

Birds respond more strongly to locally common versus locally rare songs: a playback experiment with Savannah sparrows

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Animals' learned vocalizations often show high levels of intraspecific variation, and different variants may play different roles in attracting mates and settling territorial disputes. In any animal population with variable vocalizations, certain acoustic variants may be common and others rare. The responses of animals to local versus nonlocal sounds have been well characterized in prior investigations, but few investigations have explored the reactions of animals to songs that are present at different frequencies of occurrence within a population. Using an experimental approach to investigate a breeding population of Savannah sparrows, *Passerculus sandwichensis*, we tested the responses of territorial male songbirds to playback of locally common songs, locally rare songs and heterospecific songs. Male sparrows showed strong responses to conspecific song but weak responses to heterospecific song. Males showed their strongest responses to locally common songs and weaker responses to locally rare songs. Birds did not appear to discriminate between playback songs based on whether they were of the same song type as their own. We suggest that male Savannah sparrows perceive locally rare songs as weaker threats than locally common songs, similar to birds' reactions to foreign dialects. This could be due to low familiarity with locally rare songs, reduced female preference for locally rare songs, decreased success with territory defence for males singing locally rare songs or other perceived differences between locally rare and locally common songs. Overall, our results suggest that different song types elicit different responses from territorial songbirds, even songs that are found within the same population with different frequencies of occurrence.

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Animal vocalizations often vary between individuals, giving rise to geographical patterns in signals that are important for mate attraction and territory defence (Bradbury & Vehrencamp, 2011; Podos & Warren, 2007). Understanding the origin of those differences and their consequences stands to deepen our understanding of animal behaviour. A landmark study of the songs of white-crowned sparrows, *Zonotrichia leucophrys*, revealed that birds exhibit vocal dialects, where animals exhibit stereotypy within populations but variation between populations (Marler & Tamura, 1962). Vocal dialects have been described in a number of taxa, including humans (Wolfram, 2007), whales (Whitehead et al., 1998) and birds (Wright, 1996). Subsequent studies have shown

that dialects tend to arise in species with vocal learning and short dispersal distances (Eilers & Slabbekoorn, 2003; Planqué et al., 2014; Podos & Warren, 2007). The spatial scale of vocal dialects varies tremendously. While dialects often span hundreds or thousands of kilometres, dialects also occur across small geographical distances (Date & Lemon, 1993; Hensel et al., 2022; Payne, 1978). Such 'microdialects' have been defined as dialects shared by 10 or fewer individuals and spanning less than 2 km in any given direction (Podos & Warren, 2007). At the microdialect scale, we expect to find populations composed of individuals that produce locally common vocal variants living near animals with locally rare vocal variants. Individual responses to locally common and locally rare variants provide an opportunity to explore how the behaviour of territorial animals shapes emergent properties of acoustic variation at a population scale.

The songs of oscine songbirds have received much research attention, partly due to the complex forces that shape birdsong and

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result in patterns of geographical variation (Marler & Slabbekoorn, 2004; Podos & Warren, 2007). Dialects, both macrogeographical and microgeographical, appear to be particularly common among oscine songbirds, likely due to the importance of vocal learning in this group, along with their often small dispersal distances (Podos & Warren, 2007). Song dialects have been described in various songbird species, including white-crowned sparrows (Marler & Tamura, 1962, 1964), orange-tufted sunbirds, *Cinnyris bouvieri* (Leader et al., 2000, 2008), yellow cardinals, *Gubernatrix cristata* (Fracas et al., 2023), and European wrens, *Troglodytes troglodytes* (Catchpole & Rowell, 1993). It is widely recognized that birdsong plays a dual function, both attracting mates and signalling territory ownership to conspecifics, often simultaneously (Catchpole & Slater, 2008; Mennill et al., 2002). Because birdsong is shaped by intra- and intersexual selection and shows patterns of geographical variation, we might expect that birds will react differently to different song variants based on whether they are foreign or local and common or rare.

Past research has shown that birds tend to respond most strongly to their own regional song dialect, respond less strongly to foreign song dialects and respond most weakly to heterospecific song (Slabbekoorn & Smith, 2002). This has been demonstrated in Darwin's finches (*Geospiza* spp.; Grant & Grant, 1996; Ratcliffe & Grant, 1985), song sparrows, *Melospiza melodia* (Searcy et al., 1981, 1997), white-crowned sparrows (Baker et al., 1981; Derryberry, 2011; Nelson & Soha, 2004) and swamp sparrows, *Melospiza georgiana* (Balaban, 1988), among others. These studies typically examine responses to song dialects sampled across populations, with little investigation of responses to local microdialects within populations. One example of a study that examined responses to different local songs is Ratcliffe and Grant's (1985) playback study on Española cactus finches, *Geospiza conirostris*. Male Española cactus finches on Isla Genovesa sing one of two song types (Grant, 1984), and playback experiments suggested that males reacted equally strongly to both song types, despite one song type being slightly more common in the population (Grant, 1984; Ratcliffe & Grant, 1985). Another example of a study examining responses to different local songs is Thomas et al.'s (2021) observational study of Savannah sparrows, *Passerculus sandwichensis*. Among Savannah sparrows, more aggressive calls were observed on the territories of newly established males singing songs similar to those of their neighbours compared to newly established males singing songs that were dissimilar to their neighbours' songs (Thomas et al., 2021). These findings suggest that locally rare songs may elicit different responses than locally common songs for Savannah sparrows, but further investigation is required.

We studied responses of male Savannah sparrows to locally rare and locally common songs in a breeding population on Kent Island, New Brunswick, Canada (Burant et al., 2022). Savannah sparrow songs are individually distinctive: young males incorporate song elements heard from nearby males during the song learning process (Mennill et al., 2018) and preferentially retain song variants that resemble the songs of neighbouring males through a process of selective attrition (Thomas et al., 2021). Although they are migratory, Kent Island Savannah sparrows show high site philopatry, with mean dispersal distances equivalent to the diameter of a single breeding territory (Hensel et al., 2022; Wheelwright & Mauck, 1998). Savannah sparrows display macrogeographical dialects (Bradley, 1994; Sung & Handford, 2006), with the buzz segment of the song functioning as a population marker (Fig. 1; Williams et al., 2019). Savannah sparrows also have microdialects: birds in the Kent Island population form clusters of territories guarded by individuals with similar-sounding songs (Hensel et al., 2022). Williams et al. (2013) and Hensel et al. (2022) identified six local song types that vary in the structure of the

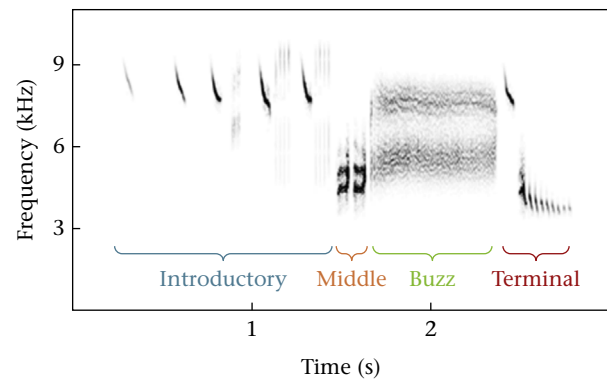


Figure 1. Sound spectrogram of a typical Savannah sparrow song from Kent Island, New Brunswick, Canada, showing the four segments of the song: the introductory segment, the middle segment, the buzz segment and the terminal segment.

middle segment of the song, comprising microdialects (spectrograms for all six song types are shown in Hensel et al., 2022). Some of these song types are very common, sung by up to 46% of local birds, while others are very rare, sung by only 1% of local birds (Hensel et al., 2022).

In this study, we used a playback experiment to study the responses of territorial male Savannah sparrows to locally common versus locally rare songs. We contrasted responses to playback of locally common and locally rare song, as well as heterospecific control song. We hypothesized that Savannah sparrows would react more strongly to locally rare songs versus locally common songs, given that a previous study revealed higher levels of territorial aggression on the territories of males singing songs that were dissimilar to their neighbours' songs (Thomas et al., 2021). We predicted that Savannah sparrows would approach the speaker more closely, show more aggressive visual and vocal displays and make more flights over and have more physical contact with the speaker when exposed to playback of locally rare songs compared to locally common songs. We also examined whether a male's response to the stimulus depended on whether the focal male sang the same or different song type as the playback treatment it received and whether responses differed with the number of 'ch' syllables in the stimulus song.

METHODS

Study Population

We used playback to simulate territorial intruders singing locally rare, locally common and heterospecific songs to territory-holding Savannah sparrows at their breeding site on Kent Island, New Brunswick, Canada (44°35'N, 66°46'W). This population has been the subject of a multidecade investigation that has yielded insights on migration (e.g. Mitchell et al., 2015; Woodworth et al., 2016), demographics (e.g. Woodworth et al., 2017), vocal communication (e.g. Mennill et al., 2018) and cultural evolution (e.g. Williams et al., 2022). Every spring, birds migrating to the island are captured in mist nets and given coloured leg bands, which facilitate individual identification by researchers (Woodworth et al., 2017). Through resighting of these coloured bands, observations of male behaviour and recording of males from song posts on their breeding territories, we mapped the territorial boundaries of all males within a 10 ha gridded study area in the middle of Kent Island, as described in Thomas et al. (2021). We performed playback during the prenesting breeding stage, during social pair formation.

Ethical Note

Our fieldwork methods were reviewed and approved by the University of Windsor Animal Care Committee (Animal Use Protocol: 20-09). All bird banding was conducted with required permits from the Canadian Wildlife Service. During banding, handling time was minimized to reduce stress to the birds. During playback, the length of the simulated territorial intrusions was minimized to reduce stress to the birds, following similar lengths of treatment that have been used previously in this population (e.g. Moran et al., 2018; Williams et al., 2024).

Playback Stimuli

We selected recordings of Savannah sparrows from our catalogue of historical recordings. To minimize neighbour effects and familiarity effects that might arise from the experimental subjects having previously encountered the playback stimuli, we selected songs from birds that were recorded between 2016 and 2019 and absent from the study site in 2023. In one case, a stimulus was created from the song of a bird that had been a former neighbour of a subject in our experiment, but this stimulus was not used for any of the trials for that particular subject. We used the two most common song types on the study site during 2016–2019 ('two ch' and 'two ch and a dash'; terminology from Williams et al., 2013) as representatives of locally common songs. We used the two rarest song types ('one ch and a dash' and 'dash') as representatives for locally rare songs (Fig. 2). Together, the 'two ch' and 'two ch and a dash' song types were sung by 75% of Kent Island birds during 2016–2019, while the 'one ch and a dash' and 'dash' song types were only sung by 3% of birds (Hensel et al., 2022). The differences between the four song types we used for playback stimuli (and also the remaining two song types in the population, as shown in

Hensel et al., 2022) are in the fine structure of the middle section of the song. The work of Hensel et al. (2022) showed that these differences are stable over extended periods. Although the structural differences between song types may seem small to us, the results of this work revealed that they are consequential for the birds singing those songs. The relative frequency of these song types was stable over the 2016–2019 period, and an assessment of recordings made in 2022 and 2023 suggests that these relative frequencies of the common and rare song types remained the same during our study period. For the heterospecific treatment, we selected recordings of black-capped chickadees, *Poecile atricapillus*, from our catalogue of historical recordings; chickadees are sympatric with Kent Island Savannah sparrows but are not known to compete directly over resources. We selected high-quality WAV files of songs with minimal background noise and a high signal-to-noise ratio from archival recordings.

We created 10 unique playback stimuli from the locally common song types and 10 unique playback stimuli from the locally rare song types. In this way, each of the four song types was represented by five different stimuli, in order to minimize pseudoreplication. We also created 10 playback stimuli from the songs of black-capped chickadees. We used Adobe Audition version 23.3 to prepare the playback stimuli using the following approach. We removed low-frequency noise from the recordings using a fast-Fourier transform filter (cutoff frequency: 3 kHz) and used the lasso selection tool to highlight and reduce the amplitude of any non-Savannah sparrow high-frequency noises and to reduce background noise. Several features of Savannah sparrow song vary between and within individuals, independently of microdialect, including the number of 'S' notes, clicks, introductory 'i' notes within the introductory segment of the song and trill notes in the terminal segment. Therefore, based on averages across all selected song stimuli, we standardized the number of 'S' notes to two, the number

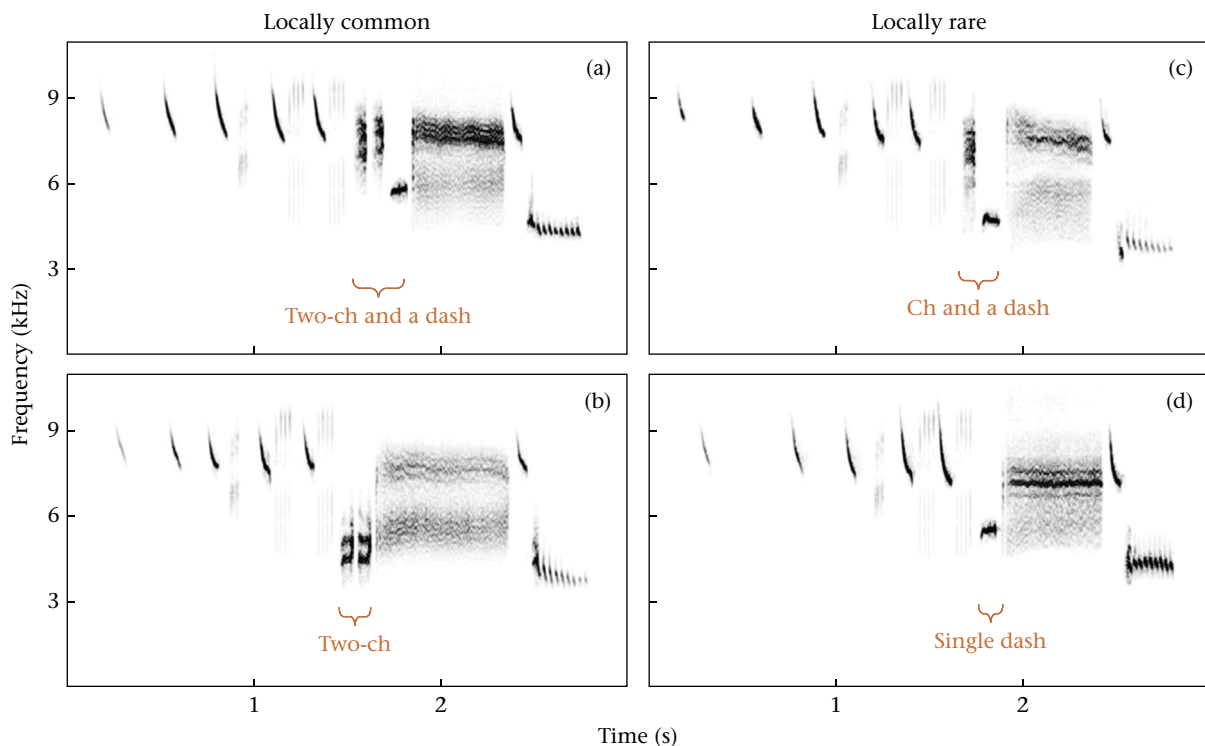


Figure 2. Sound spectrograms of four example playback stimuli used to simulate territorial intrusions on Savannah sparrow territories, each representing a different song type. (a) Locally common 'two-ch and a dash' song type. (b) Locally common 'two ch' song type. (c) Locally rare 'ch and a dash' song type. (d) Locally rare 'single dash' song type. Terminology from Williams et al. (2013).

of 'i' notes to five, the number of click notes to two clusters of four notes surrounding the final 'i' note and standardized the trill to nine notes, to avoid introducing nondialect related variation that might result in differential responses across this experiment (these modifications were made by cutting and pasting song elements in Adobe Audition). We normalized the amplitude of all stimuli to -1 dB. Savannah sparrow songs had an average duration of 2.68 s (range 2.39–2.93 s). We added the appropriate duration of silence to all Savannah sparrow songs to create a 10 s stimulus and looped these 10 s stimuli to create a playback track with a total duration of 2 min (song rate: 6 songs/min). Black-capped chickadee songs had an average duration of 1.17 s (range 1.07–1.26 s). We added the appropriate duration of silence to all chickadee songs to create a 10 s stimulus and looped these 10 s stimuli to create playback tracks with a total duration of 2 min (song rate: 6 songs/min). This ensured that all stimuli included an equal number of songs.

Playback Experiment

We conducted playback experiments from 13 May to 31 May 2023, between 0700 and 1400 hours. Males were haphazardly chosen as experimental subjects, by choosing males that had not yet received playback but avoiding performing trials on territorial neighbours on the same day. We set up a speaker (Scorpion, FoxPro Inc., Lewiston, PA, U.S.A.; power rating: 7 W) on a wooden stake located within the subject's territory, near a favoured singing perch, where a bird had been recently observed singing. The speaker was positioned at a height of 0.5 m, approximately the height of gooseberry bushes, *Ribes oxycanthoides*, which are commonly used as singing perches on Kent Island. We set up four flags in a 1 m radius circle around the speaker to help with distance estimation during each trial. A tripod-mounted shotgun microphone (Audio-Technica AT8015) connected to a digital recorder (Marantz PMD660, monaural recording; 44.1 kHz sampling rate, 16-bit depth, WAV format) was then set up approximately 10 m from the speaker. Once the male was spotted and his identity confirmed, we began a 1 min preplayback observation period to verify that the male was engaged in normal behaviours. After 1 min of observation, the playback treatment began.

The order of playback stimuli (locally common, locally rare or heterospecific) was randomized. Each stimulus was then played for 2 min, followed by a silent period of 5 min. During this entire 7 min period, the recordist noted the behaviour of the focal male, including distance to the speaker, number of flutter flights and wing waves performed, number of passes over the speaker and incidences of physical contact with the speaker. Both flutter flights and wing waves are commonly used as agonistic territorial visual signals in Savannah sparrows (Moran et al., 2018; Potter, 1972; Wheelwright & Rising, 2020). Information on the vocal behaviour of the male, particularly the number of broadcast songs, soft songs, buzz calls and decrescendo calls (sensu Thomas et al., 2021), was obtained from recordings of the playback session. Broadcast songs frequently serve as agonistic territorial signals in songbirds (Catchpole & Slater, 2008) while soft songs are correlated with physical attacks on simulated intruders in several songbird species, including Savannah sparrows (Moran et al., 2018). Both buzz calls and decrescendo calls are thought to function as agonistic vocal signals (Thomas et al., 2021; Wheelwright & Rising, 2020). Each subject received the three stimulus types on subsequent days, whenever possible. In some cases, presentation of the stimuli on subsequent days was not possible due to poor weather conditions; for 40.6% of subjects that received all stimuli (13/32), there was a delay of 3 days between the first stimulus and the final stimulus. For 15.6% (5/32) of subjects that received all stimuli, there was a delay of 4 days between the first stimulus and the final stimulus.

Two subjects disappeared from the study area before they could receive all three stimuli. In total, 34 males received playback sessions for at least one stimulus type. Of these 34 subjects, 17 had the locally common 'two ch' song type, 10 had the locally common 'two ch and a dash' song type, one had the intermediately common 'multiple ch' song type, three had the intermediately common 'short notes and a dash' song type and two had the locally rare 'ch and a dash' song type.

Statistical Analyses

We used a principal component analysis (PCA) to summarize variables related to the response of males to the experimental playback. Certain behaviours were never or rarely observed and so were excluded from the PCA; broadcast songs were only rarely recorded during the observation period, and neither soft songs nor physical contact with the loudspeaker were ever recorded, and so these three variables were omitted from the analysis. We used a PCA to summarize the following response variables: nearest approach to speaker (m), number of flutter flights, wing waves, buzz calls, decrescendo calls and passes over the loudspeaker. We performed the PCA in the R environment (version 4.2.3; R Core Team, 2023) using the function 'prcomp'. We found that our data were summarized by two principal components with eigenvalues greater than 1: PC1 ($\lambda = 2.73$, % variance = 45.5%) and PC2 ($\lambda = 1.18$, % variance = 19.6%). PC1 showed strong positive loading (i.e. eigenvectors > 0.30) from most variables (eigenvectors: flutter flights: 0.54; decrescendo calls: 0.47; wing waves: 0.46) and strong negative loading for nearest approach to the speaker (-0.35; Table 1). Birds with high PC1 scores tended to exhibit highly vocal and visual displays, giving calls, flutter flights, wing waves and closely approaching the speaker. Hereafter, we refer to PC1 as 'response intensity'. PC2 had negative loadings from buzz calls (eigenvector: -0.65) and decrescendo calls (-0.32) and positive loading from passes over the speaker (0.65; Table 1). Birds with high PC2 scores tended to pass over the speaker silently. Thus, we refer to PC2 as 'silent responses'.

We constructed two generalized linear mixed-effect models (GLMMs) to determine whether birds showed a stronger response to the locally rare, locally common or heterospecific stimulus. For variables whose GLMMs produced *P* values < 0.05, we also performed post hoc Tukey tests. We interpret the statistical tests in terms of the language of evidence, as proposed by Muff et al. (2022). We conducted these statistical analyses in the R environment using the 'lmer' function from the 'lme4' package, the 'summary' function from the 'lmerTest' package and the 'glht' function from the 'multcomp' package (Bates et al., 2015; Hothorn et al., 2023; Kuznetsova et al., 2017).

Given that not all subjects received a song stimulus of the same type as their own, we used two-sample *t* tests to determine whether birds showed a stronger response to song stimuli that were of a different song type from their own. To disambiguate the effects of song commonness and song type sharing, we only included birds with locally common song in this analysis ($N = 27$ birds) and only examined their responses to locally common songs that were the same ($N = 12$ birds) or different from their own ($N = 15$ birds). We used two-sample *t* tests to determine whether birds responded differently to common songs that were of the same or different type compared to their own, testing both their effects on response intensity (PC1) and silent responses (PC2). We conducted tests using the function 't-test' in the R environment (R Core Team, 2023).

Given that the song types differed in the number of 'ch' syllables, we also tested whether response intensity and silent responses differed with the number of 'ch' syllables in the treatment stimulus.

Table 1
Details of a principal component analysis summarizing Savannah sparrows' behavioural responses to playback

	PC1 (Response intensity)	PC2 (Silent responses)
Nearest distance of approach	-0.35	-0.09
Number of flutter flights	0.54	0.04
Number of wing waves	0.46	0.20
Number of decrescendo calls	0.47	-0.32
Number of buzz calls	0.28	-0.65
Number of passes over the speaker	0.29	0.65

Principal component (PC) loadings are shown for the first two principal components on the six variables included in the principal components analysis; variables with strong loading (i.e. eigenvectors with absolute values > 0.30) are shown in bold.

Both locally common song types include two 'ch' syllables, while one locally rare song type includes one 'ch' syllable and the other includes no 'ch' syllables. To disambiguate the effects of song commonness and the number of 'ch' syllables, we used a two-sample *t* test to determine whether birds responded differently to the 'one ch and a dash' song type versus the 'dash' song type. Again we used two-sample *t* tests.

RESULTS

Territorial Savannah sparrows presented with playback simulations of an intruder singing a locally common song, a locally rare song or a heterospecific song showed extensive variation in their responses (Fig. 3). In 95% (62/65) of trials with a Savannah sparrow stimulus, birds approached the speaker, produced decrescendo and buzz calls or performed flutter flights or wing waves. In contrast, birds exhibited these behaviours for only 47% (16/34) of trials with a heterospecific stimulus. Thus, the behaviour of the subjects was consistent with a territorial response to the playback-simulated conspecific intruder.

Responses to Locally Rare, Locally Common and Heterospecific Song

Savannah sparrows showed moderate to very strong evidence of different responses to playback of locally common, locally rare and heterospecific songs in terms of their response intensity (a principal component score summarizing different response measures; Table 2). Pairwise Tukey tests revealed moderate evidence of a difference in response intensity between the locally common

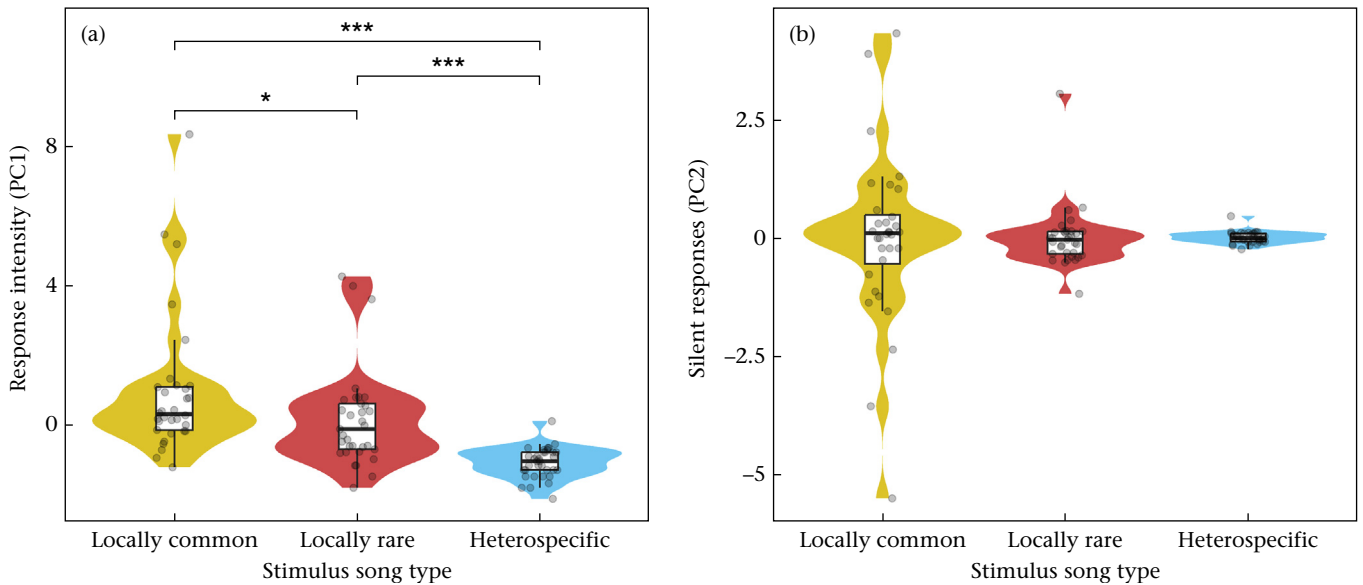


Figure 3. Male Savannah sparrows' (a) response intensity (principal component PC1) and (b) silent responses (principal component PC2) to playback of a simulated territorial intruder producing a locally common song, a locally rare song and a heterospecific control song. Data are shown as box plots, violin plots and raw data (semitransparent points). Asterisks indicate the strength of evidence: *Moderate evidence of a statistical difference (*P* ranging from 0.01 to 0.05). ***Strong evidence of a statistical difference (*P* ranging from 0.001 to 0.0001).

Table 2
Results of two generalized linear mixed models incorporating response intensity (principal component PC1) and silent responses (principal component PC2) as response variables

	Response intensity (PC1)				Silent responses (PC2)			
	Estimate	SE	<i>t</i>	<i>P</i>	Estimate	SE	<i>t</i>	<i>P</i>
Fixed effects								
(Intercept)	0.85	0.34	2.52	0.01	-0.02	0.28	-0.09	0.93
Stimulus type (rare)	-0.79	0.29	-2.71	0.008	0.03	0.26	0.10	0.92
Stimulus type (control)	-2.05	0.29	-7.04	<0.0001	0.04	0.25	0.15	0.88
Treatment order	0.05	0.10	0.45	0.65	0.001	0.09	0.02	0.99
Random effect/R²								
Residual	1.38				1.05			
Variance	0.69				0.16			
Marginal R ² /conditional R ²	0.26/0.51				0.0002/0.13			

In both models, stimulus type is included as a fixed effect with three levels (locally common, locally rare or control stimulus of a black-capped chickadee), treatment order is included as a fixed effect and subject is included as a random effect; both models have a sample size of 99 playback presentations to 34 subjects.

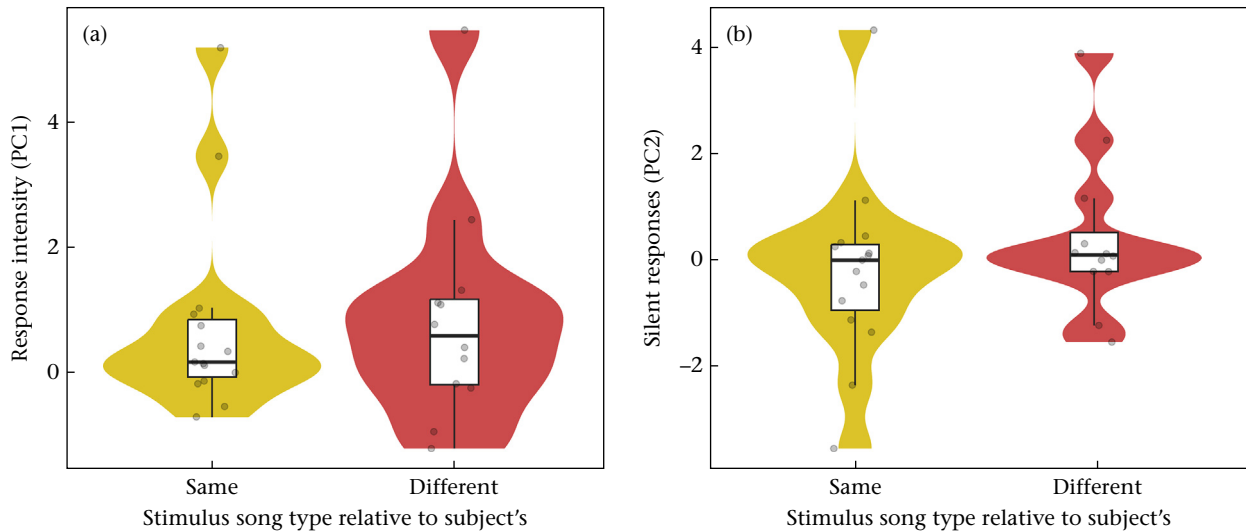


Figure 4. Male Savannah sparrows' (a) response intensity (principal component PC1) and (b) silent responses (principal component PC2) to playback of a simulated territorial intruder producing the same locally common song type as the male's own and a different locally common song type than the male's own. Data are shown as box plots, violin plots and raw data (semitransparent points).

versus locally rare treatments ($t = -2.71$, $P = 0.02$) and strong evidence for differences between both locally common versus heterospecific treatments ($t = -7.04$, $P < 0.001$) and locally rare versus heterospecific treatments ($t = -4.35$, $P < 0.001$). Response intensity was highest to playback of locally common songs, followed by the locally rare songs and lowest in response to heterospecific songs (Fig. 3a). In terms of silent responses, Savannah sparrows showed no evidence of different responses across the three treatments (Table 2, Fig. 3b).

Effect of Subject Song Type versus Stimulus Song Type

We tested whether variation in Savannah sparrows' responses to playback was related to whether the song type of the playback-simulated intruder was the same or different from the subject's song type. Of the 27 birds in this analysis, 12 received stimuli of the same locally common song type and 15 received stimuli of a different locally common song. We found no evidence that

response intensity (PC1) differed between the 'same song type' and 'different song type' stimuli ($t = -0.19$, $N = 27$, $P = 0.85$; Fig. 4a). We also tested whether the song stimulus type relative to the subject's song type had an impact on silent responses (PC2) and again found no evidence that silent responses differed between the 'different song type' and the 'same song type' stimuli ($t = -0.98$, $N = 27$, $P = 0.34$; Fig. 4b).

Effect of Number of 'Ch' Syllables

We tested whether Savannah sparrows responded more strongly to locally rare songs with one 'ch' syllable compared to locally rare songs with no 'ch' syllables. Of the 33 birds in this analysis (one subject received only the heterospecific treatment), 15 received the 'one ch and dash' song type and 18 received the 'dash' song type. We found no evidence that response intensity (PC1) differed with the number of 'ch' syllables ($t = 0.49$, $N = 33$, $P = 0.63$; Fig. 5a). We also found no evidence that silent responses

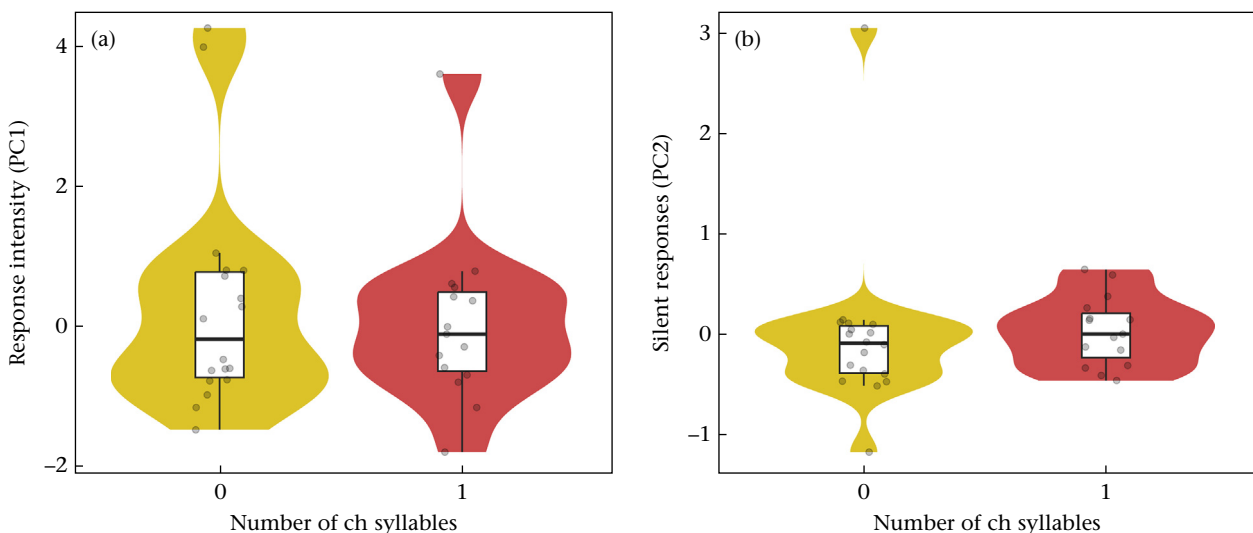


Figure 5. Male Savannah sparrows' (a) response intensity (principal component PC1) and (b) silent responses (principal component PC2) to playback of a simulated territorial intruder producing a locally rare song type with no 'ch' syllables and one 'ch' syllable. Data are shown as box plots, violin plots and raw data (semitransparent points).

(PC2) were stronger for songs with one 'ch' syllable than for songs with no 'ch' syllable ($t = -0.27$, $N = 33$, $P = 0.79$; Fig. 5b).

DISCUSSION

We investigated the responses of Savannah sparrows to simulated territorial intruders producing locally common versus locally rare songs as well as heterospecific songs. In terms of their response intensity, male Savannah sparrows reacted differently to each of the three treatments. We found stronger response intensity to conspecific song compared to heterospecific song. We found stronger responses to locally common songs compared to locally rare songs. While our observed effect sizes were relatively small, the trends observed were unequivocal. We conclude that Savannah sparrows perceive locally common songs as a stronger threat than locally rare songs and perceive locally rare conspecific song as a stronger threat than heterospecific song. We further investigated whether the observed pattern might arise as a result of the stimulus song type being the same as the subject's song type and found that playback responses did not differ as a function of whether or not the stimulus song was of the same locally common song type as the subject's song. We also investigated whether the observed trend might arise as a result of differences in the number of 'ch' syllables between the song stimuli. We found that subjects did not react more strongly to stimuli with one 'ch' syllable compared to stimuli with no 'ch' syllables. We conclude that territorial male Savannah sparrows differentiate between locally common and locally rare song types, treating the former as stronger territorial threats.

We had expected Savannah sparrows to react more strongly to locally rare songs versus locally common songs when we designed this experiment, based on a previous investigation by Thomas et al. (2021). Differences in the design, the context and the seasonal timing of our playback experiment may explain differences between our results and expectations arising from Thomas et al. (2021). Thomas et al. (2021) recorded more aggressive calls on the territories of newly established males singing songs that were dissimilar to their neighbours (a situation that we had considered to be analogous to singing a locally rare song), compared to newly established males that sang songs that were similar to their neighbours (a situation that we had considered to be analogous to singing a locally common song). Songs that are dissimilar to neighbours' songs are not directly equivalent to songs that are locally rare, and songs that are similar to neighbours' songs are not directly equivalent to songs that are locally common, and therefore our experimental design does not match directly with the results from that previous work. Furthermore, the context of Thomas et al.'s (2021) investigation was different from ours; they studied the reactions of territorial males to established neighbours during naturally occurring territorial dynamics, whereas we studied the reactions of territorial males to strangers simulated through playback. Moreover, the seasonal timing of Thomas et al.'s (2021) investigation was different from ours; they examined the number of aggressive calls on territories across two periods in May, when females were still arriving and territories were being established, whereas our study occurred later in May, when territories were more firmly established.

We argue that male Savannah sparrows perceive males with locally common songs to be more threatening than males with locally rare songs. Previous investigators have considered the idea that vocal dialects are a nonfunctional epiphenomenon that arises from vocal learning followed by limited dispersal (Podos & Warren, 2007; Slater, 1986). Our results reveal different territorial reactions to microdialect level variation and suggest that whatever the origins of this variation, locally common and locally rare songs elicit responses of different intensities. We propose several nonmutually

exclusive explanations. First, locally common songs may be stronger territorial signals than locally rare songs because singers of locally common songs are larger or more aggressive during territorial conflicts. A territorial intruder can pose a physical threat to a territory-holding male and may attempt to usurp a male's territory, and birds that are larger, more aggressive or are more effective foragers might therefore be perceived as posing a greater threat to a male and his territory. We find little support for this idea. Among the birds where we have weight data as adults, animals singing locally common songs have a similar adult body mass (mean \pm SD = 20.2 ± 1.2 g; $N = 19$ birds) to birds singing locally rare songs (20.0 ± 0.6 g; $N = 2$ birds). In white-crowned sparrows, the body size, mass and territory quality of males singing common versus 'unusual' song dialects do not differ (MacDougall-Shackleton et al., 2002). In addition, in our study population, juvenile males tend to retain song elements that match their first-breeding season neighbours (Mennill et al., 2018; Thomas et al., 2021), such that song type likely reflects the acoustic environment of a male's first breeding season, rather than his size or level of aggression. Nevertheless, future research may explore whether territorial males that sing locally common songs are more aggressive than males that sing locally rare songs.

Second, locally common song may be preferred by females because it is perceived as local, whereas locally rare song may be perceived as foreign. Such a female preference for locally common songs might result in males perceiving locally common song as a stronger territorial threat. In our study population, locally rare songs were very rare, sung by only 3% of birds on the study site (Hensel et al., 2022). Thus, it is possible that locally rare songs are perceived by females as foreign. Several studies suggest that females often prefer local song dialects over foreign song dialects. Among white-crowned sparrows, for example, females give far more copulation displays in response to local dialects compared to foreign dialects (Baker et al., 1981). Similar results have been found for song sparrows (Searcy et al., 1997), swamp sparrows (Balaban, 1988) and yellowhammers, *Emberiza citrinella* (Baker et al., 1987). Given that song is a strong driver of reproductive isolation and speciation in birds (Catchpole & Slater, 2008), it is not surprising that females prefer to mate with males that sing local dialects (and, perhaps, locally common songs). Females may mate with males who sing local dialects to avoid potentially producing nonviable offspring or offspring that are ill-suited to local conditions. In cases where dialect provides clues as to a male's geographical origin, males who sing foreign dialects may carry genes that are ill-adapted to local conditions. Among white-crowned sparrows, for example, males that sang unusual songs (likely due to dispersal) were found to carry higher parasite loads, perhaps as a result of genes that were not adapted to local conditions (MacDougall-Shackleton et al., 2002). Therefore, white-crowned sparrow females may benefit by selecting mates that sing the local dialect, both to avoid being exposed to high parasite loads and to avoid passing on nonlocally adapted genes to their offspring. However, this logic is unlikely to apply to Savannah sparrows. As we have previously emphasized, among Savannah sparrows, song is learned from nearby males on the breeding grounds, with a heavy influence from the songs of neighbours (Mennill et al., 2018). As a result, locally rare songs can persist as a result of learning rather than dispersal from nonlocal populations. Therefore, birds singing locally rare songs are perhaps unlikely to be genetically different from birds singing locally common songs, although this idea has not yet been tested explicitly.

Third, Savannah sparrows may react more strongly to locally common songs simply because they are more familiar than locally rare songs. Many studies suggest that males tend to react more aggressively to local song than foreign song (for a review, see Parker

et al., 2018). Among medium ground finches, *Geospiza fortis*, males showed increased singing and flying and closer approaches in response to local regional dialects than to foreign dialects (Podos, 2007). Similarly, white-crowned sparrows responded most strongly to current local dialects, showed similar, weaker response to historical local dialects and current nonlocal dialects and responded most weakly to dialects from a distant population (Derryberry, 2011). In addition, Savannah sparrows have been shown to reduce their responses to local song components when consistently exposed to nonlocal song (Williams et al., 2024). Therefore, it is not only song locality, but also familiarity (a bird's auditory experience with a song type) and commonness (i.e. the song type's homogeneity, or how widespread the song type is within the population) that determines how a male responds to another male's song (Williams et al., 2024). Familiar, locally common songs may be perceived as threats because males have direct experience of being challenged by rivals singing similar songs, while unfamiliar songs may not be perceived as threatening if a male has never encountered a rival with a similar song.

Future studies should attempt to disentangle why males perceive locally common songs as stronger threats than locally rare songs. A first step would be to determine whether birds with locally common songs have higher fitness than birds with locally rare songs. If they do, then this would suggest that song commonness is indeed correlated with male quality. Further tests will be needed to determine whether this is due to female preference or greater male competitive ability, as these two hypotheses are not mutually exclusive. To test whether females prefer locally common song, females could be presented with playback of locally common and locally rare songs. If females show greater interest in the locally common song, then this would suggest that locally common songs are preferred by females and consequently represent a greater threat to the fitness of males. To test whether males singing locally common songs are a greater threat to other males, researchers could determine whether characteristics such as condition, parasite load, aggression and territory quality correlate with song commonness (as in MacDougall-Shackleton et al., 2002). If males with locally common songs are in better condition, have better territories or are more aggressive than males with locally rare songs, then locally common songs may be more threatening to males because they correspond with male competitive ability. To test whether birds react more strongly to familiar song, both females and males could be presented with historical and current recordings of locally common songs. If females show greater interest in current locally common song, then this would suggest that familiar songs are a stronger territorial threat to males because they are preferred by females. If males show greater aggression in response to current locally common song in absence of a female preference, then this would suggest that familiar song is perceived as a stronger threat to males for reasons other than female preference. Regardless of the mechanisms driving these patterns, our study shows that male songbirds do indeed respond more strongly to locally common songs than to locally rare songs, suggesting that locally common songs are perceived as stronger territorial signals than locally rare songs.

Our study faces some limitations. There are only a small number of song types in the Kent Island Savannah sparrow population (six naturally occurring song types as quantified on the basis of the middle syllables; Hensel et al., 2022), and therefore we had a relatively low number of categories of songs to investigate (i.e. two locally common and two locally rare song types). This creates the possibility that the differences we report might be connected to other idiosyncratic features of the songs we tested. To guard against this in future studies, it would be worthwhile to examine responses to locally common and locally rare song in a species or population with a larger number of population level song types. Furthermore,

while our study tested the responses of birds to simulated intruders singing locally rare and locally common song, our investigation did not focus on behavioural differences between birds that sang locally common versus locally rare songs themselves (of our 34 subjects, only 2 sang locally rare songs). Future studies should examine whether birds singing locally rare song behave differently than birds singing locally common songs.

Conclusions

In contrast to prior investigations of dialects across populations separated by wide distances, we show that even songs found within the same population elicit different responses based on their frequency of occurrence. We found that male Savannah sparrows responded most strongly to playback of locally common songs and less strongly to locally rare songs, which we interpret as evidence that locally common songs are perceived as a stronger threat than locally rare songs. A male's response did not depend on the stimulus song being of the same song type as his own. We suggest that males singing locally common song may find advantages over males singing locally rare songs, either because they are preferred by females, or because they are more threatening to other males. Locally common songs may also be perceived as more threatening simply because they are more familiar. Vocal dialects remain a topic of great interest because of the insights that they offer into vocal learning and how animals perceive and react to local and foreign sounds. Although macrogeographical dialects have been examined closely in past decades, microdialects remain an understudied phenomenon, and little is known about the responses of animals to locally common and locally rare vocal variants. This study offers a glimpse into the responses of songbirds to locally common and locally rare songs, thereby illuminating the complex mechanisms that affect animal responses to the vocalizations of nearby individuals.

Author Contributions

Jaelyn A. Aubin: Conceptualization, Methodology, Formal analysis, Investigation, Writing – Original draft, Visualization. **Sarah L. Dobney:** Investigation, Writing – Review & editing. **Sarah A. M. Foreman:** Investigation, Writing – Review & editing. **Stéphanie Doucet:** Writing – Review & editing. **D. Ryan Norris:** Writing – Review & editing. **Heather Williams:** Writing – Review & editing. **Daniel J. Mennill:** Conceptualization, Methodology, Validation, Resources, Writing – Review & editing, Supervision, Project administration, Funding acquisition.

Data Availability

Data and R code are available as Supplementary material.

Declaration of Interest

The authors have no conflicts of interest to declare.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2024.03.019>.

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