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Consistency Is Key: Investigating Vocal Consistency in Field Sparrows

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Vocal consistency in birds may be a signal by which other individuals in a population assess male quality. High song consistency may be advantageous, as males that have higher consistency have higher reproductive success and can be individually distinctive in a population. Consistency may vary between different parts of songs, reflecting different functions and constraints. We ask: Do Field Sparrows exhibit vocal consistency in their simple songs over time? And, does consistency vary between the sweep and trill portions of their songs? We recorded 24 males over 5 years. Vocal consistency was measured over time through calculation of spectrographic cross-correlation and repeatability of song parameters. We analyzed cross-correlation data and calculated repeatability using a generalized linear mixed-effects model framework. We observed minor differences in song consistency between sweeps and trills, with males that sang broad bandwidth songs having the lowest song consistency scores. This suggests broad bandwidth trills may be more difficult to sing consistently. Despite these small differences, overall high within-individual song consistency over time highlights the possible importance of being individually identifiable and suggests potential links to reproductive success.

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by

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INTRODUCTION

Birdsong is a complex tool for communication in songbirds and is often used by males to maintain territory boundaries and attract females (Nowicki and Searcy 2005, Byers and Kroodsma 2016). Birds can produce, perceive, and respond to small scale differences in song features, so, even fine scale differences in song and performance may impact the quality of the signal and ultimately an individual's reproductive success (Gil and Gahr 2002, Garamszegi et al. 2006, Prior et al. 2018). Vocal performance is the ability to produce vocal signals close to defined physical limits, and it has been shown that birds will identify and respond differently to high- and low-performing songs (Welch et al. 1998, Forstmeier et al. 2002, Drăgănoiu et al. 2002, Ballentine et al. 2004, Illes et al. 2006, Byers 2007, Cramer and Price 2007, de Kort et al. 2009a, Podos et al. 2009, Caro et al. 2010, Geberzahn and Aubin 2014, Phillips and Derryberry 2017). One aspect of vocal performance, vocal consistency, refers to the ability to reproduce song elements accurately from one rendition to the next (Sakata and Vehrencamp 2012). Vocal consistency may be a signal with which individuals assess the quality of singing males in a population.

Reproducing the same renditions of songs, syllables, and notes is difficult, and largely depends on a male's morphology, physical condition, and ability to coordinate multiple neurological, physiological, and physical systems (Gil and Gahr 2002, Jarvis 2004, Ashmore et al. 2005, Reide et al. 2006, Sakata et al. 2008, Podos et al. 2009, Sockman 2009, Sprau et al. 2013, Sakata et al. 2020). Songs are physically taxing to produce and therefore incur energy costs (Ward et al. 2003, Fletcher et al. 2006, Riede et al. 2006, Mendez et al. 2012). Physical constraints like bill size and shape can affect a male's ability to repeat notes or song phrases accurately and quickly and therefore affect song performance (Podos 2001, Sprau et al. 2013, Derryberry et al. 2018). Depending on the individual's physical and physiological constraints, some songs are harder to sing than others, which may also affect their ability to be consistent. For example, in trilled songs, rapidly singing notes that cover a broad range of frequencies may be more difficult than singing notes that cover a smaller range of frequencies at that same note rate (Phillips and Derryberry 2017; although this may be species dependent, see Cramer 2013b). In some species, production of trill notes occurs through the careful coordination of the left and right sides of a bilaterally innervated syrinx, and the level of mastery of such may affect how accurately a bird can reproduce trill notes (Suthers 2004, Botero and de Kort 2013). Additionally, conditions during early development and while individuals learn song can affect later song quality (Nowicki et al. 2002, Searcy et al. 2010). These biological constraints result in variation among males with respect to their ability to produce consistent songs over time. Therefore, vocal consistency may serve as an honest signal of male quality (Murphy et al. 2008, Janicke et al. 2008, Logue et al. 2020, Sun et al. 2021).

High vocal consistency may be advantageous across many different contexts. Males that can sing with high consistency have higher reproductive success and are more likely to secure extra-pair fertilizations (Ballentine et al. 2004, Byers 2007, Botero et al. 2009, Wegrzyn et al. 2010, Cramer et al. 2011, Sakata and Vehrencamp 2012, Taff and Freeman-Gallant 2016). In a laboratory setting, female Zebra Finches preferred male courtship song that was more consistent (Wooley and Doupe 2008). Consistency can improve with age; therefore, it may be that females are using song consistency as a signal to assess male age and experience (Rossman 2007, de Kort et al. 2009b, Botero et al. 2009, Kipper and Kiefer 2010, Sprau et al. 2013, Ota and Soma 2014) and there is evidence that in some species females prefer older males (Griffith et al. 2002, Ballentine 2009, Zipple et al. 2019). Highly consistent males are also more dominant and less likely to be challenged by other males (Christie et al. 2004, Rossman 2007, Botero et al. 2009, de Kort et al. 2009b). Additionally, reproducing the same song or identifying song features with limited variation may be important for individual discrimination within a population (Goldman 1973, Fitzsimmons et al. 2008, Kennedy et al. 2009, Wilson and Mennill 2010). Individuals that can consistently produce identifying features in their vocalizations can distinguish themselves from others even in populations with a highly stereotyped song (same or similar renditions within or across individuals; Elfstrom 1990, Kennedy et al. 2009). This is particularly advantageous in species where males repeatedly interact with other males on nearby territories (dear enemy effect; Tumulty 2018, Thomas et al. 2021). Being able to identify nearby individuals is important for males managing their territory as it may alter their level of response and energy output to neighbors vs. intruders, and help avoid unnecessary, costly skirmishes. For these reasons, it is possible that higher vocal consistency is a trait selected for in birdsong by both males and females (lles et al. 2006, Botero et al. 2009, Botero and de Kort 2012, Sprau et al. 2013, Souriau et al. 2019).

Despite potential selection for individual consistency and distinctiveness, there are reasons why consistency may fluctuate over time. Variation in age, breeding season or resource availability may change the motivation or ability to invest energy in highly consistent song (Nottebohm et al. 1986, de Kort et al. 2009b, Cooper et al. 2012, Vehrencamp et al. 2013, Sprau et al. 2013, Vehrencamp et al. 2013, Zhang et al. 2016, Naguib et al. 2019, Deng et al. 2019, Souriau et al. 2019, Grabarzcyk et al. 2019). Further, plasticity may be favored depending on the environmental or social context and allow individuals to adjust to short term changes in soundscapes and social dynamics (Slabbekoorn and den Boer-Visser 2006, Tumer and Brainard 2007, Taff and Freeman-Gallant 2016, Zsebők et all. 2017, Grabarczyk et al. 2018, Dinh et al. 2020, Derryberry et al. 2020). Although plasticity may be favored in particular situations, the benefits of producing highly consistent song may outweigh the need for plasticity and select for vocal consistency, as evidenced by individualized, repeatable vocalizations across multiple time scales and contexts in some species (Murphy et al. 2007, Fitzsimmons 2008, de Kort et al. 2009b, Xia et al. 2011, Petrusková et al. 2016, Zipple et al. 2019).

Songs of many bird species may be complex, and contain different, identifiable phrases or parts combined into a unified signal. In species with small song repertoires, these song parts (instead of whole songs as seen in species with larger repertoires) may serve different functions or have different information encoded in them (Elfstrom 1990, Vallet and Kreutzer 1995, Nelson and Soha 2004 a, b, Osiejuk et al. 2007, Collins et al. 2009, Poesel et al. 2012, Bartsch et al. 2016, Nelson 2017, Grunst at el. 2018). Receivers will glean information from multiple features and parameters within a song (Nelson 1988, Nelson 1989, Lohr and Dooling 1998, Searcy et al. 2000, Dooling et al. 2002, Lohr et al. 2006, Grunst el al. 2018). As such, selective pressures stemming from male-male and male-female interactions may be acting disproportionally on different parts or parameters within a song (Collins et al. 2009). Parts of songs that are more consistent within males may communicate species or individual identity or contain an alerting component to danger (Marler 1961, Richards 1981, Thompson and Baker 1993). Alternatively, parts of songs may be more variable depending on motivational states or changing external stimuli. For example, in the White-crowned Sparrow, its suggested that the whistle portion of their song conveys species identity or serves as an alert call, the note complex portion encodes individual identity, and the trill portion conveys regional dialect or aggression (Shiovitz 1975, Soha and Marler 2000, Nelson and Poesel 2007, 2009). If song parts serve different functions, it is possible that selective pressures may act on those song parts disproportionally, which may cause the consistency of song features or parts to vary as well (see Paul et al. 2021).

We explored vocal consistency using the Field Sparrow as a model species. Field Sparrows are migratory, territorial songbirds found in grasslands and forest edges across the central and eastern United States (Best 1977). Adult Field Sparrows often return post-migration to the same territories occupied the season before (Walkinshaw 1945, Gill & Vonhof, unpubl. data). First-year birds disperse from natal sites, and songs are learned from neighbors upon arriving in a new, post-migration site in their second year and crystalize shortly after settlement (Nelson 1992). They sing two different categories of songs: simple (the subject of this study) and complex (Nelson and Croner 1991). Simple song is used in territorial advertisement and female attraction and is more frequently heard compared to complex song (Nelson and Croner 1991, Nelson 1992). Complex songs are relatively rare outside of the dawn chorus and have been shown to vary across breeding stages (Zhang et al. 2016). It is believed that their simple songs are highly stereotyped (remain identifiable from year to year), which makes them close-ended learners (Heckenlively 1976, also see Beecher and Brenowitz 2005). This, however, has not been formally investigated (Nelson 1992, Gill & Vonhof unpubl. data). Simple song typically consists of several sweep notes followed by a series of trill notes (Figure 1); within these song parts different information may be communicated to the surrounding community (Nelson 1988). Simple songs can also be sorted into recognizable song types- for this study we recognized broad and narrow bandwidth song categories (Figure 1). Song type was included to account for differences in note structure between broad and narrow bandwidth songs.

Our study sought to answer two main questions. First, do Field Sparrow song characteristics and structure change over time? Second, are there differences in the consistency of different song parts (sweeps and trills)? We examined consistency by recording singing males multiple times within and between years, and calculating repeatability and spectrographic cross-correlation of song parts within and between years. We also examined whether vocal consistency within a day changed between years as individuals aged. Overall, we predicted that song characteristics of sweeps and trills would remain highly consistent over time. While we could not address the ultimate selective pressures influencing vocal consistency, demonstrating its presence may indicate an important role in mate choice and territorial interactions. Further, if Field Sparrow songs are highly consistent across time, future field studies may also be able to identify males within a population by relying only on song recordings and territory location (see Xia et al. 2011, Kirschel et al. 2011, Ehnes & Foote 2015).

METHODS

Study Site

Field sparrows were recorded at Chipman Preserve, a 230-acre plot of land situated in Galesburg, Michigan over the summers of 2016-2020. This rurally located preserve is characterized by a mix of fields and forests with considerable edge habitats and supports a large population of Field Sparrows. A color-banded population has been maintained at this site since 2013.

Song Recordings

We utilized recordings from color-banded males recorded between 2016 to 2020. Male band IDs were confirmed prior to recording and locations of banded males were tracked using AvenzaMaps (Avenza Systems Inc., Ontario, Canada). Songs were recorded using a calibrated Sennheiser shotgun microphone and Marantz recorder. Calibration was carried out with methods specified in Gill et al. 2015. While recording each bird, the shotgun microphone was manually pointed at the male and adjusted for perch changes. We aimed to record at least 5 clear songs from each male on the day of recording. This ensured at least one good song was available for analysis. For males that sang less frequently, recordings were taken across multiple singing bouts and all songs recorded on that day were combined into one recording file. Males were opportunistically recorded again after the initial recording during the same season or in different years. In total we obtained 82 recordings of 24 male Field Sparrows. From these 24 males, 19 were recorded more than once within a single year, and 19 were recorded in two or more years.

In some cases, a male may have had more than one within-year or between-year recording comparison. In these instances, recordings were assessed for quality and number of songs, and the better-quality recordings were retained. If multiple recordings remained from a male that were of good quality and had more than five eligible songs, one pairing was randomly selected for the within-year and/or between-year category to avoid over-representation of individual males within the data set. For example, if a male was recorded twice in 2017 and twice in 2018, one year was selected for the within-year comparison. In this same scenario, there are four possible between-year comparisons, but only one combination was selected for inclusion in the analysis.

Song Analysis

We created spectrograms to visually assess each recording using the following settings: 512 Fast Fourier Transform, flat top window, 93.75% overlap, 0.73 ms temporal resolution, 86 Hz frequency resolution using AviSoft SASLab Pro v5.2 (Sprecht, R., Berlin, Germany). We identified all songs with high signal-to-noise ratios and that were not clipped or masked by other sounds and separately labeled the “sweep” and “trill” sections for each usable song from each male. Because the first and last notes of each song often had lower amplitude, and the sweep portion of songs often grades into the trill portion (Nelson and Croner 1991), we labeled only the second and third notes in each song to characterize the sweep portion, while the penultimate to n-5 trill notes were marked for the trill portion (Figure 1). This procedure allowed for consistent sampling across songs and accounts for the different spectral features found in the sweep and trill portions of Field Sparrow song (Nelson and Croner 1991).

A bandpass finite impulse response filter was applied to remove ambient sounds 200Hz above and below the minimum and maximum frequency of the song. These were determined visually using the reticule cursor in the spectrogram window. We chose and manually applied these filters for all songs in the dataset, then selected 5 songs using a random number generator (random.org). If fewer than 5 songs were recorded, then all songs for that male were included. A total of 329 sweeps and 329 trills were collected for further analysis. Males in the final data set were also assigned a song type based on whether their song was broad or narrow bandwidth (broad bandwidth songs had bandwidth greater than the median bandwidth, narrow bandwidth had smaller than median bandwidth) to account for potential differences in consistency between songs varying in overall bandwidth.

Spectrographic Cross Correlation

One way to assess song similarity is by comparing the overall shape of each song. Spectrographic Cross Correlation (SPCC) is a common method for measuring similarities between two signals in a pair-wise comparison by overlapping the spectrograms of the two signals pixel by pixel (Clark et al. 1987, Cramer 2013). We conducted the SPCC analysis using Avisoft-SASLab Pro (Sprecht, R., Berlin, Germany). The sweep and trill sections were separately subjected to spectrographic cross-correlation at five levels. Cross correlations (CC) were obtained for both within-male (two songs compared from the same male) and between-male (two songs are compared, each from different males) comparisons. At the "within-individual" level, spectrograms from recordings from the same male were compared to other spectrograms of available songs recorded on the same day, the same year, and/or different years from that male. At the "between-individual" level, spectrograms from recordings from two different males were compared from recordings taken within the same year and from different years. This was done using the batch processing tool to run "Template Cross Correlation on short files" (high-pass cutoff frequency = 500 Hz, low-pass cutoff frequency = 100,000 Hz, max frequency deviation = 0). This produced values between 0 (no similarity) and 1 (a direct match), for each pairwise comparison.

To assess whether within-day vocal consistency changed across years as individuals aged, we calculated the within-day cross-correlation scores for each year for every male that was recorded across two or more years (n=18). One male was excluded from this because one of his recordings only had a single song. For males that had more than one recording within a single year, one recording was chosen based on quality, number of songs available (>5), or random selection if multiple recordings were of sufficient quality. The first recording for a male was denoted as having come from year 1, and recordings from subsequent years were then assigned ‘relative years’ from this first recording.

Statistical Analysis

All data were initially explored following Zuur et al. (2010) and Zuur and Ieno (2016). Data were plotted to check for outliers and outliers were investigated for errors. Data was checked for zeros, and none were found in the within-male SPCC data. The SPCC data was skewed after being plotted, so a generalized linear mixed effects model with a beta distribution was applied (Douma and Weedon 2019).

To test if there were differences in cross-correlation scores across time and between song parts, we ran a generalized linear (beta regression) mixed effects model with a logit link function and using the within-male mean cross-correlation scores for each pairing as the response variable. Beta regression was chosen to analyze these data, as cross-correlation scores fall on a continuous scale between 0 and 1 and are therefore continuous proportions (Douma and Weedon 2019). Time-scale comparison (within day, within year, or between year), song part (sweep and trill), and song type (broad and narrow) were included as fixed-effect predictors and male ID was included as a random effect. Models were run using the glmmTMB package in R (Bolker et al 2009, Bolker 2016). Initially, all predictors and their two- and three-way interactions were included in the model, with male id included as a random effect. This model was later simplified to include only the two-way interactions between song part by song type and time scale by song type, the main effects, and male id as a random effect due to a lower AIC value and a comparison of AIC weight calculations (Symonds and Moussalli 2011, Table 2).

As another means of testing for vocal consistency, we analyzed whether within-day cross-correlation scores within males varied over time using an additional generalized linear (beta regression) mixed effects model. The within-day averaged cross-correlation scores for each male were used as the response variable. Relative year of recording, song part (sweep and trill), and song type (broad and narrow) were included in the model as fixed effects, male id was included as a random effect, and all two-way and three-way interactions were included. Removing interactions improved model fit, so the model was simplified to just the three main effects and the random effect of male ID (Table 4). For both models, we verified that model assumptions were satisfied using the DHARMa package in R (Hartig 2016).

Repeatability Analysis

Another way to assess song similarity is to assess repeatability of the spectral and temporal features of songs within and between recordings (see Lessells and Boag 1987). Song parameters were characterized for the same randomly selected songs used in the cross-correlation analysis. Peak frequency (Hz), minimum frequency (Hz), maximum frequency (Hz), duration (s) and bandwidth (Hz) of the sweep and trill song parts were separately extracted from each song using the automatic parameter calculation function and a threshold of -10 dB in Avisoft-SASLab Pro (Figure 2).

Repeatability was estimated using a linear mixed-effects model framework with male ID as a random effect, and 95% confidence intervals for repeatability estimates- calculated via bootstrapping using the R package rptR (1000 bootstraps; Nakagawa and Schielzeth 2010, Stoffel et al. 2017, 2019). Data were initially explored following Zuur et al. (2010). Data were plotted to check for outliers and outliers were investigated for errors. Because repeatability could be influenced by song part (sweep vs. trill) and song type (narrow vs. broad), the data set was split out into datasets representing those categories and the repeatability calculated separately to avoid the effects of those categorical variables.

RESULTS

Spectrographic Cross Correlation

We analyzed 329 songs from 81 recordings from 24 males. Within-day (n=24 males), within-year (n=19 males), and between-year (n=19 males) cross-correlation scores were calculated for a total of 21,872 between-male comparisons and 1,910 within-male comparisons.

Vocal consistency as measured by cross-correlation scores was high across all time scales, song parts, and song types, with mean scores ranging from 0.77-0.91 (N = 1,910 within male comparisons; Table 1, Figure 4). There is a clear separation between the cross-correlation scores for within-male and between-male comparisons (Figure 3), with a large majority of within-male scores >0.75 and most between-male scores falling below 0.5 for both sweeps and trills. Interestingly, in a small but notable number of cases two different males sang songs with sweeps that were similar (14.5%, scores >0.5, up to 0.95), but this was less so the case for trills (Figure 3).

We tested the effect of time scale, song part, song type and their interactions on cross-correlation scores using beta regression. The best fit model did not include the three-way interaction among these predictors, nor did it include the two-way interaction term of time scale by song part (Table 3). Model validation by the KS (Kolmogorov-Smirnov), Dispersion, and Outlier tests, and plotting residuals vs. predicted values with DHARMa in R indicated no problems. Interactions between song part and song type and between time scale and song type explained variation in cross correlation scores. Cross-correlation scores were consistently higher for sweeps than trills (Figure 4), but the interaction indicated that the cross-correlation scores for trills of males singing broad bandwidth songs were significantly lower than scores for all other song part-song type categories (Figure 5). Although high overall, cross-correlation scores consistently declined with time scale (within-day, within-year, between-year) and were higher for narrow bandwidth songs relative to broad bandwidth songs (Figure 4). The interaction between time scale and song type indicated that the difference in cross-correlation scores between narrow and broad bandwidth song types is more pronounced in within-day comparisons (Figure 6).

We tested the effect of relative age (relative year) for males recorded in more than one year, song part and song type and their interactions on within-day cross-correlation scores using beta regression. We analyzed 374 songs from 44 recordings to calculate cross-correlation means for males (n=18) that had more than one song on a within-day recording across two or more years. Of those 18 males, 16 had a “year 2” recording, 7 had a “year 3” recording, and 3 had a “year 4” recording. Some males (N= 3) did not have recording sets in each consecutive year, but 2 of the 3 “year 4” males had a within-day recording all 4 years.

While the original model included all 2 and 3-way interactions, the best fit model did not include any interactions (Table 5). Model validation by the KS (Kolmogorov-Smirnov), Dispersion, and Outlier tests, and plotting residuals vs. predicted values with DHARMa in R indicated no problems. While all three predictors explained variation in within-day cross-correlation scores, song part had the largest effect. Sweeps were more consistent than trills, and narrow bandwidth song types were more consistent than broad bandwidth song types. Regardless of male, song part, or type, almost all within-day cross-correlation scores remained high across years (>0.7; Figure 7).

Repeatability Analysis

Repeatability estimates for peak frequency, minimum frequency, maximum frequency, duration, and bandwidth were calculated for 24 males within (n=19) and between (n=19) years using a linear mixed effects model framework in rptR with male id included as a random effect and 1000 parametric bootstrap iterations used to calculate confidence intervals. We modeled repeatability estimates for each song separately by time scale, song part, and song type (N=40 repeatability estimates).

Repeatability values were moderately high for all song parameters regardless of time scale, song part, or song type, with a majority of parameters falling above 0.7 (Figure 8). While song parameters for sweeps tended to be more repeatable than those of trills and narrow bandwidth song types on average were more consistent than broad bandwidth song types, the differences between time scales, song types, and song parts were not very pronounced because of high scores across all categories. When looking at song part and song type combined, broad bandwidth trills overall were noticeably less repeatable than all other groups, with the bandwidth parameter of trills sung by males in between year comparisons scoring the lowest of all repeatability values (R=0.386; Figure 5, Table 6). Repeatability scores for bandwidth were low in all groups despite consistently high repeatability values for minimum and maximum frequency.

DISCUSSION

We recorded 24 male Field Sparrows at Chipman Preserve over five years and used those song data to explore Field Sparrow vocal consistency over time and across song parts. Song type was included to account for differences in note structure between broad and narrow bandwidth songs. Broadly stated, Field Sparrow simple song is extremely stereotyped within-individuals and remains highly consistent over time, across song parts and song types. Additionally, within-day consistency remained high with relative age. Within those high consistency scores, there were minor differences in consistency between sweeps and trills, and broad and narrow bandwidth songs. In general, trills were less consistent than sweeps, and males that sang broad bandwidth trills had the lowest consistency scores among all groups. Additionally, while narrow bandwidth songs were always more consistent than broad bandwidth songs, the disparity between the two was greater at the within-day level. Despite these distinctions, all differences are found within overall relatively high scoring song consistency scores for both cross-correlation comparisons and repeatability of song parameter traits.

Song consistency remained high within and across years, consistent with findings in other species (Murphy et al. 2007, Fitzsimmons et al. 2008, Petruskova 2016). Higher song consistency over time can be reproductively advantageous, as males that sing with higher consistency have increased reproductive success and may be more attractive to females (Wooley and Doupe 2008, Wegrzyn et al. 2010, Sakata and Vehrencamp 2012, Taff and Freeman-Gallant 2016). In some species, song consistency increases during the breeding season (Nottebohm et al. 1986, Smith et al. 1995, Smith et al. 1997, Souriau et al. 2019), and may occur just prior to the egg laying stage, when mate selection is most important (Naguib et al. 2019). In addition to attracting social mates, males with more consistent song are also more likely to secure extra pair fertilizations (Byers 2007, Cramer et al. 2011). Since our recordings of Field Sparrows were exclusively taken during the breeding season, finding high individual consistency within and between breeding seasons could mean that song consistency is linked to reproductive success in this species as well, either with social mates or through extra-pair fertilizations (Celis-Murillo et al. 2016 a, b).

High within-individual song consistency over time may also advertise individual identity. Individual distinctiveness is advantageous for both signalers and receivers in contexts where individuals are repeatedly interacting with each other (Tibbetts and Dale 2007). Generally, once territory boundaries are established, neighbors may respect these boundaries to avoid expending unnecessary energy in territorial disputes (Ydenberg et al. 1988, Elfstrom 1990, Tumullty 2022). Males can benefit from being familiar with neighboring male's identities in order to differentiate and respond to unfamiliar males who may not respect established territory boundaries (Brooks and Falls 1975, Godard 1991, Tumulty 2018). Field Sparrows return early in the spring and claim territory in a patchwork-like fashion that they defend through the breeding season, and like a number of other species (i.e. Hooded Warbler, see Godard 1991) are known to return to the same or nearby territories every year (Walkinshaw 1945, Gill & Vonhof, unpubl. data). Therefore, they likely interact with a relatively consistent set of neighbors over time (Walkinshaw 1945, Gibson 2011). Our data suggests that Field Sparrow songs are not only highly consistent, but individually distinctive because there is more variation among individuals than within (Figure 3). For these reasons, Field Sparrow simple song may be used as an identifying signal. Finding high individual consistency within and between years suggests that being individually distinctive through simple songs may be important and influence conspecific interactions.

Relative age did not impact consistency scores in Field Sparrows (Figure 7, Table 4). Song consistency has previously been observed to increase as individuals age, at least until senescence, such that males of intermediate to older ages sing more consistently (Rossman 2007, Botero et al. 2009, de Kort et al. 2009b, Wegrzyn et al. 2010, Cooper et al. 2012, Sprau et al. 2013, Berg et al. 2020). In other species, vocal consistency increased only between the first and second years (Zipple et al. 2019). It is thought that there is a period of time between breeding seasons where songbirds may enter a more plastic singing stage that allows them to practice and improve their song and singing abilities, which could explain observed, age-related increases in song consistency (Nottebohm 1981, Souriau et al. 2019). Vocal consistency in these cases is thought to be a measure by which males and females alike can assess male age, experience, and quality (Kipper and Kiefer 2010, Vehrencamp et al. 2013, Ota and Soma 2014).

In our data, individual males had minor fluctuations in within-day song consistency (which remained high overall), but we did not observe a consistent pattern of increases or decreases in consistency scores as males got older (Figure 7). It is possible that a pattern was not apparent in our data because we did not account for the exact ages of individual males, as changes in consistency can occur between specific age classes (Kipper and Kiefer 2010, Zipple et al. 2019). It may also be that our study did not track the same individual males over a long enough period of their lifespans for previously documented lifelong patterns to become apparent (see Zipple et al. 2019). Regardless, finding high within-day consistency over time further underlines the potential importance of having high individual song consistency in this species.

While the consistency of both song parts was high, sweeps on average were more consistent than trills. Different parts of song may encode different information, which may cause selective pressures from male-male and male-female interactions to drive variation in consistency among song parts (Vallet and Kreutzer 1995, Osiejuk et al. 2007, Collins et al. 2009, Nelson 2017, Paul et al. 2021). Higher consistency has been observed in song features or parts that convey species and/or individual identity, as seen in the note complex and trill portions of White-crowned sparrow (Nelson and Soha 2004, Nelson and Poesel 2007) and White-throated Sparrow songs (Grunst et al. 2018). In the Great Reed Warbler, greater consistency was observed in the whistle portion of their songs, which is thought to encode local dialect identity (Wegrzyn and Leniowski 2010). In contrast, more variable song parts may serve different communicative purposes. More variability may be observed in certain parts or features to respond to changing environmental and social contexts (Illes et al. 2006, Vehrencamp et al. 2013, Grabarczyk et al. 2019, Philips et al. 2020), or may encode information that would vary more frequently than individual identity, like motivation, reproductive state, or health (Becker 1982, Nelson and Poesel 2007, Grunst et al. 2018). We observed differences between Field Sparrow sweep and trill song consistency, providing some evidence for different parts of song serving different communicative functions. Based on findings from other species, the more consistent sweeps of Field Sparrow simple song may encode identifying information, and the more variable trills may encode information that changes on a more contextual basis.

Not only were the trilled parts of songs generally less consistent, but the trilled song parts of broad bandwidth songs had noticeably lower consistency scores than all other groups (Figure 5). Singing notes with precision quickly is difficult (Vallet and Kruetzger 1995, Podos 1997, Ballentine et al. 2004). Bird song is produced through careful coordination of neurological and muscular systems (Suthers et al. 1999, Suthers 2004, Sockman 2009, Sakata and Vehrencamp 2012, Botero and de Kort 2013). An important feature of avian song production is the syrinx, which is bilaterally divided into a right and left side that are independently controlled (Suthers et al. 1999). In some species, trilled notes require the use of both the left and right syrinx to produce the desired note, particularly when covering wider frequencies (Botero and de Kort 2013). Therefore, moving across larger frequency ranges, like in broad bandwidth trills, would require better mastery of syrinx control, and may therefore, on average, cause broad bandwidth song to be less consistent (Suthers 2004, Botero and de Kort 2013). As trill sections in Field Sparrow song require the quick repetition of the same note for a length of time, males that sing broad bandwidth trills may have a harder time quickly and accurately reproducing wider bandwidth notes, and this may account for the observed lower consistency scores.

We observed highly consistent Field Sparrow simple song over the course of this study. High within-individual song consistency, notable variation between individuals (Figure 3), and steady territory occupation once settled (Walkinshaw 1945, Gill & Vonhof, unpubl. data) make Field Sparrows a great candidate for future individual identification studies that seek to use vocalizations or songs as identifiers in the field (see Xia et al. 2011, Kirschel et al. 2011, Ehnes and Foote 2015, Deng et al. 2019, Petruskova 2021). Because they sing one highly consistent simple song, they avoid pitfalls in consistency studies that arise with species that have with multiple song types – namely, that it is difficult to assess individual consistency if those individuals sing different songs over a period of time (see Pruchova et al. 2017). In many species, males with higher song consistency have higher reproductive success and are less likely to be challenged by other males (Christie et al. 2004, Botero et al. 2009, de Kort et al. 2009b). Finding high individual song consistency across multiple time scales provides evidence that song consistency may be important in Field Sparrows and may serve as an identifying signal or a means by which females can assess male quality, but more specific questions about song consistency and its function in this species should be asked in follow up studies. Future studies on neighbor-stranger differentiation and individual identification in this species would be beneficial to determining if Field Sparrows use simple song (or its parts) as a self-identifying signal. Body condition data in conjunction with song consistency data in this species could help determine if higher song consistency scores are correlated with traditional body metric data that would indicate higher male quality. Further, collecting Field Sparrow reproductive data in conjunction with song consistency data can help determine if song consistency predicts reproductive success in this species as it does in others (Ballentine et al. 2004, Byers 2007, Botero et al. 2009, Wegrzyn et al. 2010, Cramer et al. 2011, Sakata and Vehrencamp 2012, Taff and Freeman-Gallant 2016). We detected slight differences in the consistency of Field Sparrow song parts. As seen in other species, this may indicate that sweeps and trills have different communicative functions (Nelson and Poesel 2007, Wegrzyn and Leniowski 2010, Nelson 2017), but more research is needed with playback studies to determine how and why conspecifics may react to variation in consistency of different song parts and song parameters. Further, broad bandwidth trills had the lowest consistency of all other groups, suggesting broad bandwidth songs may be harder to sing. While song type was not the focus of this study, we found evidence that song type affected song consistency, and future studies of song consistency should consider the effects of song type and its interactions with other predictors. To conclude, this exploratory study found high consistency in Field Sparrows, providing further evidence for the importance of song consistency, but there is yet more to understand about the evolutionary drivers of high song consistency in this species and what selective pressures may be driving differences in consistency between song parts.

Table 1. Mean cross-correlation scores for different male comparisons, song parts, and time scales. Scores for within-male comparisons are significantly higher than between-male comparisons, showing a clear separation between the two groups.

Male Comparison	**Time Scale**	**Song Part**	**Mean CC Score (±ci)**
Within-male	Within-day	Sweep	0.91 (±0.007)
Within-male	Within-day	Trill	0.87 (±0.012)
Within-male	Within-year	Sweep	0.86 (±0.010)
Within-male	Within-year	Trill	0.82 (±0.009)
Within-male	Between-year	Sweep	0.85 (±0.008)
Within-male	Between-year	Trill	0.77 (±0.013)
Between-male	Within-year	Sweep	0.26 (±0.007)
Between-male	Within-year	Trill	0.27 (±0.005)
Between-male	Between-year	Sweep	0.28 (±0.006)
Between-male	Between-year	Trill	0.28 (±0.004)

Table 2. Model selection using AIC values and weights for candidate beta regression mixed effects models with cross correlation scores as the response, time scale, song part, and song type as predictors, and male id as a random effect. Of the models tested, model 3 (M1.7) had the lowest AIC value, and the largest AIC weight value, making it the best fit model for the data in this set. k = the number of terms in each model plus the variance term, AIC = Akaike Information Criterion, Δi = delta AIC, wi= AIC weight, ts = time scale, sp = song part, st = song type, and id = random effect of male id.

Model #	**Candidate Models**	***k***	**AIC**	**Δ*i***	***wi***
1 (M1.6)	ts + sp + st + ts*st + ts*sp + st*sp + ts*st*sp + id	9	-353.6	7.7	0.01
2 (M1.4)	ts + sp + st + ts*st + ts*sp + st*sp + id	8	-357.5	3.8	0.09
3 (M1.7)	ts + sp + st + ts*st + st*sp + id	7	-361.3	0	0.58
4 (M1.3)	ts + sp + st + st*sp + id	6	-359.9	1.4	0.29
5 (M1.5)	ts + sp + st + id	5	-355.8	5.5	0.04

Table 3. Results of the best-fit beta regression time scale model, where the best fit model included time scale, song part, song type, and the two-way interactions of time scale by song type and song part by song type as fixed effects, and male id included as a random effect. Scores trended downwards over time, with within-day scores scoring the highest. Sweeps scored higher in consistency than trills, with broad bandwidth song type trills scoring significantly lower than narrow bandwidth song type trills (Figure 5). χ2= Chi square test statistic, df = degrees of freedom, and *P* = P-value.

	Estimate	**χ^2**	**df**	***P***
Intercept	1.708	199.923	1	< 2.2e-16 ***
Time Scale		20.176	2	4.157e-05 ***
Song Part		38.788	1	4.724e-10 ***
Song Type		0.008	1	0.931
Time Scale: Song Type		5.460	2	0.065.
Song Part: Song Type		6.548	1	0.011 *

Table 4. Model selection using AIC values and weights for candidate beta regression mixed effects models with cross correlation scores as the response, relative year, song part, and song type as predictors, and male ID as a random effect. Of the models tested, model 5 (M3.4) had the lowest AIC value, and the largest weight value, making it the best fit model for the data in this set. k = the number of terms in each model plus the variance term, AIC = Akaike Information Criterion, Δi = delta AIC, wi= AIC weight, sp = song part, st = song type, id = random effect of male id, and ry = relative year.

Model #	**Candidate Models**	**k**	**AIC**	**Δi**	**wi**
1 (m3)	ry + sp + st + ry*st + ry*sp + st*sp + ry*st*sp + id	9	-274.1	15.8	0.00
2 (m3.1)	ry + sp + st + ry*st + ry*sp + st*sp + id	8	-279.5	10.4	0.00
3 (m3.2)	ry + sp + st + ry*st + ry*sp + id	7	-281.4	8.5	0.01
4 (m3.3)	ry + sp + st + ry*sp + id	6	-286	3.9	0.12
5 (m3.4)	ry + sp + st + id	5	-289.9	0	0.86

Table 5. The results of the best-fit beta regression relative year model, where the final best fit model included relative year, song type, and song part as fixed effects, and male id as a random effect. Song part explained the most variation in the within-day cross-correlation data, although all 3 predictors explained some variation in the data. Despite differences found between each of these predictor categories, within-day cross-correlation scores were high across all years. $\chi2$= Chi square test statistic, df = degrees of freedom, *P* = P-value.

	Estimate	**χ^2**	**df**	***P***
Intercept	2.029	268.970	1	< 2.2e-16 ***
Relative Year		6.944	3	0.074 .
Song Part		21.356	1	3.815e-06 ***
Song Type		3.947	1	0.047 *

Table 6. Repeatability estimates calculated from linear mixed effects models that included each song parameter separately as a response variable, male id as a random effect, and 1000 parametric bootstrap iterations for calculating confidence intervals. Song parameter data were separated out into different data sets by time comparison, song type, and song part, so no fixed effects were included in the model. Almost all song parameters were highly consistent (R >.70). R = repeatability, LCI = lower confidence interval, UCI = upper confidence interval, P= p-value.

Within-year Repeatability Estimates

	Song Type	Song Parameter	R	LCI	UCI	*P*
Sweeps						
	broad	minimum frequency	0.925	0.761	0.970	<0.0001
	broad	maximum frequency	0.988	0.955	0.995	<0.0001
	broad	peak frequency	0.992	0.972	0.997	<0.0001
	broad	duration	0.733	0.389	0.865	<0.0001
	broad	bandwidth	0.690	0.316	0.844	<0.0001
	narrow	minimum frequency	0.969	0.904	0.986	<0.0001
	narrow	maximum frequency	0.711	0.371	0.860	<0.0001
	narrow	peak frequency	0.741	0.424	0.872	<0.0001
	narrow	duration	0.851	0.616	0.931	<0.0001
	narrow	bandwidth	0.561	0.236	0.762	<0.0001
Trills						
	broad	minimum frequency	0.938	0.784	0.974	<0.0001
	broad	maximum frequency	0.799	0.487	0.910	<0.0001
	broad	peak frequency	0.655	0.290	0.830	<0.0001
	broad	duration	0.904	0.688	0.958	<0.0001
	broad	bandwidth	0.510	0.171	0.732	<0.0001
	narrow	minimum frequency	0.918	0.783	0.962	<0.0001
	narrow	maximum frequency	0.857	0.600	0.932	<0.0001
	narrow	peak frequency	0.835	0.595	0.925	<0.0001
	narrow	duration	0.992	0.974	0.997	<0.0001
	narrow	bandwidth	0.541	0.186	0.734	<0.0001

Between-year Repeatability Estimates

	Song Type	Song Parameter	R	LCI	UCI	*P*
Sweeps						
	broad	minimum frequency	0.941	0.830	0.971	<0.0001
	broad	maximum frequency	0.993	0.978	0.997	<0.0001
	broad	peak frequency	0.948	0.856	0.974	<0.0001
	broad	duration	0.788	0.513	0.890	<0.0001
	broad	bandwidth	0.895	0.716	0.951	<0.0001
	narrow	minimum frequency	0.976	0.910	0.990	<0.0001
	narrow	maximum frequency	0.968	0.868	0.987	<0.0001
	narrow	peak frequency	0.977	0.905	0.991	<0.0001
	narrow	duration	0.882	0.613	0.947	<0.0001
	narrow	bandwidth	0.889	0.620	0.949	<0.0001

Trills

	broad	minimum frequency	0.872	0.669	0.938	<0.0001
	broad	maximum frequency	0.784	0.523	0.892	<0.0001
	broad	peak frequency	0.781	0.53	0.893	<0.0001
	broad	duration	0.932	0.811	0.968	<0.0001
	broad	bandwidth	0.386	0.116	0.591	<0.0001
	narrow	minimum frequency	0.873	0.601	0.943	<0.0001
	narrow	maximum frequency	0.977	0.905	0.991	<0.0001
	narrow	peak frequency	0.966	0.876	0.986	<0.0001
	narrow	duration	0.988	0.947	0.995	<0.0001
	narrow	bandwidth	0.694	0.297	0.859	<0.0001

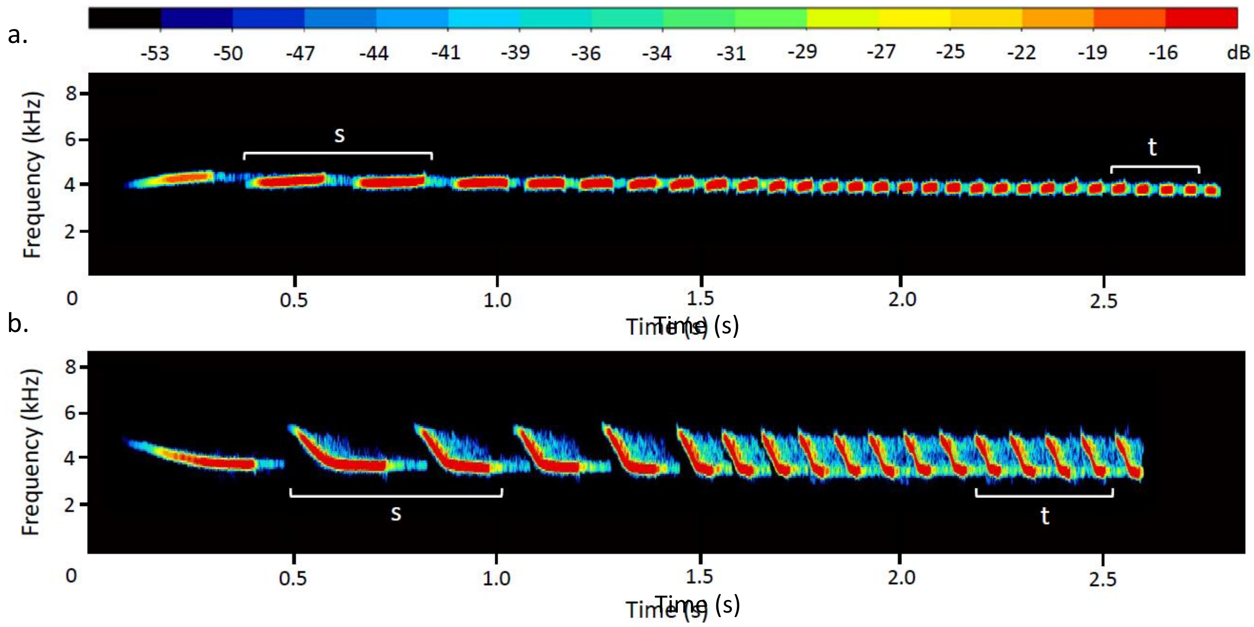

Figure 1. Two Field Sparrow simple song spectrograms with the sweep notes (s) and trill notes (t) marked. An example of narrow (a) and broad (b) bandwidth song types are shown.

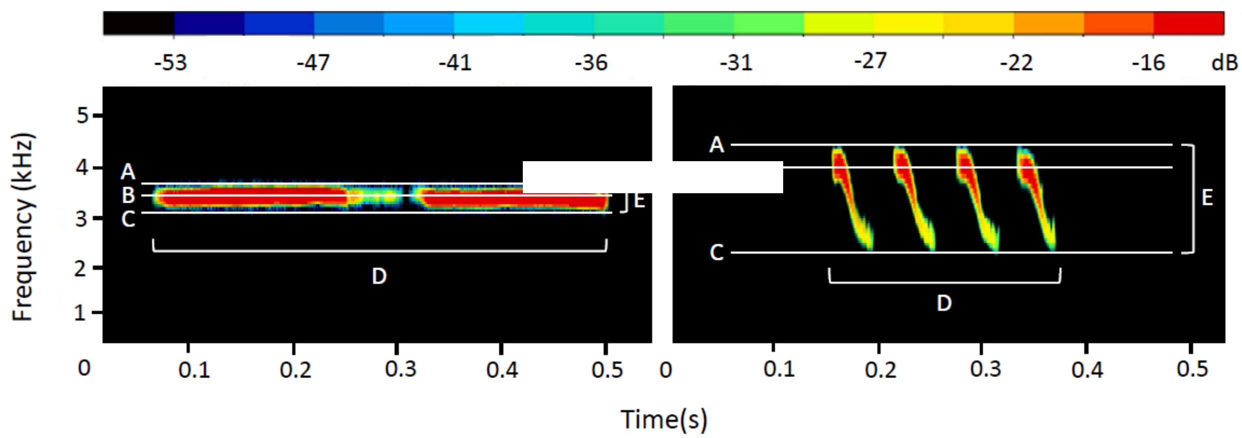

Figure 2. A sweep (left) and trill (right) section with examples of where each song parameter measurement is taken. A threshold is used to find the minimum and maximum frequencies of the spectrogram section and is set in reference to the maximum amplitude of the spectrogram. Maximum frequency (A, Hz) is the frequency where the magnitude of the spectrum first exceeds the specified threshold (-10 dB) towards higher frequencies. Peak frequency (B) is the frequency (Hz) at the point of the maximum amplitude of the song element. Minimum frequency (C) is the frequency (Hz) where the magnitude of the spectrum first exceeds the specified threshold (-10 dB) towards lower frequencies. Duration (D) is the length of time (s) from start to end of the specified spectrogram section (see Methods). Bandwidth (E, Hz) is the difference between the maximum and minimum frequencies.

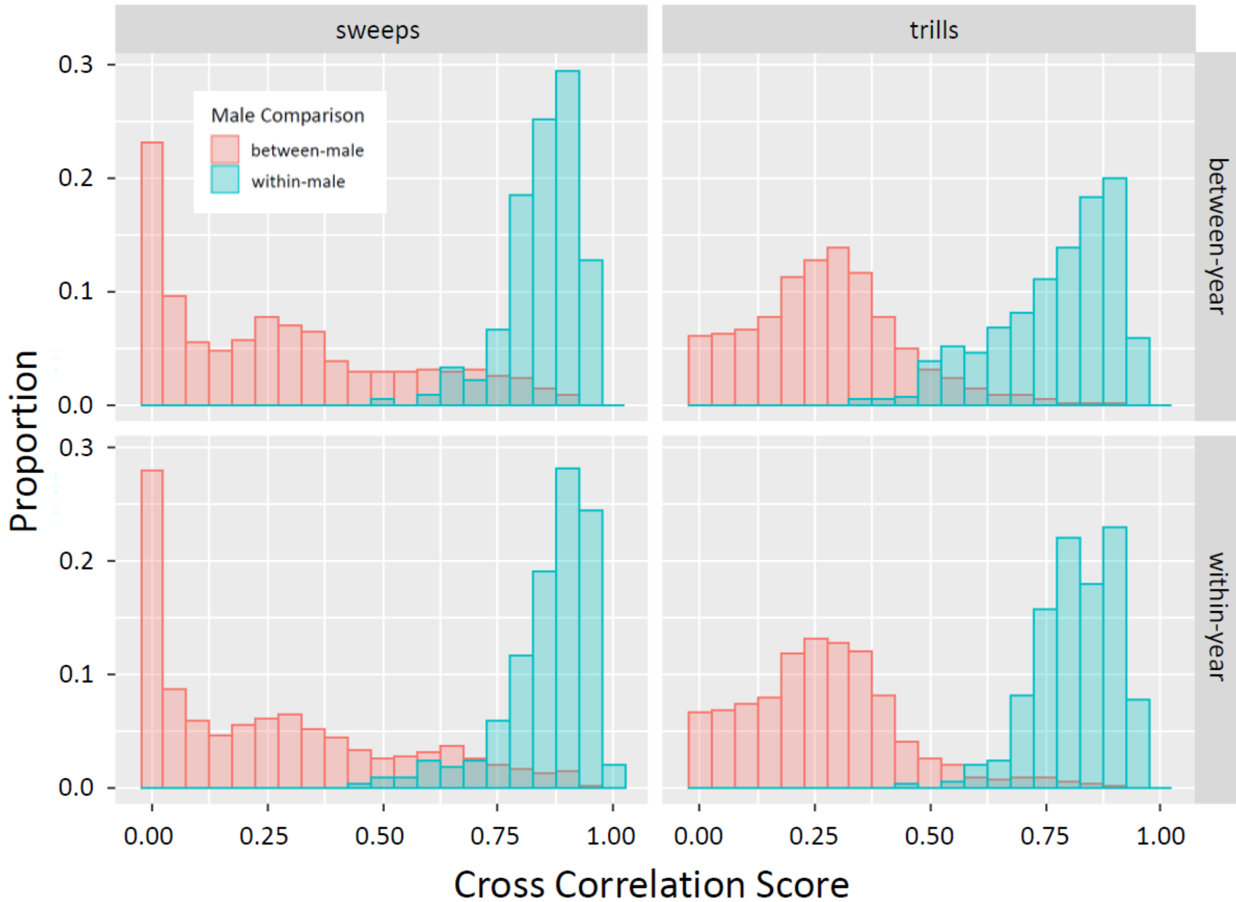

Figure 3. Frequency histogram of proportions of cross correlation scores for comparisons within and between males, between song parts, and across time scales. The cross-correlation scores for between-male and within-male comparisons show clear separation across all categories, although a small but notable proportion of between-male comparisons had high scores (>0.5). Within-male, within-day comparisons are not shown because there were no between-male, within-day comparisons.

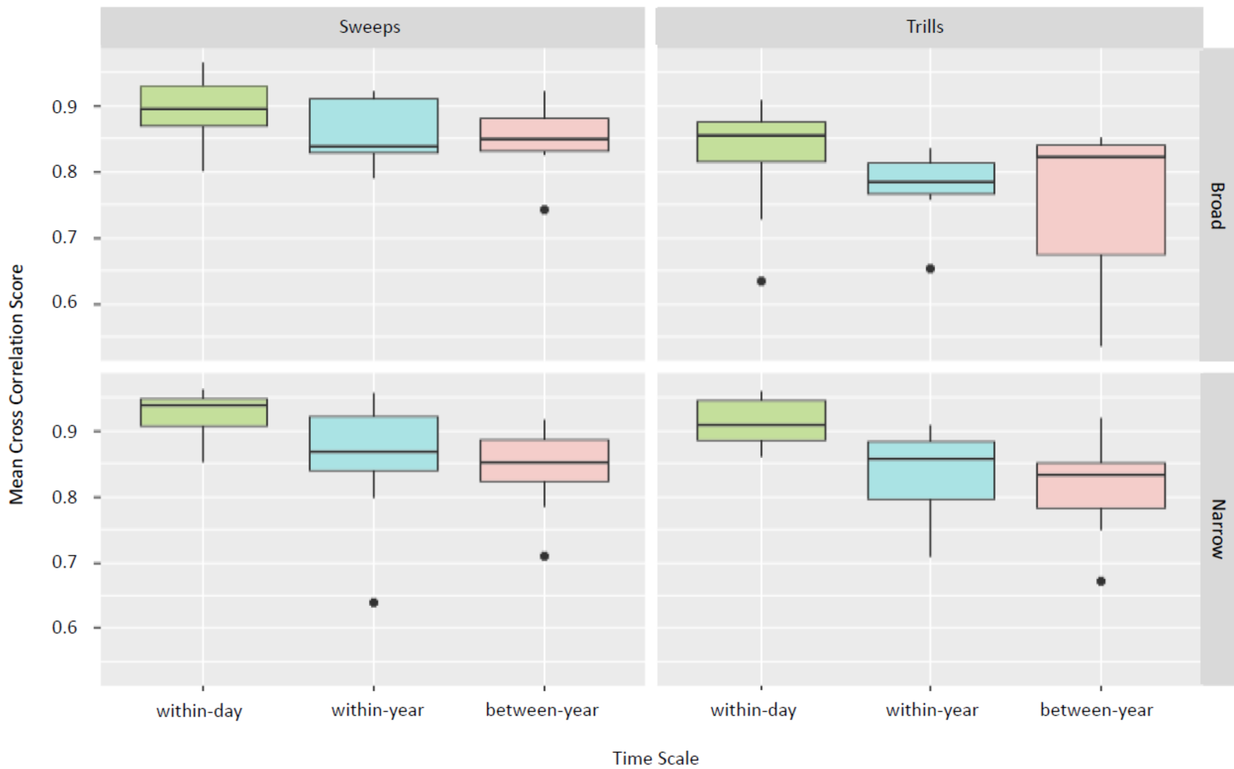

Figure 4. Mean cross-correlation scores between song parts, song types, and across time scales. Within-day cross-correlation scores were higher than within-year and between-year cross-correlation scores and had a much steeper difference between broad and narrow bandwidth song types, with within-day, narrow bandwidth song types scoring higher in consistency than any other group. Narrow bandwidth song types scored higher than broad bandwidth song types, but this difference was most notable in trills. Sweeps were more consistent than trills, but this difference was magnified in trills, with broad bandwidth trills scoring the lowest in consistency across all groups.

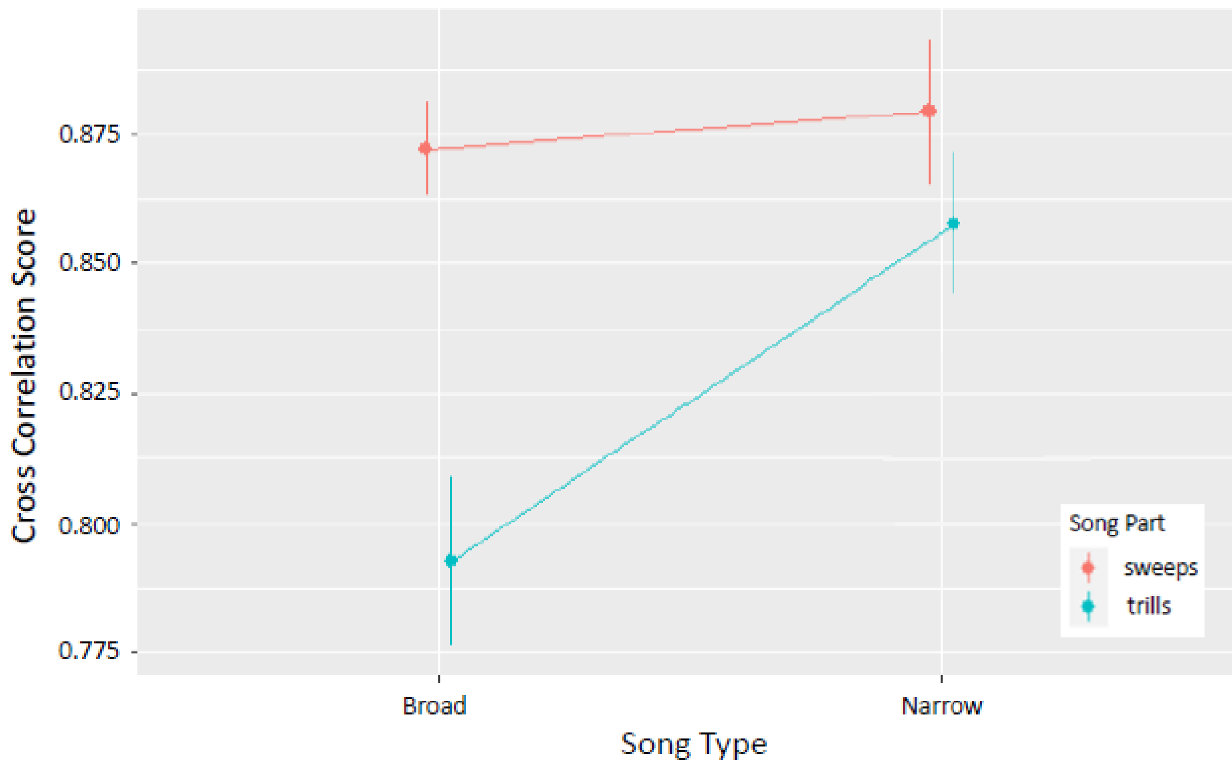

Figure 5. Mean cross correlation scores graphed across song parts and song types to test for interactions. Song type had a significant interaction with song part in the time scale model, with broad spectrum trills scoring lower in consistency than any other group. While narrow bandwidth song types were more consistent than broad bandwidth song types, this relationship is most evident when looking at trills.

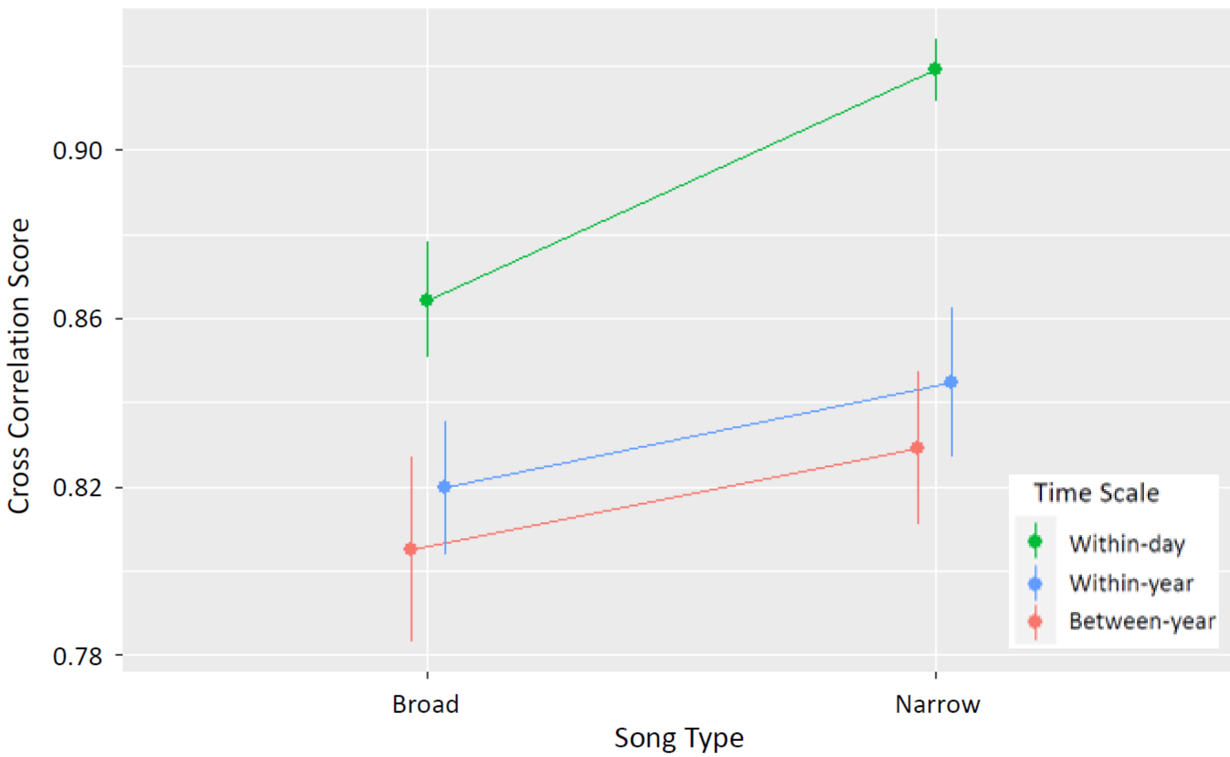

Figure 6. Mean cross correlation scores graphed across song types and time scales to test for interactions. Song type had a noteworthy interaction with time scale in the time scale model, with within-day cross correlation scores not only scoring significantly higher than within-year and between-year cross correlation scores, but also having a much more pronounced difference in consistency between broad and narrow bandwidth song types. Within-day, narrow bandwidth songs were the most consistent.

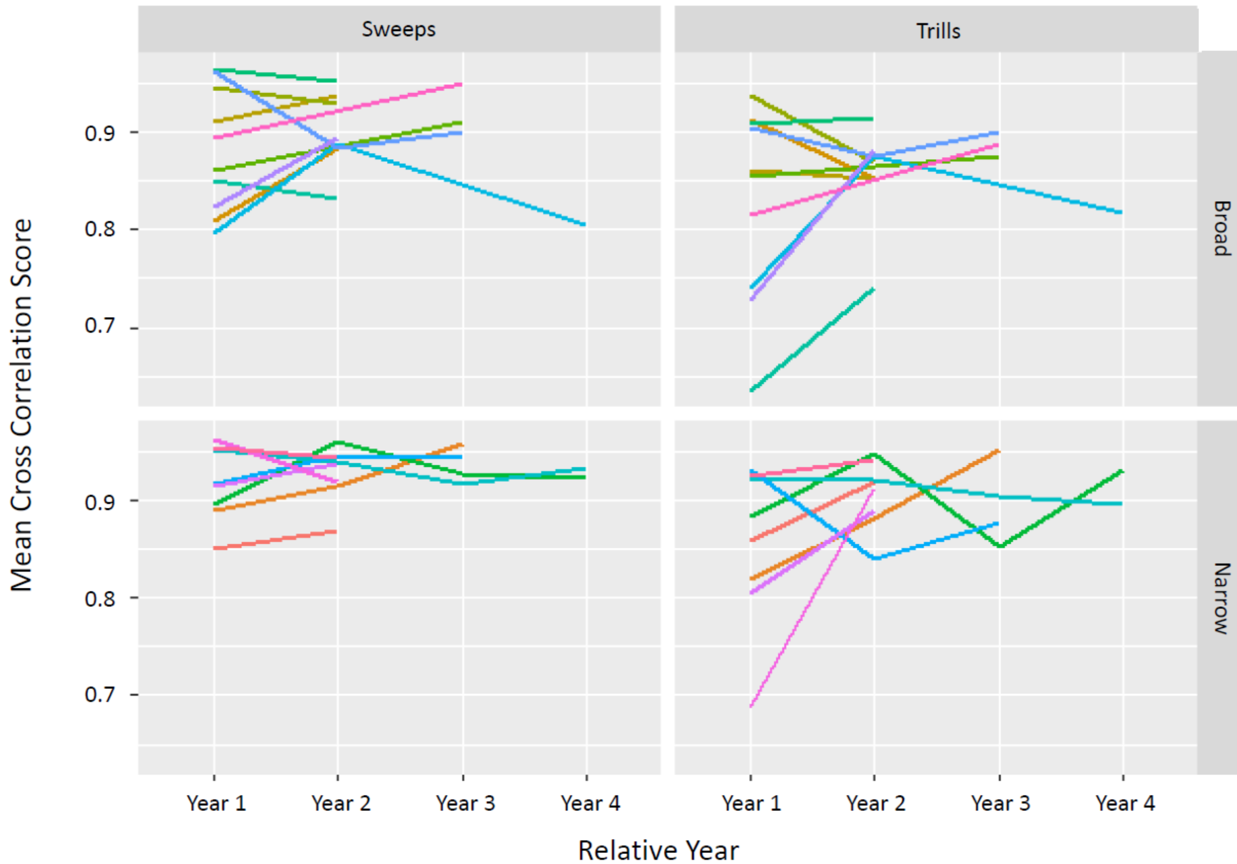

Figure 7. Mean within-day cross correlation scores for each male (color) between song parts, song types, and across relative years. Regardless of song part or song type, scored high in consistency, and those scores remained high across years.

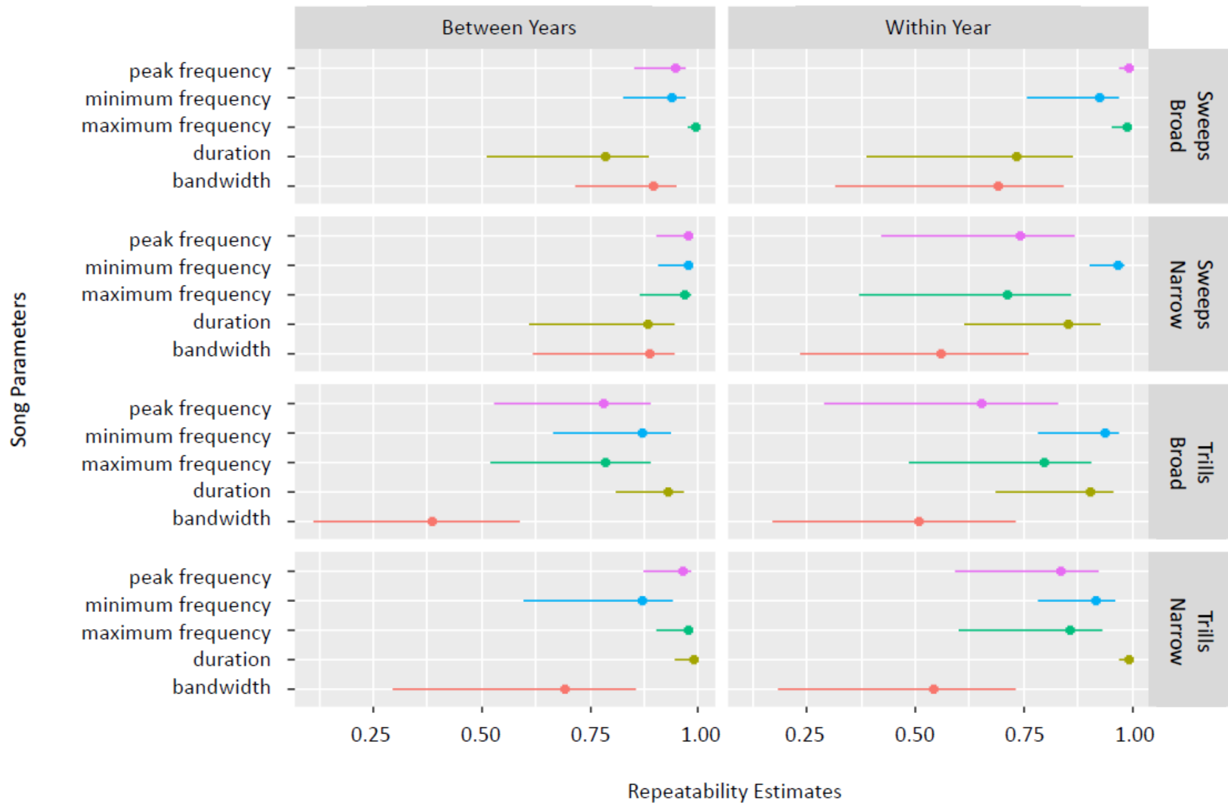

Figure 8. Repeatability estimates with confidence intervals compared between time scales, song parts, and song types. Estimates were calculated using linear mixed effects models that included each song parameter separately as a response variable, male id as a random effect, and 1000 parametric bootstrap iterations for calculating confidence intervals. Song parameter data were separated out into different data sets by time comparison, song type, and song part, so no fixed effects were included in the model. Almost all song parameters were highly repeatable (>.70), with only one instance where a song parameter scored below 0.5 (trill bandwidth for broad song type in between year comparison, R=0.386).

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