $P = 0.31$).

In 2022, 4 years after songs had last been played through long-term speakers on Kent Island, Kent Island males' responses again differed in response to different buzz types ($F_{4,64} = 3.34$, $P = 0.027$; Fig. 4c). Males' responses were longer to Kent Island standard buzzes than to Kent Island variant buzzes ($t_{48} = 3.25$, $P < 0.01$) or to Williamstown buzzes ($t_{48} = 2.25$, $P = 0.029$). However, there was no significant difference between the duration of the response to the Western (speaker) buzzes and the standard Kent Island buzzes ($t_{47} = 1.42$, $P = 0.16$).

Role of the Acoustic Distance Between the Stimulus Buzz and the Subject's Buzz

For the 2016–2017 playback studies, we calculated the acoustic distance between the buzz each subject sang as part of his song and each stimulus buzz that he experienced (see Fig. 5). We then asked whether the acoustic distance between the male's own buzz and the stimulus predicted the duration of the response to that stimulus. For the Grand Manan birds, all of which sang Kent Island standard buzzes and did not hear other buzz types from their breeding territories, response duration declined with increasing difference between the subject's buzz and the stimulus buzz ($r^2 = 0.12$, $F_{2,42} = 9.53$, $P < 0.01$; Fig. 5b). For these birds, all of the foreign buzzes, which evoked shorter (weaker) responses, were quite different from the birds' own buzzes. However, for the Kent Island birds, whose buzzes varied much more across individuals because some males had copied them from the Western (speaker) songs (see Fig. 2a), there was no significant relationship between response duration and the acoustic distance between the subject's own buzz and the stimulus buzz ($r^2 = 0.004$, $F_{2,124} = 0.86$, $P = 0.36$; Fig. 5a).

Role of the Bird's Own Buzz Type

In 2016 and 2017, when three or four generations of birds (respectively) had been exposed to Western songs broadcast through speakers on the main study site, 10 of the 34 playback subjects had copied those songs instead of the local dialect. We compared the responses of these birds to those of birds singing standard Kent Island songs and buzzes (Fig. 6a). Whether a male sang a Kent Island standard buzz or a copied a Western (speaker) buzz did not affect response duration to the different buzz types ($\chi^2_3 = 1.33$, $P = 0.72$).

Role of Auditory Experience

We asked whether age and the corresponding experience with the local dialect influenced the duration of the response to the Kent Island buzzes in the 2012 males, who had no experience of other buzz types. Males in their first ($N = 8$) and second ($N = 5$) breeding years did not differ in their responses to the different buzz types ($\chi^2_3 = 0.22$, $P = 0.97$; three birds were of unknown age and were excluded from the analysis).

In 2022, 4 full years after the end of the speaker experiment, nearly all of the breeding males on the study site (39 of 42) sang standard Kent Island songs. Of the subset of 18 males that were playback subjects, five had auditory experience with copied Western songs during the 2022 breeding season, either because they had copied a Western song ($N = 1$) or had territories adjoining those of birds that had copied a Western song ($N = 4$). There was no significant difference in the average overall response durations of the two sets of birds that differed in their auditory experience during the 2022 breeding season ($\chi^2_3 = 5.44$, $P = 0.14$; Fig. 6b). However, when responses to each individual stimulus type were examined, males who had either copied a Western song or had neighbours that sang copied Western (speaker) songs responded less strongly to the standard Kent Island buzzes ($F_{1,15} = 4.69$, $P = 0.047$) than did the younger males who only heard standard Kent Island buzzes from their neighbours.

In 2022, four of the playback subjects had heard Western songs broadcast from speakers as they were learning and developing their own songs, because they had hatched prior to 2018 (three of those birds sang standard Kent Island songs). These males, who had extensive auditory experience of the Western songs during their

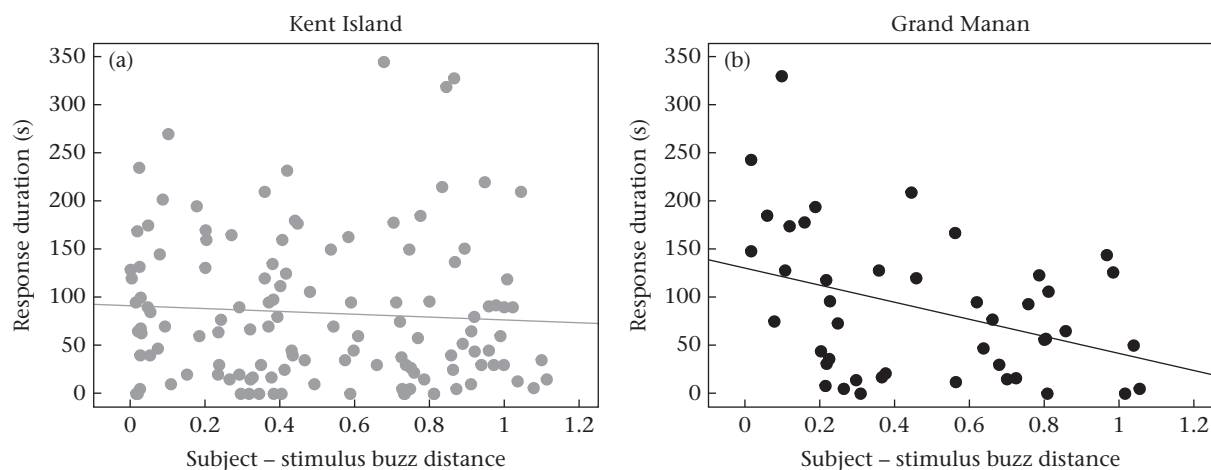


Figure 5. Response duration as a function of the acoustic difference between the stimulus buzz and the subject's buzz. Buzz mean frequency and pulse period were normalized so that ranges were between 0 and 1 and the acoustic difference between the subject's buzz and each of the stimulus buzzes he heard was determined by calculating the Euclidean distance between the two buzzes.

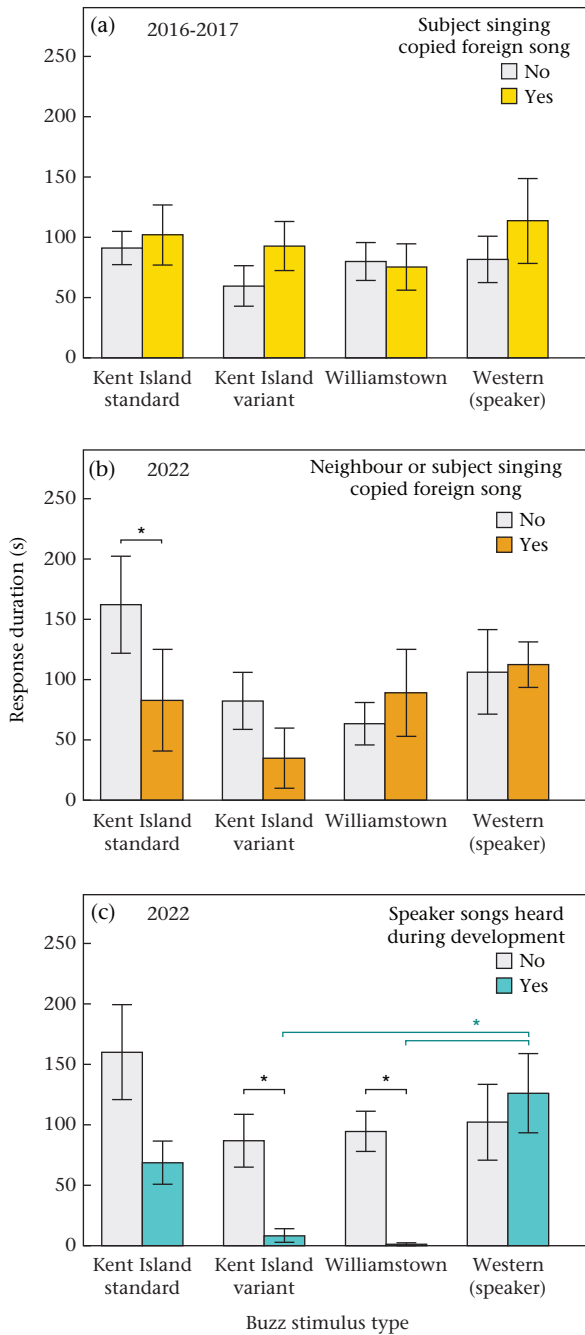


Figure 6. Effects of auditory and singing experience on responses to different buzz types. (a) Comparison of responses of birds singing copied Western songs and birds singing Kent Island standard songs in 2016–2017. (b) Responses of birds neighbouring or singing copied Western songs compared to those of birds singing and neighbouring only Kent Island standard songs in 2022. (c) Responses in 2022 of birds hatched prior to 2018 who experienced broadcast of Western songs through speakers or from song models throughout song development; their responses are compared to those of birds hatched later. Error bars represent 95% confidence intervals. Asterisks denote differences between responses to playback stimuli ($P < 0.05$).

first year, responded differently to the buzz stimulus types when compared to males that hatched in subsequent years and could only have heard Western songs sung by live birds ($F_{3,60} = 4.08$, $P = 0.012$; Fig. 6c). The older males with more extensive early auditory experience of the Western songs and the younger males who did not experience foreign songs broadcast from speakers responded similarly to the Western speaker buzz stimuli

($F_{1,15} = 2.19$, $P = 0.16$) and the Kent Island buzz stimuli ($F_{1,15} = 0.19$, $P = 0.67$; the apparent difference in Fig. 6c disappeared when trial order was included in the model). However, males that had experienced the Western speaker songs during song development had significantly shorter response durations to both the Kent Island variant buzzes ($F_{1,13} = 4.85$, $P = 0.047$) and the Williamstown standard buzzes ($F_{1,13} = 14.68$, $P < 0.01$) than did the younger males that had not heard the Western songs broadcast through speakers. Within the 2022 older males who had experienced broadcast speaker song during development, responses to the Western speaker buzzes were longer than to the other foreign buzzes (old Kent Island variant: $t_8 = 4.51$, $P < 0.001$; Williamstown: $t_8 = 4.59$, $P < 0.001$) in a model that included trial order. However, the difference between these experienced males' responses to the Western and Kent Island buzzes did not reach significance ($t_8 = 1.85$, $P > 0.05$).

DISCUSSION

As is the case for many songbird species, wild male Savannah sparrows on Kent Island in 2012 and on neighbouring islands in 2016 typically responded longer and hence more strongly to features specific to the local dialect, defined by the buzz segment. This discrimination disappeared on Kent Island in 2016 and 2017, when male Savannah sparrows had been exposed to long-term playback of Western songs via speakers in their breeding area. In those years, males' responses to all buzz stimuli were similar and equivalent to the weaker responses to unfamiliar buzzes in 2012. In 2022, after the speakers broadcasting Western songs had been absent for 4 years, discrimination returned, with most Kent Island birds again responding more strongly to buzzes from the original local dialect (and equally weakly to all other stimuli). In 2016, populations on neighbouring islands (Grand Manan Island and White Head Island) had not experienced the long-term playbacks of Western songs, and, like the 2012 Kent Island birds, responded to Kent Island standard buzzes for twice as long as to other buzz types. Longer, more aggressive responses to the local dialect occurred only when birds rarely experienced foreign songs in their breeding environment (when the dialect was homogeneous).

Although the 2022 subjects responded more strongly to Kent Island standard buzzes than to foreign buzzes, average response duration to the local buzzes was not as long as it had been in 2012. This seems likely to be due, at least in part, to differences in the subjects' experience with foreign songs. Some males had copied their songs either directly from the Western songs broadcast from speakers or secondarily from males that had copied the speaker songs (Mennill et al., 2018). As a consequence, both the males singing copies of Western songs and the males that held territories adjacent to them heard foreign buzzes during the 2022 breeding season. These birds had equivalent responses to the different buzz stimuli and did not respond more aggressively to the Kent Island standard local dialect.

In 2022, birds that had hatched in 2018 or earlier had extensive exposure to Western buzzes from speakers during their first year(s), but primarily heard standard Kent Island buzzes in subsequent years and in the current breeding year. These older males responded moderately to both Western buzzes and standard Kent Island buzzes, but very weakly or not at all to the other buzz stimuli. The significantly weaker responses to unfamiliar buzz types indicates that early auditory experience results in lasting memories that are important for defining what a bird recognizes as its local dialect.

Taken together, these results highlight the importance of auditory experience throughout an individual's life in defining an auditory representation of the local song dialect. Both early

experience of foreign songs (hearing them during song development) and current experience of foreign songs (hearing them in the same year as the playback test) reduced discrimination of the local dialect. Studies using other species have also suggested that familiarity may be the basis for recognizing and responding more strongly to a local dialect (Baker et al., 1981; Chilton et al., 1990; Vehrencamp et al., 2003). Dickcissels, *Spiza americana*, which disperse after learning their songs, respond similarly to local and foreign songs, and northern black-throated blue warblers that hear southern dialects during migration do not behaviourally discriminate between northern and southern dialects (Colbeck et al., 2010). The auditory experience in these two situations is similar to that of the Kent Island Savannah sparrows that heard foreign songs through speakers and likewise did not discriminate among buzz types. The local song environment, both as experienced during song development and during the current breeding season, thus defines how male Savannah sparrows respond to the buzz segment, a dialect marker within their songs.

In playback experiments involving pairs of related species, auditory experience is similarly important. Auditory experience with the songs of a related sympatric species heightened Japanese tits', *Parus minor*, and varied tits', *Sittiparus varus*, responses to their local dialect (Hamao, 2016). Similarly, short-toed treecreepers, *Certhia brachydactyla*, had stronger responses to the songs of common treecreepers, *Certhia familiaris*, when the two species were in sympatry (Gil, 1997), as did black redstarts, *Phoenicurus ochruros*, in sympatry with redstarts, *Phoenicurus phoenicurus* (Sedláček et al., 2006). Slater and Catchpole (1990) suggested that such a result would be expected when the two species are ecological competitors, a form of the threat hypothesis (Temeles, 1994). These results are also consistent with our finding that conspecific buzzes from unfamiliar dialects elicited weaker responses than the local dialect and that males with extensive experience with two buzz types (such as the older 2022 subjects in our study) responded equally (though not strongly) to the two buzz types they had heard previously from many sources, but did not respond at all to unfamiliar buzzes.

A possible mechanistic explanation for the reduction in average response duration to standard Kent Island buzzes (but not to other buzz stimuli) while speakers were playing Western buzzes on the study area arises from the hypothesis that auditory discrimination of conspecific songs is based on their similarity to the bird's own song. The similarity hypothesis predicts that the birds who copied Western songs should produce shorter (weaker) responses to the Kent Island buzzes. The similarity hypothesis was originally suggested by the finding that songbirds form neural representations of the songs that they hear during development, specifically in auditory mirror neurons in the song system of the brain. Such neurons fire both when the bird is singing and when it hears its own song or a similar song (Margoliash, 1983; Prather et al., 2008, 2009, 2010; Williams & Nottebohm, 1985). Past studies in other New World sparrows comparing responses of birds to their own and foreign dialects have found a correlation between response strength and acoustic similarity to the dialect of the subject (Fernández-Gómez et al., 2021; Lipshutz et al., 2017). We observed the same correlation when we plotted the responses of Grand Manan birds (all of which sang the local dialect) against the similarity between the acoustic characteristics of their own songs and those of the playback stimuli. However, our Grand Manan data and the data from past studies are not a strong test of the hypothesis that a bird's response is based on the similarity between a stimulus and its own song. When studies use stimuli from two or more dialects, and each of the subjects have sung and heard only one of the dialects, the acoustic characteristics of the stimuli fall into discrete clusters that are either similar (the same dialect) or dissimilar (a foreign dialect)

to the bird's own song, precisely because birds singing the same dialect have similar songs (Freeman & Montgomery, 2017). Our 2016–2017 Kent Island data allow for a stronger test of the similarity hypothesis because some of the subjects had copied foreign songs and the population sang a variety of buzz types. The variability of the subjects' buzzes allowed us to specifically test whether responses were related to the similarity of the features in the subject's buzz and the stimulus buzzes. When the birds' own songs were diverse, we found that the response to a stimulus buzz was not related to the similarity between the stimulus buzz and the bird's own buzz. A further test of the hypothesis that birds use comparisons to their own songs to discriminate among dialect markers comes from the responses of birds singing copies of Western songs in 2016–2017 on Kent Island. These birds' responses to different stimulus types were statistically identical to those of birds singing the standard dialect, as is also the case in western song sparrows, *Melospiza melodia* (Akçay & Beecher, 2020). Taken together, these two lines of evidence suggest that auditory experience, rather than the sensorimotor processes of song learning and production, serves as the mechanism for discriminating among different dialects and hence for the stronger responses to the local dialect.

Familiarity, in the sense of auditory experience with other birds' songs, is clearly important in determining how aggressively songbirds respond to songs of local and familiar dialects versus those of distant and unfamiliar dialects. However, familiarity alone cannot explain our results. The local song dialect was sung by the majority of birds on the Kent Island study area in 2016 (29 of 34) and 2017 (43 of 57), and so this dialect was familiar to all of the birds used as playback subjects in those years, but they did not have heightened responses to Kent Island buzzes. During those years, however, all birds on the study area were also familiar with the foreign Western songs, either as sung by their neighbours or as played back through speakers that were placed so as to be heard on all territories as part of the long-term song learning experiment. Thus, although the number of birds singing the standard Kent Island dialect was greater than the number of birds singing the foreign Western songs and the number of speakers broadcasting the foreign Western songs, birds had experience of both foreign and local buzzes as sung by live birds (as well as the foreign songs broadcast through speakers). During this period, none of the buzzes elicited the longer responses normally given to a local dialect; instead, the responses to all of the buzz stimuli were of the shorter duration typically elicited by foreign buzzes. In 2022, 4 years after the use of speakers had been discontinued, the local dialect was sung by 93% (39 of 42) of the Savannah sparrows recorded on the study site. Apart from the males that been exposed to foreign songs early in development or from neighbours during that year, males tested in 2022 had a heightened response to the local dialect's buzz. In this context, it is worth noting that the response to the local dialect's buzz type was longer only when the population sang a homogeneous (100%) or nearly homogeneous (>90%) local buzz dialect: Kent Island in 2012 and 2022 and Grand Manan in 2016.

An alternative explanation for the absence of behavioural discrimination between buzz types in 2016–2017 would be that the subjects had learned that loudspeakers were not a territorial threat, because songs were broadcast from speakers as part of a long-term learning experiment (Mennill et al., 2018), and hence the birds responded to each stimulus for only long enough to determine that it was coming from a speaker. Three points argue against this explanation. First, throughout the course of our long-term study, our observations of birds' reactions to loudspeakers suggest that differential experience with songs broadcast from speakers does not influence their response. Kent Island birds have been exposed to songs from speakers, to varying degrees, since 2004. Each year,

we lure birds into mist nets for banding, using stimuli that differ from those used in the current experiment and from those used in Mennill et al. (2018), and we have not observed any changes in responses to those playbacks over the years. We have also conducted other playback experiments during this time frame, including those reported in Moran et al. (2018) and Williams et al. (2022), and we observed strong responses to playback stimuli in those experiments. Second, the longest (strongest) responses by Kent Island birds in 2016–2017 were comparable to those of Grand Manan birds in 2016 but were distributed differently; the longest Grand Manan responses were disproportionately given to Kent Island stimuli, while those of Kent Island birds were proportional to the stimulus types. Third, when we excluded familiar stimulus types and compared habituation within playback sessions for Kent Island subjects in 2016 and 2017 (birds exposed to long-term speaker playbacks) and Grand Manan subjects in 2016 (birds without such exposure), there was no difference between the two populations in either the time course of habituation or the overall response duration. These lines of evidence argue against the possibility that the lack of behavioural discrimination of buzz types by the 2016–2017 Kent Island birds was a side-effect of habituation due to long-term exposure to songs emanating from speakers.

Homogeneity in the song dialect as well as familiarity with that dialect both appear to be important components of the auditory experience that allows Savannah sparrow males to discriminate among local and foreign buzz types and respond more strongly to familiar local buzzes. A buzz type only appears to serve as a dialect marker if it is sung by all or nearly all of the members of the population, as on Kent Island in 2012 and 2022 and in the Grand Manan population in 2016. To respond more strongly to the local buzz, males must first recognize and distinguish a local dialect buzz from other buzz types, which requires familiarity in the form of auditory experience. Older males with extensive auditory experience of foreign buzzes early in development had responses that were influenced by that experience years later, but they did not respond to foreign buzz types that they had not experienced. However, the local buzz type only achieved the special status that singled it out for heightened responses when the same buzz type was sung by more than 90% of the population. When more than one familiar dialect was present, as in 2016–2017, when both the Kent Island standard buzz and the Western (speaker) buzz were heard on the study site, the dominant Kent Island buzz elicited weaker responses, equivalent to those elicited by foreign dialects in other years. Both familiarity and homogeneity appear to be necessary for the heightened response to the local dialect that we see in Savannah sparrows, and we suggest that these two criteria are important for discrimination of local dialects in songbirds more generally.

Author Contributions

H.W. conceived the study, recorded songs, prepared playback stimuli, performed playback experiments, analysed data and wrote the original version of the paper; S.L.D. recorded songs, performed playback experiments, generated demographic data and edited the paper; C.R.R. recorded songs, performed playback experiments, analysed data and edited the paper; D.R.N. generated demographic data and edited the paper; S.M.D. generated demographic data and edited the paper; D.J.M. designed and set up the song learning study that broadcast Western songs on the study site, recorded songs, generated demographic data and edited the paper.

Data Availability

Data files including measurements of buzz segment acoustic characteristics and responses to playback experiments, as well as

audio files with playback stimuli are available at <https://doi.org/10.5061/dryad.0vt4b8h5n>.

Declaration of Interest

None.

Acknowledgments

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