Song preferences in female Java Sparrows: Familiarity or Complexity?

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Abstract

Songs play an important role in mate choice for a range of bird species. Many female birds show preferences for specific song features, such as complexity and temporal characteristics, or song familiarity. These features may indicate male quality, or help females to identify locally adapted or genetically compatible mates. Female song preference can shape mating patterns, drive sexual selection, promote local adaptation, and facilitate speciation. It is, therefore, important to understand female preferences to determine how they can contribute to selection and evolution. We examined female preference for song familiarity and song complexity in Java sparrows (*Padda oryzivora*), a species of conservation concern in the wild. Females were presented with pairs of song stimuli; females completing familiarity trials were presented with familiar (social father or social relative) and unfamiliar songs, and females completing complexity trials were presented with songs that differed in note repertoire or linearity (a measure of structural complexity, calculated as the number of note types divided by the number of unique transitions). We counted behavioural responses to determine preference, using a range of behaviours that are likely to indicate song preference in this species. Overall, females preferred their father's song over unfamiliar songs, but we did not find strong evidence to suggest that females generalized this preference to other, non-father familiar songs. Females also showed some preference for complex, rather than simple songs, responding more to stimuli with larger note repertoires. Song linearity, on the other hand, had little impact on females' responses. Our results suggest that female song preference in Java sparrow is multi-faceted, with a number of different factors affecting responses. Further investigation is necessary to work out how these, and other song features, contribute to female preference overall to understand more fully how preference could shape sexual selection, adaptation, and potentially population divergence in this species.

Keywords: song preference, sexual selection, birdsong, Java sparrow, Padda oryzivora, repertoire, linearity

Introduction

Songs play an important role in female preferences and mate choice in a range of bird species. Many female birds show preferences for specific song features, such as song familiarity (REFS), complexity (REFS), temporal characteristics (e.g., long, fast songs (Nolan and Hill, 2004)) and spectral characteristics (e.g., Tomaszycki and Adkins-Regan, 2005; Woolley and Doupe, 2008) These features can provide a range of information to females, including genetic compatibility (e.g., Clayton, 1990), local adaptation (Podos and Warren, 2007), and male quality (Gil and Gahr, 2002). As different aspects of singing behaviour provide different information (Gil and Gahr, 2002), it is likely that female song preferences are multi-faceted, depending on several axes of song variation, rather than just a single feature. How these features interact and contribute to overall song preference is likely to be complex; choosiness for one song aspect may not necessarily result in choosiness for another aspect, and multiple features may be evaluated and weighted independently (Dunning et al., 2014).

Across species, two song features than often receive attention are song familiarity and song complexity. Song familiarity may provide females with information on mate compatibility, for example individuals that are genetic compatibility or locally adapted. One mechanism by which preference for familiar songs could emerge is sexual imprinting, which is common in birds (ten Cate and Vos, 1999). In this case, the characteristics of the parental song phenotype are learned and used as a model for later sexual preference by the offspring, which is likely to be adaptive in a range of scenarios (Chaffee et al., 2013; Invernizzi and Gilman, 2015). However, very strong preferences for the exact parental phenotype, with little generalization may be maladaptive and result in inbreeding (Bateson, 1978). In line with this, there is good evidence that females are able to generalize their song preferences at different scales. At a broad scale, females often show preferences based on subspecies or macrogeographic populations dialects, preferring songs from the subspecies or dialect they were exposed to early in life (Clayton, 1990; Hernandez et al., 2009). However, females may still prefer specific songs within these broad groups, for example, those that more closely resemble the songs of their father or peers (e.g., Wang 2022).

Complex songs may incur neural costs during development (Gil and Gahr, 2002), so may provide female with information on male quality, as opposed to the information on male compatibility indicated by familiarity. This link between song complexity and quality is supported by the negative influence of developmental stress on song complexity in some species (Soma et al., 2006; Zann and Cash, 2008). Accordingly, preference for complex songs has been reported in a number of species (e.g., Hasselquist et al., 1996; Leitão et al., 2006),. A number of different measures can be used to assess complexity. Commonly, preferences for high repertoire (of notes or songs) or high syntactical complexity (e.g., linearity (Scharff and Nottebohm, 1991)) are reported.

We examined females' preferences for song familiarity and complexity in the Java sparrow (*Padda oryzivora*), an estrildid finch. Each male Java sparrow learns to produce a single song during a critical period and uses this song solely in courtship (Ota and Soma, 2014). Courtship in this species also involves co-ordinated duet dancing (Soma and Iwama, 2017). Whilst factors affecting mate choice in other Estrildid finches, such as the zebra finch and Bengalese finch, have been examined in depth, little is known about the factors affecting song preference and mate choice in the Java sparrow. A study examining preference with live males found no effect of song-related traits on the time females spent near males (Hasegawa et al., 2011). To our knowledge, preference for specific song traits has not been assessed. We used song playback trials to examine female preference, which allows us to test song preference independently of other male traits (Fujii et al., 2022). To determine females' preference for familiar songs, we measured females' responses to their father's songs and to songs similar to their father's songs compared with unfamiliar songs. We expected that females would prefer their father's song, as predicted by imprinting, and that females would be able to generalize this preference to the songs of other males that match the father's song type, which would be important for avoiding close inbreeding during mate choice. To examine preference for song complexity, we presented females with songs that varied in note repertoire, the number of unique notes in the song, and song linearity, a measure of structural complexity (Scharff and Nottebohm, 1991). If complex songs are preferred, we expected that females would respond more strongly to songs with larger note repertoires and higher structural complexity (lower linearity).

Methods

Subjects

Females were selected from a laboratory population of Java sparrows (*Padda oryzivora*) housed at Hokkaido University. Birds were housed at a temperature of 25 ± 3 °C, humidity 30 – 60 %, with a 12L:12D lighting schedule. Birds were provided with seeds as food (a 3:1:1:1 mix of Japanese millet, fox tail millet, millet, and canary seed), shell grit, fresh green vegetables, and water ad libitum. Birds were usually housed in large single-sex cages (43 × 37 × 41 or 46.5×46.5×94cm) with up to 20 individuals.

During breeding, birds were housed in family groups in cages (43 × 37 × 41cm) that were visually, but not audially, isolated from other birds. Nests were inspected regularly, and eggs were cross-fostered when multiple nests with eggs were available. In Java sparrows, sons learn their songs from their social fathers (Lewis et al., 2021). As a result, each social paternal line has a distinctive song type that can be identified visually in spectrograms. For the purpose of this study, we assumed that a song was "familiar" to an individual if it was produced by that individual's social father or by another bird in the same social line.

In total, 17 cross-fostered females raised in the lab population took part in trials examining preference for song familiarity. Twenty-four females took part in trials examining preference for song complexity: 11 cross-fostered females raised in the lab population, 3 hand-reared females, and 10 females sourced from local breeders (with unknown parental song types).

Note classification

Classification of notes was necessary to determine metrics of complexity and to assess similarity between familiar songs used in the trials. Notes were classified within social lineages based on visual inspection of the spectrogram (see Figures 1 and 2). All classifications were made by a single observer, but classifications were repeatable between observers. In a sample of 146 songs (containing 4915 notes), a second observer was able to correctly classify 95.2% of notes using a provided list of exemplars (NB this dataset includes some songs from birds not represented in this study, and all birds in this study do not appear in the dataset). At the level of classification used in this study, it is not possible to compare notes between different social lines. This would require using broader categories of notes that hold across lines (as in Lewis *et al.*, 2021), and such broad categories might not fully capture song complexity or similarity within lines.

Stimulus assignments

Familiarity trials

Three types of stimuli were created for use in familiarity preference tests: 'Father', 'Line', and 'Unfamiliar.' Stimuli were presented to females in the study in pairs (see 'Experimental trials' below). The 'Father' stimulus was made up of songs recorded from the female's social father (henceforth referred to as 'father'). 'Line' stimuli were made up of songs from a bird that had the same song type as the female's father, i.e., from the same social family. Where fathers had been reared in the presence of a subtutor, visual inspection was used to confirm the father's social line. In all but one case, the father's (and therefore the female's) social line was that of the father's main tutor (father's social father). In one case, the female's father closely resembled his subtutor's song, and so was assigned to the subtutor's social line. Similarity between 'Father' and 'Line' stimuli was calculated based on a) the number of the father's notes appearing in the 'Line' stimulus, and b) the overall number of shared notes between 'Father' and 'Line' stimuli. Across familiar pairs, an average of 91.4% of fathers' note types appeared in the 'Line' stimuli (interquartile range 81.8-100%; range 57.1-100%) and 72.7% of notes were shared between 'Father' and 'Line' stimuli (interquartile range 58.6-93.8%; range 26.8-100), i.e., the note types appeared in both the 'Father' and 'Line' stimuli. 'Unfamiliar' stimuli were made up of songs from a bird that had a different song type to the father.

Each female was assigned two unfamiliar stimuli to reduce the probability of habituation to a single unfamiliar individual (Figure 1). Line and unfamiliar birds were selected at random for each female. Where possible, clutch mates were avoided, but in two cases alternative familiar birds were not available. Figure 1 shows an example set of stimulus songs used for a single female (Father, Line, Unfamiliar 1, Unfamiliar 2).

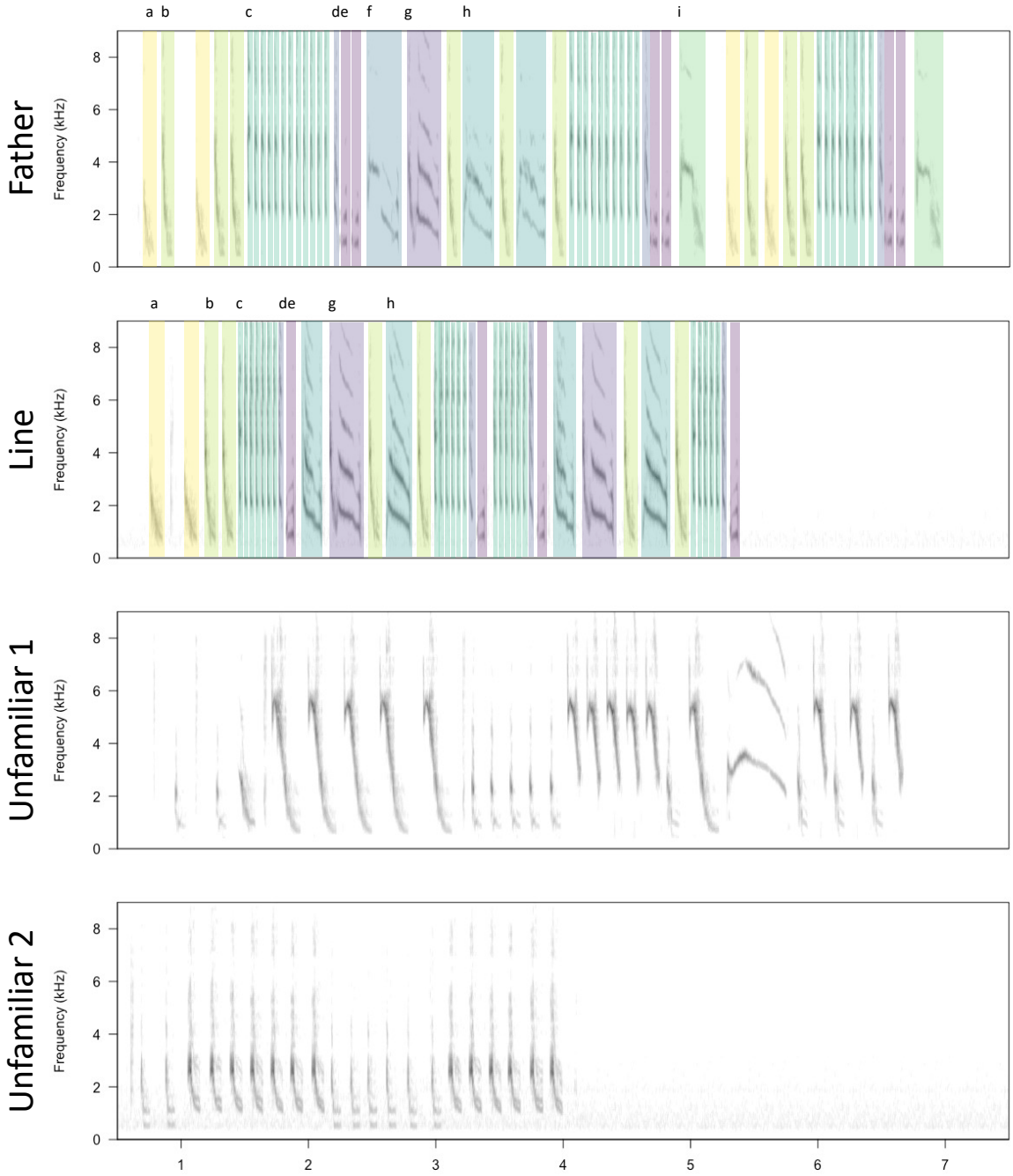


Figure 1: Example of stimuli presented to a single female in familiarity preference tests. The 'Father' and 'Line' stimuli have been marked to show equivalent note types. Due to the variable nature of songs between different family lines, it is not possible to extend this level of classification to songs of

other family lines, so 'Unfamiliar' stimuli have not been marked. Spectrograms were created using Seewave (Sueur et al., 2008) (sample rate = 44.1kHz, window length = 512, overlap = 90%).

Complexity

We used two measures of complexity to assess females' preference for complex songs; note repertoire and song linearity. Note repertoire is a measure of note diversity, defined as the number of unique note types used by a bird within their song, with a high note repertoire associated with complexity. Linearity is a measure of structural complexity of a song, defined as the number of unique note types divided by the number of unique note-to-note transitions, with low linearity associated with high complexity. Four types of stimuli were created for use in complexity preference tests, 'High note repertoire', 'Low note repertoire', 'High linearity', and 'Low linearity', which were presented in 'High' vs. 'Low' pairs for each measure. Individual males for each stimulus type were selected for each social line from the available archival recordings. The differences between 'High' and 'Low' in each category varied among social lines based on individual variability and the availability of archival recordings. For each stimulus, females heard three songs from the same male (see Stimulus Construction), so the average note repertoire and song linearity across all three songs was used for analysis.

Each female was assigned a set of four stimuli from the same social line. This reduces the potential impact of differences in attractiveness between the song types of the different social lines. Where females were reared by parents in the main population, they received a set of familiar stimuli (i.e., all stimuli were from their father's social line). If females were hand-reared or were reared outside of the main population they received a set of unfamiliar stimuli from the same social line. Where females received familiar songs, songs from the father or clutchmates were avoided where possible. For one female, only three familiar stimuli were available, so one stimulus was repeated in each of the trial types.

Figure 2 shows an example set of stimulus songs used for a single female (High Repertoire, Low Repertoire, High Linearity, Low Linearity).

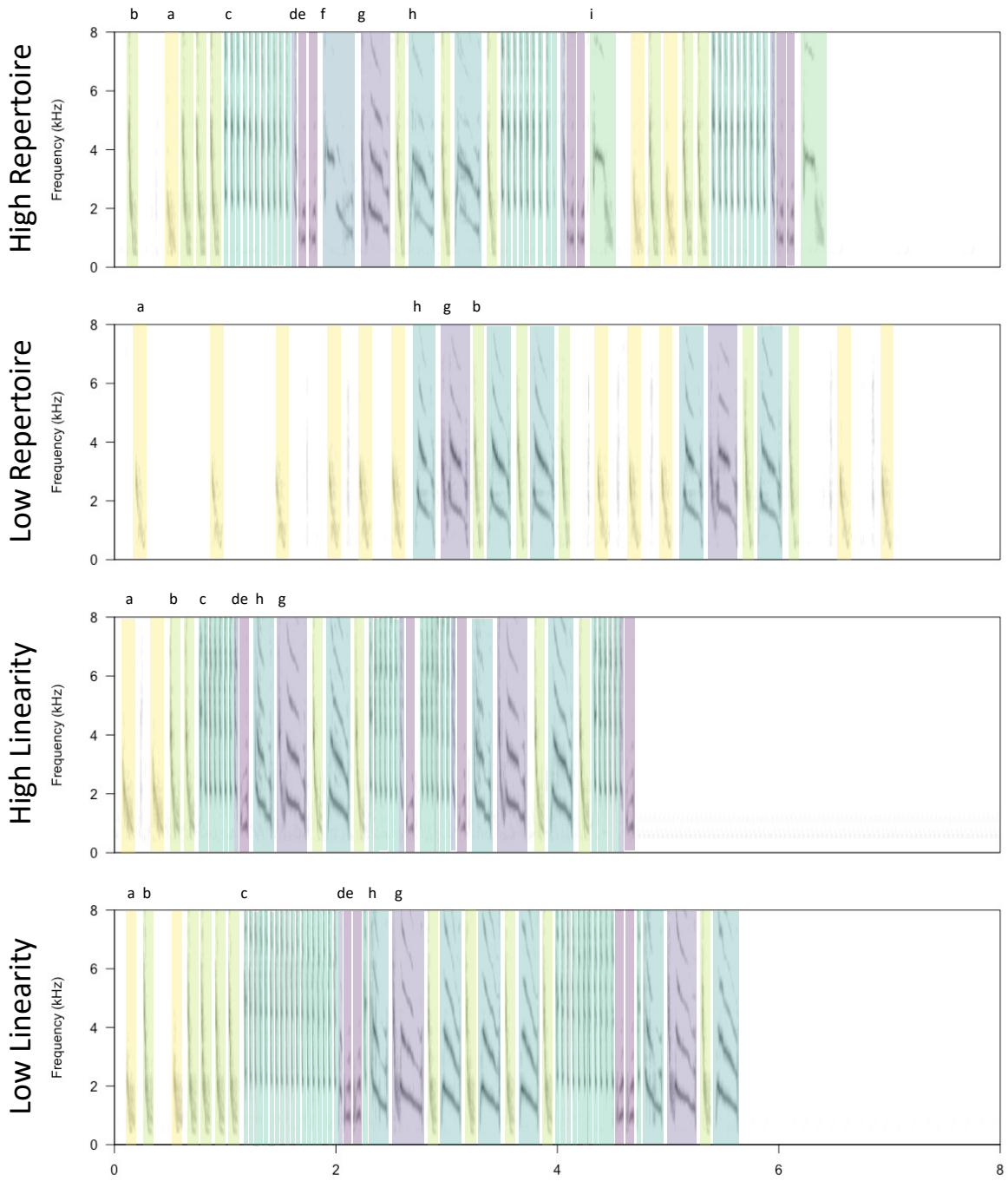


Figure 2: Example of stimuli presented to a single female during complexity preference tests. Stimuli have been marked to show equivalent note types. Spectrograms were created using Seewave (Sueur et al., 2008) (sample rate = 44.1kHz, window length = 512, overlap = 90%).

Stimulus construction

Stimuli were constructed using available archival recordings from individuals in the lab population. Archival recordings had 44.1 kHz sampling rate and 16-bit resolution and consisted of an individual bird singing alone. Recordings were taken recorded using a digital sound recorder (Marantz PMD 661,

Zoom Q3HD, TASCAM DR-100 MKIII). Recordings were high-pass filtered at 375 Hz in Raven Pro (1.6.3) to remove background noise. Recordings from four birds from one social line in the dataset had been pre-processed with a high pass filter of 1 kHz. We do not expect this to have an effect on preference tests; a high pass filter of 1 kHz is unlikely to have removed any important song features, and the closely related zebra finch (as well as other song birds) are reported to have a narrow hearing range with highest sensitivity between 1-6 kHz (Hashino and Okanoya, 1989).

For each stimulus, three songs from a single male were selected from those available in archival recordings. The three songs were repeated at a constant rate (one song every 10s) for two minutes, alternating between songs. As such, a full stimulus contained 12 songs in the pattern ABCABCABCABC. Many of the archival songs had been recorded with recorders using stop start direction (so only significant noise events were recorded), or, had been segmented into individual songs prior to storage. As such, we did not have information on the natural song rates of individuals in our dataset, and there is little published information on song rates in this species. Since song rate can influence preference (Forstmeier 2004; Nolan & Hill 2004), we chose to control for song rate during playback. The chosen rate may differ to natural song rates, and natural song rates are likely to differ between individuals and social contexts, as in other species (e.g., zebra finch (Dunn & Zann 1996; Naguib et al. 2008; Jesse & Riebel 2012)). Due to our methods of stimulus construction, the total time occupied by songs differed between stimuli, as individuals had differing song lengths. However, familiar and unfamiliar song stimuli differed for each individual female, and, as such, song density is unlikely to have systematically differed with familiarity.

Across all stimuli, amplitude was equalized by matching peak amplitude between stimuli, as song amplitude may influence preference (Ritschard et al., 2010).

Experimental trials

Familiarity

There were two types of trials during the familiarity preference tests, Father vs. Unfamiliar and Line vs. Unfamiliar, with each pairing using a different unfamiliar stimulus. For two birds, recordings of the father's song were not available, so two Line vs. Unfamiliar stimulus pairs were presented, with a different familiar and unfamiliar bird in each pair.

Females completed four trials during the experiment, with each trial taking place on a different day. Each trial type was completed twice, with the order of presentation reversed in each repeat (Figure X2). The order of trials was randomized among birds. Prior to each trial, females in individual cages were placed in a soundproof chamber and allowed to habituate overnight. At the start of each trial,

females completed a short habituation period (5 minutes). After this, females were presented with four stimuli (2 minutes), alternating between familiar and unfamiliar, with a 30 second gap between each stimulus presentation (Figure 3). Each trial lasted 10 minutes. All playbacks used XXX. One of the 17 birds was removed from the study after completing a single trial. In total, 65 trials (4 trials for each of 16 birds plus one trial for one bird) were recorded for analysis.

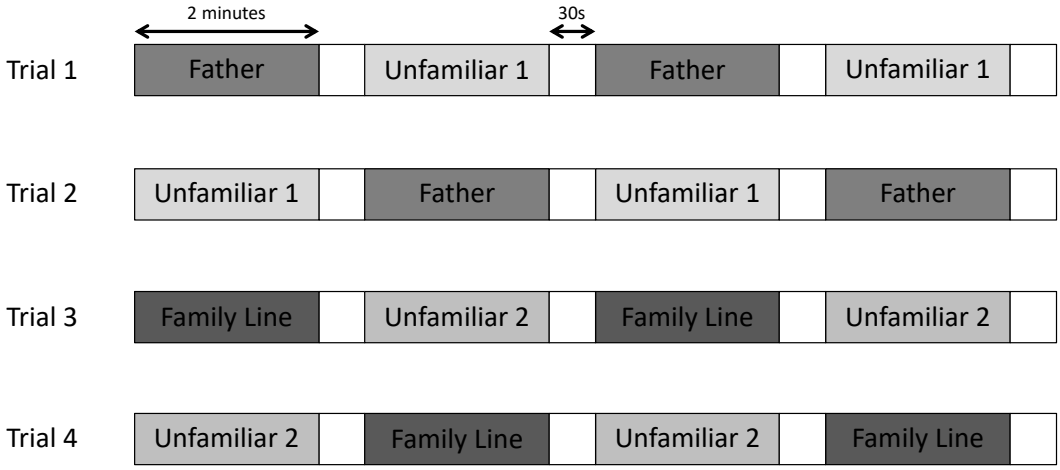


Figure 3: Example experimental set up for a female completing the familiarity preference tests.

Complexity

Complexity preference tests also comprised of two trial types, 'high' vs. 'low' note repertoire and 'high' vs. 'low' linearity. As with the familiarity preference tests, females completed four trials during the experiment and each trial took place on a different day. Each trial type was completed twice with the order of presentation reversed in each repeat (Figure 4), and the order of trials was randomized among females. Trial presentation was identical to that for the familiarity preference tests, with a short habituation period (5 minutes) followed by the presentation of stimuli. Based on females' responses in the familiarity preference tests, overnight habituation was not deemed necessary, as birds habituated quickly to the soundproof chamber. All trials used XXX for playbacks. In total, 96 trials were recorded for analysis. One trial could not be analysed due to equipment malfunction, so data was extracted from 95 trials.

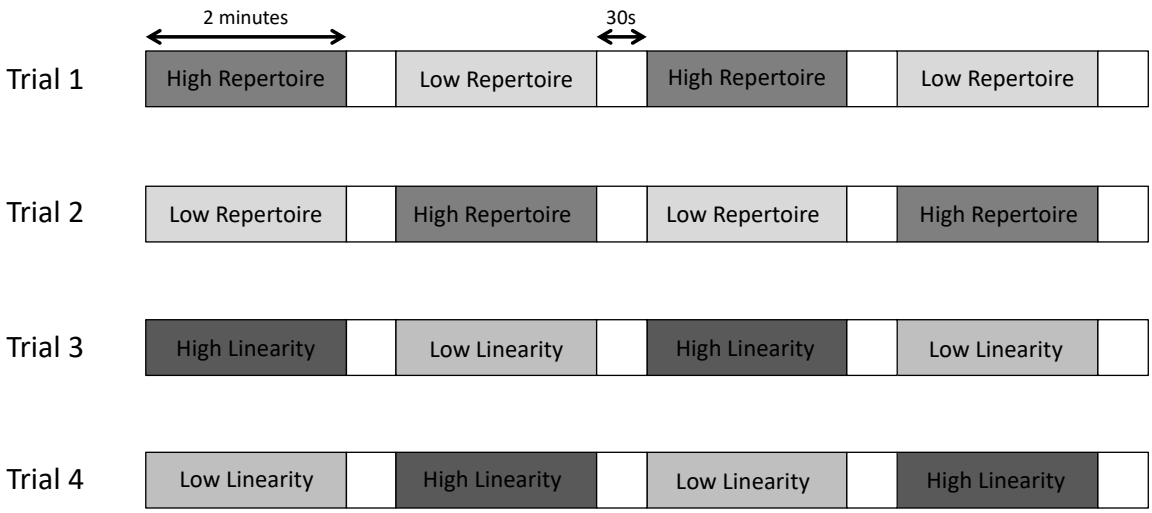


Figure 4: Example experimental set up for a female completing the complexity preference tests.

Behavioural data

The extraction of behavioural data was the same for both familiarity preference and complexity preference tests. Information on behavioural responses to stimuli was extracted from video footage taken during experimental trials. We examined four behaviours that are performed in a range of social situations by Java sparrows: calls, hops, bill wiping and fluffing. These behaviours were chosen to cover a wide range of social responses, including behaviours used in courtship displays, as these may indicate mate preference. In Bengalese finches, calls were a reliable indicator of preference, showing similar patterns to copulation solicitation displays (Dunning et al., 2014). In Java sparrows, both hopping and bill wiping are associated with courtship dancing (Soma and Iwama, 2017), so may indicate mate preference. In zebra finches, fluffing behaviour is associated with mate preference and is performed in response to complex, attractive songs (Vyas et al., 2009). Juveniles experiencing more fluffing behaviour in response to songs also developed more accurate songs (Carouso-Peck et al., 2020; Carouso-Peck and Goldstein, 2019).

Instances of each behaviour were counted for each stimulus presentation (i.e., each 2-minute block of song playback), and these values were used in the analysis presented in the main text. Motivations behind behaviours performed during the silent gaps may be hard to interpret. However, responses in the silent gaps were correlated with the number of responses in the preceding stimulus presentation for most behaviours examined. The inclusion of behaviours performed in the silent intervals did not qualitatively affect our results and interpretation (Appendix 1).

Data analysis

All analyses were conducted in R (ver. 4.1.2). Within each set of tests (familiarity preference tests and complexity preference tests), we conducted separate tests for each of calls, hops, bill wiping and fluffing. Due to the number of non-responses from females, it was possible that our data were zero-inflated. Models were initially constructed without zero-inflation and checked using the performance package in R (Ludecke et al., 2021). Where likely zero-inflation was detected, we re-ran the models including a zero-inflation term. As a result, some behavioural responses were analysed with a generalized linear mixed effect model (with Poisson error distribution) using the lme4 and lmerTest packages (Bates et al., 2015; Kuznetsovs et al., 2017), and others were analysed using a zero-inflated Poisson models using the glmmTMB package (Brooks et al., 2017). Models for familiarity and complexity preference tests were broadly similar, but differed in some predictors, as outlined below.

Familiarity

For each model, the behaviour of interest was used as the response variable. We included the type of stimulus (familiar or unfamiliar), the type of trial (Father vs. Unfamiliar or Line vs. Unfamiliar), the order of the stimulus within the trial (played 1st, 2nd, 3rd or 4th), and the order of the trial within the experimental period (1st trial, 2nd trial, 3rd trial or 4th trial) as fixed effects in the model. The order of the stimulus was included to account for habituation within the 10-minute trial. The order of the trial was included to account for habituation over the course of the overall experiment. We also included the interaction between the type of stimulus and the type of trial to determine if the difference in response to familiar songs was different in Father vs. Unfamiliar or Line vs. Unfamiliar trials. We included the female ID, the ID of the male's song used and female ID x male ID as random effects in the models. Where used (calling and hopping behaviour), the zero-inflation formula included an intercept and a random effect of the individual female. This accounted for the fact that females may not respond during the presentation of a stimulus during the trial, and that the likelihood of not responding differed among females.

Complexity

As with familiarity preference tests, the behaviour of interest was used as the response variable. We included the average note repertoire and average linearity of the stimulus as fixed effects. Complexity measures were included as numerical values, rather than 'high' or 'low'. This is because the difference between the 'high' and 'low' values differed depending on the social line from which stimuli were selected based on the availability of archival recordings. As with the familiarity preference tests, we included the order of the stimulus within the trial and the order of the trial within the experimental period as fixed effects to account for habituation at different scales. We also included a fixed effect of stimulus familiarity (familiar vs. unfamiliar), as birds may respond differently to a familiar stimulus set compared to an unfamiliar set. As hand-reared birds had less experience with adult song models,

their responses and preferences may be different to parent reared birds. To account for this, hand-rearing status was included as a fixed effect in the models. We included the same random effect outlined above female ID, the ID of the male's song used and female ID x male ID. Where used (calling, hopping, and bill wiping behaviour), the zero-inflation formula was the same as that used in the analyses for familiarity preference tests, and included an intercept and a random effect of the individual female.

Ethical approval

This study was approved by The University of Manchester Animal Welfare and Ethics in Research Board (Permit Number D0062) and Hokkaido University (Permit Numbers 16-0020 and 22-0052).

Data availability

Data and code associated with this study can be found on Figshare: https://doi.org/10.48420/25142780.v1.

Results

Familiarity

Overall, we found evidence that Java sparrow females responded more strongly to their father's song compared to unfamiliar songs. Significantly fewer calls, hops and fluffs were performed during playback of unfamiliar songs (Table 1, Figure 5). The number of bill wipes followed the same pattern, but this did not reach marginal significance (Table 1, Figure 5). Females did not show significantly stronger responses to familiar 'Line' songs compared to unfamiliar songs (Table 1, Figure 5). However, in all cases, the direction of effect suggested that females responded more strongly to the line stimulus, although marginal significance was not reached.

There was limited evidence that females responded more strongly to their father's song than to the familiar 'Line' song. At marginal significance, females performed a greater number of fluffs to their father's song than to other familiar songs. Other behaviours followed the same pattern, but dd not reach marginal significance (Table 1)

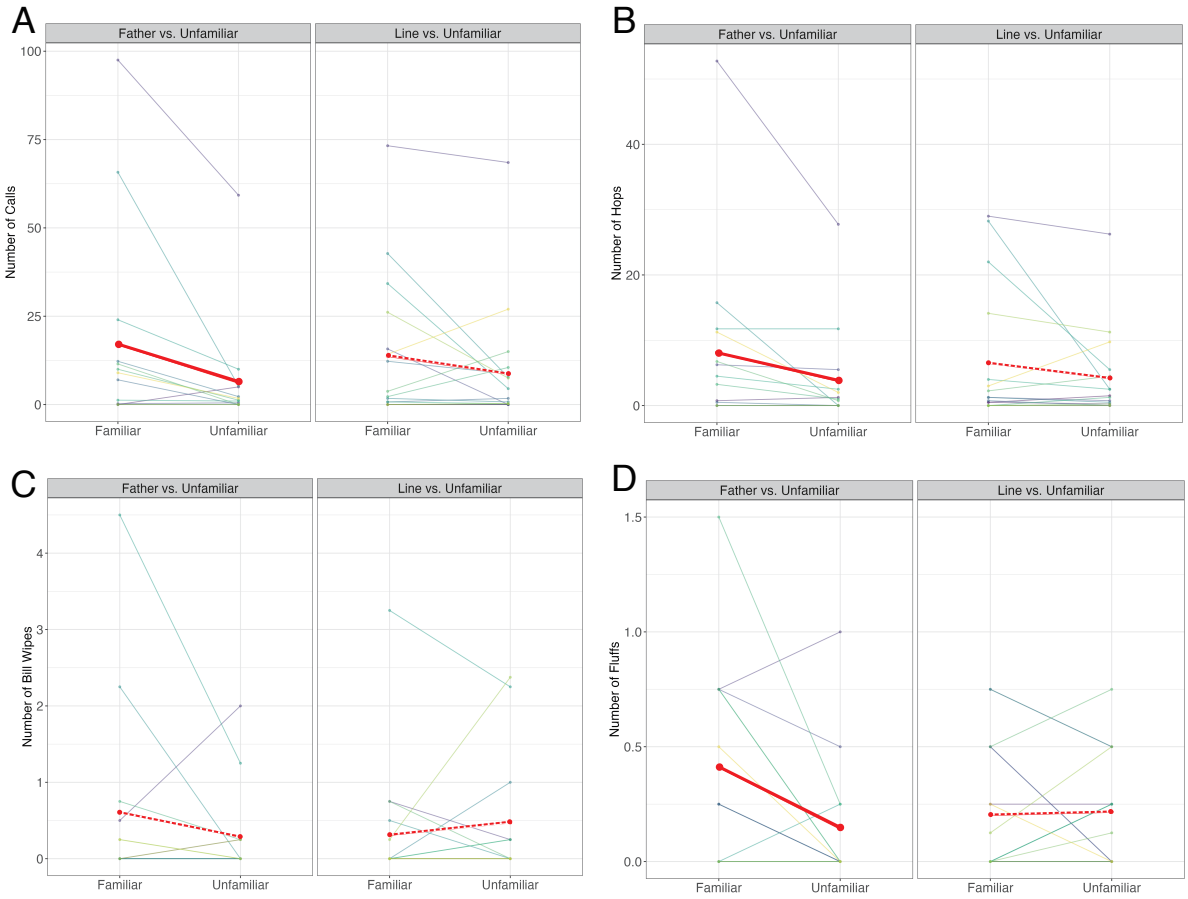


Figure 5: Behavioural responses from females to familiar and unfamiliar songs in Father vs. Unfamiliar and Line vs. Unfamiliar trials A) calls B) hops C) bill wiping D) fluffing. Transparent lines represent individual females' responses. Bold red lines indicate the average response across individuals within the trial type. Significant comparisons are indicated by solid lines, non-significant comparisons are indicated by dashed lines.

Table 1: Results of mixed effect models for behavioural responses to song familiarity.

	Estimate	p-value	Direction of effect
Number of Calls			
Father vs. Unfamiliar	1.093	0.011	Greater response to father's songs
Line vs. Unfamiliar	0.241	0.401	N.S (direction of greater response to familiar songs)
Father vs. Line	-0.160	0.630	N.S.
Test Order	0.178	<0.001	Acceleration effect
Stimulus order	-0.216	<0.001	Habituation effect
Number of Hops			
Father vs. Unfamiliar	1.289	<0.001	Greater response to father's songs
Line vs. Unfamiliar	0.487	0.121	N.S (direction of greater response to familiar songs)
Father vs. Line	0.485	0.117	N.S (direction of greater response to father's song)
Test Order	-0.108	<0.001	Habituation effect
Stimulus order	-0.089	<0.001	Habituation effect
Number of Bill Wipes			
Father vs. Unfamiliar	0.551	0.386	N.S. (direction of greater response to father's songs)
Line vs. Unfamiliar	0.500	0.374	N.S (direction of greater response to familiar songs)
Father vs. Line	0.759	0.210	N.S (direction of greater response to father's song)
Test Order	0.357	<0.001	Acceleration effect
Stimulus order	0.088	0.312	N.S.
Number of Fluffs			
Father vs. Unfamiliar	1.092	0.014	Greater response to father's songs
Line vs. Unfamiliar	0.072	0.854	N.S (direction of greater response to familiar songs)
Father vs. Line	0.672	0.072	Greater response to father's song
Test Order	0.078	0.518	N.S.
Stimulus order	-0.275	0.019	Habituation effect

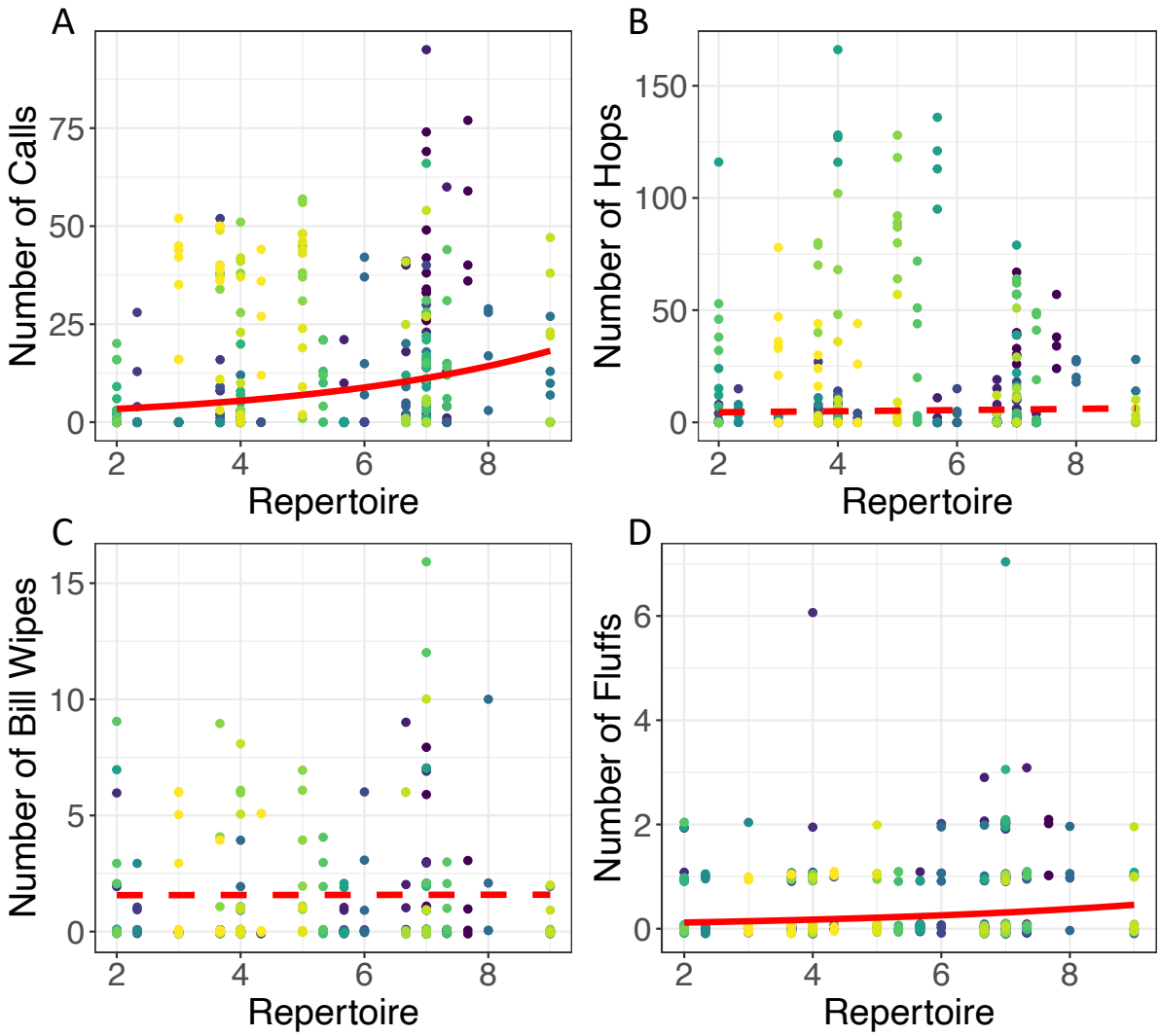
Generally, birds habituated to stimulus presentation within the 10-minute trial, responding less to stimuli presented later in the trial. We found a significant decrease in in calling, hopping, and fluffing over the trial (Table 1). Although the effect was in the same direction, there was no significant effect of habituation when considering bill-wiping behaviour (Table 1).

Our results for changes in behaviour over the course of the whole experiment were less clear-cut. Whilst there was an apparent decrease in hopping behaviour across experimental trials, this was not the case for other behaviours (Table 1). We found no significant differences in fluffing behaviour across the course of the experiment (Table 1). However, for calling and bill-wiping behaviour, we found evidence for an acceleration effect; birds showed greater responses in later trials (Table 1). This may suggest a change in preferred response type over the course of the experiment.

Complexity

Overall, we found evidence that Java sparrow females preferred songs with larger note repertoires Table 2; Figure 6). Females performed more calls and fluffing behaviour with increasing size of the singer's note repertoire. The number of hops followed the same pattern, but did not reach marginal significance (Table 2, Figure 6). We did not find evidence for an effect of song linearity. There was no significant relationship between females' responses and song linearity for any of the behaviours examined (Table 2, Figure 7).

Figure



6: Behavioural responses from females to stimuli in complexity preference tests compared to stimulus repertoire A) calls B) hops C) bill wiping D) fluffing. Coloured points represent individual female's responses to stimuli. Bold red lines show the model predictions for each behaviour, significant results are represented by solid lines, non-significant results are represented by dashed lines.

As in the familiarity tests, birds habituated to stimulus presentation within the 10-minute trial, responding less to stimuli presented later in the trial. There was a significant decrease in calling, hopping and bill wiping behaviour over the trial, although there was no change in fluffing behaviour (Table 2). Across trials, we found evidence for an acceleration effect for all behaviours, with birds responding more in later trials (Table 2).

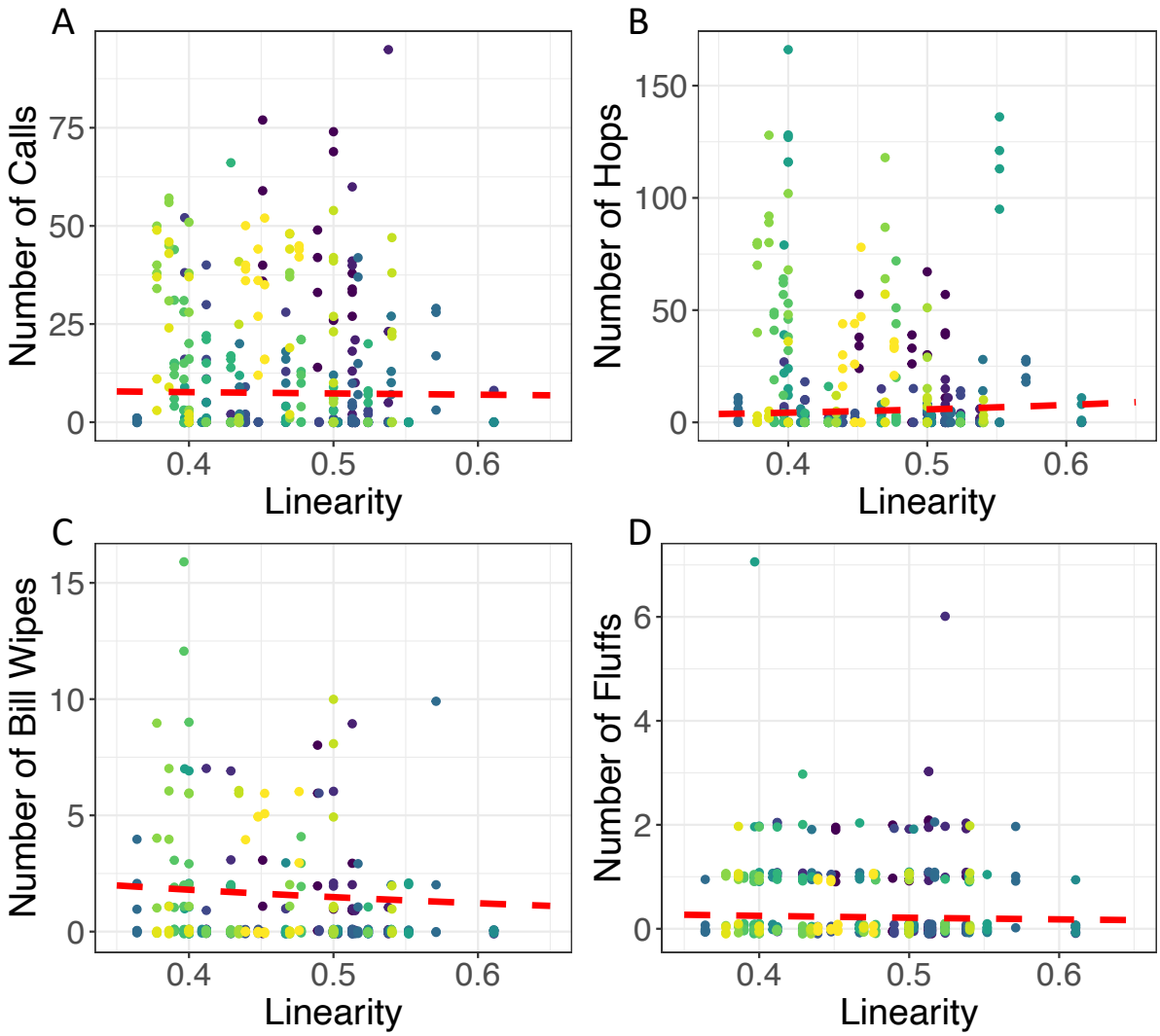


Figure 7: Behavioural responses from females to stimuli in complexity preference tests compared to stimulus linearity A) calls B) hops C) bill wiping D) fluffing. Coloured points represent individual female's responses to stimuli. Bold red lines show the model predictions for each behaviour, significant results are represented by solid lines, non-significant results are represented by dashed lines.

Despite the finding that birds responded more to familiar song stimuli, we found no evidence for an effect of familiarity on responses during the complexity tests; birds did not respond more to familiar song sets (Table 2). For most behaviours, hand-reared birds did not significantly differ from parent-reared birds in their responses. However, hand-reared individuals produced significantly less calls over the course of the experiment (Table 2).

Table 2: Results of mixed effect models for behavioural responses to song complexity. Estimates show comparison of unfamiliar to familiar songs, and hand-reared compared to parent-reared birds.

	Estimate	p-value	Direction of effect
Number of Calls			
Note Repertoire	0.241	**<0.001**	Response increases as repertoire increases
Song Linearity	-0.445	0.817	N.S.
Test Order	0.070	**<0.001**	Acceleration effect
Stimulus Order	-0.180	**<0.001**	Habituation effect
Familiar vs. Unfamiliar	0.639	0.243	N.S.
Hand-reared	-1.730	0.023	Less response from hand-reared females
Number of Hops			
Repertoire	0.048	0.433	N.S.
Linearity	2.934	0.125	N.S.
Test Order	0.164	**<0.001**	Acceleration effect
Stimulus Order	-0.060	**<0.001**	Habituation effect
Familiar vs. Unfamiliar	0.607	0.336	N.S.
Hand-reared	0.570	0.575	N.S.
Number of Bill Wipes			
Repertoire	-0.002	0.973	N.S.
Linearity	-1.948	0.355	N.S.
Test Order	0.237	**0.005**	Acceleration effect
Stimulus Order	-0.156	**0.008**	Habituation effect
Familiar vs. Unfamiliar	0.219	0.369	N.S.
Hand-reared	-0.437	0.235	N.S.
Number of Fluffs			
Repertoire	0.193	**<0.001**	Response increases as repertoire increases
Linearity	-1.607	0.373	N.S.
Test Order	0.140	**0.050**	Acceleration effect
Stimulus Order	-0.035	0.607	N.S.
Familiar vs. Unfamiliar	-0.241	0.578	N.S.
Hand-reared	0.011	0.987	N.S.

Discussion

Java sparrow females showed distinct song preferences across song features. Females preferred their father's song over unfamiliar songs, but did not show significant preferences for other familiar songs over unfamiliar songs. Females also preferred songs with higher note repertoires, but did not show a preference based on structural complexity measured as linearity.

Preference for father's song is found in other, closely-related species (Fujii et al., 2021; Fujii and Okanoya, 2022; Kato et al., 2010; Riebel, 2000) and is reported in both studies using operant tasks (Kato et al. 2010; Riebel 2000) and those measuring behavioural responses, including copulation solicitation displays (Fujii et al., 2021; Fujii and Okanoya, 2022). Whilst we did not find a significant preference for non-father familiar songs, this does not necessarily mean that Java sparrow females were unable to generalize their preferences. For all behaviours measured, the direction of effect was towards a stronger response to familiar non-father songs compared to unfamiliar songs. . A wide range of song features, including song and note structure, are socially inherited in this species (Lewis et al., 2021a), meaning that song type and song similarity likely indicate that birds are (socially) related. There is some evidence for generalization of preference from other Estrildid finch species, with birds showing greater responses to songs that were more similar to those of their father (Fujii and Okanoya, 2022; Miller, 1979; Wei et al., 2022). However, this is not the case in all studies. Zebra finches that had previously shown a preference for father's song over unfamiliar song did not show a similar preference for an unfamiliar brother's song (which was similar to the father's song) (Riebel and Smallegange, 2003). In our study, the familiar stimuli were very similar, with a high proportion of the father's song notes present in the line song (mean 91.4%) and a large proportion of notes shared between father and line songs (mean 72.3%), so we may have expected females to prefer familiar non-father songs over unfamiliar songs. In zebra finches, birds exhibited stronger preferences for songs sharing more elements with father's song (Wei et al., 2022). We found limited evidence to suggest that females preferred their father's song over the non-father familiar song; females showed a stronger response to their father's song for one behaviour, with a similar direction of effect in other behaviours. Whilst these findings provide support for the fact that father's songs are more strongly preferred, we cannot draw definitive conclusions about the differences in preference strength. To limit the number of trials undertaken by females we did not directly compare preference for father and line songs. Overall, our results suggest that females' responses to non-father familiar songs are an intermediate between responses to father's and unfamiliar songs. However, our sample size was limited by the number of females with father's songs available in the song archive, and further studies with larger sample sizes are needed to explore this pattern in more depth.

Java sparrow females showed some preferences based on song complexity, responding more to songs with higher note repertoires. However, females did not show song preferences based on syntactical complexity, measured as song linearity. Preferences for large note repertoires has been reported in other estrildid finch species. In zebra finches, songs with larger syllable repertoires were preferred in tests using both phonotaxis and operant tasks (Holveck and Riebel, 2007). A similar preference for repertoire was found in another study examining behavioural responses to stimulus playback across females with different early acoustic experiences (Vyas et al., 2009). In other estrildid species, there is some evidence for song preferences relating to syntactical complexity, which were not apparent in Java sparrows. Bengalese finch females stimulated with syntactically complex songs carried more nesting material than those stimulated with simple songs (Okanoya, 2012). In an operant task, four of eight females preferring complex songs, suggesting that syntactical complexity may play a role in shaping female preferences (Morisaka et al., 2008). However, there was clear inter-individual variation, with half of the females taking part showing no or reversed song preference. In a meta-analysis of the effects of song complexity on male reproductive success, song versatility, which is associated with structural complexity, was less correlated with reproductive success than song repertoire (Soma and Garamszegi, 2011), suggesting that structural complexity may not be as important to females when selecting a mate. There are several reasons why we may not have found preference for structural complexity in Java sparrows. Firstly, females may not pay attention to the syntactical complexity of songs. Secondly, females may prefer syntactical complexity, but the measurement used, song linearity, may not fully reflect how birds assess complexity. Finally, it is possible that females do show preferences for song linearity, but we were unable to detect this preference in our study. For example, it is possible that preference for note repertoire in Java sparrows is greater than preference for song linearity. In this case, we may have been unable to detect preference for song linearity, as the natural songs used varied in both features simultaneously.

Previous studies of female song preferences have used operant tasks (e.g., Riebel & Smallegange 2003; Wei et al. 2022) or examined few behavioural responses, such as copulation solicitation displays (Fujii and Okanoya, 2022) or approach (Miller; Clayton 1988). In the present study, we examined the combined evidence from multiple behaviours in a naturalistic context and without interventions such as hormone implants, allowing us to more readily assess the social role of songs in this species. Whilst females' behavioural responses could indicate social response to songs, the behaviours we examined are likely to indicate song *preference*, rather than a simple response. Calls are associated with female preference in Bengalese finches; calls and copulations solicitation displays were correlated in determining song preferences (Dunning et al., 2014). In zebra finches, fluffing behaviours were performed more frequently in response to complex songs in both untreated and hormone-treated females (Vyas et al., 2009). Finally, both hops and bill wipes are used by Java sparrows in courtship display dancing (Soma and Iwama, 2017). Therefore, these behaviours are likely to correlate with mate preference.

Female song preferences can have implications for male reproductive success, and may result in changes in songs over time or contribute to assortative mating within or between populations. Preferences for familiar songs in a mate choice context can assist in the correct choosing of subspecies or local population (Slabbekoorn and Smith, 2002). However, strong preferences for familiar songs, and in particular songs similar to those of the father, may contribute to the formation of pre-mating reproductive barriers (Gilman and Kozak, 2015) and contribute to inbreeding through the promotion of assortative mating based on social (genetic) background (Soma 2011). Assortative mating based on familiarity could also negatively affect population management strategies that bring birds from multiple populations together, for example, during conservation breeding programmes (Lewis et al., 2021b). Preference for song complexity during mate choice may result in improved reproductive success for birds with complex songs (Soma and Garamszegi, 2011). This may drive changes in song complexity over time due to sexual selection. In Bengalese finches, it has been suggested that a release from selection pressure, coupled with a female preference for complex songs, has driven increases in song complexity during the domestication process (Okanoya, 2012).

Mate choice in natural situations may not always reflect preference in controlled settings. Other factors, such as additional song parameters (Dunning et al., 2020; Nolan and Hill, 2004) and male traits (Hasegawa et al., 2011), may influence pairing. However, there is some evidence that preference for familiar or complex songs may affect real-world pairings. In zebra finches, females preferentially paired with males whose song matched their population of rearing and that more closely resembled songs of their adolescent peers in semi-natural conditions (Wang 2022). Our results show that Java sparrows, like zebra finches, show preferences for familiar songs, so it is possible that similar patterns of mate choice could occur. For song complexity, although a meta-analysis revealed a small but significant link between song complexity and male reproductive success, the effect of complexity was reduced when considering genetic reproductive success (i.e., the number of genetically related offspring produced), rather than social measures (e.g., number of females acquired, number of offspring produced within a pair) (Soma and Garamszegi, 2011). This suggests that, in natural settings, females may show different song preferences for social mates and extra-pair mating, making it difficult to predict the real-world effect of preferences measured in controlled conditions. Java sparrow females' preferences for song complexity may result in males with larger note repertoires having greater reproductive success, and may result in sexual selection for complex songs over time. Even if females do not show a preference when pairing, investment in breeding may be reduced with non-preferred males. In Bengalese finches, females produced heavier eggs and showed a trend towards male-biased broods when their mate had a longer song duration (Soma and Okanoya, 2013). Across tests, female Java sparrows varied in their preference and strength of responses. Therefore, individual differences may also contribute to mate choice and investment in real-world scenarios. Further investigation of mate choice in natural conditions is necessary to

understand the implications of female preference for assortative mating and sexual selection, and whether this could contribute to pre-mating barriers between populations or drive vocal change across generations.

In summary, Java sparrow females showed clear preferences for specific song characteristics across the experimental tests. This suggests that overall song preference in this species is likely to be multi-faceted, with multiple song features contributing. In this study, we identified that song familiarity and complexity in the form of note repertoire may be important in influencing females' preferences. However, other song features not tested here may also contribute to females' overall preferences. As natural songs vary on multiple axes, and these axes may covary, it can be difficult to determine which specific features are more strongly preferred. Artificial song stimuli that vary in only one aspect may be useful in determining females' preferences for specific aspects of the song and allow us to build a more comprehensive overview of female preference as a whole.

Author contributions

RL and MS conceptualized the study and were responsible for the experimental design. Data collection and extraction of behavioural data from videos was carried out by HM and RL. Data analysis was conducted by RL, MS, and TG. The initial draft of the manuscript was written by RL, with RL, MS, and TG contributing to reviewing and editing. MS and TG provided supervision throughout the project.

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Appendices

Appendix 1: Results of models using combined behavioural data from stimulus presentation and the adjacent silent gap

The statistical models used to analyse the combined behavioural data from stimulus presentation and the adjacent silent gap follow the same format as those described in the 'Data Analysis' section. For bill wiping behaviour, zero-inflation was detected in the combined behavioural data, even though it was not for behavioural data in the stimulus presentation, so a zero-inflation term was included in the model. In some cases, models did not fully converge using the zero-inflation formation specified in the 'Data Analysis' section of the paper. In these cases, an alternative zero inflation formula was used, as indicated in results tables (Table A1.1, Table A1.2)

Table A1.1: Results of mixed effect models for behavioural responses to song familiarity using combined data from stimulus presentation and adjacent silent gap. Estimates show comparison of unfamiliar to familiar songs and Line vs. Unfamiliar (L vs. U) to Father vs. Unfamiliar test types.

	Estimate	p-value	Direction of effect
Number of Calls*			
Father vs. Unfamiliar	0.929	0.068	Greater response to father's songs
Line vs. Unfamiliar	0.359	0.429	N.S (direction of greater response to familiar songs)
Father vs. Line	-0.229	0.643	N.S.
Test Order	0.172	**<0.001**	Acceleration effect
Stimulus order	-0.226	**<0.001**	Habituation effect
Number of Hops			
Father vs. Unfamiliar	1.343	<0.001	Greater response to father's songs
Line vs. Unfamiliar	0.435	0.170	N.S (direction of greater response to familiar songs)
Father vs. Line	0.617	0.067	Greater response to father's song
Test Order	-0.116	<0.001	Habituation effect
Stimulus order	-0.098	<0.001	Habituation effect
Number of Bill Wipes			
Father vs. Unfamiliar	0.603	0.276	N.S. (direction of greater response to father's songs)
Line vs. Unfamiliar	0.369	0.440	N.S (direction of greater response to familiar songs)
Father vs. Line	0.299	0.570	N.S (direction of greater response to father's song)
Test Order	0.264	<0.001	Acceleration effect
Stimulus order	-0.031	0.721	N.S.
Number of Fluffs			
Father vs. Unfamiliar	1.032	0.004	Greater response to father's songs
Line vs. Unfamiliar	-0.164	0.854	N.S (direction of lesser response to familiar songs)
Father vs. Line	0.817	0.010	Greater response to father's song
Test Order	0.064	0.542	N.S.
Stimulus order	-0.275	0.009	Habituation effect

*Model uses a simplified zero inflation formula including an intercept for convergence

Table A1.2: Results of mixed effect models for behavioural responses to song complexity using combined data from stimulus presentation and adjacent silent gap. Estimates show comparison of unfamiliar to familiar songs.

	Estimate	p-value	Direction of effect
Number of Calls*			
Note Repertoire	0.241	<0.001	Response increases as repertoire increases
Song Linearity	-0.877	0.652	N.S.
Test Order	0.059	<0.001	Acceleration effect
Stimulus Order	-0.170	<0.001	Habituation effect
Familiar vs. Unfamiliar	0.696	0.231	N.S.
Hand-reared	-1.780	0.027	Less response in hand-reared birds
Number of Hops			
Repertoire	0.049	0.417	N.S.
Linearity	1.841	0.342	N.S.
Test Order	0.170	<0.001	Acceleration effect
Stimulus Order	-0.060	<0.001	Habituation effect
Familiar vs. Unfamiliar	0.647	0.330	N.S.
Hand-reared	0.694	0.509	N.S.
Number of Bill Wipes			
Repertoire	-0.031	0.535	N.S.
Linearity	-0.926	0.627	N.S.
Test Order	0.122	0.093	Acceleration effect
Stimulus Order	-0.164	0.003	Habituation effect
Familiar vs. Unfamiliar	-0.336	0.120	N.S
Hand-reared	-0.219	0.484	N.S.
Number of Fluffs			
Repertoire	0.162	0.003	Response increases as repertoire increases
Linearity	-2.256	0.214	N.S.
Test Order	0.185	0.006	Acceleration effect
Stimulus Order	-0.015	0.818	N.S.
Familiar vs. Unfamiliar	-0.057	0.891	N.S.
Hand-reared	-0.101	0.872	N.S.

*Model uses a simplified zero inflation formula including an intercept for convergence