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Song repertoire size in male song sparrows correlates with detour reaching, but not with other cognitive measures

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Song learning is a cognitive task in which juvenile birds acquire, store and use information about adult song to shape their own song production. Comparative studies show that across bird species, performance on different cognitive tasks is usually positively correlated. If the same holds true within species, then the complexity of a male's learned song ought to be correlated with other cognitive abilities. To test this hypothesis, we measured correlations between song repertoire size and cognitive performance in wild song sparrows, *Melospiza melodia*. Females prefer males with larger song repertoires in this species, and song repertoire size correlates with various fitness measures. We recorded males' song repertoires in the field and tested these males in captivity on motor, colour association and reversal learning tasks, as well as on a detour-reaching task that measures inhibitory control. We found that individuals' performance on the colour association task correlated positively with their performance on the reversal task, but performance did not correlate across the other learning tasks. Males with larger song repertoires were faster to solve the detour-reaching task, but performed worse on the reversal task than males with smaller song repertoires. Although our results suggest that song repertoire size does correlate with one measure of cognitive performance, more detailed song analyses and further cognitive tests are required to answer the questions raised by our findings.

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Cognition is usually defined to include any mechanism by which an animal acquires, processes, stores and uses information (Shettleworth 2010). By such a definition, song learning is clearly a cognitive task: young birds acquire information about the correct form of song by listening to adults of their own species, store this information in memory, and subsequently use the stored information to shape their own song production (Marler 1990; Beecher & Brenowitz 2005). In this study, we tested the hypothesis that sexually selected characteristics of an individual's song are correlated with, and thus signal, that individual's cognitive abilities in general (Nowicki et al. 2000; Boogert et al. 2008; Searcy & Nowicki 2009).

Comparative studies show that across bird taxa, performance on different cognitive tasks tends to be positively associated. Corvids,

for example, show higher frequencies of innovation and tool use in their natural habitats, and perform better on tests of learning in captivity, than species in the pheasant and crane orders (Timmermans et al. 2000; Lefebvre et al. 2004). At the within-species level, covariation in the performance of individuals across cognitive tasks has been considered evidence for a general cognitive ability (*g*) in mammals. The most convincing evidence for such covariation comes from humans (Plomin 2001; Deary et al. 2010), although evidence for *g* in mice, *Mus musculus*, is accumulating (reviewed in Matzel & Kolata 2010; but see Locurto et al. 2003). With regard to evidence for a general cognitive ability in birds, results are mixed. On the one hand, Bouchard et al. (2007) tested pigeons, *Columba livia*, on two tasks, involving problem solving and social learning, and found a strong positive correlation in performance (Bouchard et al. 2007). On the other hand, Keagy et al. (2009) presented male satin bowerbirds, *Ptilonorhynchus violaceus*, with two novel problem-solving tasks, and found a correlation in performance close to zero. Similarly, Boogert et al. (2010) found no concordance in the performance of Zenaida doves, *Zenaida aurita*, on three tasks, involving a novel foraging mode test, a colour association test and a colour reversal test. One study has tested whether a measure of song complexity correlated with learning

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performance in zebra finches, *Taeniopygia guttata*, and found a positive correlation between the number of elements in males' songs and the speed with which they learned to solve a foraging task (Boogert et al. 2008). This previous study focused on a domesticated species lacking song repertoires and tested the birds on a single cognitive task. In the present study, we focused on a wild songbird, the song sparrow, *Melospiza melodia*, and measured correlations between song repertoire size and performance on several cognitive tasks related to foraging.

Song sparrows sing repertoires of 5–15 or more distinct song types (Podos et al. 1992; Nordby et al. 2002). In the laboratory, the details of these song types are learned during a critical period that extends from approximately 20 to 90 days posthatching (Marler & Peters 1987). In the field, young males learn most of their song types from older males other than their fathers that they encounter during their first year (Beecher et al. 1994; Nordby et al. 1999). Larger numbers of song types induce more copulation solicitation displays in captive females (Searcy & Marler 1981; Searcy 1984) and male song repertoire size correlates with earlier pairing dates in the field (Reid et al. 2004), suggesting that this measure of song complexity affects female choice of mates. Female preferences for larger song repertoires seem likely to be adaptive, because song repertoire size correlates positively in male song sparrows with a number of traits important to fitness, such as territory tenure, heterozygosity, immune system quality, longevity and lifetime reproductive success (Hiebert et al. 1989; Reid et al. 2005a, b; Pfaff et al. 2007). Because song repertoire size is an important display attribute that emerges from song learning, it is a logical song feature to investigate as a signal of general cognitive ability.

Song and other cognitive abilities are affected by common genetic and environmental factors, suggesting mechanisms by which the two could become associated. For example, in zebra finches the volumes of the brain structures underlying song learning (the 'song control nuclei') are positively correlated with the volume of the telencephalon, a brain area activated during other forms of learning (Airey et al. 2000). Both brain areas are negatively affected by nutritional stress in a close relative of the song sparrow, the swamp sparrow, *Melospiza georgiana* (Nowicki et al. 2002a), and female swamp sparrows are more responsive to songs of males with good early growth histories than to songs of males with poor growth histories (Searcy et al. 2010). The same negative effects of developmental stress on the volume of song control nuclei and on song quality and attractiveness have been reported for various other species, including song sparrows (reviewed in Catchpole & Slater 2008; Searcy & Nowicki 2009). Developmental stressors have also been shown to have negative effects on the brain structures underlying spatial learning in western scrub jays, *Aphelocoma californica* (Pravosudov et al. 2005) and rats, *Rattus norvegicus* (De Souza et al. 2008; McCormick et al. 2010), and on other measures of cognitive ability in several birds (Kitaysky et al. 2003, 2006; Pravosudov et al. 2005; Fisher et al. 2006; Donaldson 2009) and mammals (Castro et al. 1989; Levitsky & Strupp 1995; Fukuda et al. 2002; Erhard et al. 2004; De Souza et al. 2008; Lupien et al. 2009).

Regardless of whether cognitive traits in birds are heritable or not, the fact that developmental stresses affect both song learning and more general cognitive processes suggests that females who prefer males with higher song quality may obtain direct benefits: these males may also be more proficient in other cognitively demanding behaviours, such as learning when, where and how to feed (Nowicki et al. 2000; DeVoogd 2004), and how to cope with environmental change (Botero et al. 2009). The one previous study of the association of song and cognition measured three aspects of zebra finch song: number of elements per phrase, number of unique elements per phrase and song duration (Boogert et al.

2008). Cognitive performance was measured as the number of trials required to learn a novel motor task in a foraging context, in which the bird had to remove a lid from a small well to obtain a food reward. Stepwise linear regression showed that one of the song measures, the number of elements per phrase, was a significant predictor of speed of learning to solve the motor task (Boogert et al. 2008).

In the present study, we tested the prediction that a single measure of song, song type repertoire size of wild-caught adult song sparrows, correlates positively with the singers' speed of learning to solve four cognitive tasks in captivity: (1) a novel motor task, similar to that used by Boogert et al. (2008); (2) a colour association task; (3) a reversal of the colour association task; and (4) a detour-reaching task that tests inhibitory control (Santos et al. 1999; Amici et al. 2008; Vlamings et al. 2010). This last task requires subjects to learn to inhibit a nonfunctional but automatic response.

METHODS

Song Recording

We recorded at least 200 songs for each of 52 adult song sparrow males in Crawford County, PA, U.S.A., between 24 April and 8 June 2009 ($N = 24$), and between 3 May and 2 June 2010 ($N = 28$) (mean \pm SD = 330 ± 38 songs per bird, range 207–413). We are confident that we recorded the complete repertoire of each male. A range of 200–300 songs has been shown to be sufficient to document all song types in a song sparrow's repertoire exhaustively (Searcy et al. 1985; Hughes et al. 1998). For 47 of the 52 birds, we recorded >300 songs and the number of songs recorded for the remaining five males ranged from 207 to 289. For all 52 males no new song types were detected in a male's repertoire after an average of 100 ± 45 songs were inspected. Furthermore, after the last new song type was detected we recorded at least 87 more songs per male (with a maximum of 346 more songs). Finally, across all the males in the sample there was no relationship between the number of songs recorded and the number of song types detected (Spearman rank correlation: $r_s = -0.047$, $N = 52$, $P = 0.743$). Playback of song sparrow song was used to locate territory owners and their territory boundaries, and was used occasionally to initiate singing when necessary. Once a male started to sing, however, playback was not used further; males were not recorded countersinging with playback and they switched spontaneously between song type bouts in the absence of playback. Depending on a male's singing rate, recording a repertoire took between 1.5 and 6 h per individual. Thirty-two of the 52 males were recorded during one morning session, 19 males were recorded over two consecutive mornings and one male was also recorded on two different mornings but with a 4-day gap between recordings. For the 20 males recorded on two different mornings, we visually inspected song spectrograms (see below) and confirmed that song types recorded one morning were virtually identical to those in the second recording to ensure that we had recorded the same male on both mornings. For recordings, we used a Marantz PMD 670 digital recorder connected to a Shure SM-57 microphone mounted in a Sony PBR-330 parabola.

Capture and Housing

After being recorded in the field, males were caught on their territories with mist nets and transported to the laboratory where they were weighed and individually colour-banded. Field sites were located ca. 12 km from the laboratory, and time between capture and release into a holding cage was ca. 30 min. Subjects were housed singly in metal wire cages (46 \times 23 cm and 23 cm high,

'double breeder' type, Prevue Pet, Chicago, IL, U.S.A.) within individual sound attenuation chambers (69 × 65 cm and 52 cm high, AC-1, Industrial Acoustics, Bronx, NY, U.S.A.) that isolated males both acoustically and visually. Birds were kept on a 15:9 h light:dark cycle (lights on at 0600, off at 2100 hours) at 22–24 °C. Cages contained two perches and a cuttlebone, and birds were given free access to water and mixed songbird seed (Canary Forti Diet, KayTee, Chilton, WI, U.S.A.) except prior to and during testing (see below). Birds were in captivity for an average of 12.2 ± 2.2 days. All birds maintained good health while in captivity and several individuals banded and tested in 2009 were observed to breed and defend territories in 2010.

Cognitive Testing Procedures

We tested subjects on cognitive tasks starting at 0945 hours each day. Birds were presented with four cognitive tasks in the same order: (1) motor task; (2) colour association task; (3) colour reversal task; and (4) detour-reaching task. Food was removed from the cages at 0545 hours, so that subjects were deprived of food for 4 h before testing, as pilot trials indicated that a period of food deprivation was necessary to ensure that all subjects were motivated to perform the cognitive tasks. During testing, subjects were able to earn ample rewards of a highly favoured food item: larvae of the mealworm beetle, *Tenebrio molitor*. We observed that all test subjects started to feed on seed immediately when this was provided upon completion of the learning trials each day, suggesting that individuals still had high levels of feeding motivation at the end of our experimental sessions.

The first three tasks used a foraging grid consisting of two plastic blocks (13.5 × 9 cm and 2.5 cm high), placed adjacent to each other, and each containing six wells (1.3 cm diameter, 0.8 cm deep). During all task trials, four of the 12 wells contained one mealworm each. These cognitive tasks required flipping blue or yellow circular plastic lids (2.2 cm diameter, 0.05 cm high) from the top of a well to access the mealworm reward underneath. Attached to the bottom of each lid was a vinyl bumper (1.3 cm diameter, 0.3 cm high) that fitted exactly into the well. Each trial started with the presentation of the foraging grids and lasted 10 min, after which the foraging grids, lids and any uneaten mealworms were removed. Birds received trials every 30 min until six 10 min trials had been completed. If a bird did not reach the learning criterion during the 3 h test period on one day, the task was presented again on subsequent days, until the learning criterion was reached. We continued the tally of correct trials from one day to the next.

Motor task

We adopted a shaping procedure slightly modified from that described in Boogert et al. (2008) to test each individual's capacity to learn to flip lids off wells to obtain mealworm rewards. Test subjects learned this motor task in five stages. In stage 1, four mealworms were placed in four randomly selected wells with no lids on the grids; in stage 2, four lids (two yellow, two blue) were positioned adjacent to the four baited wells; in stage 3, the coloured lids were placed to half-cover the baited wells; in stage 4, the lids were propped up in the wells, so that they fitted loosely while hiding the mealworms underneath; and in stage 5, the vinyl bumpers of the lids were fitted snugly into the wells, so that the test subject would have to pry the lids from the wells using its beak or feet. We recorded the number of wells from which each bird had obtained a mealworm after it had been presented with the task for 10 min. For each task level, 'success' was defined as obtaining three or four mealworms, 'failure' was defined as obtaining zero or one mealworm, and a 'neutral' result was defined as obtaining two mealworms. If a subject failed during three consecutive trials, it

regressed to the previous stage. When a male succeeded during three consecutive trials, it proceeded to the next stage. When a male obtained a neutral result, it was kept on the same stage. To pass the final level, stage 5, of the motor task, a bird had to obtain three or four mealworms in six out of seven consecutive trials.

Colour association task

Immediately after passing the motor task, the subject proceeded to the colour association task. For each bird, we randomly chose one colour lid (yellow or blue) to be rewarded. In each trial, eight of the 12 wells were used, four of which were covered by yellow lids and four by blue lids. Only wells covered by lids of the rewarded colour contained mealworms. For each trial, the positions of blue and yellow lids were determined randomly. Each trial was observed through a window in the door of the acoustic chamber in which the test subject was housed, and the order of the colours of the lids the test subject flipped was recorded. For each trial, a bird obtained 'success' if it flipped all four rewarded lids before flipping any of the unrewarded lids. 'Failure' was defined as flipping the unrewarded colour during any of the first four flips. To pass the colour association task, the test subject had to flip the rewarded colour for the first four flips in a trial during six out of seven consecutive trials. Video 1 in the Supplementary material shows the performance of a female song sparrow on the colour association task, presented on her territory in Crawford County, Pennsylvania, U.S.A.

Reversal task

Here, we rewarded the colour lid that had been unrewarded during the colour association task. Otherwise, the task proceeded as did the colour association task described above.

Detour-reaching task

Inhibitory control is the ability to inhibit ineffective prepotent responses, or to inhibit responses to irrelevant stimuli, while pursuing a cognitively represented goal (Rothbart & Posner 1985; reviewed in Hauser 1999). Prepotent responses can exist because of past reinforcement or because they are preprogrammed. In humans and nonhuman animals, inhibitory control is thought to be a strong predictive measure of problem-solving skills (Mischel et al. 1989; Diamond 1990; Dempster 1992; Hauser 1999; Carlson & Moses 2001; Vlamings et al. 2010). A common measure of inhibitory control is obtained with the detour-reaching task, in which a desired object (a toy or preferred food) is placed in a transparent enclosure or behind a transparent barrier, requiring the subject to make a detour around the barrier to obtain the object. When presented with a desired object viewed through a Plexiglas box, for example, human infants and many nonhuman animals consistently reach directly for the object, despite tactile feedback from the Plexiglas and failure to obtain the object (reviewed in Vlamings et al. 2010). However, after experience with an opaque enclosure, most species are able to learn to inhibit their grabbing response when the object is in an identical transparent enclosure, and instead detour to the opening of the enclosure to reach the object (Diamond 1990; Santos et al. 1999; Amici et al. 2008; Vlamings et al. 2010). Thus, the speed at which species or individuals learn to inhibit the automatic grabbing response and solve the detour-reaching task is used as a measure of inhibitory control.

In 2010, we added a detour-reaching task to our cognitive test battery and tested the final 22 of the birds we sampled that season. This task employed a different apparatus: a plastic cylinder (5 cm length, 4 cm diameter) fashioned from plastic sheeting (0.1 cm thickness), open at both ends and glued to a wooden base (5 × 4 cm and 0.6 cm high). During the habituation and training phases, the cylinder was opaque (wrapped in black window film), whereas it was transparent during the test phase (Fig. 1). Each individual was

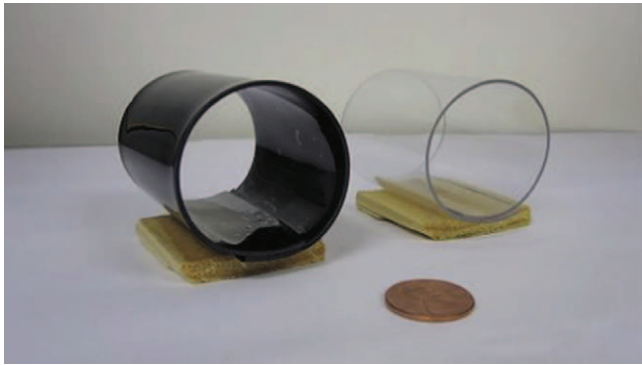


Figure 1. The opaque and transparent cylinders used for the detour-reaching task. An American penny is added for scale.

presented with the cylinder for a maximum of 20 trials per day, containing on each trial one freshly killed mealworm, starting the day after the subject had passed the colour reversal task. Testing was preceded each day by 90 min of food deprivation.

The task proceeded in three phases: habituation, training and test. The goal of the habituation phase was to reduce a subject's fear of the cylinder as a novel object. We presented the black opaque cylinder containing a freshly killed mealworm in the right side of the cage, equidistant from, and with the openings facing, the front and back of the cage. Every 10 min we checked whether the test subject had consumed the worm. Each trial was followed by a 2 min time-out, during which the cylinder was left inside the cage. If the mealworm had been consumed, a different cylinder was baited and swapped with the empty cylinder at the start of the next trial. The test subject passed the habituation phase and started the training phase if it consumed the mealworm in three consecutive 10 min trials.

The goals of the training phase were to reinforce subjects' learning that food was inside the cylinder, and that they could obtain the food by reaching with their beaks into the open ends of the cylinder. The training phase proceeded similarly to the habituation phase. However, each trial was observed by the experimenter, who recorded whether the test subject pecked at the sides of the cylinder in an attempt to remove the mealworm (incorrect) before retrieving it from one of the open ends (correct). Test subjects moved on to the test phase once they had retrieved the mealworm from the opaque tube on their first attempt, without pecking the sides of the cylinder first, in four out of five consecutive trials. Only one of the 22 test subjects pecked the side of the opaque cylinder during a trial. Thus, only a few trials were needed to establish that the test subjects had learned how to obtain the worm in the training phase.

The test phase employed the transparent cylinder, baited with a mealworm. As the test subjects could see the mealworm through the transparent sheeting, most attempted to obtain the mealworm by pecking through the transparent sides of the cylinder (incorrect) rather than using the previously acquired detour movement to the open ends of the cylinder (correct). With successive trials, however, all subjects learned to detour to one of the cylinder openings to obtain the mealworm. A test subject had to obtain the mealworm from the transparent tube on its first attempt (i.e. without pecking the sides of the cylinder first), in six out of seven consecutive trials to pass the detour-reaching task. Video 2 in the Supplementary material shows a song sparrow's performance on the detour-reaching task.

Once an individual had passed all four cognitive tasks, it was provided with seed and mealworms ad libitum for several hours, after which it was fitted with a U.S. Fish and Wildlife service

aluminium band and released at its site of capture. All experiments were conducted under University of Pittsburgh IACUC protocols 090510107-A (2009) and 0904772A-1 (2010) and Duke University IACUC protocol A090-08-04.

Analyses

Song sparrow song types are easily identified by visual inspection of spectrograms (e.g. Podos et al. 1992). All song recordings were digitized at 22 050 pts/s and 16-bit resolution, and spectrograms displayed with a 172.3 Hz frequency resolution and 5.8 ms time resolution using Syrinx-PC version 2.6h (John Burt 2006; www.syrinxpc.com). Each male's repertoire was inspected twice. Either N.J.B. or R.C.A. inspected all songs recorded per male and scored the number of song types sung by each song sparrow male. A third observer (S.P.) inspected all songs a second time to double check the repertoire size assigned to each male. All scoring of repertoire size was done blind to the cognitive performance of the test subjects.

For the motor task, we planned to use task stages 1, 2 and 3 as measures of habituation to captivity and neophobia. However, all test subjects passed these stages in the minimum number of trials, possibly because the mealworms were visible and could thus be easily obtained. As there was no interindividual variation in scores for these first task stages, we omitted them from subsequent analyses. We summed the number of trials that each male required to pass task stages 4 (hinged lids) and 5 (snugly fitted lids), where the mealworms were no longer visible, and used this cumulative number of trials to learn to flip lids as the motor task score for each bird (following Boogert et al. 2008). Each male's score for the colour association task was the total number of trials it required to reach the criterion of choosing the rewarded colour lid for the first four flips in six of seven consecutive trials (i.e. including the final six successful trials). The same scoring method was used for the reversal task. A song sparrow's score on the detour-reaching task was the number of trials it required to pass the test phase (i.e. obtaining the reward from the transparent tube), and included the final six successful trials as well.

We first performed pairwise correlations to explore how performance on the learning tasks related to each other. We used nonparametric Spearman rank correlation tests because these minimize assumptions about the distribution of the data. As cognitive task scores and song repertoire sizes did not differ significantly between 2009 and 2010 (Mann–Whitney U tests: motor task: $U = 316.5$, $N_{2009} = 23$, $N_{2010} = 28$, $P = 0.916$; colour association: $U = 276.0$, $N_{2009} = 24$, $N_{2010} = 28$, $P = 0.269$; reversal: $U = 237.0$, $N_{2009} = 24$, $N_{2010} = 27$, $P = 0.100$; repertoire size: $U = 284.5$, $N_{2009} = 24$, $N_{2010} = 28$, $P = 0.335$), we pooled the data across years for these correlation analyses.

We then performed a principal components analysis (PCA), based on the correlation matrix with unrotated factor solution, to investigate whether the variance in the cognitive task performances could be explained by a single factor extracted from the data. If so, this would suggest the existence of a general cognitive ability underlying these behaviours (Galsworthy et al. 2002, 2005; Locurto et al. 2003; Matzel et al. 2006; Herrmann et al. 2010). We conducted a PCA on the 2009 and 2010 samples separately to explore whether the variance in cognitive task performances was distributed in the same way in both years. For the 2010 data, we first conducted a PCA that excluded the detour-reaching task performance to make it directly comparable to the PCA of the 2009 data. The second PCA of the 2010 data included all four cognitive task measures collected in that year.

Finally, we tested whether any of the principal components with an eigenvalue ≥ 1.0 extracted from the 2009 and 2010 data

correlated with song repertoire size using Spearman rank correlation tests.

We conducted all analyses in SPSS version 15.0 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

The repertoires of males in our sample ranged from five to 11 song types ($N = 52$, mean \pm SD = 7.9 ± 1.6). The cumulative number of trials required to pass stages 4 (hinged lids) and 5 (lids fitted in wells) of the motor task ranged from nine to 22 ($N = 51$, mean \pm SD = 12.5 ± 3.1 ; the first test subject of 2009 was tested with a different motor task protocol from the rest of the birds and was omitted from motor task analyses). The number of trials to pass the colour association task ranged from eight to 36 ($N = 52$, mean \pm SD = 16.2 ± 6.2), and the number to pass the reversal task ranged from 13 to 40 ($N = 51$, mean \pm SD = 23.7 ± 7.2 ; one test subject from the 2010 sample was omitted from reversal task analyses as he stopped flipping lids during this task). The detour-reaching task showed the largest variation in performance, with males requiring between six and 48 trials to pass this task ($N = 22$, mean \pm SE = 21.3 ± 10.8).

Correlations among Learning Performances

The results of the Spearman rank correlation tests that were conducted to explore the relationships between performance on the motor, colour association, colour reversal and detour-reaching tasks and song repertoire size across years are summarized in Table 1. This table shows that performance on the colour association task correlated positively with performance on the motor task and performance on the colour reversal task, although these results were no longer significant after applying the Bonferroni correction. Performance on the colour reversal task correlated positively with song repertoire size, suggesting that males with larger song type repertoires were slower at passing the reversal task, but again this result did not withstand the Bonferroni correction. The only correlation still significant after Bonferroni correction was that between performance on the detour-reaching task and song repertoire size: males that were faster to inhibit their impulsive reaction to peck the side of the tube to obtain the food reward inside had larger song repertoires (Fig. 2). None of the other learning task performances correlated significantly with each other or with song repertoire size (all $P > 0.30$; Table 1).

Table 1

Spearman correlation matrix of all cognitive task performances and song repertoire size

	Motor task	Colour association	Colour reversal	Detour reaching
Colour association				
r_s	0.275			
P	0.051			
N	51			
Colour reversal				
r_s	0.039	0.292		
P	0.789	0.038		
N	50	51		
Detour reaching				
r_s	0.060	-0.233	-0.185	
P	0.792	0.298	0.409	
N	22	22	22	
Song repertoire				
r_s	-0.052	0.094	0.336	-0.621
P	0.718	0.506	0.016	0.002
N	51	52	51	22

Results that remain significant after Bonferroni correction (reducing the α level of significance to $0.05/10 = 0.005$) are indicated in bold.

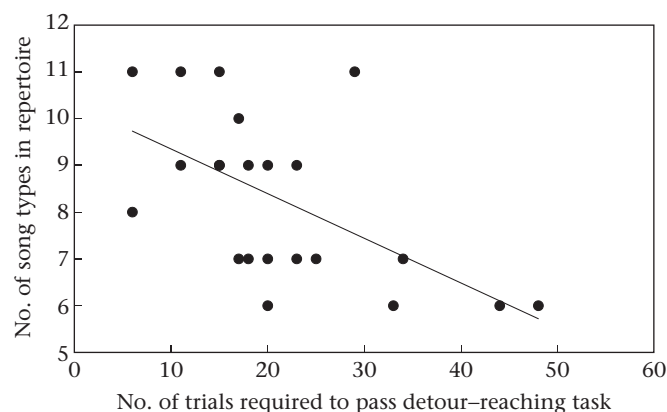


Figure 2. The relationship between the song repertoire size of song sparrow males ($N = 22$) and their performance on the detour-reaching task. Note that two data points overlap: two males required 15 trials to solve the detour-reaching task and had nine songs in their repertoire.

Variance in Learning Performance

The unrotated solution of a PCA of the first three learning test measures from the 2009 sample showed that the motor, colour association and reversal task performances all loaded positively on the only principal component extracted, which explained 50.92% of the variance in the data (Table 2). Similarly, the PCA of the learning test measures from the 2010 sample showed that colour association and reversal task performances loaded positively on the first component extracted (Table 3). Motor task performance in 2010, however, loaded weakly and negatively on this first principal component, which explained 45.99% of the variance in the data, but strongly and positively on the second principal component, which explained an additional 33.48% of the variance (Table 3). The PCA results for the 2010 sample were very similar with regard to the motor, colour association and reversal task performances including and excluding performance on the detour-reaching task (Table 4). Detour-reaching task performance loaded negatively on the first component, however, which explained 36.65% of the variance in the data (Table 4).

Principal Components and Repertoire Size

Individuals' scores for the only principal component extracted for the learning task measures of the 2009 sample (Table 2) did not correlate significantly with their song type repertoire size (Spearman rank correlation $r_s = 0.033$, $N = 23$, $P = 0.880$). Neither of the two principal components extracted for the first three learning task measures of the 2010 sample (i.e. motor, colour association and reversal task; Table 3) correlated significantly with song type repertoire size (PC1: $r_s = 0.328$, $N = 27$, $P = 0.094$;

Table 2

Results of a principal components analysis of the learning task scores of 23 song sparrow males tested in 2009

Learning task	Component 1
Motor	0.70
Colour association	0.78
Reversal	0.66
Eigenvalue	1.53
% Total variance explained	50.92

Unrotated component loadings, eigenvalue and percentage of total variance in the cognitive performance data explained by each component are shown.

Table 3
Results of a principal components analysis of the learning task scores of 27 song sparrow males tested in 2010

Learning task	Component 1	Component 2
Motor	–0.21	0.97
Colour association	0.80	0.27
Reversal	0.83	–0.02
Eigenvalue	1.38	1.00
% Total variance explained	45.99	33.48

Unrotated component loadings, eigenvalues and percentage of total variance in the cognitive performance data explained by each component are shown.

PC2: $r_s = 0.134$, $N = 27$, $P = 0.505$). However, when detour-reaching task performance was added to the PCA (Table 4), individuals' scores on the first principal component showed a marginally significant positive correlation with their song repertoire size ($r_s = 0.417$, $N = 22$, $P = 0.054$), whereas the second principal component did not ($r_s = 0.195$, $N = 22$, $P = 0.385$).

DISCUSSION

We tested the prediction that performance on a range of learning tasks should increase with increasing song repertoire size in male song sparrows. We found that birds with larger song repertoires were also faster to solve the detour-reaching task. The detour-reaching task measures the ability to inhibit an automatic response, an ability that has been argued to be crucial to promoting behavioural flexibility and thus to problem solving (Diamond 1990). Santos et al. (1999) suggested that the difficulty cottontop tamarins, *Sanguinus oedipus*, had in solving a detour-reaching task similar to the one used here might be responsible for their difficulties mastering other cognitive problems involving search. Amici et al. (2008) found that performance on inhibitory control tasks was better among primates with fission–fusion social systems than among those with more stable societies, and argued that ability on this task reflected higher behavioural flexibility in general. Thus there are reasons for considering inhibitory control an important cognitive ability.

Reversal learning is also thought to be an aspect of behavioural flexibility (Hauser et al. 2002; Boogert et al. 2010; Tebbich et al. 2010), and has been argued to reflect similar cognitive mechanisms as inhibitory control (Bond et al. 2007). Surprisingly, we found that birds with larger repertoires were slower to pass the reversal learning task, and performance on this task was not correlated with that on the detour-reaching task. However, as behavioural flexibility is a broad concept that can encompass a variety of cognitive mechanisms (Jones 2005; Bond et al. 2007; Sol 2009), different measures of flexibility need not necessarily correlate within or among individuals.

Finally, we found that song repertoire size was not correlated with performance on the motor task or with performance on the

Table 4
Results of a principal components analysis of the learning task scores of 22 song sparrow males tested in 2010 on the detour-reaching task in addition to the motor, colour association and reversal learning tasks

Learning task	Component 1	Component 2
Motor	–0.10	0.93
Colour association	0.80	–0.02
Reversal	0.69	0.34
Detour reaching	–0.58	0.21
Eigenvalue	1.47	1.03
% Total variance explained	36.65	25.64

Unrotated component loadings, eigenvalues and percentage of total variance in the cognitive performance data explained by each component are shown.

colour association task. That song repertoire size is positively correlated with one learning measure and negatively with a second is possible only because the learning measures were not themselves uniformly positively associated with one another. This result contrasts with what has been found in mammals, where performance on different learning tasks tends to be positively correlated, for example in humans (Carroll 1993; Plomin 2001), mice (Galsworthy et al. 2002, 2005; Matzel et al. 2003; although see Locurto et al. 2003) and chimpanzees, *Pan troglodytes* (Herrmann et al. 2010). A positive association between performances on different cognitive tasks has also been demonstrated in honeybees, *Apis mellifera* (Chandra et al. 2000). Even in the mammal studies, however, correlations, although positive, are often low and nonsignificant. For example, Matzel et al. (2003) measured the performance of 56 laboratory mice on five learning tests, and assessed associations between performances on the different tasks using Pearson correlations. All 10 correlations were positive, but only two were nominally significant. Similarly, Galsworthy et al. (2002) administered eight learning tests to 40 mice and found eight of 28 between-test correlations to be significant, with a maximum correlation of 0.48 and a mean of 0.20. Furthermore, previous evidence on birds does not uniformly support positive associations of cognitive test results.

The one previous study relating song to measures of cognitive ability found a significant positive correlation in zebra finches between performance on a novel motor task and one of three measures of song complexity (Boogert et al. 2008). The motor task used in that study was highly similar to the one used here, involving removal of lids from wells. However, the zebra finches tested by Boogert et al. (2008) were domesticated, whereas the song sparrows used in our study were caught from the wild. Zebra finches are grass-seed specialists (Zann 1996), whereas song sparrows feed on invertebrates, seeds and berries, a diet that requires a range of foraging techniques, including flipping over the fronds of plants in search of amphipods (Arcese et al. 2002). One can be confident that the domesticated zebra finches, born and raised under standardized conditions, had never experienced anything like the motor task before, and were thus all equally naïve to this novel foraging task. It is conceivable, however, that the song sparrow males differed in the extent to which they had acquired relevant experiences in the wild before they were subjected to our experiments. Interindividual differences in relevant experience obtained in the wild may have obscured a possible relationship between motor task performance and song repertoire size. Perhaps the lack of a correlation between colour association test performance and song repertoire size can be explained along the same lines, with individuals differing in their experiences with colour cues. Only tests with hand-reared song sparrows can elucidate the role of previous experience on learning test performance (Kotrschal & Taborsky 2010; Light et al. 2010; Roth et al. 2010).

One result that is consistent with the findings of other studies is the positive correlation between latency to learn the colour discrimination and performance on the reversal test. Reversal learning tests are most commonly adopted in comparative analyses of animal learning (e.g. Bitterman 1965, 1975; Day et al. 1999; Bond et al. 2007; Tebbich et al. 2010). Data from Tebbich et al. (2010) for three species of Galapagos finches and Day et al. (1999) for a species of desert-dwelling lizard demonstrate that discrimination and reversal learning performance generally show positive correlations, even if significant in only one case, perhaps because of small sample sizes (*Cactospiza pallida*: Spearman correlation: $r_s = 0.562$, $N = 16$, $P = 0.023$; *Camarhynchus parvulus*: $r_s = 0.596$, $N = 8$, $P = 0.119$; *Geospiza fortis*: $r_s = 0.180$, $N = 8$, $P = 0.671$; *Acanthodactylus scutellatus*: Pearson correlation: $r_s = 0.630$, $P = 0.130$).

A potential criticism of our colour association and reversal tasks is that there was no penalty for making errors; individuals that flipped the rewarded colour three times and the unrewarded colour once (and thus 'failed') did not experience a significantly greater cost than individuals that flipped the rewarded colour four times in a row (and thus 'succeeded'). Since all individuals had acquired facility with flipping lids by the time they were tested on the colour association and reversal tasks, the cost in terms of time delay until reward was small. In contrast, during the detour-reaching trials a bird usually pecked numerous times against the sides of the plastic cylinder without obtaining any reward, and this may have represented a more negative experience for the test subjects.

The fact that we did not find that song sparrows' performances across the four learning tasks were all positively correlated with each other or with song repertoire size in the 2 years of our study could be interpreted as a lack of evidence for a general cognitive ability in this species. However, as the development of such cognitive test batteries for birds is clearly in its infancy, more studies are required to clarify the mixed results we found. In addition, it would be useful for future studies to assess interindividual differences in variables such as (feeding) motivation, body condition, age, sex, reproductive success, neophobia, exploratory behaviour and habituation to captivity, to test whether these and other factors may be associated with variation in individuals' cognitive performance on different tasks (e.g. Reader & Laland 2003; Boogert et al. 2006; Biondi 2010). It may also be that a clearer relationship between song and cognitive ability could be discerned using song measures that reflect song-learning ability more directly than does song repertoire size. Perhaps the most direct measures of song-learning quality are ones that estimate the accuracy with which learners copy specific song models (Nowicki et al. 2002b). Use of such metrics requires that song models be identified, which, depending on the species, can be done with more or less difficulty in the field (Nordby et al. 1999), and may involve heterospecific song models (e.g. Coleman et al. 2007). Alternatively, song models can be assigned in laboratory experiments using either live or tape tutors. Thus laboratory experiments that examine both song learning and performance on cognitive tests may be the best route to making further progress on the relationship between song and cognition.

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Supplementary Material

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