



4-22-2019

The meaning of song type: exploring behavioral responses of field sparrows to three simple song types

Eliza Foli

Western Michigan University, elizafoli@outlook.com

Follow this and additional works at: https://scholarworks.wmich.edu/honors_theses



Part of the Biology Commons

Recommended Citation

Foli, Eliza, "The meaning of song type: exploring behavioral responses of field sparrows to three simple song types" (2019). *Honors Theses*. 3109.

https://scholarworks.wmich.edu/honors_theses/3109

This Honors Thesis-Open Access is brought to you for free and open access by the Lee Honors College at ScholarWorks at WMU. It has been accepted for inclusion in Honors Theses by an authorized administrator of ScholarWorks at WMU. For more information, please contact wmu-scholarworks@wmich.edu.



The meaning of song structure: exploring behavioral responses of field sparrows to three simple song types

Introduction

Acoustic communication is critical for avian taxa for species recognition, courtship, and competition (Nowicki and Searcy 2005; Reichard and Anderson 2015; Phillips and Derryberry 2017; Poesel et al. 2017). Characteristics of bird song are pertinent to signal function, and variation in characteristics could potentially change the information that the signal communicates to the receiver (Poesel et al. 2012; Reichard and Anderson 2015, Zhang et al. 2015). A male's song is an effective signal for establishing and defending territory as well as attracting mates when visual cues are not possible, such as in long-distance communication. Due to the role of bird song in species recognition and courtship, the presence of significant variation in song between individuals can be a driver of processes that may lead to reproductive isolation, such as assortative mating (Dingle et al. 2010, Podos 2010; Tinghitella et al. 2018). Trait divergence may be influenced by multiple processes simultaneously, including ecological adaptation, cultural drift, genetic drift, and female choice in sexual selection if some characteristics are favored over others (Podos and Warren 2007; Tinghitella et al. 2018).

Variation in song is widely researched, since song is an essential signal within species. In some species, even slight variation in song characteristics such as frequency or note duration have been shown to be meaningful to the signal function. For example, chipping sparrows (*Spizella passerina*), which only sings a simple song type, shorten the duration of the song during aggressive interactions (Liu and Kroodsma 1999). Species may have multiple song types, which are characterized by distinct differences in structure of song parts. However, even slight variations can be significant enough to be classified as separate song types, such as in male red-winged blackbirds (*Agelaius phoeniceus*), which have two to eight song types distinguished by drastically different trill rates, and which respond differently to playback of songs with differing trill rates (Nowicki and Searcy 2005; Cramer and Price 2007). Another example is substantial variation of song type used within white-throated sparrows (*Zonotrichia albicollis*) populations, which arises consistently in all distinct populations across their widespread breeding range (Borror and Gunn 1965). Song types may cluster spatially within a population due to social learning of a local song from parents or neighbor tutors (Lachlan et al. 2014) or eventual matching of neighbor's songs after settling in new territories, as in field sparrow (*S. pusilla*) populations after two years (Nelson 1992). Since slight variations in song characteristics can affect species recognition and signal function and song is critical for competitive and sexual interactions, variations in song may directly affect the reproductive pairing of individuals within populations and could lead to divergence of signal variants over time.

Since song is learned socially by juveniles from conspecific male tutors, song characteristics that are successful within the population will be taught by adult males to the next generation of juveniles during the first few months of life, resulting in potential for modification

of song characteristics over time based on which are selected (Nelson 1992; Date and Lemon 1993; Lachlan et al. 2014; Poesel et al. 2017; Sebastian-Gonzalez and Hart 2017). In species with large breeding ranges, local dialects can form over time, defined as existing variation in song at a local scale that may be associated with specific behavioral responses. These behavioral responses are typically stronger in response to the local dialect than to a foreign dialect due to the role of song in species recognition (Ramsay and Potter 2015). If individuals with particular dialects become reproductively isolated due to differential behavioral responses, divergence can occur based on the song variations, or dialects, and could eventually lead to development of subspecies. However, subspecies with slight differences in song may still respond to heterospecific songs, as in Thick-billed grasswren subspecies *A. m. raglessi* and *A. m. indulkanna*, in which *A. m. raglessi* responded similarly to playback of both hetero- and conspecific song, but *A. m. indulkanna* responded more strongly to heterospecific song (source?). Songs can be correlated to morphological characteristics, such as in small and large beak morphs of Darwin's finches *Geospiza fortis*, in which a playback study revealed that males responded significantly more strongly to songs of their own beak morph than to songs of the other morph. This result shows the finches discriminated between song, and recognized which song correlated to the morphological characteristics similar to themselves. This implies that intruders who are of the same morph as the focal male represent a larger competitive threat, supported by the increased response to similar morph songs (Podos 2010). Even without visually distinct morphological differences, theoretically males would respond most strongly to song most similar to their own, since even frequency characteristics of a song are critical to the signal function of species recognition, which informs all competitive or mating interactions (Dingle et al. 2018).

One species that exhibits significant within-population song variation is the field sparrow, a socially monogamous passerine with a breeding range in Canada and the eastern USA and a winter range in southeastern USA (Celis-Murillo et al. 2016). Field sparrows sing two different song types, which are defined by number of parts and are distinct in function (Nelson 1992). Complex songs are sung mainly during the dawn chorus and have more than two parts, while simple songs have only two parts. Simple songs are sung throughout the day and typically begin with longer-duration introductory notes followed by a trill made up of the same note repeated in short succession (Nelson 1992; Celis-Murillo et al. 2016). Complex songs are mainly used in intrasexual functions such as territory defense between males, while simple songs function intersexually between singing males and potential female mates (Celis-Murillo et al. 2016). From recordings of 65 male field sparrows in southwest Michigan, cluster analysis revealed four common clusters, or categories, of variation in frequency characteristic in simple song emerged of which three were common: Type 1) completely broadband, Type 2) narrowband introductory notes with a lower frequency, broader bandwidth trill, and Type 3) completely narrowband with a higher frequency trill (Gill & Vonhof, unpubl. data).

The presence of these distinct variations in song within southwest Michigan raises the question of possible difference in signal function communicated by the variations. These variations could represent the aftereffects of selective pressures such as assortative mating, the outcome of male competition, or even female choice if preference for certain song variations dictated mating choices over time (Poesel et al. 2017). In order to investigate any potential

difference in salience, or meaning, communicated by the signal, we can observe the behavioral response of male field sparrows to playback of songs of these three variation types. Playback experiments, or simulated territory intrusions, represent a direct method of observing specific behavioral responses known to be used in aggressive interactions, including counter-singing, flights or perch changes, and approaching the source of playback (simulated intruder) (Moseley et al. 2013). Songbirds of many species are responsive to playback and can distinguish between different playback songs, including songs with subtle changes in structure (Moseley et al. 2013; Lachlan et al. 2014; Freeman and Montgomery 2017; Phillips and Derryberry 2017; Slender et al. 2018). If analysis of aggressive male responses to playback of the three simple song variation types shows patterns, it could indicate, primarily, that males discriminate between songs based on variations in frequency characteristics. Since a male's own song can influence how he perceives other males in competitive interactions (e.g. Podos 2010), any patterns in response to the variation paired with which variation the male himself sings could indicate further that a male discriminates between the variations, and perceives the type that is most similar to his own. We hypothesized that males discriminate between the three song type variants, and that males respond more strongly to variants most similar to their own song.

Methods

Definition of song type clusters

Songs used for playback were all simple songs previously recorded in 2012 and 2013 from field sparrows in southwest Michigan (Gill and Vonhof unpublished data). Songs selected for use as experimental playbacks represented three variations that persisted commonly throughout the population. These three variations were defined as three song types categorized by frequency characteristics including bandwidth and minimum frequency of trill breadth with Type 1) completely broadband, Type 2) narrowband introductory notes with a broader bandwidth trill with a lower minimum frequency, and Type 3) completely narrowband with higher frequency trill. Recordings of focal males during playback experiments were examined and each male was designated as singing Type 1, 2, or 3 song based on the spectrogram of his song during playback and dichotomous key based on the findings of Gill and Vonhof.

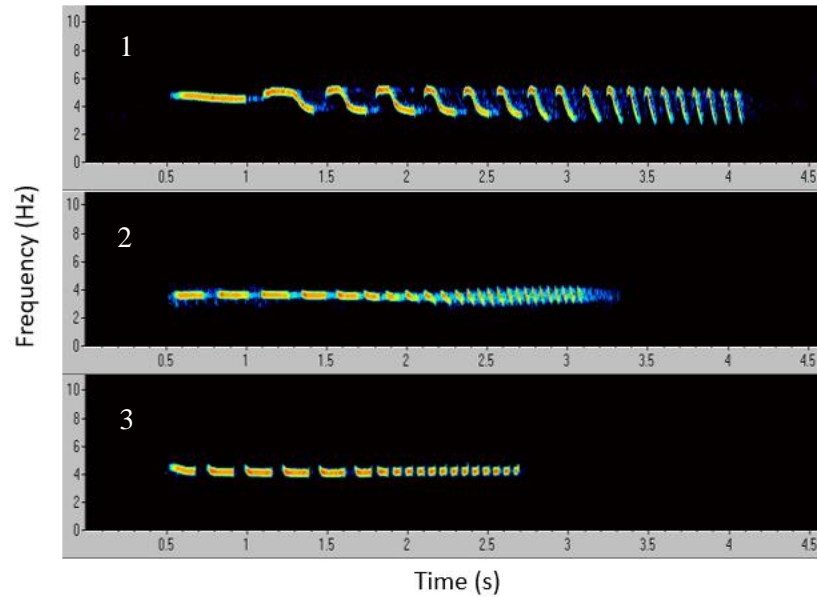


Fig. 1 Spectrograms of the three clusters of simple song variation (Gill and Vonhof, unpublished data).

Playback Experiments

Study Site

Playback experiments were conducted at the Southwest Michigan Land Conservancy preserve, Chipman Preserve, Galesburg, MI, from May 5, 2018, to June 6, 2018. The preserve consists of 228 acres of grassland, savanna, and forest habitat.

Source of Recordings

Recordings of field sparrows were taken across southwest Michigan by Gill and Vonhof to build an existing song library of 66 recordings of simple song. From this library, 26 songs representing all three song type categories were used to create exemplars for playback experiments.

Playback Exemplar Design

To observe behavioral response to each variation category, playbacks were designed as sets including three nine-minute sound files consisting of three minutes of silence pre-treatment, three minutes of playback treatment, and three minutes of silence post-treatment. Each file represented one of the three variation categories, with 32 sets of playbacks created in total for 32 trials in the field.

Exemplars were designed to emulate natural field sparrow vocal patterns of mean song rate of (± 1 sd) 3.15 ± 1.33 seconds and mean song duration of 2.65 ± 0.36 seconds from a sample of 66 field sparrow recordings from 2012-2013 (Nelson and Croner 1991; Gill and Vonhof unpublished data). Modification of recorded songs used for exemplars to fit these

parameters was done using Avisoft SASLab Pro v 5.1 (R. Specht, Berlin, Germany). If shortening the song was necessary to fit the mean song duration of natural song, trill notes excluding the first or last were cut from the song so that it did not alter the trill rate. Once the original exemplar was edited to match the natural song duration, silence was added after the song to match the natural song rate. This song with silence afterwards was copied and pasted within the sound file until 180 seconds, 3 minutes, made up the playback treatment period. The pre-treatment and post-treatment silent periods consisted of 180 seconds of added silence before and after the created playback treatment period. All exemplar song files were normalized to 75% peak amplitude within the software and saved as separate nine-minute audio files. Audio files were played during experiments using an Apple iPod Nano music player and an OontZ Angle 3 blue tooth speaker connected via chords to ensure consistent signal strength throughout the experiment.

Field Design

To present all three song variations to each male, focal males received three trials during the same day, each separated by an hour to minimize the potential of carry over effects. The order of playback sets was randomized, and the order of variation type was randomized within those sets to prevent bias of order presentation. Since 26 recorded songs were used to create playback exemplars and 32 playback sets were used, some songs were used more than once during the entirety of the experiment, though each playback set was only used once and one male never received the same song twice. Further, a focal male was never presented with a recording of his own individual song or that of a neighbor. If neighboring males were both tested, they were not tested on successive days. All focal males were banded in previous years or banded more than a day before an experiment was performed in their territory, using target mist-netting and short playback of field sparrow song.

Experiments attempted to sample all males during the same stage of the breeding season, which lasts roughly 10-12 weeks for field sparrows, starting in May (Celis-Murillo et al. 2016). Experiments were performed between the hours of 07:00 and 12:00 when weather was clear, and winds were not over seven miles per hour. Prior to experiments, I observed focal males flight and space use patterns and determined the most likely center of their territory. Location of males was recorded on a gps grid laid over a satellite image of the site using the Avenza Maps app (Avenza Systems Inc.). Once the center of territory was determined, I placed the blue tooth speaker at the center, on the ground at the base of a shrub or other vegetation that may serve as a perch for a simulated intruder and placed wire flags every 2 meters for a total of 12 meters north, south, east, and west of the speaker to assist in recording movement of the focal male as horizontal distance from the speaker. After speaker and flag set up, I retreated at least 12 meters from the center of the territory and began the nine-minute trial playback file using the Apple iPod Nano. To minimize the effect of my presence in the territory as much as possible, I attempted to the best of my ability to observe from a viewpoint with adequate visibility of the focal male but substantial covering of myself. I stayed close to the ground and minimized movement as much as possible during the trial. For the entirety of each trial, I dictated observations of all movements including distance from speaker, perch changes, songs, chips, flying over the speaker, scanning, preening

and ruffling of feathers, foraging, and time the focal male was out of sight during continuous audio recordings into a WAV. file Audio Recorder app on my cell phone. From at least twenty meters from the center of the territory, vocalizations of the focal male during the trial were recorded using a Marantz PMD661 MK-11 and Sennheiser microphone with a mE-66 condenser. After data collection, I transcribed the dictated trial observations onto sheets I designed to record distance from speaker, perch changes, vocalizations, and other observed behaviors in ten second blocks for the duration of the trial. Pre, during, and post treatment three-minute sections were specified on the transcription sheets, with categories of distance from the speaker separated into within 0-2, 2-4, 4-6, 6-8, 8-10, 10-12, and over 12 meters from the speaker. Perch changes within distance categories were recorded as tallies within the relevant category so it was clear how much time the focal male spent a certain distance from the speaker.

Univariate Linear Mixed Models

Univariate linear mixed models were used to examine the effects of playback on focal males depending on the song type cluster their own song belongs to, defined as cluster 1, 2, and 3 to correspond directly to song type 1, 2, and 3. Predictors were treatment type (that is, the cluster to which the playback song belonged) and male song cluster, with male identity as a random effect since males were tested in repeated observations. Number of focal males for each cluster type was $n_1=10$, $n_2=17$, and $n_3=4$. Due to small sample size of tested individuals that belonged to cluster 3, cluster 3 males were not included in analysis. Robust linear mixed models were used when assumptions could not be met.

Results

Males changed their behavior in response to playbacks, shown by the significant increase in number of perch changes from before the playback to during and after the playback (Fig. 1). This allowed further analysis of the other behavioral responses (perch changes, songs, and time spent within distance categories of within two meters and within two and six meters of the speaker) observed with confidence that response was due to the presented playback.

Focal males that sang Type 2 songs responded more than males that sang Type 1 songs. Type 2 males gave more perch changes overall (Fig. 3), showed a decrease in latency to respond (Fig. 4) and spent more time spent within 6 to 12 meters from the speaker, regardless of the playback cluster. There was some evidence that males responded more to playbacks of Type 2 and 3 than playbacks of Type 1, due to more time spent within 2 meters of the speaker during playbacks of Type 2 compared to Type 1 (Fig. 2). Males sang more songs during the post playback period than before or during, with no significant differences in number of songs sang during the three playback treatments (Fig. 5).

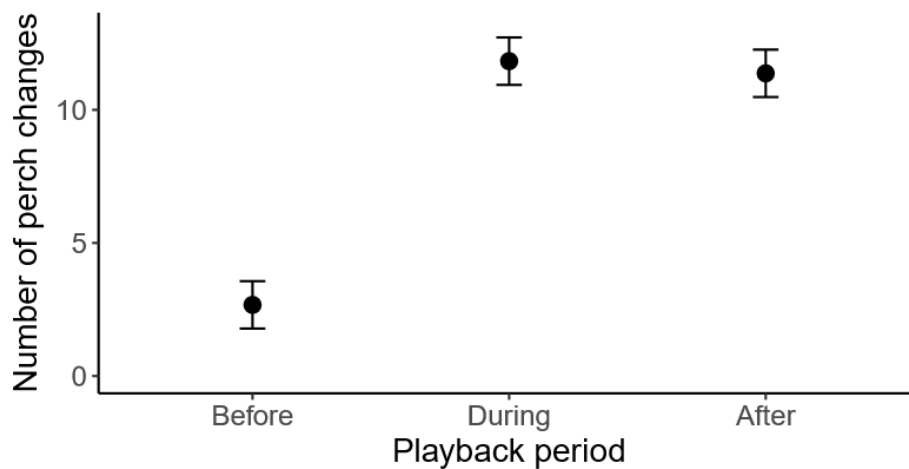


Figure 1. The number of perch changes of focal males before, during, and after playback of the three song variations.

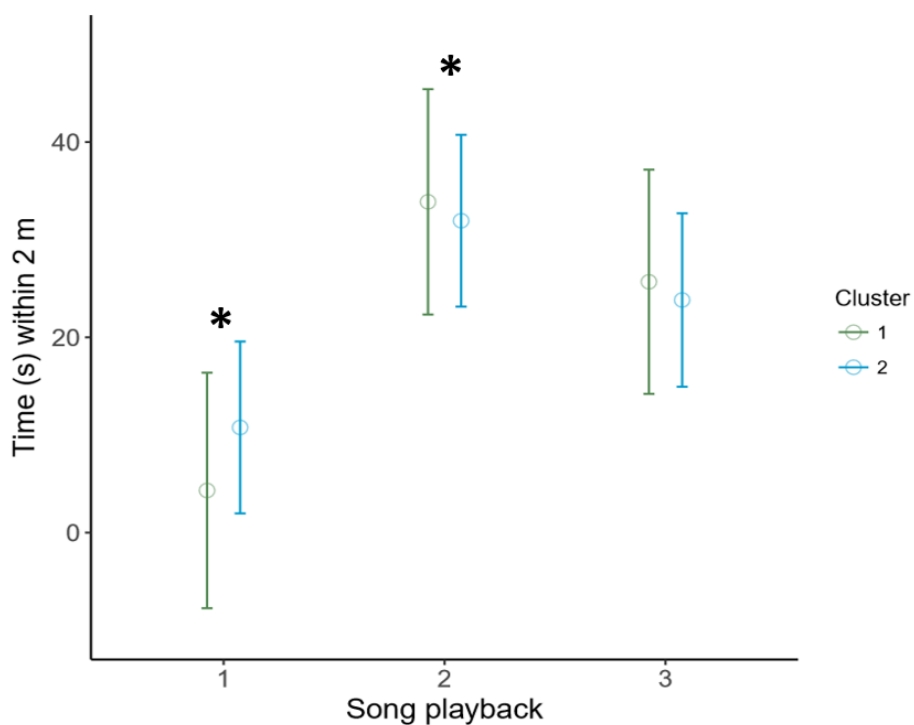


Figure 2. Time spent within 2 meters of the speaker during playback of the three song variations. Asterisks indicates significant differences in response to playback types 1 and 2.

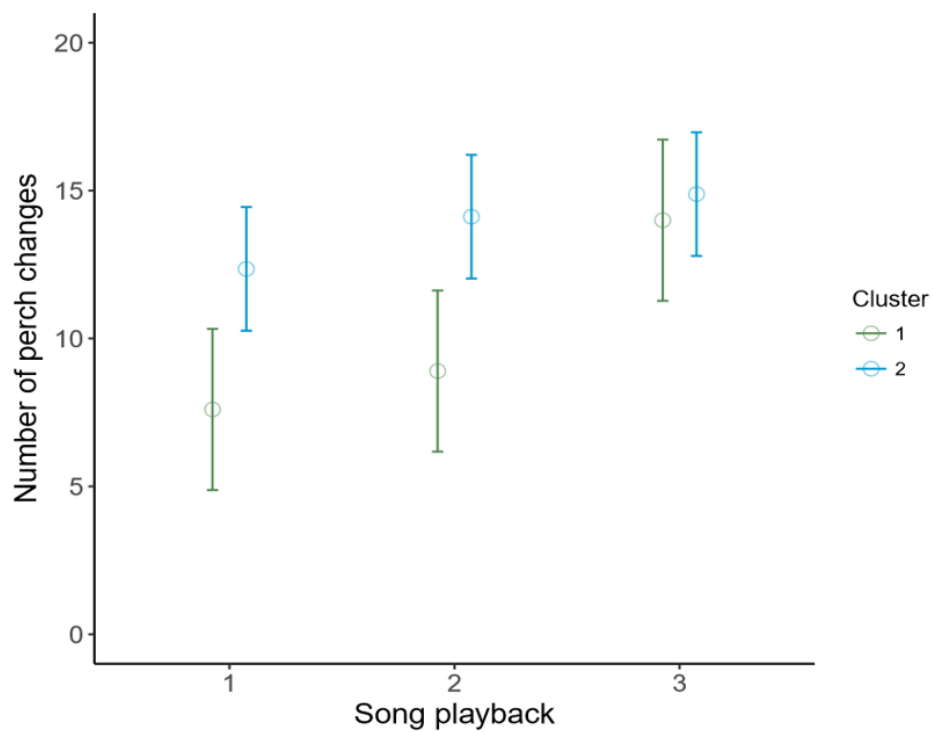


Figure 3. the number of perch changes during playback of the three song variations.

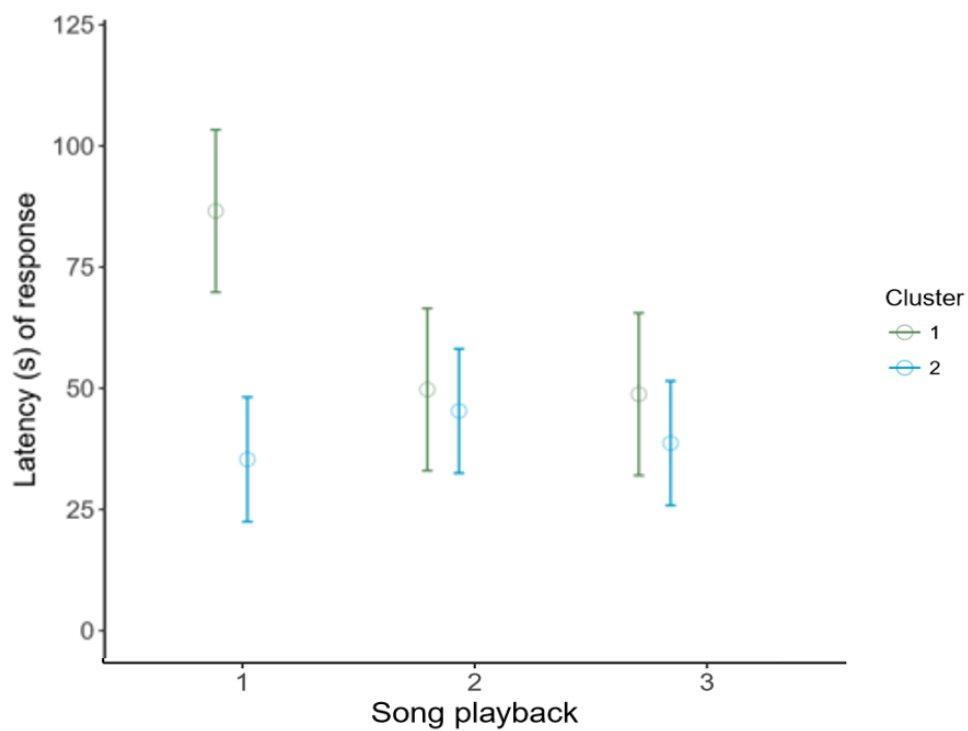


Figure 4. The latency of response to playback of the three song variations.

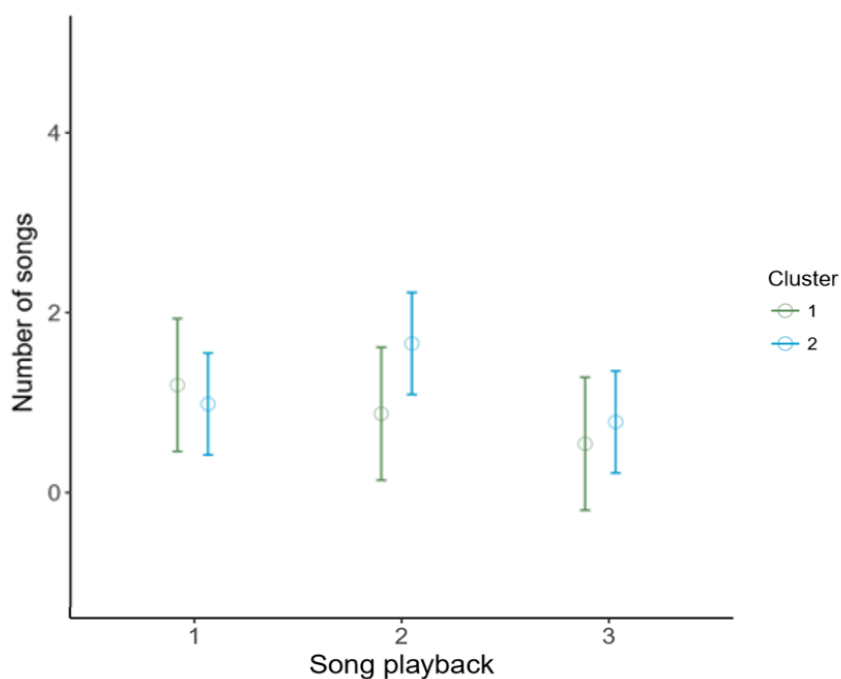


Figure 5. The number of songs sang during playback treatment.

Discussion

From the results of our playback experiments, it is clear that males responded to playback of the song variations. The increase of perch changes in response to playback treatment (Fig. 1) allowed us to analyze behavioral responses during playback treatment (Figure 2-5). The results show that there is not a clear-cut pattern of responses to type 1, 2, or 3 songs. There is evidence that males discriminated between the playback song clusters, though the response was varied across different behaviors. There was not a significant difference in number of songs sung in response (Fig. 5), which could indicate that the males did not discriminate between the songs and therefore did not change responses. However, the other behaviors recorded, included time spent within 2 meters of the speaker, showed that males responded differently to each playback type, but similarly to each other even though they sing different song variations (Fig. 2). This result supports the first hypothesis that males discriminate between playback of the three song types.

The type of song a male sings appeared to influence his response to playback. Males that sang type 2 songs changed perch more often than males that sang type 1 songs (Fig. 3). Also, males that sang type 1 songs took longest to respond to playback of their own song type (Fig. 5), which echoes the trends in Figure 2 and 3 of least response to type 1 playback overall. This result of least response to type 1 song in number of perch changes, time spent within 2 meters of the speaker, and speed to respond suggest that type 1 song was either perceived as less of a threat or less crucial to respond to than type 2 or 3 songs. Type 1 song consists completely of broad

bandwidth notes, which differs significantly visually and audibly from type 2 and 3 song, which have narrower bandwidth notes in both the introductory notes and the trill.

More experimental playbacks should be performed to gather more statistical power to the analysis as well as produce a large enough sample size of males that sing type 3 song. While the experiment was completed in about a month in an attempt to observe behavior during the same period of the breeding season, active tracking of the breeding status and presence of female in the territory during the experiment could be taken into account, as field sparrows change their use of complex and simple songs throughout the breeding season (Celis-Murillo et al. 2016) and presence of a female can influence behavioral response to playback in several species (Beletsky et al. 1990; Slender et al. 2018). Accuracy of behavioral observations could be increased by having two observers dictating behavior during the trial, as the focal male could be hidden within the territory area by vegetation and may have been seen more often from multiple angles. Fighting with neighboring males should be tracked in the future, as it could affect the stress level of the focal male and therefore potentially his behavioral response to any playback treatment occurring soon after aggressive interactions with other males. Bird song is influenced by many processes to varying degrees, including dispersal patterns, time of song learning, and long-term ecological processes, which could all have an impact on the presence of song variations in field sparrow populations across their range (Poesel et al. 2017; Podos and Warren 2007).

This variation existing in simple song in this study may be explained as a ‘simple song repertoire’, occurring more often in field sparrows new to territory settlement (Nelson 1992). Repertoires could remain within the population because of song sharing through late acquisition or selective attrition (retaining only matching songs from their repertoire) between males in the same population, resulting in similar songs between neighbors (Nelson 1992; Liu and Kroodsma 1999; Podos and Warren 2007; Poesel et al. 2017). Song sharing may be beneficial for males, seen in the male Puget Sound white-crowned sparrows (*Z. l. pugetensis*) found to be more likely to attract a social mate in their first year if they sang a song similar to their neighbor (Poesel et al. 2012). If matching of neighbors is a leading process in field sparrows, analysis of the locations of males singing the three variant song types could reveal if spatial clustering of the simple song types occurs within a population. Genetic drift, or random morphological changes that develop within lineages, can influence song characteristics if the anatomical features related to producing song are affected, such as the syrinx. Songbirds with larger syrinxes can sing songs at lower frequency than birds with smaller syrinxes, which could lead to an increase of lower frequency song in a population. Beak shape, which also affects the frequency characteristics of songs, can be influenced by diet through natural selection, and therefore also put pressure on song characteristics if individuals with certain beak shapes are more successful over time. The evidence in this study of significant variation in frequency characteristics within one song type in a small geographical range of birds could potentially indicate future divergence of song characteristics. If variation extends across a wider area of the field sparrows range, it could lead to differential adaptation of local populations to their environments and dialects, also influenced by the many processes affecting birdsong populations over time (Podos and Warren 2007).

In conclusion, there are three types of defined variability in frequency characteristics of the simple song of field sparrows in southwest Michigan. Since song is the key signal for mate attraction, variation such as these three types could lead to genetic divergence between individuals over time (Poesel et al. 2017). However, there is still more to learn about to what degree divergence or evolution of vocal signals influences rates of speciation (Mason et al. 2016). This variability may be important to the competitive interactions of males, with songs that have broad bandwidth introductory notes and trill potentially being perceived as less threatening than songs with narrow bandwidth introductory notes due to a decreased aggressive response to playback of broad bandwidth songs (type 1) regardless of song type the focal male sings. While the acoustic qualities of a song are known to be influenced by physical attributes, the information communicated by specific attributes and the weighting of variations against each other is not well understood in most species (Moseley et al. 2013; Phillips and Derryberry 2017). This study aimed to understand the salience of variations of field sparrow simple song by examining the direct behavioral response elicited in a male upon hearing a specific song variation. The presence of the variations implies there may be some selection occurring for them, whether it be directly through male competition, female choice, or larger scale ecological pressures. Our playback experiments support the hypothesis that males actively discriminate between song based on frequency characteristics, based on the distinct response of males to playback of the three variation types in time spent within 2 meter of the speaker in Figure 2. While it appears that the song a male sings himself does influence the way he responds to playback of songs, with males who sing broad bandwidth songs changing perch less often in response to playbacks (Fig. 3) more playback experiments could provide more clarity to this, particularly if the response of males who sing type 3 narrow bandwidth, higher frequency songs could be included in comparisons. If these three simple song variations are further found to elicit significantly different response from focal males, it could indicate the potential for development of dialects through male competition, song sharing, and subsequent learning of successful songs which could potentially lead to reproductive isolation between dialect neighborhoods. Since behavioral traits affect reproductive strategies, and song often informs these behaviors, understanding changes in song can be the first step to tracking the progress of diversification in a species (Mason et al. 2016). This documentation of variation within the simple song of field sparrows may provide a look into the early stages of divergence and is important to track in the future to understand the interactions and development of the species as well as the process of diversification as it applies to songbirds and vocalizations.

Acknowledgements

I thank the Southwest Michigan Land Conservancy for use of Chipman Preserve for experimental playbacks and bird banding, as well as setting up a grid across the entire preserve to use with the Avenza Maps app.

For assistance recording during playback experiments in the field, I thank Annie Lilac, Kelsey Cushway, Nicole Bays, and Jonathan Eiseman. I thank Mike Dreibelbis for banding Field sparrows at Chipman Preserve to allow playback experiments on banded males.

I thank the Lee Honors College at Western Michigan University for funding this research with the Research and Creative Activities Award in 2018.

Many thanks go to Dr. Maarten J. Vohhof for training in field techniques and prior data that led to development of this project. Dr. Sharon A. Gill was essential from the beginning to the end of this project, including statistical modeling, editing of the paper, poster, and presentation of the project as well as critical advice and support.

References

- Borror, D. J. and W. H. Gunn. 1965. Variation in White-throated sparrow songs. *The Auk* 82:26-47.
- Celis-Murillo, A., K. W. Stodola, B. Pappadopoli, J. M. Burton, and M. P. Ward. 2016. Seasonal and daily patterns of nocturnal singing in the Field Sparrow (*Spizella pusilla*). *Journal of Ornithology* 157:853-860.
- Cramer, E. R. A. and J. J. Price. 2007. Red-winged blackbirds *Agelaius phoeniceus* respond differently to song types with different performance levels. *Journal of Avian Biology* 38:122-127.
- Dingle, C., Poelstra, J. W., Halfwerk, W., Brinkhuizen, D. M., and Slabbekoorn, H. 2010. Asymmetric response patterns to subspecies-specific song differences in allopatry and para-patry in the gray-breasted wood-wren. *Evolution*, 64, 3537–3548.
- Lachlan, R. F., R. C. Anderson, S. Peters, W. A. Searcy, and S. Nowicki. 2014. Typical versions of learned swamp sparrow song types are more effective signals than are less typical versions. *Proc. R. Soc. B* 281: 20140252.
- Mason, N. A., Burns, K. J., Tobias, J. A., Claramunt, S., Seddon, N., and Derryberry, E. P. 2016. Song evolution, speciation, and vocal learning in passerine birds. *Evolution*, 71, 786–796.
- Moseley, D. L., D. C. Lahti, and J. Podos. 2013. Responses to song playback vary with the vocal performance of both signal senders and receivers. *Proc. R. Soc. B* 280:20131401.
- Nelson, D. A. 1992. Song overproduction and selective attrition lead to song sharing the Field sparrow (*Spizella pusilla*). *Behavioral Ecology and Sociobiology* 30:415-424.
- Nelson, D. A. and L. J. Croner. 1991. Song categories and their functions in the field sparrow (*Spizella pusilla*). *The Auk* 108:42-52.
- Nowicki, S. and W. A. Searcy. 2005. Song and mate choice in birds: how the development of behavior helps us understand function. *The Auk* 122:1-14.
- Phillips, J. N. and E. P. Derryberry. 2017. Vocal performance is a salient signal for male-male competition in White-crowned Sparrows. *The Auk* 134:564-574.
- Podos, J. 2010. Acoustic discrimination of sympatric morphs in Darwin's finches: a behavioral mechanism for assortative mating? *Phil. Trans. R. Soc. B* 365:1031-1039.

- Podos, J. and P. S. Warren. 2007. The evolution of geographic variation in birdsong. *Advances in the Study of Behavior* 37:403-458.
- Poesel, A., D. A. Nelson, and H. L. Gibbs. 2012. Song sharing correlates with social but not extrapair mating success in the white-crowned sparrow. *Behavioral Ecology*: 627-634.
- Poesel, A., A. C. Fries, L. Miller, H. L. Gibbs, J. A. Soha and D. A. Nelson. 2017. High levels of gene flow among song dialect populations of the Puget Sound white-crowned sparrow. *Ethology* 123:581-592.
- Ramsay, S. M. and K. A. Otter. 2015. Geographic variation in White-throated Sparrow song may arise through cultural drift. *J Ornithol* 156: 763-773.
- Reichard, D. G. and R. C. Anderson. 2015. Why signal softly? The structure, function and evolutionary significance of low-amplitude signals.
- Sebastian-Gonzalez, E., and P. J. Hart. 2017. Birdsong meme diversity in a fragmented habitat depends on landscape and species characteristics. *Oikos* 126:1511-1521.
- Tinghitella, R.M., A. C.R. Lackey, M. Martin, P. D. Dijkstra, J.P. Drury, R. Heathcote, J. Keagy, E. S.C. Scordato, and A. M. Tyers. 2018. On the role of male competition in speciation: a review and research agenda. *Behavioral Ecology* 29:783-797.
- Wood, W. E. and S. M. Yezerinac. 2006. Song Sparrow (*Melospiza melodia*) song varies with urban noise. *The Auk* 123: 650-659.
- Zhang, V. Y., A. Celis-Murillo, and M. P. Ward. 2015. Conveying information with one song type: changes in dawn song performance correspond to different female breeding stages. *Bioacoustics* 25:19-28.