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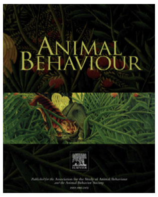

Inheritance of temporal song features in Java sparrows

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The inheritance of structural characteristics and individual note parameters is often studied in oscine passerines. However, other song features, such as the temporal characteristics of song, are less well studied. Inheritance of these features could be influenced by a range of factors, including social inheritance, mechanical constraints, genetic relatedness and the developmental environment. Using archived song data, we examined patterns of inheritance of temporal song features, relating to song duration, song tempo and internote intervals, in a laboratory population of Java sparrows, *Padda oryzivora*, some of which had been cross fostered. Overall, we found strong evidence for cultural inheritance of temporal song features, that is, temporal song features were learned from the social father. We found that song duration was, at most, weakly socially inherited and constrained by a correlation between song tempo and number of notes. Internote gap durations were also influenced by other song features, in particular the duration of the preceding and following notes, although social learning was still apparent when controlling for these features. Across all measures, we found no evidence that temporal song features were affected by genetic relatedness or the developmental environment. Our findings, and those in other species, suggest that temporal song features are likely to be inherited through a combination of the learning of song structure and spectral structure of notes, and specific learning of temporal song features during development.

Birdsong is a complex social signal with an important role in courtship and mate choice. The inheritance of birdsong structure (e.g. note repertoire or structural complexity) and specific note parameters (e.g. frequency, duration and amplitude) are frequently studied. These features can be honest indicators of male quality (Gil & Gahr, 2002) and can shape female preferences (Collins, 2004; Ritschard et al., 2010) and thus sexual selection (Ryan, 1997). A range of mechanisms, including social learning (Beecher & Brenowitz, 2005; Lewis, Soma, et al., 2021), genetic inheritance (Forstmeier et al., 2009), motivation (Leedale et al., 2015) and developmental stress (Nowicki & Searcy, 2004), can influence song development and adult song phenotype. Understanding the contribution of these different components to adult song phenotype is therefore vital to making predictions about song evolution over time.

Many of the same principles apply to the temporal features of song, such as tempo (i.e. notes/s). The silent features of birdsong, such as internote intervals, may be particularly interesting. In both zebra finches, *Taeniopygia guttata* (Glaze & Troyer, 2006) and Bengalese finches, *Lonchura striata domestica* (Tachibana et al., 2015), variation in internote interval was considerably greater than variation in note duration within individuals. Temporal features are salient to females, and females show preference for songs with particular temporal features (Dunning et al., 2020; Nolan & Hill, 2004). Although temporal song features could contribute to sexual selection, their inheritance has received less attention than other song features.

Temporal features may be learned from a tutor. Untutored birds can show unusual song timing (e.g. Kagawa et al., 2014), suggesting that a tutor may be necessary in developing species-specific temporal features. In a study by James et al. (2023), zebra finches

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showed no significant difference in gap durations between fathers and sons for identical note-to-note transitions. This pattern was also seen when birds were experimentally tutored with songs constructed to have the same gap durations for all note-to-note transitions (James et al., 2023), suggesting that gap duration may have a learned component which is separate from the notes themselves. However, temporal features can also be mechanistically linked to other song features. In Bengalese finches, individuals with larger note repertoires sang slower songs, suggesting a trade-off between repertoire size and tempo (Soma, Takahasi, Hasegawa, et al., 2006). Note repertoire can be socially inherited (Lewis, Soma, et al., 2021; Soma, 2011), so learning of note repertoire may result in similar tempos between fathers and sons due to a shared repertoire and repertoire size. In Bengalese finches, the duration of silent gaps was significantly correlated with the duration of the preceding note (Tachibana et al., 2015). Gap duration was also affected by the note-to-note transition; stereotyped transitions, that is, transition types that occur repeatedly in a singer's repertoire, were significantly shorter than branching points, where a syllable may be followed by more than one different syllable type (Matheson & Sakata, 2015; Tachibana et al., 2015). Specific note-to-note transitions and branching points are often shared between fathers and sons (James et al., 2020). While the duration of silent gaps could be learned directly from the tutor's song, it is possible that it is learned indirectly through the learning of note repertoires and sequences. As such, apparent learning of a broad range of temporal features may simply be a by-product of the learning of note types and song sequences.

Genetic background can also influence temporal song features. In Bengalese finches, genetic background influenced the fidelity of learning for temporal features; the learning of tempo was more accurate when the tempo of the tutor's song was more similar to that of the genetic father's song (Mets & Brainard, 2018). Temporal features may also be affected by morphological characteristics such as beak shape and body size (Derryberry et al., 2012, 2018; Friedman et al., 2019; García & Tubaro, 2018; Huber & Podos, 2006; Podos, 2001), the heritability of which may result in the genetic inheritance of some song traits. If genetic background influences temporal song features, we would expect to see correlations in traits between related individuals, even if birds were not raised by their genetic fathers.

Temporal song features may be honest indicators of male quality (Gil & Gahr, 2002). The syllable rate of zebra finch nestlings with food-restricted parents was lower than that of those without restrictions (Zann & Cash, 2008), suggesting that temporal song features could indicate early developmental stress. If the developmental environment plays a role in shaping temporal song features, we would expect to see correlations in traits among individuals with shared developmental history, for example clutch mates. Song tempo is also positively correlated with age in a number of estrildid finch species (Glaze & Troyer, 2013; James & Sakata, 2014, 2015, 2019; Ota & Soma, 2014), whereas gap duration (i.e. the duration of silent intervals between notes) and age appear to be negatively correlated (Glaze & Troyer, 2013; James & Sakata, 2014, 2015). There is a positive relationship between age and male quality through selective attrition (Kokko, 1998). Temporal song features could, therefore, be used as a basis for males to advertise individual quality and to inform female mate choice.

Temporal features can play a role during courtship and mate choice. Preference for some temporal song features has been reported in a number of species (Bengalese finches, Dunning et al., 2020; canaries, *Serinus canaria*, Drăgănoiu et al., 2002; Lerch et al., 2011, 2013; swamp sparrows, *Melospiza georgiana*, Ballentine et al., 2004; house finches, *Carpodacus mexicanus*, Nolan & Hill, 2004). The importance of temporal features is further highlighted when comparing undirected versus female-directed songs. Bengalese finches increase song tempo and decrease internote intervals when performing female-directed rather than undirected song (James & Sakata, 2015; Matheson & Sakata, 2015). Female-directed songs also have higher levels of consistency (Sakata et al., 2008), which is often related to higher reproductive success (Sakata & Vehrencamp, 2012). In addition, in blue tits, *Cyanistes caeruleus*, where both sexes sing, males sang with higher consistency than females, and consistency increased towards the female fertile period when females make daily mating choice decisions (Sierro et al., 2022), supporting the hypothesis that consistency is important for mate choice. As such, temporal features may be important in sexual selection, especially if they reveal information about the singer's learning ability, genetic background, developmental environment or individual traits.

Estrildid finches, particularly zebra finches and Bengalese finches, are frequently used as a model group for the study of song development and inheritance. We studied patterns of inheritance of temporal song features in another estrildid species, the Java sparrow, *Padda oryzivora*. We used the same data set as Lewis, Soma, et al. (2021), which contains song recordings from Java sparrows over multiple generations. Some birds were raised by their genetic fathers, while others were cross-fostered and raised by social fathers that were not their genetic fathers. As such, this data set offers the potential to disentangle social learning and genetic heritability. We examined the data set for evidence of social learning, genetic heritability and rearing environment on the inheritance of temporal song features. We expected that temporal song features would be socially inherited, as is the case with other song features in this species (Lewis, Soma, et al., 2021), but with potential contributions from genetic inheritance and the developmental environment.

METHODS

Study Species

The Java sparrow is an endangered finch native to South East Asia and frequently kept in captivity (BirdLife International, 2021; Restall, 1996). Each juvenile male learns to sing a single song type during a critical period (Ota & Soma, 2014) and, as adults, males use these songs for courtship. Song learning requires social interaction with the tutor, so in laboratory settings juvenile males are most likely to learn from their social fathers even if they are not auditorily isolated from other birds (Soma, 2011). Previous studies suggest that a range of song features, such as song structure and note characteristics, are inherited from the social father and not related to the genetic pedigree (Lewis, Soma, et al., 2021). However, spectrogram inspection suggests that copy accuracy of the temporal features of songs, such as the duration of internote intervals, may be lower than that of other song features (Soma, 2011). The relative contributions of cultural and genetic inheritance, as well as rearing environment, to a wide range of temporal song features have not, to our knowledge, been formally assessed in this species.

Data Set

To investigate the inheritance of temporal song features, we used the data set from Lewis, Soma, et al. (2021). This data set contains information on individual notes in 676 undirected songs from 73 Java sparrows (mean 9.3 songs per individual, range 3–10) from multiple generations with known social and genetic pedigrees (see Lewis, Soma, et al., 2021). Founding individuals were obtained from pet shops and breeders. Adult birds were housed in large (43 × 37 cm and 41 cm high or 46.5 × 46.5 cm and 94 cm high), single-sex cages with up to 20 individuals per cage. During breeding, breeding pairs were kept in separate cages (43 × 37 cm and 41 cm high) and inspected regularly. Eggs were cross fostered when multiple nests were available. During rearing, cages were visually but not auditorily isolated, and juveniles remained in the cages with their social parents until they were approximately 180 days old. A small number of birds had the opportunity to learn from multiple tutors. These birds were not included as ‘sons’ in the data set. However, these individuals were included in the data set as fathers if they raised or fathered sons.

Recordings consisted of an individual bird singing alone in a recording chamber with a recording device placed ca. 20 cm away from the bird. All recordings were taken at a sample rate of 44.1 kHz. Archival recordings were collected using a number of different recorders (Marantz PMD 661, Zoom Q3HD, TASCAM DR-100 MKIII). In total, 58 father–son pairs were present in the data set. Sons were raised by their genetic fathers ($N = 28$) or by social fathers that were not their genetic fathers ($N = 30$).

A song was defined as a series of notes with internote intervals of <1 s (Kagawa & Soma, 2013; Lewis, Soma, et al., 2021). Songs were manually segmented into individual notes using the software Koe (window length = 512, window overlap = 50%, time-axis zoom = 400%, contrast = 100%; Fukuzawa et al., 2020; Lewis, Soma, et al., 2021). In total, 22 972 notes were classified into 16 note types based on a suite of characteristics (presence of harmonics, frequency modulation, duration and presence of nonlinear phenomena). Classification was repeatable across observers (Lewis, Soma, et al., 2021). We cleaned the original data set to remove eight notes separated from their songs by internote intervals of >1 s. In addition, we added two notes from a single song that were not included in the original data set despite being separated by <1 s from the body of their song. These two notes were segmented and classified as in Lewis, Soma, et al. (2021). Thus, the final data set used for the present study included 22 966 notes.

Measurement of Song Features

Identification of introductory notes

Songs frequently contained a series of introductory notes, which, although spectrally similar to other notes in the song, are indicated by note repetition and variable, uncharacteristically long gap durations. These notes may represent a period of preparation prior to the main song, as reported in zebra finches (Kalra et al., 2021; Rajan & Doupe, 2013; Rao et al., 2019). In zebra finches, the acoustic structure and the number of introductory notes before the main body of the song is not only learned from a tutor, but also shaped by biological predispositions (Kalra et al., 2021). This suggests that these notes are not solely related to preparation and may be important in song learning and development. This does, however, create some problems when considering temporal features of songs. Introductory sections were more variable than the main bodies of songs and were characterized by relatively long silent intervals between notes (>0.25 s but <1 s). Although in other species, these introductory notes appear to be structurally distinct from the main song motif (Kalra et al., 2021; Rajan & Doupe, 2013; Rao et al., 2019), in Java sparrows, introductory notes were structurally similar to notes found elsewhere in the song, making them harder to define. The presence and number of introductory notes was highly variable both within and between individuals. As such, the presence of introductory notes in songs may influence our estimates of inheritance. For example, if a son generally uses introductory notes, but his social father does not, then the son's gap durations and standard deviation will be inflated compared to that of his father, potentially masking any pattern of inheritance in the main body of the songs. In Java sparrows, while a 1 s internote interval is often used to describe songs (Kagawa & Soma, 2013; Lewis, Soma, et al., 2021), other studies have used a smaller internote interval for inclusion to exclude introductory notes (Ota & Soma, 2014). To account for the presence of introductory notes, all analyses were conducted twice, once with and once without introductory notes, to determine whether patterns were still apparent when these notes were excluded.

To remove introductory notes, we reduced the internote interval for inclusion in the song to 0.25 s, rather than 1 s. However, birds sometimes had gaps of >0.25 s in the middle of their main songs, and birds often sang more than one introductory note in quick succession followed by a long gap. To account for these features, we excluded notes separated from the main song by >0.25 s until five consecutive notes with an internote interval of <0.25 s had been identified. We considered the first note in the series of five notes to be the start of the song (Fig. 1). Our full data set included 22 290 gaps when song introductions were included and 20 911 gaps when song introductions were removed.

Temporal song features

Temporal song features were extracted from the processed data set, which contained information on the start time, end time and duration of notes in each song. We defined gaps as the period of silence between the end of one note and the beginning of the next (i.e. the internote interval). Across the data set, each gap was assigned a transition type based on the note types immediately preceding and following the gap, using the note types defined by Lewis, Soma et al. (2021). Gap durations differed between transition types (see Results), and the transition types sung by individuals in the data set differed. Thus, we chose some metrics that examine the overall temporal features of songs, and others that control for differences in the duration of different transition types. We focused on six temporal features that we computed for each individual bird: (1) the mean song duration (s); (2) the mean log song tempo (log (notes/s)); (3) the mean log gap duration (log(s)); (4) the standard deviation of the log gap duration (log(s)); (5) the gap score (unitless); and (6) the gap variability score (unitless). All logarithms are natural logarithms.

Gap score is a measure of vocal performance that compares an individual's gap durations to the gap durations of the rest of the population for the same transition types. For each transition type, we computed the deviation of each individual's mean log gap duration from the population mean log gap duration for the same transition type. Thus, shorter-than-average gap durations produced by an individual had negative values, and longer-than-average gap durations had positive values. The gap score for an individual was the weighted mean of its deviations across all the transition types it used. Thus, transition types that a bird produced more frequently contributed more to its gap score. Overall, birds that produced systematically shorter-than-average gap durations would have negative gap scores, and those that produced systematically longer-than-average gap durations would have positive gap scores. The motivation for this measure is that gap duration is influenced by transition type in other species (Matheson & Sakata, 2015), and this is also the case in Java sparrows (see Results). The gap score allowed us to investigate whether social fathers that sang with longer gap durations also produced sons that sang with longer gap durations, while controlling for the transition types that each bird uses.

The gap variability score is a measure of consistency of the gap durations in an individual's songs, while controlling for transition types. We computed the variance, σ_{jb}^2, for the log gap duration of each transition type j as produced by each bird b. Then, we computed the weighted population mean variance, σ_j^2, for each transition type j in the population. Thus, $\sigma_j^2 = \sum \sigma_{jb}^2 (n_{jb} - 1) / \sum (n_{jb} - 1)$ where n_{jb} is the number of times

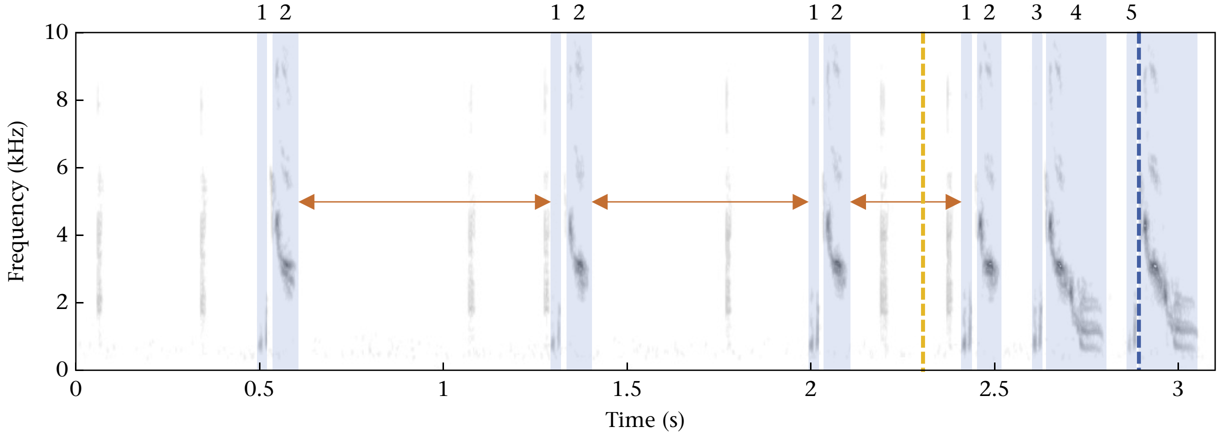

Figure 1. Spectrogram of Java sparrow song showing the identification of introductory notes. Orange arrows represent internote intervals larger than 0.25 s. Working from the beginning of the note sequence, we excluded notes that were separated from the main body of the song by gaps of >0.25 s until we encountered five consecutive notes separated by gaps of <0.25 s (blue dashed line). The start of the main song is identified as the point at which the string of five consecutive notes started (yellow dashed line). Unhighlighted sounds represent bill clicks, which were not included in analyses, as we focused on vocalizations rather than mechanical sounds.

bird *b* produced transition type *j* and the summations run over all birds that produced transition type *j* at least twice. Then, the variability score for bird *b* producing transition type *j* is $z_{jb} = \log(\sigma^2_{jb}/\sigma^2_j)$ and the overall gap variability score for bird *b* is $z_b = \sum z_{jb}(n_{jb}-1)/\sum(n_{jb}-1)$ where the summations run over all transition types that bird *b* produced at least twice. Similar to the gap score, this statistic enabled us to investigate gap duration variability while controlling for differences in variability between transition types.

Temporal song features may be influenced by other song features due to constraints associated with vocal production. As gap duration is an important feature in all the temporal song features described above, we further examined how additional song features, including the preceding and following notes, note repertoire and song complexity, affected the inheritance of gap duration in this species in addition to social learning. These additional features were examined for both all gap durations in the data set and for only transition types that were shared between sons and their social fathers (i.e. only those transition types that appeared in both the song of the son and his social father; see Data Analysis section; Fig. 2).

Finally, we explored the relationship between song length and tempo, as this may impact overall song duration.

Data Analysis

We investigated the potential social and genetic inheritance of the six temporal song features we measured for individual birds using linear mixed-effects models fitted with the lmekin function from the coxme package in R, which accounts for the genetic pedigree via a relatedness matrix (Therneau, 2018). For each song feature, we regressed the son's phenotype against the social father's phenotype and log age of the son at the time of recording. Age was included because Java sparrow songs change with age after the crystallization period (Ota & Soma, 2014). As fathers were not always recorded at the age when they raised sons, and due to the possible effects of age on temporal features (James & Sakata, 2014, 2015, 2019; Ota & Soma, 2014), we corrected the social father's phenotype to represent his phenotype when rearing sons using the methods described in Lewis, Soma et al. (2021). Briefly, we fitted a model to the data and then adjusted the social father's phenotype by subtracting the difference in his log age at the time of recording and the time at which the son was reared, multiplied by the fitted coefficient for log age. We repeated this process in a loop which terminated when the fitted coefficient for log age changed by less that 10^{-5} between iterations. Inclusion of age correction did not qualitatively affect our findings (Tables A1, A2). Clutch and the genetic pedigree were included in the model as random effects. We modelled the genetic pedigree using a relatedness matrix produced by the kinship2 R package (Sinnwell et al., 2014). Using a relatedness matrix, rather than only information from genetic fathers, allowed us to use information about more distantly related individuals, which increased our ability to detect genetic effects in the data set. Clutch was included to account for the shared environment among nestmates. To test whether the clutch, the genetic pedigree or the two factors together affect the temporal features of Java sparrow song, we fitted reduced models with those random effects removed. We compared the reduced models to the full model using likelihood ratio tests. We conducted each regression twice: once with the introductory notes included in the songs and once with the introductory notes removed. We conducted a similar regression to examine the patterns of inheritance for the mean log number of introductory notes that each bird produced across all songs. Some birds had songs with no introductory notes. Since a value of zero cannot be log-transformed, we set the number of introductory notes to 0.5 in songs without observed introductions. This approach maintains the desired relationship among songs with one or more introductory notes and assumes that songs with no introductory notes differ from songs with one introductory note in the same way that songs with one introductory note differ from songs with two introductory notes. Thus, it makes conservative use of the information provided by songs without introductory notes (Anderson et al., 2006).

To examine the factors that influence gap durations, we conducted two additional regression analyses. In the first, we regressed the log duration of each gap produced by each bird simultaneously on (1) the log duration of the note that preceded the gap, (2) the log duration of the note that followed the gap, (3) the log number of notes in the song, (4) the log repertoire size of the singer, (5) the first-order entropy of the singer's repertoire, (6) the proportion of all transitions produced by the singer that were of the same type as the focal gap, (7) the log duration of the song in which the gap appeared, (8) the position of the gap in the song in which it appeared, (9) the log age of the singer, (10) the size of the brood in which the singer was reared, (11) the mean log gap duration of notes produced by the singer's social father, (12) the

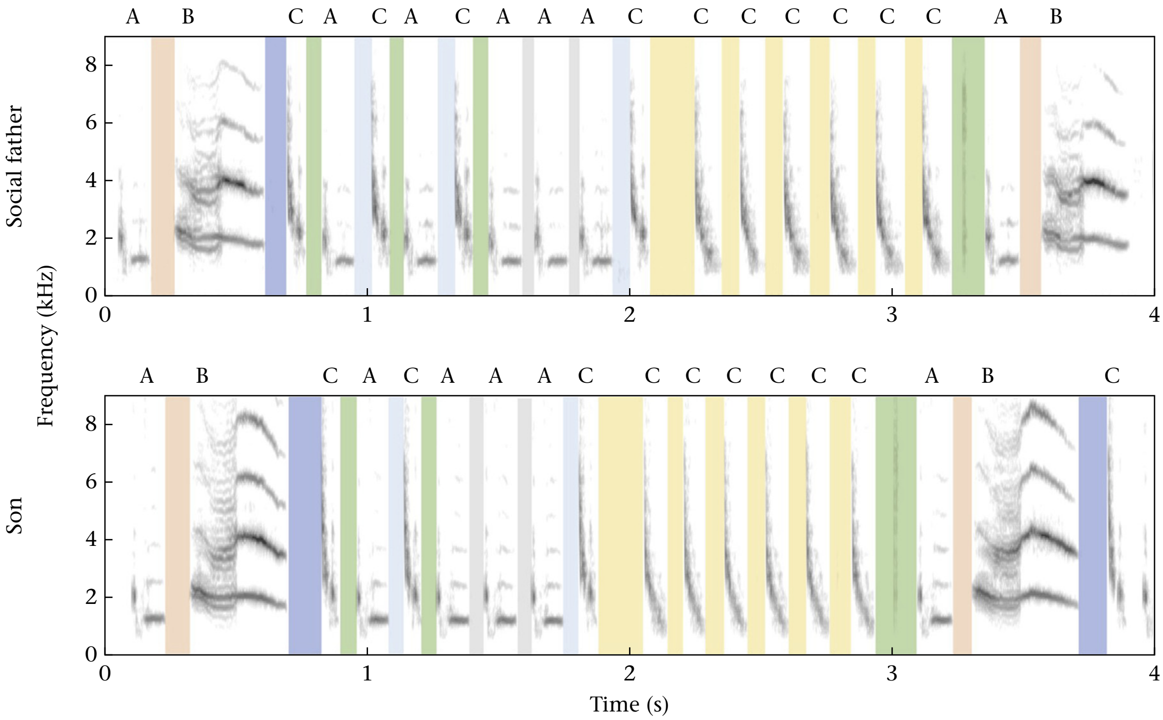

Figure 2. Identification of shared transition types between a son and his social father. Spectrograms show a truncated 4 s section of each song. Coloured blocks indicate each transition type present in the songs. Where coloured blocks appear in both son and social father songs, they are considered to be shared. Transition types were defined based on the note type preceding and following the silent gap (as defined in Lewis, Soma, et al., 2021), with note types indicated by letters above the spectrogram.

gap score of the singer's social father and (13) the interaction between the singer's brood size and the mean log gap duration of the social father. The observed gap durations in our data set were not independent and identically distributed. For example, gaps produced by the same bird or gaps with the same transition type were more similar than gaps produced by different birds or gaps with different transition types. To account for correlations in gap duration within groups of similar gaps, we included random intercepts in our regression for the following factors: (1) the song in which the gap appeared, (2) the identity of the singer, (3) the class of the note before the gap, (4) the class of the note after the gap, (5) the transition type, (6) the clutch of the singer, and the two- and three-way interactions between the identity of the singer, the class of the note before the gap and the class of the note after the gap. We fitted these models using the lmer command in the package lmerTest in R (Kuznetsovs et al., 2017). There were too many predictors in this full model for us to study all the possible submodels nested within it, so we looked for a best model for our data using backwards selection. First, we removed random effects to which no variance was assigned in the fitted model. This prevents model singularities and allows accurate estimation of the fixed effects. Then, we removed fixed predictors one at a time, starting with the fixed predictor with the largest t statistic. We computed Akaike's information criterion (AIC) for the fitted model using the AICc command in the R package AICcmodavg (Mazerolle, 2020). We continued removing fixed predictors until the AICc stopped declining. The reduced model we obtained was the best model that we encountered for our data. To ensure that there were no better models we could achieve by the addition of single predictors, we reintroduced each fixed predictor that we had removed from the full model back to our ‘best’ model one at a time and computed a new AICc value. Our best model was better (i.e. had a lower AICc value) than any of the models with predictors reintroduced. All predictors that remained in the best model were statistically significant throughout the backwards selection process, which suggests that our inferences from this analysis are robust to the model selection process.

Our second regression, examining shared transitions, was similar to the first, but we removed the gap score and overall mean log gap duration of the social father from the set of predictors, and replaced these with (1) the mean gap duration of the social father when he produced the focal transition type, (2) the proportion of the social father's transitions that were of the focal transition type, (3) the Jaccard similarity index between the repertoires of the son and social father, (4) the interaction between (1) and (2) and (5) the interaction between (1) and (3). We mean centred (1) to make models with interactions easier to interpret. This analysis asked whether sons learn how to produce specific transition types from their social fathers, whether they learn transition types more accurately if they hear them more often, and whether they learn transition types more accurately when they also learn more of their social father's repertoire. Shared transition types were defined solely based on the notes preceding and following the gap, and were not related to position within the song. If the same transition type appeared at any point in the songs of the son and his social father, then we considered it to be shared (Fig. 2). Focusing on specific transition types comes at a cost because we could only study gaps produced by sons if their social fathers produced the same transition types, whereas in the first analysis we could study all the gaps produced by sons as long as their social fathers were part of the data set. Thus, the first analysis included 17 387 and 16 163 gaps in songs with and without introductions, respectively, while the second analysis included 16 192 and 15 065 gaps in songs with and without introductions, respectively.

Finally, to examine the relationship between tempo and number of notes, we regressed the mean log song tempo of each bird on the mean number of notes in the songs that bird produced.

Ethical Note

This study used archival recording data from a laboratory population of Java sparrows housed at Hokkaido University. The archival data were collected between 2011 and 2019 under the following approvals: Hokkaido University (Permit numbers: 11-0028, 16-0020) and the University of Manchester AWERB (Permit number: D042). The data were collected for a range of purposes, including use in other studies and training of laboratory members. The sample size in our study was dictated by the number of individuals in the archival data for which recordings were available and that (1) had recordings available and (2) had social fathers that also had recordings in the archive. Birds were housed at a temperature of 25 ± 3 °C, humidity 30–60%, with a 12:12 light:dark 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 cm and 41 cm high or 46.5 × 46.5 cm and 94 cm high) with up to 20 individuals per cage. During breeding, birds were housed in family groups in cages (43 × 37 cm and 41 cm high) which were visually, but not aurally, isolated from other birds. For recording, birds were housed singly in small cages (27 × 36 cm and 18 cm high), which were placed in a soundproof recording chamber to ensure recordings contained only songs from a single individual with a high signal-to-noise ratio, as this is important for analysis. To ensure sufficient recordings were obtained for analyses, individuals remained in the recording chamber for up to 72 h, although if enough recordings were obtained in a shorter time period, birds were removed from the recording chamber and returned to their usual environment. Most birds spent <24 h in the recording chamber. Food and water were provided ad libitum during this time. Individuals are not strongly bonded with cagemates (M. Soma, personal communication, 2018). As such, single housing for this time period was unlikely to have detrimental effects on birds' welfare. Birds were checked regularly during single housing to ensure that they did not show signs of distress.

RESULTS

When considering full songs, we found evidence for social inheritance in all traits measured except song duration and gap score (Table 1, Fig. 3). That is, birds' temporal song features were more similar to the song features of their social fathers than to those of other birds. Results were similar when introductory notes were removed (Table 2, Fig. 4), except for song duration, which showed evidence of social inheritance (Table 2). Our inability to detect social learning of song duration when introductory notes were included is consistent with the finding that the production of introductory notes is not socially learned (Table 1); if introductory notes are not learned, then including them in songs may obscure the social learning of song duration. Across all features measured, both in full songs and in songs without introductory notes, there was no evidence for an effect of genetic inheritance (pedigree) on temporal features of songs (Tables 1, 2). Thus, birds' song features were not significantly correlated with the song features of their genetic relatives. Similarly, there was no evidence for an effect of the developmental environment (clutch) on temporal features (Tables 1, 2).

Evidence for age effects was more variable (Tables 1, 2, Figs 5, A1, A2). When considering full songs we found an effect of age on song duration, with older birds singing longer songs (Table 1, Fig. 5). However, the patterns were slightly different when considering songs without introductory notes. First, while the effect was in the same direction, the effect of age on song duration was not significant (Table 2, Fig. A1). This is consistent with the finding that the number of introductory notes, which impacts song duration, increased with age (Table 1), so removing introductory notes could reduce apparent age effects. Second, we found a marginally significant effect of age on the gap score: older birds had shorter internote intervals when controlling for the transition type (Table 2, Fig. 5).

Since patterns relating to both age and inheritance were influenced by the removal of the introductory notes, we further examined the removed introductory phrases. We found no evidence that the number of introductory notes was socially inherited; social fathers with more introductory notes did not have sons with more introductory notes (Table 1). However, older birds had more introductory notes than younger birds (Table 1).

Different transition types had different mean gap durations (Fig. A3). Among transition types that were observed more than 10 times, the mean gap duration ranged from 0.015 s to 0.156 s. Because gap duration contributes to many of the temporal song features that we examined, we studied the factors affecting gap duration directly. First, we examined all gaps in the data set. In full songs (introductory notes included), the log gap duration was positively correlated with the log durations of the preceding ($\beta = 0.294$, $P < 0.001$) and following ($\beta = 0.422$, $P < 0.001$) notes. The log gap duration was negatively correlated with the proportion of the singer's notes that belonged to the focal transition type: transition types sung more frequently had shorter durations ($\beta = -1.104$ log(s), $P < 0.001$), were positively correlated with the

Table 1
Results from mixed-effect models of full songs

Response	Social Father's phenotype	log(Age)	Pedigree	Clutch	Either
Mean song duration	0.18 P=0.195	**0.76** **P=0.018**	P=0.166	P=0.338	P=0.109
Mean log song tempo	**0.62** **P<0.001**	−0.049 P=0.169	P=0.254	P=1	P=0.506
Mean log gap duration	**0.65** **P<0.001**	−0.0096 P=0.872	P=0.396	P=1	P=0.698
Standard deviation of log gap duration	**0.54** **P<0.001**	0.051 P=0.171	P=1	P=0.127	P=0.311
Gap score	0.066 P=0.646	−0.022 P=0.474	P=0.376	P=1	P=0.676
Gap variability score	**0.38** **P=0.007**	0.074 P=0.463	P=0.615	P=0.626	P=0.646
Log number of introductory notes	−0.0038 P=0.980	**0.39** **P=0.008**	P=0.290	P=0.431	P=0.219

Model coefficients and P values from the mixed-effect models are presented for the effect of social fathers' phenotype and log(age). P values for random effects are from likelihood ratio tests comparing full models to reduced models with the random effects removed. Significant results are indicated in bold.

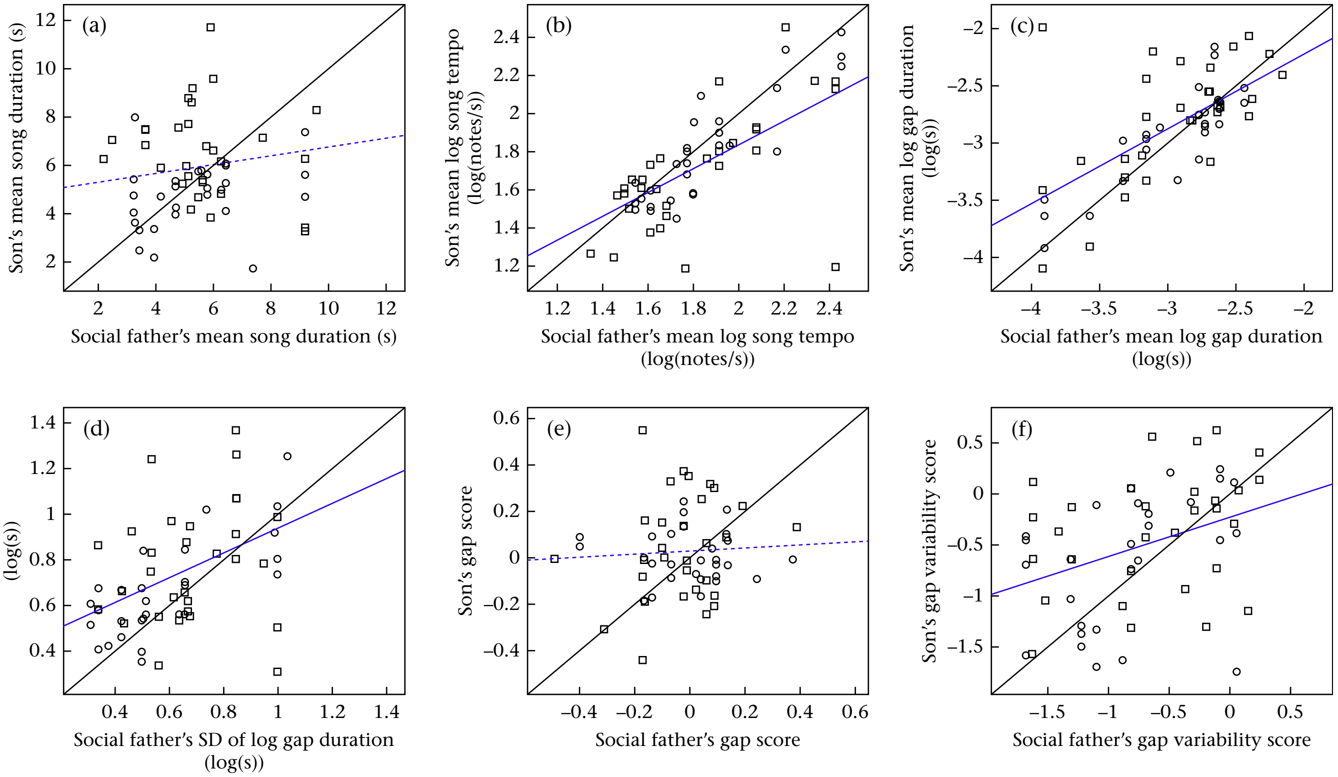

Figure 3. Relationships between the temporal song features of sons and social fathers in full songs (including introductory notes): (a) mean song duration, (b) mean log song tempo, (c) mean log gap duration, (d) standard deviation of log gap duration, (e) gap score and (f) gap variability score. Each point represents the mean value of an individual's temporal features across their songs in the data set ($N = 58$ sons). Cross-fostered sons are indicated by squares and sons raised by their genetic fathers by circles. Regression lines are shown in blue. Dotted lines indicate that the result was not significant. The identity line (y = x) is shown in black.

log song length ($\beta = 0.081$ log(s)/note, $P < 0.001$) and negatively correlated with the position of the gap in the song ($\beta = -0.005$ log(s)/position, $P < 0.001$). Sons' log gap durations were positively correlated with the mean log gap durations of their social fathers ($\beta = 0.489$, $P < 0.001$). Thus, when controlling for the position of gaps in songs, sons sang shorter gaps if their fathers sang shorter gaps. Results were similar in songs with introductory notes excluded. Again, the log durations of both the preceding ($\beta = 0.281$, $P < 0.001$) and following ($\beta = 0.374$, $P < 0.001$) notes were positively correlated with the log gap duration, as was the social father's mean log gap duration ($\beta = 0.337$, $P < 0.001$). Gap duration was negatively correlated with the proportion of the singer's gaps that belonged to the focal transition type ($\beta = -0.825$ log(s), $P < 0.001$). However, neither log song length ($P = 0.55$) nor the position of the gap in the song ($P = 0.65$) was correlated with log gap duration, suggesting that the effects of these variables may be due in part to the long gaps between introductory notes at the beginning of songs.

Table 2
Results from mixed-effect models of songs with introductory phrases removed

Response	Social Father's phenotype	log(Age)	Pedigree	Clutch	Either
Mean song duration	**0.27** ***P*=0.044**	0.29 *P*=0.180	*P*=0.175	*P*=0.219	*P*=0.071
Mean log song tempo	**0.65** ***P*<0.001**	−0.0065 *P*=0.817	*P*=0.231	*P*=1	*P*=0.489
Mean log gap duration	**0.64** ***P*<0.001**	−0.041 *P*=0.43	*P*=0.428	*P*=1	*P*=0.730
Standard deviation of log gap duration	**0.80** ***P*<0.001**	0.020 *P*=0.547	*P*=1	*P*=0.487	*P*=0.786
Gap score	0.010 *P*=0.942	**−0.053** ***P*=0.050**	*P*=0.392	*P*=1	*P*=0.694
Gap variability score	**0.33** ***P*=0.018**	0.0084 *P*=0.931	*P*=0.684	*P*=0.337	*P*=0.524

Model coefficients and *P* values from the mixed-effect models are presented for the effect of social father's phenotype and log(Age). *P* values for random effects are from likelihood ratio tests comparing full models to reduced models with the random effects removed. Significant results are indicated in bold.

We also investigated the factors associated with log gap duration for transition types that were shared between sons and their social fathers to determine whether sons learn how to produce specific transition types from their social fathers. In full songs (i.e. with introductory notes included) the log gap duration for shared transition types was positively correlated with the log durations of the notes preceding ($\beta = 0.269$, $P < 0.001$) and following ($\beta = 0.457$, $P < 0.001$) the gap. Log gap durations were also positively correlated with the first-order entropy of the singer's repertoire ($\beta = 0.223$ log(s), $P = 0.012$), indicating that birds with more complex songs may produce longer gaps between notes. Gap durations were longer in songs with more notes ($\beta = 0.070$ log(s)/note, $P = 0.001$), but shorter when they appeared later in songs ($\beta = -0.004$ log(s)/position, $P < 0.001$). Sons' log gap durations were positively correlated with the mean log duration of their social fathers' gaps for the same transition types ($\beta = 0.83$, $P < 0.001$ for father–son pairs with identical repertoires; Fig. 6) but became less correlated as the Jaccard distance between the fathers' and sons' repertoires increased ($\beta = -0.45$, $P < 0.001$).

In songs with introductory notes removed, log gap durations were positively correlated with the durations of the preceding ($\beta = 0.237$, $P < 0.001$) and following ($\beta = 0.387$, $P < 0.001$) notes, but neither the first-order entropy of the singer's repertoire ($P = 0.08$) nor the position of the gap in the song ($P = 0.40$) was significantly correlated with log gap duration. Sons' log gap durations were positively correlated with the mean log duration of their

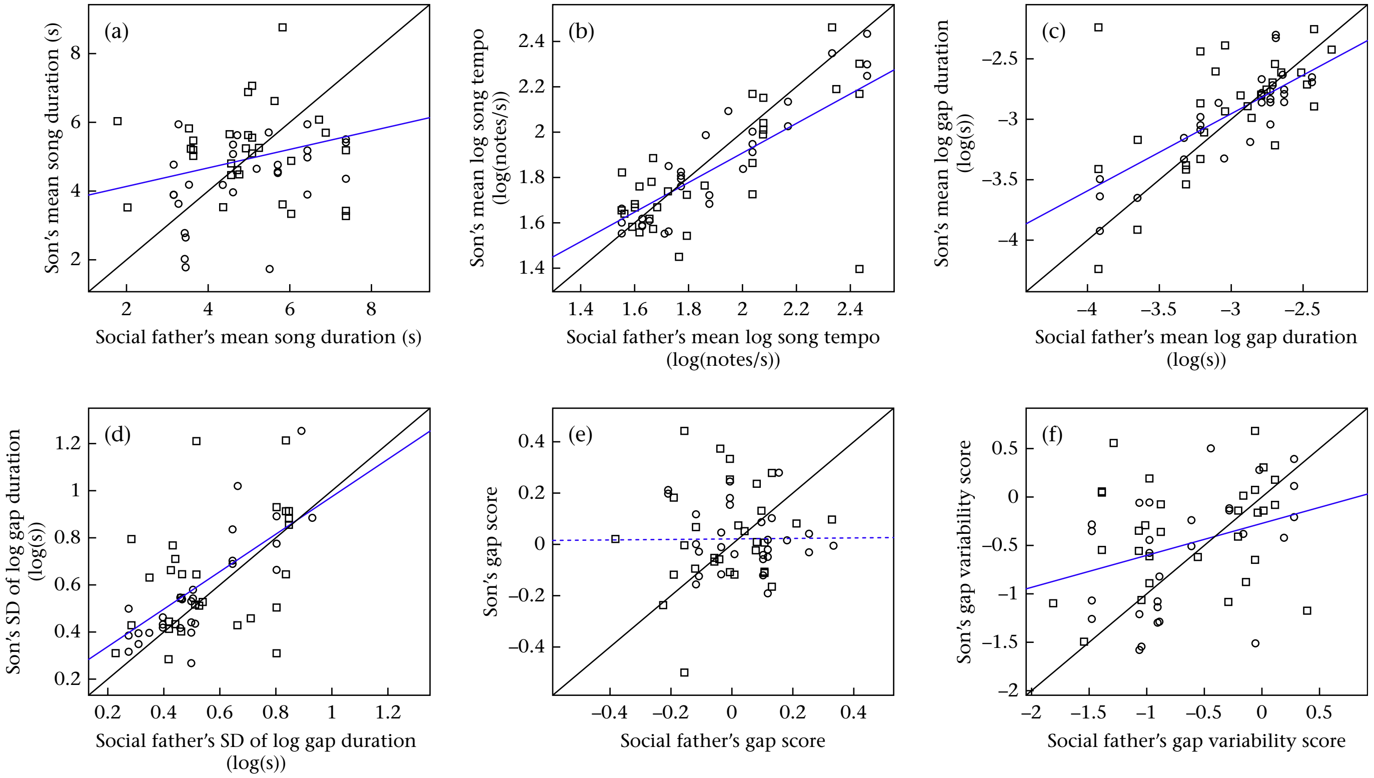

Figure 4. Relationships between the temporal song features of sons and social fathers in songs without introductory notes: (a) mean song duration, (b) mean log song tempo, (c) mean log gap duration, (d) standard deviation of log gap duration, (e) gap score and (f) gap variability score. Each point represents the mean value of an individual's temporal features across their songs in the data set ($N = 58$ sons). Cross-fostered sons are indicated by squares and sons raised by their genetic fathers by circles. Regression lines are shown in blue. Dotted lines indicate that the result was not significant. The identity line ($y = x$) is shown in black.

social fathers' gaps for the same transition types ($\beta = 0.88$, $P < 0.001$ for father–son pairs with identical repertoires) but became less correlated as the Jaccard distance between the fathers' and sons' repertoires increased ($\beta = -0.55$, $P < 0.001$). Sons' gap durations were positively correlated with the Jaccard distance between the fathers' and sons' repertoires ($\beta = 0.289$ log(s), $P = 0.019$), suggesting that sons that learned repertoires less accurately produced slightly longer gap durations across all shared gap types.

Finally, song tempo was positively correlated with the number of notes in the song for both full songs ($\beta = 0.013$, $P < 0.001$) and those with introductory notes removed ($\beta = 0.015$, $P < 0.001$).

DISCUSSION

We examined the inheritance of temporal song features including song duration, tempo and gap duration in the Java sparrow, using archival data both for birds that were cross-fostered and for birds that were raised by their genetic fathers. We found strong evidence that temporal features of birds' songs were socially inherited. There was no evidence that temporal features were genetically inherited or affected by the developmental environment. In addition, we found that temporal song features were also influenced by other song features, as gap durations were influenced by the durations of both the preceding and the following notes.

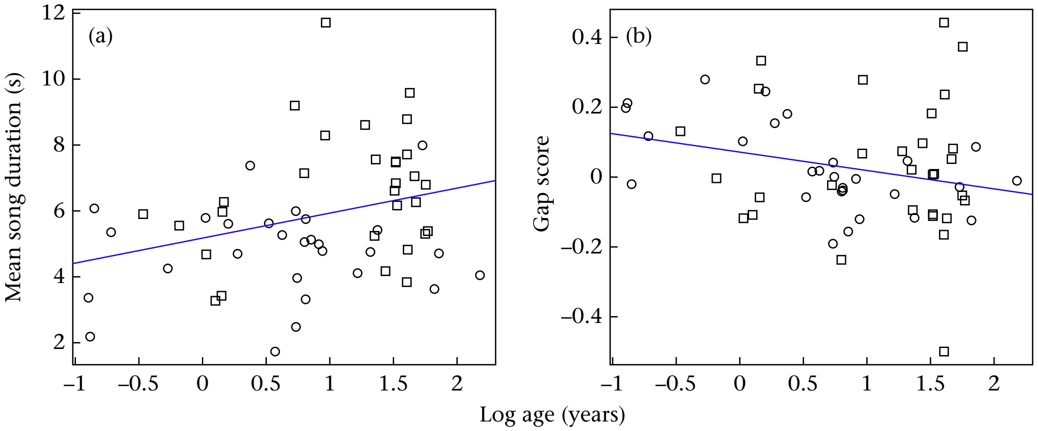

Figure 5. Significant relationships between birds' age at recording and the temporal features of their songs: (a) mean song duration in the full song (introductory notes included) and (b) gap score in songs with introductory notes removed. A full set of plots for all temporal features can be found in Figs A1 and A2. Each point represents the mean value of an individual's features across their songs in the data set ($N = 58$ sons). Regression lines are shown in blue.

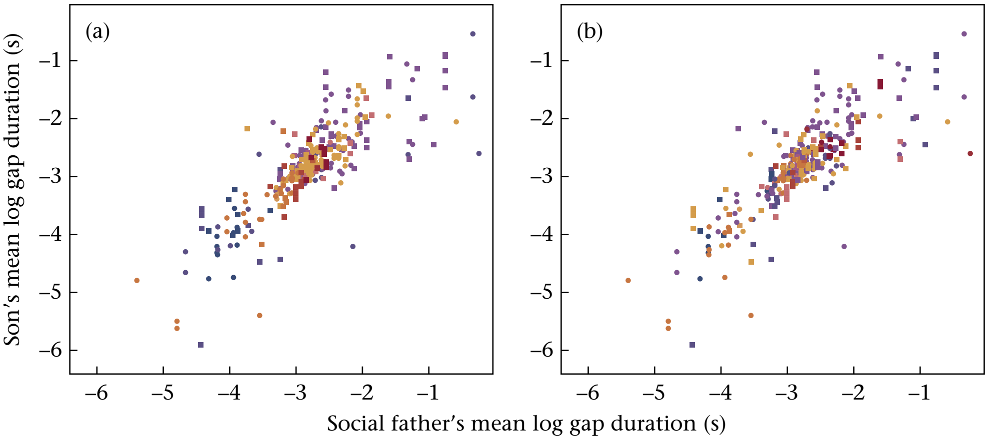

Figure 6. Relationship between social fathers' and sons' mean log gap durations for shared transition types in full songs (with introductory notes included). Each point represents the mean log gap duration for one shared transition type. (a) Note type preceding the gap; (b) note type following the gap. Point colours represent note types. Cross-fostered sons are indicated by squares and sons raised by their genetic fathers by circles.

Most temporal features in songs showed strong evidence of social inheritance. Sons' song features correlated strongly with those of their social fathers for song tempo, mean log gap duration, mean log gap duration of shared transitions, standard deviation of log gap duration and gap variability score. Similar results were found for the inheritance of song tempo in the closely related Bengalese finch when raised with a live tutor present (Mets & Brainard, 2018) and for gap durations in live-tutored zebra finches (James et al., 2023). However, the variability of gap durations for shared transitions was not correlated between fathers and sons in zebra finches (James et al., 2023). Although examining similar patterns relating to the variability of gap durations, our measure, gap variability score, assessed variation across all transitions sung by an individual, rather than focusing on shared transitions. While most temporal song features examined were socially inherited, we found no evidence of social inheritance for gap score, which quantifies gap durations controlled for transition type compared to the rest of the population. That is, social fathers with longer average gap durations across all transition types did not raise sons with longer average gap durations across all transition types. This lack of pattern might occur if birds learn the features of transition types independently, that is, singing some transition types with a longer-than-average duration and others with shorter-than-average duration, rather than learning general features (e.g. ‘long gap durations’) that they apply to all transition types.

Apparent learning of temporal song features could be achieved in three ways: learning of temporal song features, similarity in temporal features due to the learning of song sequencing and spectral structure or a combination of the two. A number of features of vocal production, including note repertoire, the number of note types and note durations are socially inherited in Java sparrows (Lewis, Soma, et al., 2021; Ota & Soma, 2014; Soma, 2011), so vocal production learning may contribute to the apparent learning of song temporal features through matching of note types, trade-offs and mechanical constraints. When further examining factors influencing gap duration, we found that durations of the notes both preceding and following the gap were positively correlated with gap duration, suggesting that gap duration could be influenced by learning of note durations. In Bengalese finches, larger note repertoires (more note types) were associated with slower song tempo (Soma, Takahasi, Ikebuchi, et al., 2006). However, we found no evidence that note repertoire influenced gap duration in Java sparrows, although high first-order entropy, which relates to structural complexity, was associated with longer gaps when considering shared transition types in full songs. This is in line with other findings in Bengalese finches, where branching points (where notes may be followed by more than one different note type) in songs, which contribute to higher first-order entropy, are associated with longer gap durations (Matheson & Sakata, 2015). The social father's gap durations were also significant predictors of the son's gap durations. This may mean that gap durations have a learned component independent of their association with vocal production learning. However, this pattern could also be explained by other shared features of vocal production. A number of additional note features, such as frequency change, are shared between fathers and sons (Lewis, Soma, et al., 2021), and these features could influence gap duration (e.g. due to mechanical constraints). To fully understand whether sons learn specific features of gap durations independent of the learning of song sequencing and spectral structure, experimental tutoring to decouple these potential mechanisms would be necessary. In zebra finches, birds tutored with songs manipulated to have uniform gap durations across all transition types produced songs with gap durations significantly correlated with those of their artificial tutors (James et al., 2023), suggesting that the specific learning of gap duration plays a role in song development in at least some species.

We did not find strong evidence for social inheritance of song duration; the effect of the social father's phenotype was not significant when considering full songs, and only weakly correlated with son's phenotype for songs without introductory notes. At first, this seems surprising, since gap duration, note duration (within note types) and song structural characteristics, such as number of notes and complexity, are all socially inherited (Lewis, Soma, et al., 2021). We might, therefore, expect song duration to be socially inherited. A lack of social learning in full songs is likely to be partially mediated by introductory notes. These are characterized by long internote intervals, so they can strongly impact overall song duration; the number of introductory notes in the song was not socially inherited and increased with age, which could contribute to differences between fathers and sons. However, other song features may affect the inheritance of song duration. Song duration is determined by the number of notes in a song and by the song tempo. In our data, these two features were correlated: birds with more notes in their song sang at faster tempos, and this effect was apparent in both full songs and those with introductory notes removed. In this way, it appears that duration is partially constrained: birds cannot simply double their song duration by doubling the number of notes they sing, which may relate to energetic costs. If duration is constrained in this way, then it may act as an honest indicator of male quality. However, birds might also constrain their song duration for reasons unrelated to male quality. For example, species-typical song durations might be important for species recognition and social cohesion, or females might prefer intermediate song durations, in which case the ability to produce longer songs might not signal male quality. As such, further investigation into the factors affecting song duration is necessary before drawing broad conclusions.

Contrary to our predictions, we found no evidence that genetic pedigree influenced temporal features in Java sparrow song. Consistent with this finding, other song features in Java sparrows, specifically those relating to overall song and note structure, also showed no evidence of genetic inheritance (Lewis, Soma, et al., 2021). This is contrary to findings in other estrildid finch species. In Bengalese finches, there was an interaction between learning environment and genetic background for song tempo (Mets & Brainard, 2018, 2019). Birds tutored with identical songs produced songs with tempos correlated with those of their genetic fathers (Mets & Brainard, 2018) and computer-tutored birds learned more accurately if song tempo was more similar to that of their genetic fathers (Mets & Brainard, 2019). However, when birds were live-tutored, the relative contribution of genetics to song phenotype was dramatically reduced, while the relative contribution of the tutor's song increased, suggesting that live tutoring may mask genetic contributions to song temporal features (Mets & Brainard, 2018). Given the findings in Bengalese finches, and as birds in our data set were live-tutored, it is possible that the relative contribution of genetic inheritance was reduced to a point where it was not detectable in our analyses. It is also possible that genetic variation in this domesticated and strongly selected population was too small to reliably assess genetic inheritance.

We also found no effect of the developmental environment (clutch) on temporal features. The developmental environment captures attributes such as provisioning, brood size and parental feedback during song learning (Carouso-Peck et al., 2020). Previous studies in Java sparrows found that note consistency, that is, spectral similarity between consecutive notes, but not song or note structure, was affected by an individual's clutch of origin (Lewis, Soma, et al., 2021). Our ability to detect overall clutch effects in this study may have been limited as all clutches were raised in captivity in relatively similar conditions, and there may have been variability within clutches due to asynchronous hatching. In zebra finches, higher developmental stress (restricted foraging, Zann & Cash, 2008; large clutch size, Holveck et al., 2008) affected temporal song features. However, developmental stress did not affect song speed in Bengalese finches, but larger birds (which were generally from smaller clutches) produced song bouts with longer durations (Soma, Takahasi, Ikebuchi, et al., 2006). Despite evidence that clutch size can influence song features in other estrildid finch species, we did not find a significant effect of clutch size on gap durations in Java sparrows. Further research and experimental manipulation are likely needed to fully understand the effect of the developmental environment on song phenotype in this species.

Changes in song characteristics with age have been frequently reported across birds (Kipper & Kiefer, 2010). Delayed maturation of song characteristics may result in song characteristics being an honest signal of age (De Kort et al., 2009; Kochvar et al., 2022; Zipple et al., 2019). This can signal male quality, as older males have demonstrated an increased survival ability (Kokko, 1998). We did not find strong evidence that temporal features were affected by age at recording, although we found some effect of age on song features in certain scenarios. This is in contrast to previous findings in this and other species (Java sparrows, Ota & Soma, 2014; Bengalese finches, James & Sakata, 2014, 2015; Matheson & Sakata, 2015; zebra finches, Glaze & Troyer, 2013; James & Sakata, 2019).

Many previous studies (Glaze & Troyer, 2013; James & Sakata, 2014, 2015, 2019; Ota & Soma, 2014) assessed the effects of age on song using longitudinal data from the same individuals at different ages. In our study, each bird was recorded only once, so we cannot study changes over time within birds. Thus, variability in temporal features among birds might mask changes with age even if those changes did exist. In willow warblers, *Phylloscopus trochilus*, longitudinal and cross-sectional analysis of age-related changes in song gave different results, with changes in element rate not detected using cross-sectional analysis (Gil et al., 2001). We did find that song duration increased with age, as has previously been reported in Java sparrows (Ota & Soma, 2014), but this pattern was only significant when considering full songs, which is likely due to a corresponding increase in the number of introductory notes with age. There was also weak evidence that gap score, a performance-related measure examining gap duration across transitions compared to the rest of the population, decreased with age when considering the main body of the song (i.e. without introductory notes). As such, it remains unclear whether age-related differences in temporal song features are potential signals of male quality in this species.

Social inheritance has the potential to influence song evolution and divergence in this species, and possibly to impact conservation efforts. The effect sizes in our models indicate that, while learning of traits is very faithful, it is not completely accurate and error is likely to be introduced in each generation. The build-up of copying errors in different populations may result in divergence of temporal features among captive populations, and between wild and captive populations. If differences in temporal features are salient and influence mate choice, as is true in other species (Dunning et al., 2020; Nolan & Hill, 2004), these differences could influence the success of conservation programmes by influencing mating patterns (Lewis, Williams, et al., 2021). Little is known about the features that influence mate choice in Java sparrows, so it is not possible to predict the effects that sexual selection may have on temporal song features. Even if silent features are not under direct selection during mate choice, selection for other features, such as note duration, note repertoire or number of notes, may influence temporal song features through associated changes in internote intervals, as these traits are linked in this and other species (e.g. Bengalese finch, Soma, Takahasi, Hasegawa, et al., 2006).

Overall, our findings suggest that social learning is the main mode of inheritance for many temporal features in Java sparrow song. We found that gap durations were also mediated by other song features, particularly the duration of the notes preceding and following the gap. However, even when controlling for other influences, there was still evidence that the social father's song phenotype influenced temporal song features. In contrast to results from other species, we found no evidence to support an effect of genetic inheritance or the developmental environment, and little evidence to support the effect of age on most of the features examined. Based on findings in this and other species, it is likely that learning of temporal song features interacts with learning of song sequencing and spectral structure in the development of the adult song phenotype in Java sparrows.

Author Contributions

R.L. was responsible for the initial idea and R.L., A.K. and T.G. conceptualized the study. The original data set was collated by R.L. and M.S. R.L., M.S., S.d.K. and T.G. contributed to data extraction. R.L., A.K. and T.G. conducted data analysis. The initial draft was written by R.L., with all authors involved in reviewing and editing the manuscript. T.G. provided supervision throughout the project.

Data Availability

Data and code associated with this paper can be found at FigShare http://doi.org/10.48420/22550149. Data and code from the original Lewis, Soma, et al. (2021) paper can be found at FigShare: https://doi.org/10.48420/14555247.

Declaration of Interest

None.

Acknowledgments

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Appendix

Table A1
Results for mixed-effect models on whole songs, with no age correction for social father's phenotype

Response	Social Father's phenotype	log(Age)	Pedigree	Clutch	Either
Song duration	0.15 *P*=0.322	**0.77** ***P* =0.018**	*P* =0.135	*P* =0.423	*P* =0.111
Mean log song tempo	**0.66** ***P* <0.001**	−0.052 *P* =0.141	*P* =0.341	*P* =1	*P* =0.628
Mean log gap duration	**0.65** ***P* <0.001**	−0.010 *P* =0.863	*P* =0.408	*P* =1	*P* =0.710
Standard deviation of log gap length	**0.57** ***P* <0.001**	0.058 *P* =0.114	*P* =1	*P* =0.224	*P* =0.478
Gap score	0.067 *P* =0.643	−0.022 *P* =0.471	*P* =0.387	*P* =1	*P* =0.687
Gap variability score	**0.41** ***P* =0.004**	0.076 *P* =0.442	*P* =0.597	*P* =0.731	*P* =0.697
Log number of introductory notes	**0.13** *P* =0.423	0.42 ***P* =0.005**	*P* =0.334	*P* =0.404	*P* =0.254

Model coefficients and *P* values from the mixed-effect models are presented for the effect of social father's phenotype and log(Age). *P* values from likelihood ratio tests comparing the full model to a reduced model with random effects removed are reported for pedigree, clutch and the effect of either pedigree or clutch. Significant results are indicated in bold.

Table A2
Results for mixed-effect models on songs with introductory phrases removed, with no age correction for social father's phenotype

Response	Social Father's phenotype	log(Age)	Pedigree	Clutch	Either
Song duration	**0.22** ***P* =0.103**	0.29 *P* =0.192	*P* =0.152	*P* =0.275	*P* =0.066
Mean log song tempo	**0.65** ***P* <0.001**	−0.0069 *P* =0.80	*P* =0.226	*P* =1	*P* =0.481
Mean log gap length	**0.65** ***P* <0.001**	−0.044 *P* =0.395	*P* =0.526	*P* =1	*P* =0.818
Standard deviation of log gap length	**0.79** ***P* <0.001**	0.023 *P* =0.491	*P* =1	*P* =0.584	*P* =0.861
Gap score	0.003 *P* =0.986	**−0.053** *P* =**0.049**	*P* =0.396	*P* =1	*P* =0.697
Gap variability score	**0.33** ***P* =0.018**	0.0086 *P* =0.928	*P* =0.685	*P* =0.343	*P* =0.531

Model coefficients and *P* values from the mixed-effect models are presented for the effect of social father's phenotype and log(Age). *P* values from likelihood ratio tests comparing the full model to a reduced model with random effects removed are reported for pedigree, clutch and the effect of either pedigree or clutch. Significant results are indicated in bold.

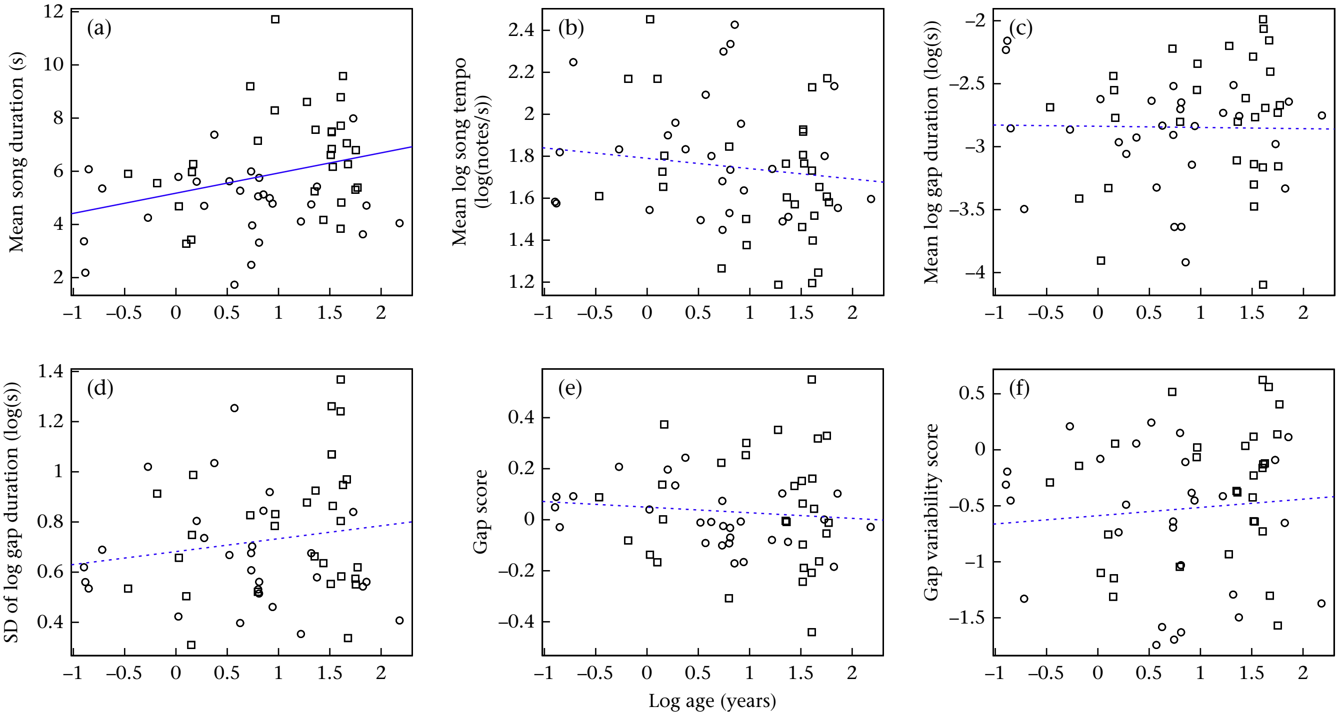

Figure A1. Relationship between birds' age at recording and the temporal features of their full songs (introductory notes included): (a) mean song duration, (b) mean log song tempo, (c) mean log gap duration, (d) standard deviation of log gap duration, (e) gap score and (f) gap variability score. Each point represents the mean value of an individual's features across their songs in the data set (N=58 sons). Regression lines are shown in blue. Dotted lines indicate that the result was not significant.

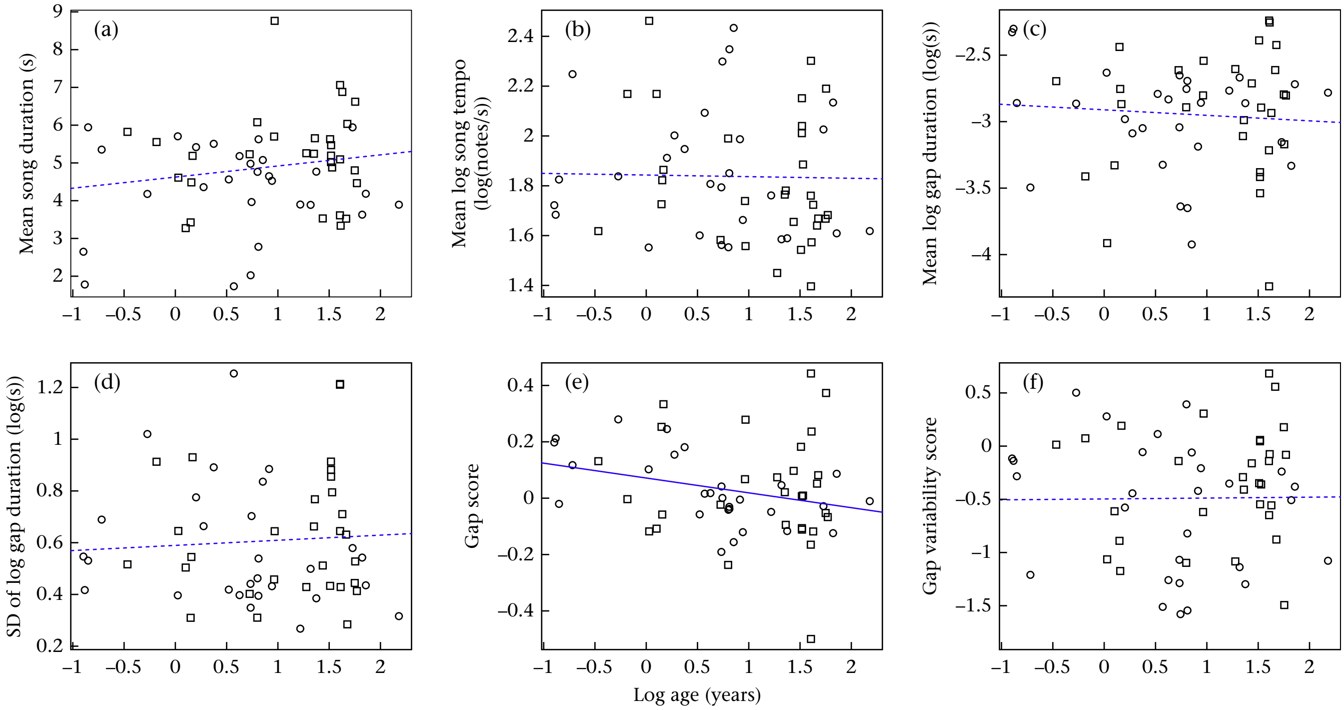

Figure A2. Relationship between birds' age at recording and the temporal features of songs with introductory notes removed: (a) mean song duration, (b) mean log song tempo, (c) mean log gap duration, (d) standard deviation of log gap duration, (e) gap score and (f) gap variability score. Each point represents the mean value of an individual's features across their songs in the data set (N=58 sons). Regression lines are shown in blue. Dotted lines indicate that the result was not significant.

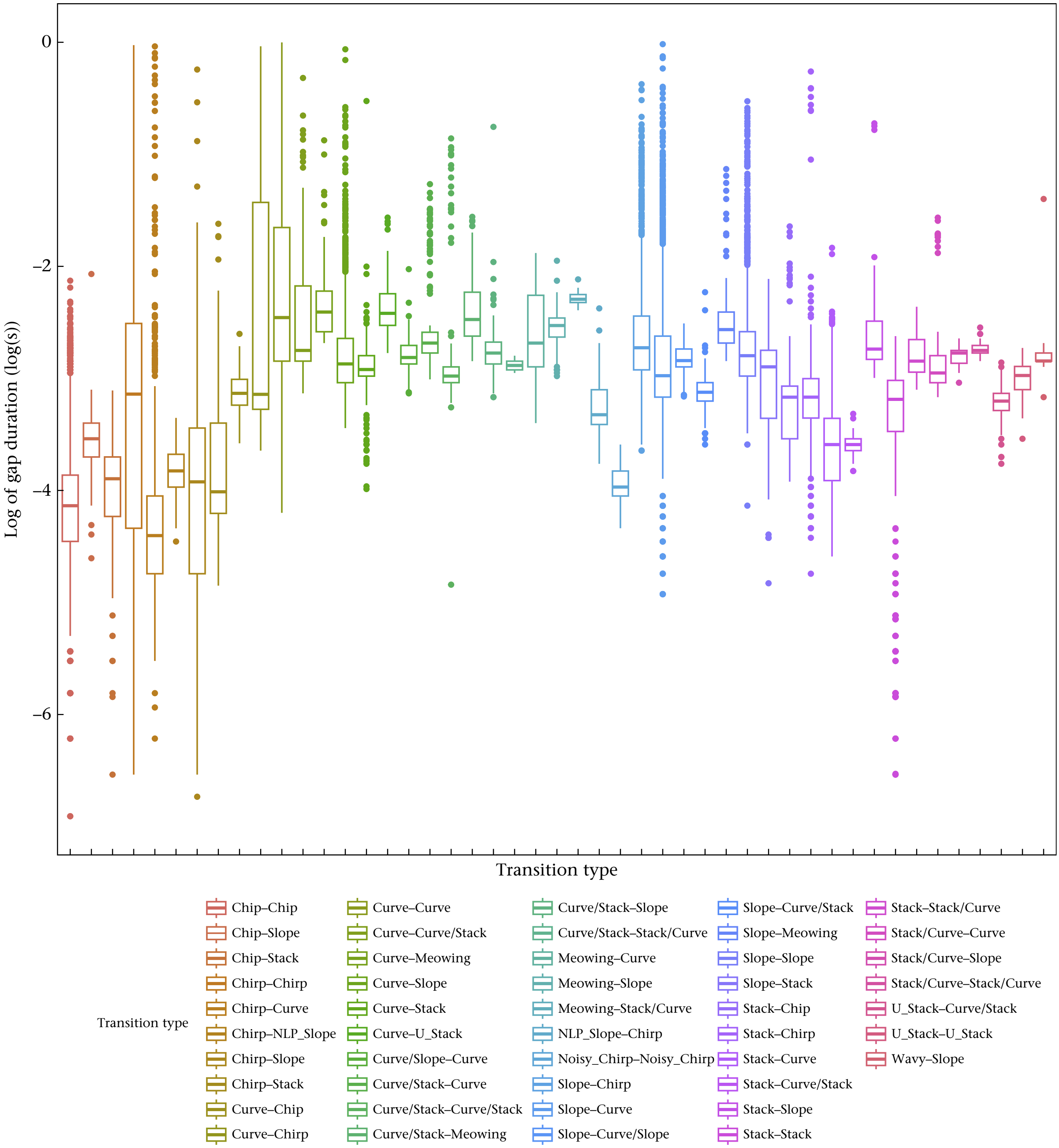

Figure A3. Lengths of transition types from full songs (introductory notes included) sung by Java sparrows in the study population. The internal line represents the median, with boxes indicating the interquartile range. Whiskers extend from the hinge to the largest (or smallest) value above (or below) the box that is within 1.5 times the interquartile range. Points falling outside this limit are shown as individual points. Transition types with more than 10 instances across the population are included. Note names associated with transition types reflect the categories described in Lewis, Soma, et al. (2021).