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Song complexity correlates with learning ability in zebra finch males

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In species with mate choice, the choosy sex selects its mate based on traits that are thought to indicate the mate's quality. In several bird species, females prefer males that sing more complex songs but it is unclear which aspect of male quality is signalled by this trait. Here we tested the hypothesis that a male's song complexity conveys information about his learning capacity. We recorded the songs of 27 male zebra finches, *Taeniopygia guttata*, and quantified their complexity by measuring average song phrase duration, the total number of elements and the number of unique elements per song phrase. We then presented each male with a novel foraging task and recorded the number of trials he required to solve the task. We found a positive correlation between song complexity and learning proficiency: males with more song phrase elements required fewer learning trials to solve the novel foraging task. This result suggests that a male's song complexity signals his learning ability, which may have contributed to the selective pressures driving females to choose males with more complex songs.

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A trait is under sexual selection when variation in its expression affects success in mating competition and reproduction (Andersson 1994). A prominent example of a sexually selected trait is bird song: females prefer males with specific song features that may involve the song's structure, rate of output and quality of vocal performance (see reviews in Nowicki & Searcy 2004; Kipper et al. 2006; Byers 2007). A commonly studied structural trait is 'song complexity', which is related to the number of different songs, syllables or elements that a male produces (i.e., 'song repertoire'; Neubauer 1999; Buchanan & Catchpole 2000; Pfaff et al. 2007), but can also include the total number of syllables or elements and song phrase duration (Airey & DeVoogd 2000; Spencer et al. 2005a; Zeng et al.

Correspondence: N. J. Boogert, Biology Department McGill University, 1205 Dr. Penfield Avenue, Montréal, QC H3A 1B1, Canada (email: njboogert@gmail.com). L.-A. Giraldeau is at the Département des sciences biologiques, Université du Québec à Montréal, Case postale 8888, succursale Centre-ville, Montréal, QC H3C 3P8, Canada. 2007). Virtually all studies on mate choice and song complexity report that females prefer males that sing more complex songs (reviewed in Searcy 1992; Nowicki et al. 2002; Nowicki & Searcy 2004). This is true for species widely ranging in repertoire size, from the zebra finch, *Taeniopygia guttata*, in which each male sings a single song consisting of 3 to 14 different syllables (Clayton & Pröve 1989), to species such as the song sparrow, *Melospiza melodia*, with 4 to 13 distinct songs (Reid et al. 2004) and starling, *Sturnus vulgaris*, whose repertoire can contain up to 68 different songs (Mountjoy & Lemon 1996).

Whereas there is a consensus, based on empirical evidence from many species, that song complexity is a sexually selected trait, there is no such agreement concerning the information this trait conveys about the quality of its bearer. The 'developmental stress hypothesis' (Nowicki & Searcy 2004) currently guides the majority of research efforts on this topic and revolves around the link between song complexity and the brain structures underlying song learning. These 'song-control nuclei' develop most during the first few months after hatching, the life stage in which birds are also most vulnerable to developmental stresses (e.g. food scarcity, parasite infections, social stressors) that may negatively affect brain development. The proper development of the song system would act as a phenotypic revealer of the animal's ability to cope with environmental challenges (Nowicki & Searcy 2005). Chicks that can afford to develop better song-control nuclei and associated neural structures should also be able to learn more complex songs (Nowicki & Searcy 2004). Females choosing on the basis of song complexity would then be selecting males who demonstrate superior genotypic and/or phenotypic quality (Nowicki et al. 2002).

A series of recent experimental studies has confirmed the detrimental effects of developmental stress on song complexity and the brain structures underlying song learning (Buchanan et al. 2003, 2004; Spencer et al. 2003. 2004. 2005a. b: MacDonald et al. 2006: Soma et al. 2006; Zann & Cash 2008; but see Gil et al. 2006). Concurrently, various studies were performed to determine which mate quality traits might be signalled by song complexity. Thus far, most empirical data support the hypothesis that a male's song complexity indicates his body condition and fitness. For example, in great reed warblers, Acrocephalus arundinaceus, females obtained extrapair fertilizations from neighbouring males with greater song repertoires than their social mates. Offspring resulting from these extrapair fertilizations by complex singers had greater postfledgling survival (Hasselquist et al. 1996). In sedge warblers, A. schoenobaenus, males infested with parasites had smaller song repertoires and weighed less than nonparasitized males (Buchanan et al. 1999). In pied flycatchers, Ficedula hypoleuca, males with more complex songs were in better body condition and defended higher quality territories (Lampe & Espmark 2003). In common nightingales, Luscinia megarhynchos, males with larger repertoires had longer wings, were heavier and arrived at their territories earlier (Kipper et al. 2006). In song sparrows, males with larger repertoires were in better body condition and had a more robust immune system than those with smaller song repertoires (Pfaff et al. 2007), and also lived longer, raised a greater proportion of chicks to independence and recruited more offspring as well as grand-offspring (Reid et al. 2005).

How can song complexity be an indicator of body condition and longevity? Several authors have suggested that a male's cognitive capacity may provide a link between his song complexity and his quality as a mate (Catchpole 1996; Nowicki et al. 2000; DeVoogd 2004). This hypothesis is tenable from a neuroanatomical perspective in view of three findings made on zebra finches: first, song complexity (i.e. song element repertoire, total number of song phrase elements and song phrase duration) is strongly correlated with the volumes of the song-control nuclei in the brain (Airey & DeVoogd 2000); second, these song-control nuclei volumes are positively correlated with the volume of the telencephalon, a brain region associated with complex learning; third, the volumes of both the song-control nuclei and the telencephalon are heritable (Airev et al. 2000). Thus, females selecting males on the basis of song complexity may, in effect, be selecting for particular neuroanatomical qualities that underlie both song development and cognitive processing in general. Males with more complex songs might be more proficient in other cognitively demanding behaviours, such as learning when, where and how to feed and how to recognize and avoid predators (Nowicki et al. 2000; DeVoogd 2004; Griffin 2004). Females choosing such mates might obtain direct fitness benefits such as more reliable food supplies, a high-quality territory or a lower risk of predation. Females may also gain indirect fitness benefits when they produce offspring bequeathed with the father's cognitive capacity, which would in turn increase the offspring's fitness (DeVoogd 2004).

The cognitive capacity hypothesis implies that song complexity correlates positively with learning performance, but this crucial prediction has never been addressed empirically. We tested this prediction in the zebra finch, the model system of bird song and mate-choice studies, by quantifying the song complexity of males and measuring their learning speed on a novel foraging task. Here, we present the first empirical evidence that zebra finch males with more complex songs are faster learners.

METHODS

Subjects and Housing Conditions

We obtained domesticated adult male and female zebra finches from a local breeder in 2005, ensuring that the birds were not related to one another. Upon arrival in the lab, each individual was fitted with one numbered light blue leg band (A.C. Hughes, Hampton Hill, U.K.) and housed with one or two other birds of the same sex in wire-mesh housing cages $(57 \times 29 \times 42 \text{ cm})$ containing two perches and two reed nest baskets. Males and females were kept in separate rooms. Except during experiments, birds had ad libitum access to mixed millet seed. fresh water, cuttlefish bone and crushed ovster shells. Laboratory rooms were illuminated with standard 40-W and widespectrum Gro-Lux fluorescent tubes (Osram Sylvania, Danvers, Massachusetts, U.S.A.) on a 12:12 h light:dark cycle (lights on at 0600, off at 1800 hours) and kept at 24 ± 2 °C ambient temperature. These experiments were approved by the Animal Care Committee of the Université du Québec à Montréal, Protocol 0807-592-0708, and conformed to all guidelines of the Canadian Council on Animal Care.

Procedure

We recorded the songs and learning performance of 27 adult male zebra finches. We tested four birds at a time, so that we could film all trials, for 3 consecutive days in a laboratory room that was isolated visually and acoustically from the housing rooms.

On test day 1, we stimulated each male to sing directed song (Zann 1996) by transferring it to a wire-mesh cage $(53 \times 29 \times 38 \text{ cm})$ adjacent to a similar cage containing a female zebra finch (see Brumm & Slater 2006). The two cages were surrounded by an anechoic shell $(92 \times 70 \times 42 \text{ cm})$ made of high-density Fiberglas covered with

cotton cloth, carton and plastic sheets, to reduce the background noise volume on the song recordings. We recorded males' songs with an AT835b Shotgun condenser microphone and a Tascam DP-01FX/CD digital hard disk recorder. We presented the same stimulus female to the four males in a test group. When a male did not sing, we returned it to the housing room and made another attempt to record its song later that day. If the second song recording attempt failed, we replaced the female with another bird from the set of five stimulus females we used to elicit directed song. Zebra finch males are 'critical-period learners' that sing the same stereotyped sequence of elements after their song has crystallized at around 90 days (Williams 2004). When males are courting females, their songs have a faster tempo, the sequence and fundamental frequency of the syllables are less variable and they are less likely to start in the middle of a phrase than when these males sing the same song but without a female audience (Williams 2004; Woolley & Doupe 2008). Although the calls of the stimulus female in response to the courting male may affect the probability that the male truncates or adds a note to his song phrase (Williams 2004), we analysed complete song phrases only. Thus, we consider it unlikely that any small changes induced in the males' song phrase structures affected our results. Song recordings were made between 0700 and 1500 hours.

At 1500 hours, we transferred each of the four birds to its own wire-mesh cage ($53 \times 29 \times 38$ cm) containing four perches and water, mixed millet seeds and oyster shell ad libitum. Cages were positioned next to each other but were separated by cardboard partitions so that males could hear but not see each other. We deprived the birds of food from 1700 until 0730 hours the next day. The 2.5 h of light during which the birds were food-deprived increased the birds' motivation to engage in solving the foraging task, whereas this amount of time not spent feeding is within the range observed in the wild (Zann & Straw 1984) and in captivity (Dall & Witter 1998).

We started the learning performance test at 0730 hours on test day 2 by presenting each bird with a foraging task containing 20 seeds. If the test subject did not solve the task during the 15-min learning trial it was given free access to the 20 seeds at the end of the trial. We gave each bird one 15-min trial per hour for a total of 17 trials: nine trials on test day 2 and eight trials on test day 3. After the final trial of a day, test subjects could feed ad libitum for 2 h, after which we deprived them of food for another 2.5 h of light (and 12 night hours), until the next learning-test day. Most birds had solved the task by the end of the second learning-test day.

Task Apparatus and Learning Test Protocol

The base of the task apparatus consisted of a wooden foraging grid $(26 \times 22 \times 2 \text{ cm})$ containing 10 wells (0.8 cm deep and 1.3 cm wide) with centre points 6 cm apart. Each well contained two white millet seeds and was covered with a lid. The lids consisted of blue cardboard circles (3.5-cm diameter) with small metal rings (1.2-cm diameter, 0.1 cm high) taped on top to weigh them down. We covered the upper sides of the lids and

the metal rings on top with blue electrical tape, whereas the undersides had vinyl bumpers (1.3-cm diameter, 0.3 cm high) taped in the centre that fitted exactly in the wells of the foraging grid. Lids weighed 4.26 ± 0.1 g. To solve the task, a bird had to flip the lid off the well to gain access to the seeds. The difficulty of the task varied across four levels. At level 1, the lids were positioned next to the wells; at level 2, half of each well was covered by the lid; at level 3, the wells were fully hidden from view by the lids; and at level 4, the lids' vinyl bumpers were fitted into the wells. Thus, in the final, most difficult level of the task, the test subject had to flip the lid up to lift the vinyl bumper out of the well to reach the millet seed reward.

We used a systematic shaping procedure (Seferta et al. 2001) to lead the subject progressively through the levels of the task. When the bird managed to reach the seeds in two of the 10 wells, it passed on to the next level of difficulty on the next trial, whereas failure to do so (i.e. feeding from one or no well) returned it to the previous difficulty level on the next trial. After a trial ended, we uncovered the wells that the test subject had not accessed during the trial, to provide the zebra finch with the 20 seeds per hour required to fulfil its energetic demands (Zann 1996). Just before the start of the next trial, we removed the foraging grids and lids from the individual cages, refilled the wells with seeds and covered them again with the lids. The next trial started with the presentation of the replenished foraging grids. We recorded all learning trials using a Panasonic 3CCD mini-DV recorder with a wide-angle lens.

Analyses

We analysed the zebra finch song recordings with Avisoft-SASLab Pro 4.36 software (Avisoft Bioacoustics, Berlin, Germany). All song recordings were first high-pass filtered (cutoff frequency 0.4 kHz; Hamming window 1024 coefficients) to remove low-frequency background noise (Brumm & Slater 2006). For each bird's song, we analysed 10 song phrases and averaged the results. We used the same song measures and methods as Airey & DeVoogd (2000) to estimate song complexity, recording the total number of elements per song phrase, the number of unique elements per song phrase and song phrase duration in milliseconds. Introductory elements were not considered part of the song phrase and were excluded from analyses. The waveform amplitude was used to distinguish song elements: when it returned to baseline, we treated adjacent elements as separate. We used duration, the number and distribution of harmonics, and frequency modulation to categorize elements as 'same' or 'different' (Fig. 1). Such classifications of complicated song structures are somewhat subjective and different researchers are likely to make slightly different judgements. To check if we had applied our criteria in accordance with the song analysis methods in Airey & DeVoogd (2000), we asked Professor T. DeVoogd (T.D.V.) to score our song recordings. We also asked an independent expert on zebra finch song, Professor H. Williams (H.W.), to analyse our songs. Neither of these experts had information on the learning

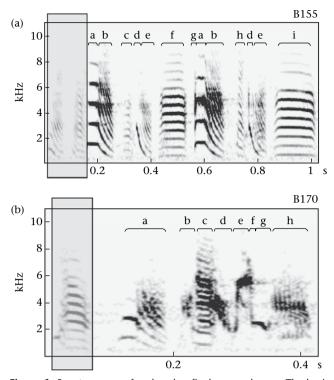


Figure 1. Spectrograms of male zebra finch song phrases. The horizontal axis represents time in seconds, the vertical axis is the sound frequency in kilohertz. The transparent boxes cover introductory elements that were excluded from analyses. The brackets distinguish song elements, and letters indicate which elements were categorized as being unique (new letter) or the same (reused letter) within each bird's song phrase. (a) The characteristic song phrase of bird 155 contained a total of 13 elements a, b, d and e. (b) Bird 170's characteristic song phrase contained a total of eight song elements, with each element being different from the others, as this male did not repeat any of its song elements.

performance of individual birds. We estimated agreement between our scores and those of H.W. by computing intraclass correlation coefficients (ICCs) with a two-way random-effects model (accommodating variation due to raters as well as due to bird performance) that tested for absolute agreement. In this model, the expected correlation coefficient ('test value') with which the observed correlation coefficients were compared was 0.5. We also computed Cronbach's α , a measure that describes internal consistency based on the average interitem correlation. Cronbach's α increases with increasing correlations up to $\alpha = 1$, which indicates absolute agreement between the items under study.

Our measure of zebra finch learning performance was the cumulative number of trials required by each male to solve the final level of the lid-flipping task. One male required 10 learning trials to feed from a well with the lid next to it (task level 1) and was excluded from all analyses. We considered this test subject to be too neophobic and/ or unmotivated to participate in the test (Sanford & Clayton 2008) and its learning score might not have been representative of its learning capacity. Of the remaining 26 test subjects that fed next to the lid in <10 trials, males that did not solve the final level of the learning task within the 17 trials of the experiment were assigned a learning score of 18 trials (i.e., the maximum of 17 + 1). As the assigned value of 18 is arbitrary, we analysed our learning data with and without nonsolvers and report both results.

We used the Kolmogorov–Smirnov test to check whether the data conformed to a normal distribution and resolved nonnormality with a natural-log transformation. We used Pearson correlations to explore the relationships between the three song measures and tested for an association between these song measures and learning performance with linear regressions including ln(phrase duration), ln(total no. of song phrase elements) and ln(no. of different song phrase elements) as predictors of ln(cumulative no. of learning trials required to solve the foraging task). Independent variable selection followed a stepwise procedure, in which the statistical significance of *F* tests determined whether the independent variables were included ($\alpha \le 0.05$) or excluded ($\alpha \ge 0.10$) from the model. We conducted all analyses in SPSS version 15.0.

RESULTS

Agreement between our song complexity analyses and those of T.D.V. and H.W. was high. T.D.V. found virtually the same total number of elements and number of unique elements (± 1) for all birds but one that differed by two unique elements. The number of unique song phrase elements assigned to this bird did not influence the results. Our element counts and those of H.W. differed by one or two elements for 18 birds, by three elements for one bird and by four elements for two birds, owing to our exclusion of introductory elements and our tendency to divide syllables into more elements. Cronbach's α and the ICCs (lower-upper bounds of 95% confidence intervals) between our song variable scores and those of H.W. were, for the total number of song phrase elements, $\alpha = 0.91$ and ICC = 0.91 (0.79–0.96), $F_{0.05,25,26} = 5.47$, P < 0.001; for the total number of different song phrase elements $\alpha = 0.78$ and ICC = 0.78 (0.51-0.90), $F_{0.05,25,25} = 2.27$, P = 0.022; and for song phrase duration $\alpha = 0.97$ and ICC = 0.97 (0.93–0.99), $F_{0.05,25,26} = 16.98$ and P < 0.001.

With regard to the relationships between our three song measures, we found that the total number of elements in a song phrase correlated positively with average song phrase duration (Pearson correlation test: r = 0.70, N = 26, P < 0.001) and with the number of different song phrase elements (r = 0.41, N = 26, P = 0.037). Song phrase duration did not correlate with the number of different song phrase elements (r = 0.08, N = 26, P = 0.70).

Six of the 26 males that required <10 learning trials to feed next to the lid in task level 1 did not solve the final level of the lid-flipping task and were assigned a learning score of 18 trials. We found the same qualitative relationship between song complexity and learning performance whether we included or excluded nonsolvers. Linear stepwise regressions showed that total number of song phrase elements was the only significant predictor of learning performance: males whose song phrases contained more elements required fewer trials to solve the final level of the lid-flipping task (R = 0.53, $F_{1,24} = 9.50$, P = 0.005; Fig. 2). When nonsolvers were excluded, the total number of song phrase elements still predicted learning performance (R = 0.57, $F_{1,18} = 8.63$, P = 0.009) and explained slightly more of the variance in the data ($R^2 = 0.32$, N = 20) than when the regression included both solvers and nonsolvers ($R^2 = 0.28$, N = 26).

Residuals of both regressions were normally distributed.

DISCUSSION

We found that in domesticated zebra finches, males with more complex songs were faster at learning the solution to a novel foraging task. This finding supports the hypothesis that song complexity might be an honest indicator of learning capacity. Thus, females that select males with more complex songs are effectively choosing mates that may learn more quickly than less complex singers where and when to find food sources and how to exploit them efficiently.

In our study, the total number of song phrase elements was the only song measure that explained a significant proportion of the variance in learning performance. Number of song components is an important character in zebra finch mate choice, given that females prefer the songs of control males over songs of developmentally

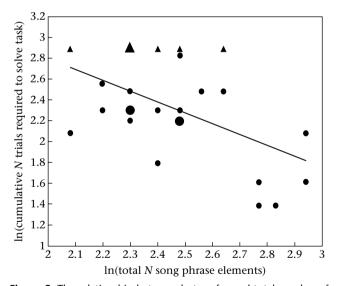


Figure 2. The relationship between In-transformed total number of song phrase elements in a zebra finch male's song and Intransformed cumulative number of learning trials it required to solve the final level of the foraging task. Each filled circle represents the data for one zebra finch male that solved the task, whereas each filled triangle represents the data for one zebra finch male that did not solve the final level of the task and was assigned a maximum learning score of 18 trials. The enlarged symbols represent two data points lying on top of each other. The equation of the regression line (\pm SE) for all test subjects shown is ln (cumulative no. of trials required to solve task) = 4.868 (\pm 0.832) - 1.035 (\pm 0.336) × ln(total no. of song phrase elements). When nonsolvers are excluded, the intercept is 4.371 (\pm 0.762) and the slope -0.892 (\pm 0.304).

stressed males that contain fewer syllables (Spencer et al. 2005a) and that, of nine song measures, it is one of the best predictors of mate choice (Holveck & Riebel 2007).

It is unclear, however, whether female zebra finches' preference for songs with more syllables (Spencer et al. 2005a; Holveck & Riebel 2007) extrapolates to songs with more elements, as operational definitions of syllables and elements vary between studies (Jones et al. 2001; Holveck & Riebel 2007). The fact that our song element counts were mostly consistent with those of two independent experts indicates that this song measure is robust. The lower agreement between our repertoire size estimates and those of Professor H. Williams suggests that the procedure of categorizing elements as 'same' or 'different' is more susceptible to subjectivity. Even if all experimenters agreed on an exhaustive set of criteria to distinguish syllables or elements, however, the right set of criteria can be obtained only by asking the truly relevant raters, zebra finch females.

The number of song phrase elements explained 28– 32% of the variance in learning performance in our experiment. It should be noted, however, that we tested zebra finches that were not experimentally stressed during development. Our finding suggests that even in captivity, where resource availability should meet developmental needs, individual differences in genetic constitution and/ or social stimulation resulted in sufficient variation in cognitive development to detect a significant relationship between a sexual display and learning performance. Exposure to harsher environmental conditions and various stressors in the wild is likely to result in more individual variation in development, which could lead to more pronounced differences in learning performance.

The cognitive capacity to learn how to adapt quickly to variable foraging conditions might make the difference between life and death for individuals of many bird species. Although the hypothesis that greater learning capacity enhances fitness seems to be widely accepted, it has been tested only with comparative analyses of brain sizes at the species level. Sol et al. (2007) showed that bird species with larger brains experience lower mortality in the wild than species with smaller brains. We are not aware of any long-term field study that has explored the relationship between individuals' cognitive traits and their fitness, even though it would be feasible to incorporate a cognitive test in the series of ornithological measures commonly taken. A study by Both et al. (2005) on avian personality illustrates that simple and reliable tests can be developed to collect data on the explorativeness of hundreds of individuals from a wild bird population and relate this behavioural trait to birds' fitness. Similarly, learning proficiency could be measured in wild bird populations, potentially using single tests that involve methods and tasks very similar to ours. Such tests have already been conducted on wild birds in short-term captivity and resulted in learning measures that correlated strongly with relevant traits in several species (e.g. in pigeons, Columba livia, and doves, Zenaida aurita, learning performance versus neophilia: $R^2 = 0.78$. Seferta et al. 2001: in starlings. learning versus dominance: mean $R^2 \pm SD = 0.77 \pm 0.11$, Boogert et al. 2006, and learning versus innovativeness: $R^2 = 0.55$, Boogert et al. 2008). We encourage those researchers working on long-studied bird populations to include measures of cognitive traits, so that these can be related to song complexity, body condition, mate choice and fitness and improve our understanding of the selective forces driving passerine evolution.

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