



Title	Age-dependent song changes in a closed-ended vocal learner: elevation of song performance after song crystallization
Author(s)	Ota, Nao; Soma, Masayo
Citation	Journal of avian biology, 45(6), 566-573 https://doi.org/10.1111/jav.00383
Issue Date	2014-11
Doc URL	http://hdl.handle.net/2115/60287
Rights	The definitive version is available at www.blackwell-synergy.com
Type	article (author version)
File Information	JAV_45_566-.pdf



[Instructions for use](#)

Age-dependent song changes in a closed-ended vocal learner: elevation of song performance after song crystallization

Nao Ota¹ and Masayo Soma^{2*}

1 Behavioral Neurobiology Group, Biosystems Science Course, The Graduate School of Life Science, Hokkaido University

2 Behavioral Neurobiology Group, Department of Biology, Faculty of Science, Hokkaido University

*Corresponding author

Hokkaido University, Kita 10 Nishi 8, Kita-ku, Sapporo, Hokkaido 060-0810, Japan

Tel: +81-11-706-2995

E-mail: nao_ota@mail.sci.hokudai.ac.jp (N. Ota),

masayo.soma@sci.hokudai.ac.jp (M. Soma).

Abstract

Birdsong is a sexual signal that serves as an indicator of male quality. There is already abundant evidence that song elaboration reflects early life-history because early developmental stress affects neural development of song control systems, and leaves irreversible adverse effects on song phenotypes. Especially in closed-ended vocal learners, song features crystallized early in life are less subject to changes in adulthood. This is why less attention has been paid to lifelong song changes in closed-ended learners. However, in the eyes of female birds that gain benefits from choosing mates based on male songs, not only past but also current conditions encoded in songs would be meaningful, given that even crystallized songs in closed-ended learners would not be identical in the long term. In this study, we examine within-individual song changes in the Java sparrow *Lonchura oryzivora*, with the aim of shedding light on the relationship between song and long-term life history. Specifically, we compared song length, tempo, and song complexity measures between the point just after song crystallization and around 1 year later, and also compared those traits between fathers and sons to clarify the effect of vocal learning. While it is not surprising that song complexity did not differ depending on age or between fathers and sons, we found that song length and tempo increased with age. Follow-up analyses have revealed that frequency bandwidth and peak frequency of song notes also elevated with age. Our results show that song performance related to motor skills can be improved even after song crystallization. We also suggest that song performance in closed-ended vocal learners gives a reliable clue for mate choice by reflecting male quality with aging.

Introduction

Birdsong is a sexually selected acoustic ornament that consists of multiple factors. In a wide range of passerines, females are reported to prefer males that sing complex and high performance songs (reviewed in Catchpole and Slater 2008, Andersson 1994). To date, studies on birdsong sexual selection have tried to understand indicator mechanisms of such song traits by shedding light on how songs honestly reflect the quality of males (Gil and Gahr 2002). Such approaches were successful in showing that early developmental condition is one of the key factors responsible for song quality, especially learning-based acoustic features such as repertoire size, which accords with the prediction from the developmental stress hypothesis (Nowicki et al. 1998, reviewed in MacDougall-Shackleton and Spencer 2012). It has been reported that developmental stress, such as physical development, hormone level and early rearing condition, affects various song traits in a wide range of oscine species (Bengalese finch *Lonchura striata* var. *domestica*: Soma et al. 2006b, zebra finch *Taeniopygia guttata*: Spencer et al. 2003, swamp sparrow *Melospiza Georgiana*: Nowicki et al. 2002, song sparrow *Melospiza melodia*: Schmidt et al. 2013, European starling *Sturnus vulgaris*: Buchanan et al. 2003). All of these studies demonstrate that early developmental conditions affect song traits soon after their song-learning phase, but we know little about song changes long after song crystallization.

Birdsong reflects life history, and age is a crucial limiting or mediating factor for it. Learning-based song features of closed-ended learners hardly change after sexual maturation, by which time they crystallize their songs, while open-ended learner species can change song / note repertoire size and structures plastically every year (Brenowitz and Beecher 2005). A notable example of age-related song changes is increase in repertoire size (e.g. Sedge warbler *Acrocephalus schoenobenus*: Nicholson et al. 2007, Common nightingale *Luscinia megarhynchos*: Kiefer et al. 2009, European starling *Sturnus vulgaris*: Mountjoy and Lemon 1995) and elevation of performance (nightingale *Luscinia megarhynchos*: Sprau et al. 2013).

The improvement of song quality with age can be explained by two

scenarios (Kipper and Kiefer 2010). First, song quality reflects viability because individuals with low song quality have low survival rate (Jennions et al. 2001). Second, they improve with age at the within-individual level. It is impossible to disentangle these two scenarios only in cross-sectional comparisons, therefore a longitudinal approach is needed. Such investigations are usually conducted using open-ended learner species as described above.

However, less attention has been paid to, and little is known about, the factors responsible for plasticity in the closed-ended learner song after song crystallization. What we currently know is that songs in closed-ended learners retain some variability after song crystallization. In other words, closed-ended learner males have a long-term stable song motif that is performed with some flexibility. It has been reported that real-time auditory feedback is necessary to maintain the normal syntactical structure of their crystallized songs in some Estrildid finches (zebra finch: Lombardino and Nottebohm 2000; Bengalese finch: Okanoya and Yamaguchi 1997, Woolley and Rubel 1997, Tumer and Brainard 2007, Kagawa et al. 2012; white-rumped munia *Lonchura striata*: Kagawa et al. 2012). Therefore, song variability is actively driven by neural circuits in the avian forebrain that control song behavior (Hampton et al. 2009).

Song quality can basically be determined by two measures: the degree of elaboration and the intensity of performance (Nowicki and Searcy 2005, Soma et al. 2006a). The former is linked to song acoustical complexity, such as song repertoire size, note repertoire size and ordering complexity of notes, which is acquired through vocal learning, and hence remains unchanged after the song-learning period. The latter is associated with the amount of song production, such as song length, tempo, song amplitude and song consistency. So far it has been shown in closed-ended learners that performance-related traits (e.g. song length) can be affected by body size (Soma et al. 2006b) and early stress (Holveck et al. 2008, Tchernichovski and Nottebohm 1998), but few studies have focused on the effect of age on these traits, and we still do not have an understanding of age-related changes in bird song. There have been some reports of acceleration of tempo with age in

closed-ended learners (zebra finch: Brainard and Doupe 2001, banded wren *Thryophilus pleurostictus*: Vehrencamp et al. 2013).

Female preference for older males is a common phenomenon among animals (reviewed in Brooks and Kemp 2001). In socially monogamous birds, females often choose older males as extra-pair mates (reviewed in Griffith et al. 2002). Such a preference can lead to direct and indirect benefits for females (reviewed in Martin 1995). Older males have proved their viability through their longevity and have more experience in foraging or in breeding behavior. It is therefore likely that male signals that vary with age enable rapid assessment by female receivers in mate choice. We therefore assume that in closed-ended vocal learners, song can work as an age indicator mechanism.

The aims of this paper are grouped into one major and two minor themes. The main goal is to shed light on age-related song changes after song crystallization in the closed-ended learner. We also seek to understand how developmental stress can affect various song traits, and to test if a father's song quality has an influence on songs, considering that its acoustic features are socially transmitted in the process of song learning early in life (Soma 2011). To address these questions, we adopted three approaches in our study of Java sparrow *Lonchura oryzivora* songs. First, we compared songs between fathers and sons. Second, we tested within-individual song changes depending on age. Third and additionally, we considered other factors expected to affect song traits, such as early rearing conditions and body size.

Materials and Methods

Study species

The Java sparrow belongs to the family Estrildidae, which includes well-studied songbirds such as the zebra and Bengalese finch. Java sparrows are native to Java and Bali in Indonesia. Each male Java sparrow sings one stereotyped song for courtship, which is composed of 2–8 different note types and characterized by note ordering patterns (Hasegawa et al. 2011, Kagawa and Soma 2013). Because song learning in the Java sparrow needs social interactions, juvenile males in cage-bred conditions usually learn songs from

their fathers (Soma 2011). According to our observation, the song-learning period of the subject species is estimated to end at around 150–180 days old (see also Supplementary material Appendix 1, Fig. A1) as note repertoire size, note structure and song complexity do not change from that age onwards.

Subjects

Java sparrows maintained and bred in our laboratory (Hokkaido Univ.) were used as subjects. When breeding, each pair was introduced into an individual breeding cage equipped with one nest box. Each cage was visually, but not audibly, isolated, which is sufficient to confine their song learning only from their father (Soma 2011). Java sparrows were allowed to start laying a second brood soon after the first brood fledged. This study is therefore based on a total of 18 broods from 14 breeding pairs taken from April 2011 to February 2013. In some cases of breeding, eggs were cross-fostered. Sexing of juvenile birds was based on singing behaviors or otherwise done with molecular markers (Griffiths et al. 1998). A total of 34 males were used as subjects, which includes 29 sons (including five foster sons) and 14 fathers, as nine individuals served as both fathers and sons.

Throughout the study, the birds were maintained in a controlled environment suitable for breeding (temperature of $25 \pm 3^\circ\text{C}$, humidity of 30–60%, 12L: 12D photoperiod) and provided with finch seed mixture, foxtail millet coated with egg yolk, rice, water, shell grit, and green vegetables ad libitum. All subject birds were marked with colored leg rings and aluminum bands for individual identification.

Song recordings

When sons ($n = 29$) were fully mature and had crystallized their songs (age \pm SD = 202 ± 35.1 days), their undirected songs were recorded. Seventeen sons were recorded again to examine age-related change (age \pm SD = 416 ± 55.1 days); the other males were omitted because they were used in other experiments. Songs of their fathers ($n = 14$) were also recorded before or during breeding (age \pm SD = 590 ± 94.8 days). When recording, each

bird was individually introduced into a soundproof room, and its vocal output was recorded using a digital audio recorder (Marantz PMD 661) with a sampling rate of 44.1 kHz with 16-bit resolution. We sampled an average of 28.2 songs (total 1466, range 12–30) from each male subject, which took 1–3 days. Because we did not control the time spent recording each subject, the total number of songs we obtained was arbitrary and had no relationship with other variables.

Song analysis

Recorded songs were digitized and sonogrammed at 44.1 kHz and 16-bit resolution using avisoft Saslab pro ver 5.1.21 (Avisoft Bioacoustics, Berlin, Germany). We measured (a) song performance from each song, (b) song complexity from each individual, and (c) song note feature from each note.

(a) Song performance

Based on the computed sonogram of each song, the following three measurements were taken: song duration, total number of notes included in one song, and tempo taken as number of notes per second. We defined one song as a sequence of notes with less than 0.3-second intervals (Fig. 1), because introductory notes were likely to be emitted sparsely with unstable long note-to-note intervals and were excluded in past song investigations of the Bengalese finch (Woolley and Rubel 1997). In this measurement, each male contributes a plural data point, which is equal to the number of sampled songs.

(b) Song complexity

We measured note repertoire size and note order complexity of each individual. In this measurement, each male contributes one data point. Note repertoire size was calculated as the number of different note types subjects used in their songs. Note order complexity was measured as the entropy of a first-order Markov model, which estimates the syntactical complexity of note orders. This model was originally developed in information theory, but is

gaining popularity in studies of songs sung by Bengalese finch (Nakamura and Okanoya 2004, Soma et al. 2006a) and other songbirds (American redstart *Setophaga ruticilla*: Lemon et al. 1993, European starling *Sturnus vulgaris*: Gentner and Hulse 2000). The index will be larger if the note-to-note transition is more versatile (i.e. complex).

(c) Song note features

To conduct additional analyses (see also statistical analysis and result of age-related song changes), we also measured four song note features: note duration, frequency bandwidth, peak frequency (loudest frequency throughout a note), and note-to-note intervals. We sampled a total of 300 notes from each son ($n = 10$) between the first and second year. To do this, only the recordings taken under identical setups were used. Songs were band pass-filtered from 1 to 20 kHz, and the dynamic range was normalized. We measured song note features at 24–48 dB relative to the peak amplitude frequency of each note, which was fixed within but not among individuals as it was difficult to set a common threshold to individually distinctive songs with variable amplitude modulations.

Morphological Measurements

In February 2013 (after all birds were recorded at least once), we caught 29 sons and measured the following five morphological characters using digital calipers: natural wing length, tarsus length, bill length, width, and height. Tail length was not included in the data because some sons had tail feathers that were worn down. We conducted a principal component analysis of the five body measurements and used the first principal component (PC1) score as an index of body size (Table 1). The data set was suited for such a data reduction (Kaiser–Meyer–Olkin measure of sampling adequacy: 0.640; Bartlett’s test of sphericity: $\chi^2 = 28.166$, $df = 10$, $p = 0.002$).

Statistical analyses

We used linear mixed effect (LME) models to analyze duration, tempo and entropy, and generalized linear mixed effect models (GLMM) with

a Poisson distribution to analyze total number of notes and note repertoire size. In all analyses, we considered song lineage/family ID/bird ID as random effects to control for non-independence of the data. All results are based on the full model.

To investigate differences in songs of sons and fathers, we entered the subject's attributes (i.e. father or son) as a fixed effect. We used song data from 29 sons soon after song crystallization and song data from 14 fathers at around the same time when sons were recorded.

To assess the effect of age on five song variables, we entered age on the day when subjects were recorded as a fixed effect using song data of 17 sons who were recorded twice at different ages. At that time, we also added further acoustical analyses using song note feature data described in song analysis (c) to examine how each individual changed vocal acoustics associated with age-related increases in song length and tempo using 6000 note data from 10 sons. We tested the effect of recording age on four song note variables: note duration, frequency bandwidth, peak frequency, and note-to-note intervals using LME.

To explore other possible factors that could affect 29 sons' individual variations in song variables soon after song crystallization, we considered the following six factors; brood order (first or second), brood size, brood sex ratio (the proportion of males in brood) and the interaction of brood size \times sex ratio, and body size (PC1) in addition to recording age as fixed effects.

Because we confirmed that song variables used in this study were not dependent on each other (Kagawa and Soma unpublished data), we did not adopt corrections for multiple testing. All statistical analyses were performed using R 2.13.2 (R Development Core Team 2011).

Results

Song comparison between fathers and sons

Most sons ($n = 24 / 29$), including three foster sons learned their fathers' full note repertoires; however, three sons including two foster sons had smaller note repertoire sizes and two sons had larger note repertoire sizes than their fathers. There was no statistically significant difference in

note repertoire size, entropy, and tempo between fathers and sons (Table 2). However, the song length of sons was significantly shorter than that of fathers (sons' total number of notes: average \pm SE = 22 ± 0.392 , sons' song duration: average \pm SE = 3.609 ± 0.042 sec; fathers' total number of notes: average \pm SE = 29 ± 0.672 , fathers' song duration: average \pm SE = 4.505 ± 0.082 sec; Table 2; Figs. 2a, 2b).

Age-related song changes

We found statistically significant within-individual changes in song length and tempo but not in note repertoire size and entropy (Table 2). The song length and tempo of sons after one year was significantly higher than those of sons just after song crystallization (just after song crystallization: total number of notes: average \pm SE = 20.1 ± 0.44 , song duration: average \pm SE = 3.147 ± 0.064 sec, tempo: average \pm SE = 6.557 ± 0.095 ; after one year: total number of notes: average \pm SE = 25.395 ± 0.543 , song duration: average \pm SE = 3.652 ± 0.064 sec, tempo: average \pm SE = 6.941 ± 0.096). These are partially in accordance with the aforementioned result from father-son comparisons, in that note repertoire size and entropy were confined by song learning and did not change with age, and song length was more plastic and increased with age (Figs. 3a, 3b). As shown in Figure 3c, though tempo was stable within individuals, it showed slight but statistically significant elevation with age (Table 2).

Additional LME analysis on song note features revealed statistically significant increases in frequency bandwidth and peak frequency with age, but not note duration. We also found that note-to-note intervals got shorter with age (Table 3).

Effects of early rearing conditions and body size

Total number of notes was significantly positively associated with body size ($p = 0.027$, Supplementary material Appendix 2, Fig. A2, Table A1), but the effect disappeared when we removed two outliers ($p = 0.149$, Supplementary material Appendix 2, Fig. A2). Song duration, tempo, note repertoire size and entropy were not associated with any factors ($p > 0.081$).

Discussion

In accordance with our prediction, performance-related song traits (i.e. song length and tempo) elevated with age within individuals, while learning-based song traits (i.e. note repertoire size and entropy) did not change. Overall, Java sparrow males produced higher-performance songs in the second year compared with when they had just crystallized songs. Song complexity (i.e. note repertoire size and entropy) did not differ between father and son, and we could not find any effects of early rearing condition and body size on song complexity. These results indicate that sons developed acoustically similar songs, probably due to social song learning. We also confirmed that there was no change in note repertoire size and entropy with age, as expected. Our results thus support the second scenario of age-related differences described in introduction (i.e. song traits improve with age at the within-individual level) even in the closed-ended learner.

Surprisingly, even in a well-studied closed-ended learner such as the zebra finch, few studies have investigated long-term song changes within individuals (c.f. Pytte et al. 2007, de Kort et al. 2009). Meanwhile, birdsong research has mainly focused on testing how developmental stress affects learning-based song traits (Nowicki et al. 1998, Nowicki and Searcy 2004, 2005), and plasticity of performance-related song traits has been overlooked. Our results suggest that performance-related song traits can serve as an honest signal of male age and condition, providing reliable clues for female mate choice.

Body size effect on song length and tempo has been reported in previous studies in related species (Spencer et al. 2003, Soma et al. 2006b, Holveck and Riebel 2007), but the effect of age is a novel finding. It is possible that age-related body size change is the underlying cause, and it would be of value for future studies to test if aging under better nutritional conditions leads to a higher rate of increment in song length compared with aging under mal-nutritional conditions. Although we do not have a full understanding of female preference in estrildid finches (but see Okanoya 2004, Riebel 2009), in the zebra finch, females are reported to prefer longer

song duration, which is both within the normal range (Vyas et al. 2009) and beyond the male zebra finch's capacity (Neubauer 1999), and in the Bengalese finch, preference for longer songs has also been reported (Soma and Okanoya 2013). Presumably this preference is because longer songs guarantee better mates in terms of physical condition and age. There is a possibility that longer songs contain on average more different elements and this, rather than song length, seems to be the cause of the preference for long songs (Vyas et al. 2009). However, based on our results that song length became longer with age while song complexity did not, we assume that song length but not complexity is likely to affect female preference.

Tempo accelerated with age, even though tempo was influenced by song learning to some degree and was quite constant within individuals at a time. Acceleration of tempo with age has been reported in other closed-ended learners (zebra finch: Brainard and Doupe 2001, banded wren: Vehrencamp et al. 2013), but this is the first report of detailed acoustical changes (but see Ballentine 2009). Our follow-up analyses have revealed that birds could sing with shorter note-to-note intervals in the second year compared with the first year, while note duration did not change. Therefore, the increase in tempo was caused by the decrease in note-to-note intervals.

Frequency bandwidth and peak frequency of song notes also elevated with age. As shown in the famous examples of 'sexy' syllables in the canary (Vallet and Kreutzer 1995, Drăgănoiu et al. 2002), faster repetition of syllables that cover a wider frequency range is more demanding to produce and thus more attractive for females (Ballentine et al. 2004, Caro et al. 2010, Podos 1996). The age-related rises in acoustic features observed in the Java sparrow suggest that males in the second year were able to sing higher-performance songs, which can be achieved only by precise coordination of vocal tract movements and air flow (Podos 1996, Hoese et al. 2000, Suthers and Margoliash 2002).

Because frequency bandwidth is dependent on sound pressure (Zollinger et al. 2012), we cannot deny the possibility that older males had louder vocalizations, which contributed to the wider frequency bandwidth. However, elevation of tempo and peak frequency is independent of changes

in vocal amplitude. Although more detailed investigations are needed, our results imply that performance of trilled parts, which are effected by body size (Kagawa and Soma 2013), improve with age. Regarding the factors associated with age-related elevation of peak frequency, we do not have clear answers, but it is possible that modulation of frequency occurred under a noisy environment (Schuster et al. 2012). During trials, we housed subjects in a room where they were able to hear many other individuals' vocalizations, so elevation of peak frequency might have occurred as a result of this noise. Nevertheless, it can be said that male Java sparrows can elevate or modulate their song performance within individuals over time.

In general, it is assumed that closed-ended learners' song traits become more stereotyped with age (Pytte et al. 2007, de Kort et al. 2009) and the function of undirected song is to maintain song structure by auditory feedbacks. However, our results imply that undirected songs play a role in improving, rather than maintaining, song performance. As in many species, females choose mates based upon their evaluations of male motor performance (reviewed in Byers et al. 2010). Therefore, improving their motor skills by singing and practicing undirected song would contribute to their reproductive success.

Does song performance decrease again in old age after reaching a plateau? In the Bengalese finch, a decrease in song tempo and frequency with senescence was observed (Cooper et al. 2012) although the sample size was very small (four individuals only). Senescence is another important perspective that we should consider when trying to understand the associations between aging and sexual signals (Torres and Velando 2007). To resolve this, investigation of the relationships between intra-individual variability and observation of long-term changes in closed-ended learner songs is needed, and will allow us to better understand the function of birdsong.

Acknowledgements

We thank Chihiro Mori, Raimu Imai and Shin Hayase for advice and technical assistance on the molecular sexing of chicks, and Kazutoshi

Sasahara, Hiroko Kagawa and Eri Ohgushi for advice on song analysis. This study was supported by JSPS Grants-in-Aid for Young Scientists (22800002, 23680027) to M.S.

References

- Andersson, M. 1994. Sexual selection. – Princeton Univ. Press, Princeton.
- Ballentine, B. 2009. The ability to perform physically challenging songs predicts age and size in male swamp sparrows, *Melospiza georgiana*. – Anim. Behav. 77: 973–978.
- Ballentine, B., Hyman, J. and Nowicki, S. 2004. Vocal performance influences female response to male bird song: an experimental test. – Behav. Ecol. 15: 163–168.
- Brainard, M. S. and Doupe, A. J. 2001. Postlearning consolidation of birdsong: stabilizing effects of age and anterior forebrain lesions. – J. Neurosci. 21: 2501–2517.
- Brenowitz, E. A. and Beecher, M. D. 2005. Song learning in birds: diversity and plasticity, opportunities and challenges. – Trends Neurosci. 28: 127–132.
- Brooks, R. and Kemp, D.J. 2001. Can older males deliver the good genes? – Trends Ecol. Evol. 16: 308–313.
- Buchanan, K. L., Spencer, K. A., Goldsmith, A. R. and Catchpole, C. K. 2003. Song as an honest signal of past developmental stress in the European starling (*Sturnus vulgaris*). – Proc. R. Soc. B-Biol. Sci. 270: 1149–1156.
- Byers, J., Hebets, E. and Podos, J. 2010. Female choice based upon male motor performance. – Anim. Behav. 79: 771–778.
- Caro, S. P., Sewall, K. B., Salvante, K. G. and Sockman, K. W. 2010. Female Lincoln's sparrows modulate their behavior in response to variation in male song quality. – Behav. Ecol. 21: 562–569.
- Catchpole, C. K. and Slater, P. J. B. 2008. Bird song: biological themes and variations. – Cambridge Univ. Press.
- Cooper, B. G., Mendez, J. M., Saar, S., Whetstone, A. G., Meyers, R. and Goller, F. 2012. Age-related changes in the Bengalese finch song motor

- program. – *Neurobiol. Aging* 33: 564–568.
- de Kort, S. R., Eldermire, E. R., Valderrama, S., Botero, C. A., and Vehrencamp, S. L. 2009. Trill consistency is an age-related assessment signal in banded wrens. – *Proc. R. Soc. B-Biol. Sci.* 276: 2315–2321.
- Drăgănoiu, T. I., Nagle, L. and Kreutzer, M. 2002. Directional female preference for an exaggerated male trait in canary (*Serinus canaria*) song. – *Proc. R. Soc. B-Biol. Sci.* 269: 2525–2531.
- Gentner, T. Q. and Hulse, S. H. 2000. Female European Starling preference and choice for variation in conspecific male song. – *Anim. Behav.* 59: 443–458.
- Gil, D. and Gahr, M. 2002. The honesty of bird song: multiple constraints for multiple traits. – *Trends Ecol. Evol.* 17: 133–141.
- Griffith, S. C., Owens, I. P. F. and Thuman, K. A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. – *Mol. Ecol.* 11: 2195–2212.
- Griffiths, R., Double, M. C., Orr, K. and Dawson, J. G. 1998. A DNA test to sex most birds. – *Mol. Ecol.* 7: 1071–1075.
- Hampton, C. M., Sakata, J. T. and Brainard, M. S. 2009. An avian basal ganglia–forebrain circuit contributes differentially to syllable versus sequence variability of adult Bengalese finch song. – *J. Neurophysiol.* 101: 3235–3245.
- Hasegawa, A., Soma, M. and Hasegawa, T. 2011. Male traits and female choice in Java Sparrows: preference for large body size. – *Ornithol. Sci.* 10: 73–80.
- Hoese, W. J., Podos, J., Boetticher, N. C. and Nowicki, S. 2000. Vocal tract function in birdsong production: experimental manipulation of beak movements. – *J. Exp. Biol.* 203: 1845–1855.
- Holveck, M. J., de Castro, A. C. V., Lachlan, R. F., ten Cate, C. and Riebel, K. 2008. Accuracy of song syntax learning and singing consistency signal early condition in zebra finches. – *Behav. Ecol.* 19: 1267–1281.
- Holveck, M. J., and Riebel, K. 2007. Preferred songs predict preferred males: consistency and repeatability of zebra finch females across three test

- contexts. – *Anim. Behav.* 74: 297–309.
- Jennions, M. D., Møller, A. P. and Petrie, M. 2001. Sexually selected traits and adult survival: a meta-analysis. – *Q. Rev. Biol.* 76: 3–36.
- Kagawa, H. and Soma, M. 2013. Song performance and elaboration as potential indicators of male quality in Java sparrows. – *Behav. Process.* 99: 138–144.
- Kagawa, H., Takahashi, R., Ikebuchi, M., and Okanoya, K. 2012. Song Complexity and Auditory Feedback in Birds: A Comparison between Two Strains of Bengalese Finches with Different Degrees of Song Complexity. – *Zool. Sci.* 29: 645–651.
- Kiefer, S., Sommer, C., Scharff, C., Kipper, S. and Mundry, R. 2009. Tuning towards tomorrow? Common nightingales *Luscinia megarhynchos* change and increase their song repertoires from the first to the second breeding season. – *J. Avian Biol.* 40: 231–236.
- Kipper, S. and Kiefer, S. 2010. Age-related changes in birds' singing styles: on fresh tunes and fading voices? – *Adv. Study. Behav.* 41: 77–118.
- Lemon, R. E., Dobson, C. W. and Clifton, P. G. 1993. Songs of American Redstarts *Setophaga ruticilla*: sequencing rules and their relationships to repertoire size. – *Ethology* 93: 198–210.
- Lombardino, A. J. and Nottebohm, F. 2000. Age at deafening affects the stability of learned song in adult male zebra finches. – *J. Neurosci.* 20: 5054–5064.
- MacDougall-Shackleton, S. A. and Spencer, K. A. 2012. Developmental stress and birdsong: current evidence and future directions. – *J. Ornithol.* 53: 105–117.
- Martin, K. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. – *Am. Zool.* 35: 340–348.
- Mountjoy, J. D. and Lemon, R. E. 1995. Extended song learning in wild European starlings. – *Anim. Behav.* 49: 357–366.
- Nakamura, K. Z. and Okanoya, K. 2004. Neural correlates of song complexity in Bengalese Finch high vocal center. – *Neuroreport* 15: 1359–1363.
- Neubauer, R. L. 1999. Super-normal song length preferences of female zebra

- finches (*Taeniopygia guttata*) and a theory of the evolution of bird song. – *Evol. Ecol.* 13: 365–380.
- Nicholson, J. S., Buchanan, K. L., Marshall, R. C. and Catchpole, C. K. 2007. Song sharing and repertoire size in the sedge warbler, *Acrocephalus schoenobaenus*: changes within and between years. – *Anim. Behav.* 74: 1585–1592.
- Nowicki, S. and Searcy, W. A. 2005. Song and mate choice in birds: how the development of behavior helps us understand function. – *Auk* 122: 1–14.
- Nowicki, S., Peters, S. and Podos, J. 1998. Song learning, early nutrition and sexual selection in songbirds. – *Am. Zool.* 38: 179–190.
- Nowicki, S., Searcy, W. A. and Peters, S. 2002. Brain development, song learning and mate choice in birds: a review and experimental test of the “nutritional stress hypothesis”. – *J. Comp. Physiol. A* 188: 1003–1014.
- Nowicki, S. and Searcy, W. A. 2004. Song function and the evolution of female preferences—why birds sing, why brains matter. – *Ann. NY Acad. Sci.* 1016: 704–723.
- Okanoya, K. 2004. The Bengalese finch: a window on the behavioral neurobiology of birdsong syntax. – *Ann. N.Y. Acad. Sci.* 1016: 724–735.
- Okanoya, K. and Yamaguchi, A. 1997. Adult Bengalese finches (*Lonchura striata* var. *domestica*) require real-time auditory feedback to produce normal song syntax. – *J Neurobiol.* 4: 343–356.
- Podos, J. 1996. Motor constraints on vocal development in a songbird. – *Anim. Behav.* 51: 1061–1070.
- Pytte, C. L., Gerson, M., Miller, J. and Kirn, J. R. 2007. Increasing stereotypy in adult zebra finch song correlates with a declining rate of adult neurogenesis. – *Dev. Neurobiol.* 67: 1699–1720.
- R Development Core Team 2011. R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>.
- Riebel, K. 2009. Song and female mate choice in zebra finches: a review. – *Advan. Study Behav.* 40: 197–238.

- Schmidt, K. L., Moore, S. D., MacDougall-Shackleton, E. A. and MacDougall-Shackleton, S. A. 2013. Early-life stress affects song complexity, song learning and volume of the brain nucleus RA in adult male song sparrows. – *Anim. Behav.* 86: 25–35.
- Schuster, S., Zollinger, S. A., Lesku, J. A., and Brumm, H. 2012. On the evolution of noise-dependent vocal plasticity in birds. – *Biol. Lett.* 8: 913–916.
- Soma, M. F. 2011. Social factors in song learning: A review of Estrildid finch research. – *Ornithol. Sci.* 10: 89–100.
- Soma, M. and Okanoya, K. 2013. Differential allocation in relation to mate song quality in the Bengalese finch. – *Behaviour* 150: 1491–1508.
- Soma, M., Takahasi, M., Hasegawa, T. and Okanoya, K. 2006a. Trade-offs and correlations among multiple song features in the Bengalese Finch. – *Ornithol. Sci.* 5: 77–84.
- Soma, M., Takahasi, M., Ikebuchi, M., Yamada, H., Suzuki, M., Hasegawa, T. and Okanoya, K. 2006b. Early rearing conditions affect the development of body size and song in Bengalese finches. – *Ethology* 112: 1071–1078.
- Spencer, K. A., Buchanan, K. L., Goldsmith, A. R. and Catchpole, C. K. 2003. Song as an honest signal of developmental stress in the zebra finch (*Taeniopygia guttata*). – *Horm. Behav.* 44: 132–139.
- Sprau, P., Roth, T., Amrhein, V., and Naguib, M. 2013. The predictive value of trill performance in a large repertoire songbird, the nightingale *Luscinia megarhynchos*. – *J. Avian Biol.* 44: 567–574.
- Suthers, R. A. and Margoliash, D. 2002. Motor control of birdsong. – *Curr. Opin. Neurobiol.* 12: 684–690.
- Tchernichovski, O. and Nottebohm, F. 1998. Social inhibition of song imitation among sibling male zebra finches. – *Proc. Natl. Acad. Sci. U.S.A.* 95: 8951–8956.
- Torres, R. and Velando, A. 2007. Male reproductive senescence: the price of immune induced oxidative damage on sexual attractiveness in the blue-footed booby. – *J. Anim. Ecol.* 76: 1161–1168.
- Tumer, E. C. and Brainard, M. S. 2007. Performance variability enables

- adaptive plasticity of 'crystallized' adult birdsong. – *Nature* 450: 1240–1244.
- Vallet, E. and Kreutzer, M. 1995. Female canaries are sexually responsive to special song phrases. – *Anim. Behav.* 49: 1603–1610.
- Vehrencamp, S. L., Yantachka, J., Hall, M. L. and de Kort, S. R. 2013. Trill performance components vary with age, season, and motivation in the banded wren. – *Behav. Ecol. Sociobiol.* 67: 409–419.
- Vyas, A., Harding, C., Borg, L., and Bogdan, D. 2009. Acoustic characteristics, early experience, and endocrine status interact to modulate female zebra finches' behavioral responses to songs. – *Horm. Behav.* 55: 50–59.
- Woolley, S. M. N. and Rubel, E. 1997. Bengalese finches *Lonchura striata domestica* depend upon auditory feedback for maintenance of adult song. – *J. Neurosci.* 17: 6380–6390.
- Zollinger, S. A., Podos, J., Nemeth, E., Goller, F. and Brumm, H. 2012. On the relationship between, and measurement of, amplitude and frequency in birdsong. – *Anim. Behav.* 84: e1–e9.

Figures

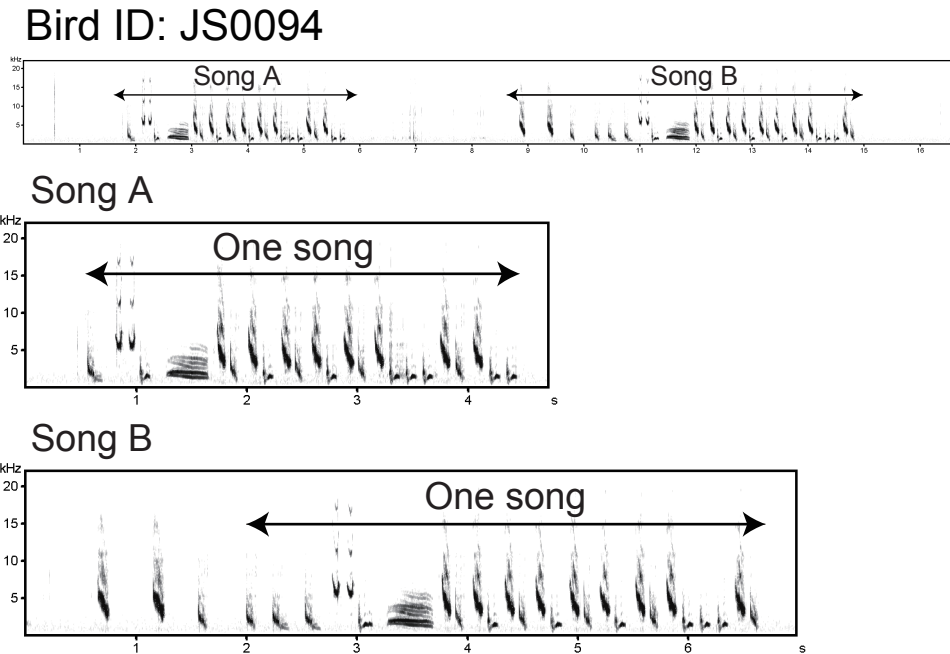


Figure 1. Examples of unstable note interval at the beginning of one individual's songs. To obtain reliable measures of tempo, we defined one song as a sequence of notes in which intervals were less than 0.3 seconds.

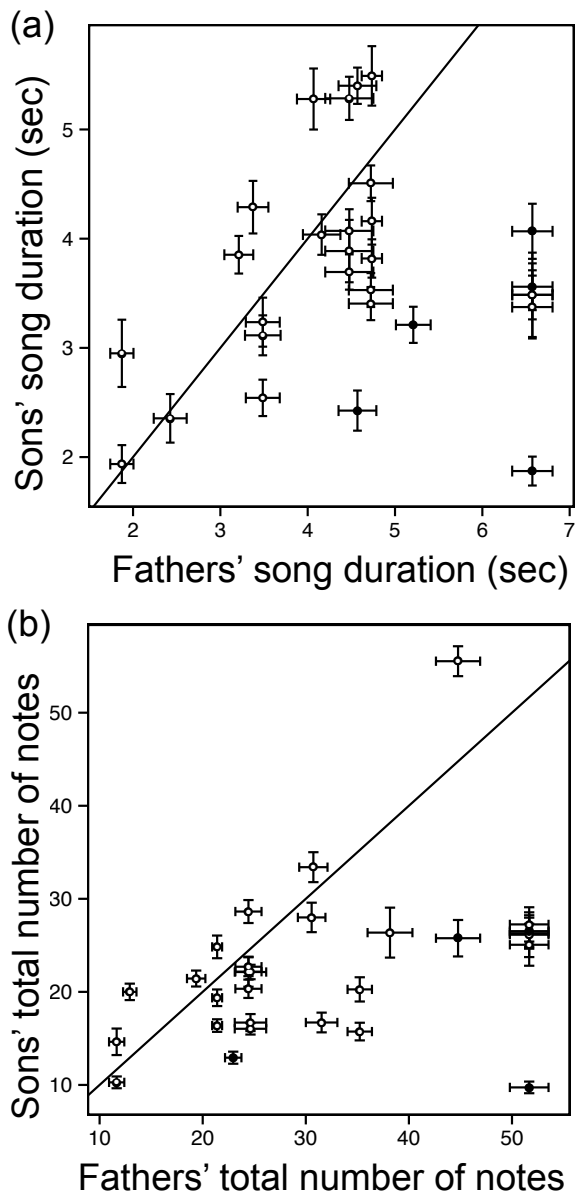


Figure 2. Comparison of (a) average (\pm SE) song duration and (b) average (\pm SE) total number of notes between fathers and sons. Many of the plots are near or below the solid line ($y = x$), indicating that sons tended to sing shorter songs than fathers (open circles: genetic son, $n = 24$, filled circles: foster son, $n = 5$).

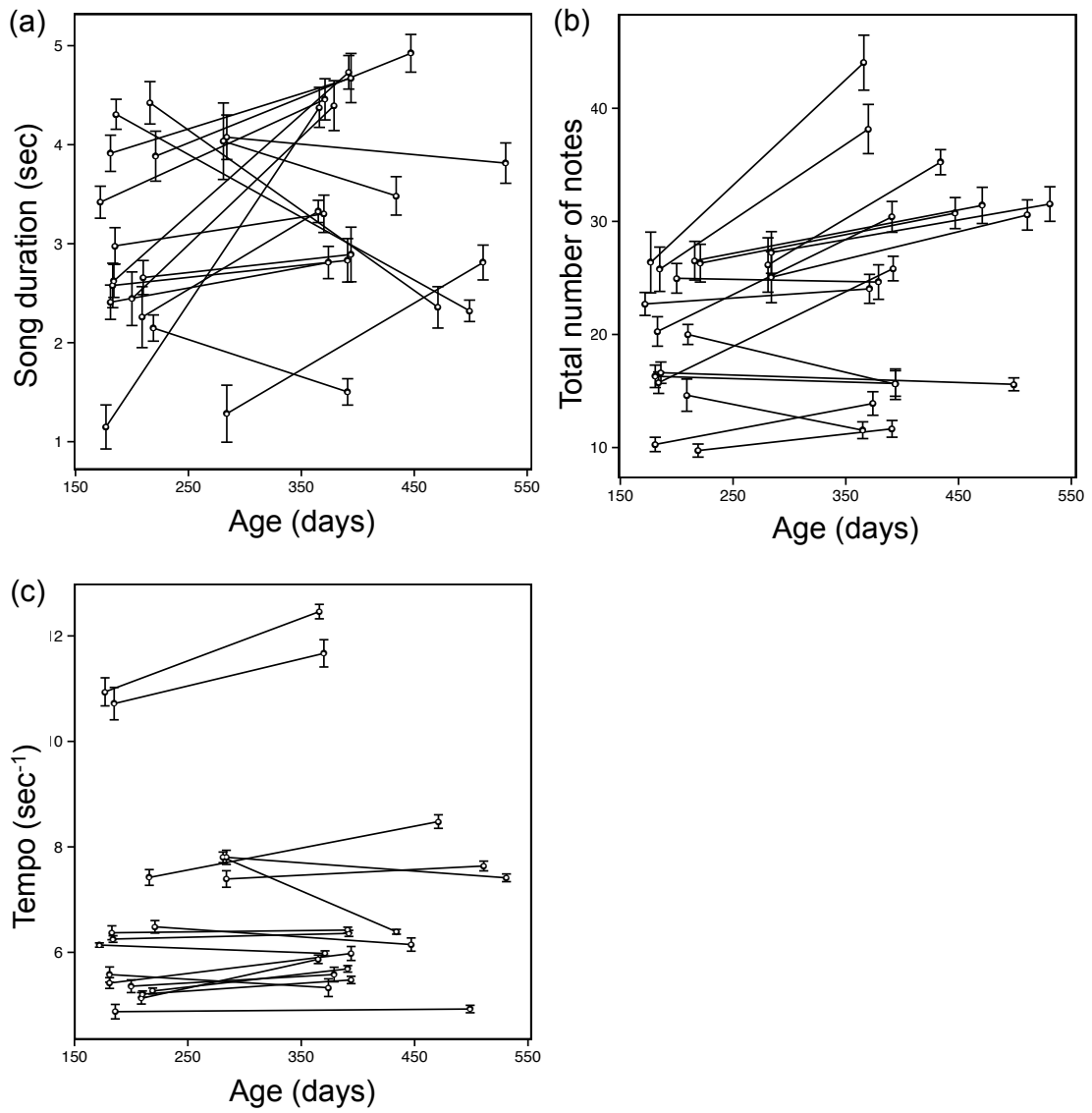


Figure 3. Within-individual's elevation of average (\pm SE) (a) song duration, (b) total number of notes and (c) tempo with age.

Tables

Table 1. Principal component analysis on body measurements (eigenvalue > 1). We adopted PC1 as index of body size.

Variable	PC1	PC2
Bill length	0.316	-0.639
Bill width	0.563	<0.001
Bill height	0.536	0.250
Tarsus length	0.346	-0.659
Natural wing length	0.419	-0.306
Eigenvalue (%)	2.148 (43)	1.146 (23)

Table 2. Changes in five song variables between father and son (a), and in relation to age (b) were analyzed using LME and GLM (random effect: song lineage/family lineage/bird ID). The former used 801 songs from 29 sons and 397 songs from 14 fathers. The latter used 445 songs at age \pm SD = 210 \pm 38.0 days and 504 songs at age \pm SD = 416 \pm 55.1 days from 17 sons.

Response variable	Fixed effect	Total number of data points	Estimate	SE	t/z	p	
(a)							
Song duration	Father or son	1198	-0.701	0.328	t=-2.139	0.041	LME gaussian
Total number of notes	Father or son	1198	-0.240	0.108	z=-2.218	0.027	GLMM poisson
Tempo	Father or son	1198	-0.303	0.214	t=-1.414	0.169	LME gaussian
Entropy	Father or son	43	-0.040	0.074	t=-0.544	0.591	LME gaussian
Note repertoire	Father or son	43	-0.054	0.137	z=-0.393	0.694	GLMM poisson
(b)							
Song duration	Age	949	0.002	<0.001	t=5.368	<0.001	LME gaussian
Total number of notes	Age	949	0.001	<0.001	z=13.250	<0.001	GLMM poisson
Tempo	Age	949	0.001	<0.001	t=6.131	<0.001	LME gaussian
Entropy	Age	34	<0.001	<0.001	t=-1.743	0.101	LME gaussian
Note repertoire	Age	34	<0.001	<0.001	z=0.465	0.642	GLMM poisson

Table 3. Results of LME analysis (random effect: song lineage/family lineage/bird ID) on age-related changes in four note structures. This analysis used 3000 notes at age \pm SD = 188 \pm 13.3 days and 3000 notes at age \pm SD = 393 \pm 39.1 days from 10 sons.

Response variable	Fixed effect	Total number of data points	Estimate	SE	t	p
Note duration	Age	6000	<0.001	<0.001	0.478	0.633
Frequency bandwidth	Age	6000	1.362	0.209	6.510	<0.001
Peak frequency	Age	6000	1.165	0.151	7.719	<0.001
Note-to-note interval	Age	6000	<-0.001	<0.001	-5.113	<0.001