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Male satin bowerbird problem-solving ability predicts mating success

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Mate choice and mate attraction are important behaviours influencing the evolution of elaborate traits. It is possible that male general cognitive performance plays an important role in sexual attractiveness, but there has been no direct test of this hypothesis. Satin bowerbirds, *Ptilonorhynchus violaceus*, are an excellent species for testing this hypothesis because their complex male courtship, including use of decorations of certain colours, suggests a selective advantage to individuals with superior cognitive abilities. We used males' strong aversion to red objects on their bowers to design two unique problem-solving tests. We presented males with these problems to test the hypothesis that males that are better problem-solvers have higher mating success. We confirmed this prediction and demonstrate that neither age nor motivational level significantly influenced problem-solving scores. Our findings suggest that general cognitive performance is related to male mating success. This is the first evidence that individuals with better problem-solving abilities are more sexually attractive.

Since Darwin there has been great interest in both sexual selection (Darwin 1871) and mental processes (Darwin 1871, 1872), both of which have important effects on fitness. Perhaps because many evolutionary biologists have underappreciated the significance of mental processes in nonhuman organisms, their influence on fitness, in conjunction with that of sexual selection, has received scant attention. Recently, the greater appreciation that cognitive performance can affect fitness (Shultz et al. 2005; Sol et al. 2005, 2007, 2008; Roth & Pravosudov 2009), the obvious large investments in tissue associated with cognition (Aiello & Wheeler 1995) and the high level of complex behavioural interactions in sexual displays (e.g. Balsby & Dabelsteen 2002; Patricelli et al. 2002) all suggest there may be important effects of cognition on sexual display and mate choice (see also Miller 2001; DeVoogd 2004). Here we test the 'cognitive performance hypothesis', which suggests a positive relationship between general cognitive performance and reproductive success. We assess general cognitive performance using problem-solving tests, an accepted measure of general cognitive ability (Roth & Dicke 2005). This hypothesis has not been directly tested in any species.

A positive relationship between general cognitive performance and reproductive success could result through at least four processes, as follows. (1) Assuming general cognitive ability is heritable in the target species (e.g. humans: Deary et al. 2006; mice: Galsworthy et al. 2005), cognitively superior males may confer 'good genes' advantages on their offspring, and females may have evolved to choose males for these advantages. For example, females choosing cognitively adept males might have offspring with better cognitive abilities, such as sons with better behavioural displays (Airey et al. 2000b) or daughters with more effective mate discrimination (Leitner & Catchpole 2002). Also, given that there is a connection between levels of parasitism and cognitive functions such as learning and decision making (Kavaliers et al. 1995; Gegear et al. 2005, 2006), offspring of cognitively superior males may inherit greater parasite resistance (Buchanan et al. 1999; Spencer et al. 2005). (2) In socially monogamous species, males that have better cognitive performance may be better at provisioning young (Isler & van Schaik 2006a, 2008). (3) Males may be able to use their cognitive abilities to attract or coerce females into mating with them in ways that may not be beneficial for females but increase male reproductive success (e.g. sensory exploitation: Ryan & Rand 1990). (4) Females may have different requirements for sexual display depending on their age (Coleman et al. 2004) or level of

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experience (Hebets 2003), and males with better cognitive performance might be better able to respond to these diverse needs. All of these examples predict that females will tend to choose males with superior cognitive abilities.

One approach to testing the role of cognition in mate choice has been to conduct comparative studies investigating the relationship between the mean brain size of a species and the elaboration of a sexually selected trait. The results of these studies have been inconsistent, with different studies finding either a positive relationship between total brain size and trait size (e.g. bower complexity: Madden 2001; but see Day et al. 2005), a negative relationship (e.g. testes size: Pitnick et al. 2006), or no relationship (e.g. song complexity: Garamszegi et al. 2005; Spencer et al. 2005). This lack of agreement among studies could result from the use of different sexually selected traits, but it is also likely that cognitive evolution is subject to multiple selective forces that can differentially affect brain size. For example, brain size may be a poor measure of behavioural complexity because many regions of the brain have specific purposes (e.g. vision, spatial memory) that will evolve in response to different selection pressures (Iwaniuk & Hurd 2005; Healy & Rowe 2007). This was demonstrated in the study by Spencer et al. (2005), where song complexity did not correlate with brain size, but did correlate with the size of the HVC, an important song control nuclei (see also Nottebohm et al. 1981; Canady et al. 1984; Airey et al. 2000a; Nowicki et al. 2002).

A more direct approach for testing the cognitive performance hypothesis is to compare problem-solving ability to reproductive success. Problem-solving ability has not been used in sexual selection studies as a measure of cognitive performance, but has a well-established history of use in studying such diverse topics as innovation and behavioural flexibility (Webster & Lefebvre 2001; Biondi et al. 2008; Liker & Bokony 2009), cooperation (Cronin et al. 2005; Seed et al. 2008), tool use (Taylor et al. 2007), theory of mind (Hare et al. 2001), transitive inference (Bond et al. 2003) and neurobiology of spatial memory (Pravosudov & Clayton 2002; Cristol et al. 2003). We conducted the first direct test of the cognitive performance hypothesis using satin bowerbirds, *Ptilonorhynchus violaceus,* by presenting males novel problem-solving tests and comparing their scores to their mating success.

Satin bowerbirds are well suited for testing the cognitive performance hypothesis. Males have many behavioural traits that suggest cognitive performance may be important in their sexual display: they build a stick bower on the ground where courtship occurs (Borgia 1985b), they react to female signals during courtship and adjust their display accordingly (Patricelli et al. 2002), they steal from and destroy neighbouring bowers that are not within view of each other, which implies a mental map of bower locations (Borgia 1985a; Borgia & Gore 1986; Pruett-Jones & Pruett-Jones 1994; Hunter & Dwyer 1997), and they accurately mimic several species of birds during courtship (Loffredo & Borgia 1986; Coleman et al. 2007). Bowerbirds have the seven attributes that Emery (2006) suggests are associated with intelligence, including large relative brain size (Madden 2001; cf. Day et al. 2005; Iwaniuk et al. 2005), extended longevity (males in this study were 7–21 years old) and a long developmental period (7 years to maturity). Finally, bowerbirds have a large skew in male mating success (Borgia 1985b), which indicates strong sexual selection. This measure of mating success is obtained from automated monitoring of bowers where copulations occur (Borgia 1985b; Reynolds et al. 2007) and it accurately reflects paternity (Reynolds et al. 2007).

Each assessment of male problem-solving ability consisted of three related tests. First, we evaluated the hypothesis that there was a positive relationship between problem-solving ability and mating success. Second, we tested males to determine how motivational level affected their problem-solving scores. Motivational level can greatly influence problem-solving performance because unmotivated individuals will score lower on a problem-solving task even when they are capable of solving the problem (Cronin & Snowdon 2008). If a measure of motivation is correlated with problem-solving scores, this could mean that problem-solving scores are not by themselves reliable indicators of cognitive ability because of the difficulty in separating the effects of motivation and cognitive performance. In this situation, one way to separate these effects is to calculate the residuals of a regression between problem-solving ability and motivation to construct a new problem-solving variable with the effect of motivation statistically controlled. Third, we examined the relationship between male age and male problem-solving ability. Differences in performance on particular cognitive tasks have been found in adult animals, with performance increasing with age (e.g. birds: Botero et al. 2009), decreasing with age (e.g. macaques: Tsuchida et al. 2002), or remaining stable until old age (e.g. humans: Thornton & Dumke 2005; orang-utans: Anderson et al. 2007). Therefore, we were interested in understanding not only how problem-solving scores relate to mating success, but also how age and motivational level influence problem-solving scores.

We developed problem-solving tests that took advantage of male satin bowerbirds' strong aversion to red objects on their bower platforms, which they immediately attempt to remove (Morrison-Scott 1937; Borgia et al. 1987; Borgia & Keagy 2006). This behaviour suggests that red objects have a great deal of salience to male satin bowerbirds and that males are highly motivated to remove them. Each problem-solving test involved something that hindered the removal of red objects. In one experiment, a clear container was placed over three red objects on the bower platform. In the other experiment, a red object was glued to a long screw and fixed into the bower platform.

We measured motivation by presenting males with the simple task of moving a small red object away from the bower. Males frequently move objects on and off the bower, a behaviour that probably requires little cognitive ability to complete and therefore should only be influenced by differences in motivation. Both motivation and cognitive ability could affect performance on novel problem-solving tests such as ours that involve more complicated solutions than simply picking up and moving an object. Therefore, we tested for an association between our tests of motivation and problem-solving ability. Absence of an association would suggest that motivation does not drive problem-solving scores, whereas a positive correlation would suggest that motivation may drive problem-solving scores, and that the effects of motivation on problem-solving scores should be statistically removed (Fig. 1).

METHODS

Study System

This study was conducted in 2004 and 2005 at Wallaby Creek (28°28′S, 152°25′E), NSW, Australia (Borgia 1985b). Males court females at bowers that are at least 100 m apart (Borgia 1985a), and females visit a mean $\pm$ SE of 2.64 ± 0.18 adjacent bowers per mating season (range 1–8; Uy et al. 2001). The number of certain types of decorations, especially blue decorations, is an important predictor of male mating success (Borgia 1985b). Females are less likely to startle and prematurely end courtship if males have more blue decorations (Patricelli et al. 2003), and young females mate more with males whose blue bower decorations have been experimentally increased (Coleman et al. 2004). Males procure most blue decorations by stealing them from other male bower-holders (Borgia & Gore 1986; Hunter & Dwyer 1997; Wojcieszek et al. 2007), and blue objects are rare in the environment (Borgia et al.

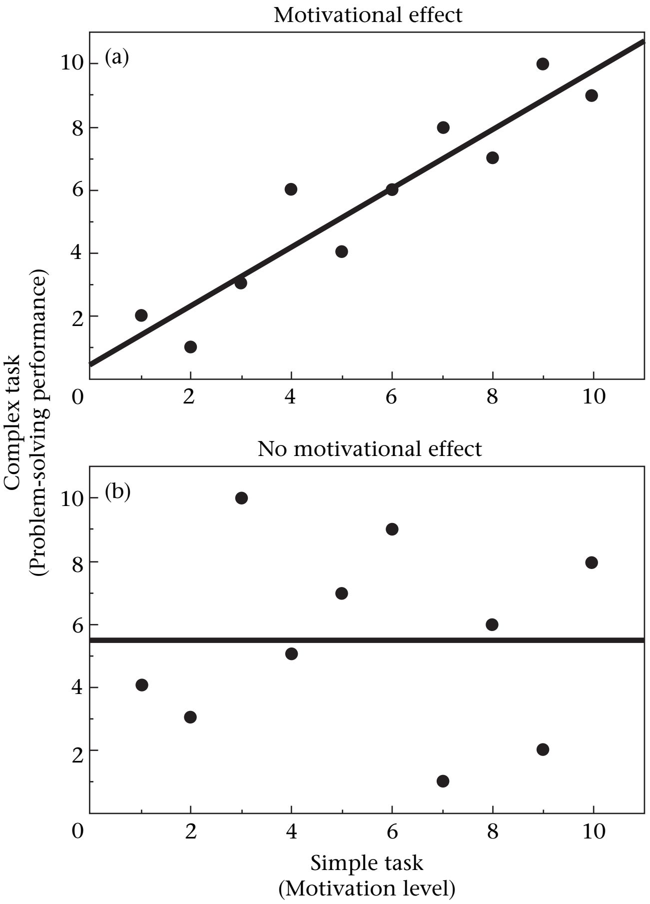

Figure 1. Two potential possibilities for the relationship between measures of motivational level and problem-solving performance. (a) First, if differences in motivation directly influence performance on problem-solving tasks, there should be a correlation between the two scores. (b) Alternatively, if there is no correlation, this suggests that male motivational level does not significantly influence problem-solving scores.

1987), suggesting that the number of blue objects on a male's bower is a measure of male quality. Male bowerbirds have highly specific colour preferences and actively remove red objects on or near their bower platform (Morrison-Scott 1937; Borgia et al. 1987; Borgia & Keagy 2006). This behaviour may be related to the use of specific colour combinations on their bower platform (blue on a yellow background of straw and leaves). In previous tests, male bowerbirds responded much more quickly to problems where red objects had to be removed from their bowers than they did to problems where blue objects had to be collected for their bowers (J. Keagy, personal observation). We took advantage of the males' strong aversion to red objects on their bowers to design problem-solving tests that they would be highly motivated to solve. Males in the present study responded rapidly to tests presented at their bowers, and only the bower owner attempted to solve the tests presented at his bower.

All males were bower-holders in full adult plumage, and each male could be identified by a unique combination of three coloured plastic bands on each leg (Borgia 1985b). We monitored bowers throughout the mating season using an automated video-monitoring system to provide a complete record of behaviour at these bowers. We scored the number of copulations that each male achieved during the breeding season from these videos (Uy et al. 2001), which is an accurate measure of genetic paternity (Reynolds et al. 2007). Monitoring has been uninterrupted at our field site since 1995, providing us with detailed age information for birds in the present study. Capture, banding and experimental protocols were approved by the University of Maryland's Institutional Animal Care and Use Committee (R-04-37) and, locally, by the University of Wollongong Animal Ethics Committee (AE02/18 and AE02/18/r05). Research was conducted in New South Wales under New South Wales National Parks and Wildlife Services licence number S10516, and birds were captured for banding under Australian Bird and Bat Banding Scheme authority numbers 2594 (J. Keagy), 2539 (J-F Savard) and 946 (G. Borgia).

Barrier Experiment

Males were presented with a problem in which a clear barrier was placed over three small red objects on each male's bower platform. The male could not remove the red objects until he solved the problem by removing the barrier. The barrier was a clear plastic container (10 cm diameter, 10 cm tall), placed over three cylindrical red objects (plastic battery terminal covers, 2 cm diameter, 2.5 cm tall) 25 cm from the bower entrance at 25 bowers (Fig. 2). We videotaped all behaviours for 24 h, then removed the experimental apparatus. As a measure of problem-solving ability, we scored the time that each male took to remove the barrier and gain access to the red objects. Males that were better problem-solvers were expected to remove the barrier faster. Time to solve the problem was recorded in two ways. (1) 'Total elapsed time': interval between when the male first encountered the problem (was oriented towards and within 20 cm of the barrier) and when he removed the barrier. This measure allowed for the possibility that males could have been mentally working on the problem when doing other activities. (2) 'Time attentive to task': the number of seconds spent within 20 cm of the barrier and oriented towards it. This measure did not penalize individuals for activities not directly related to solving the problem (e.g. moving decorations around in the area near the barrier, looking away from the barrier, etc.). For both measures, time to solve was rank-transformed so that males that did not solve the task could be included in the analysis (fastest solve time = smallest rank; unsolved = largest rank). The motivation measure was the time that males took to move a red object far enough from the bower to not be visible on video (>20 cm) after the barrier was removed. This measure meant that males that did not solve the barrier task were not scored for motivational level.

Figure 2. Male satin bowerbird attempting to solve barrier problem. Three red objects were placed under a clear container on the bower platform of 25 males.

Red Coverage Experiment

Males were presented with a problem in which they were unable to move an undesirable red object from their bower platform because it was fixed into the ground. In an unrelated experiment, we observed males covering screws inserted into their platforms, which led us to predict that males could solve the current problem by covering the object with naturally available materials (leaf litter, bower decorations, etc.). Males that were better problem-solvers were expected to be more effective in covering the red object. Red, blue and green square plastic tiles (2.54 cm on each side) were placed in fixed positions in the ground 20 cm apart in a triangular configuration at 33 bowers (Fig. 3). We predicted that the tiles would be covered in order of colour preference, and that males would react to the problem by covering the undesirable red tile the most. Tiles were rendered unmovable by super-gluing them to 15 cm screws and sinking the screws into the bower platform and the ground below. At each bower, we randomly assigned the three coloured squares to one of six possible configurations. After 24 h, we took digital photographs of each configuration and measured the uncovered area on each square using Image J (v. 1.34i, National Institutes of Health, Washington, D.C.). We used the area of the red tile that was covered as a measure of problem-solving ability. To measure motivation, we presented males with a red tile that was not fixed into the ground. We did not record the time that males took to move the red tile, but we did record the distance that they moved the red tile after 4 h. We used this distance as our measure of motivation and assumed that males that were more motivated to move red objects would move the red tile further from their bower. We conducted the motivation experiment before presenting the problem-solving task so that the males' motivation scores would not be influenced by prior experience with immovable red tiles.

Figure 3. Layout of the red coverage experiment. A blue, green and red tile were evenly spaced on the bower platform of 33 males. Below are representative pictures showing coverage of the red tile varying from 0% to 100%.

Statistical Analyses

Data were analysed using Statistica 6.0 (Statsoft Inc., Tulsa, OK, U.S.A.). We used regression analysis to test the hypothesis that problem-solving ability predicts mating success. In addition, we tested for the possible influences of age and motivation on problem-solving scores, including a multiple regression analysis to examine how age and motivational level independently affected problem-solving ability. Because we knew a priori that age can be associated with cognitive performance (e.g. Botero et al. 2009) and that age is sometimes positively associated with mating success in satin bowerbirds (J. Keagy, J.-F. Savard & G. Borgia, unpublished data), we performed a partial correlation analysis that removed the effect of age, however small, from both variables.

Our data set consists of performance scores on two problem-solving tests presented in different years, along with each year's associated mating success scores. We used canonical correlation analysis (James & McCulloch 1990; Bond & Diamond 2005) to analyse the combined data to determine the overall correlation between problem-solving ability and mating success. This multivariate approach simultaneously generates weighted linear combinations (called 'canonical variates', CVs) specific to each variable set (e.g. problem-solving ability and mating success) such that the correlation between the predictor and response canonical variates is maximized (i.e. problem-solving CVs versus mating success CVs). This relationship can then be tested for statistical significance. Canonical correlation analysis differs from another common approach in which a measure of association is calculated between the first principal component of each variable set, because when creating canonical variates, all the variation in both sets is considered, whereas construction of principal components maximizes the variance explained in a given variable set without taking into account the variance in any other variable set. This ignored variance may be biologically important to the overall relationship between the variable sets (Lesser & Parker 2006).

Residuals were analysed for normality and, when necessary, variables were transformed. Mating success was rank-transformed because of the strongly skewed distribution of copulations among male satin bowerbirds (2004: range 0–55, mean = 9, median = 5; 2005: range 0–33, mean = 9.52, median = 7). Although rank transformation often results in a uniform distribution, rank transformation of our mating success data resulted in distributions that were sufficiently normal and nearly identical to those achieved through log transformations. We preferred to use ranks because it is a male's relative genetic contribution that determines the strength of sexual selection, and using ranks also seemed more appropriate for analyses that used data from different years with different ranges of mating success. Results were qualitatively the same for all analyses if we used log transformations of mating success instead. Time to solve the barrier experiment was rank-transformed so that males that did not solve the experiment could be included in the analysis (nonsolvers were all given the largest, i.e. worst, rank), and the distribution of this rank-transformed data was sufficiently close to normal. Measures of red tile coverage and motivation did not need to be transformed. Statistical tests of our a priori directional hypothesis that problem-solving ability positively predicts mating success are one tailed (Quinn & Keough 2002). All other tests are two tailed.

RESULTS

Barrier Experiment

We measured the time that males took to solve the barrier problem in two ways. First, we ranked males based on the time that they took to solve the problem after they first encountered the barrier ('total elapsed time'). Males that solved the barrier problem fastest achieved higher mating success (regression: $R^2 = 0.29$, $F_{1,23} = 9.43$, $P = 0.003$; Fig. 4a). For the second measure ('time attentive to task'), we ranked males based on the time they spent within 20 cm of the problem either oriented towards or touching it. This test also significantly predicted male mating success ($R^2 = 0.27$, $F_{1,23} = 8.31$, $P = 0.004$; Fig. 4b). These two measures were highly correlated (Pearson correlation: $R^2 = 0.84$, $t_{23} = 11.08$, $P < <0.0001$).

We tested for the possibility that male age or motivation affected male problem-solving ability. Male age did not predict the time that males took to solve the barrier problem (total elapsed time: $R^2 = 0.01$, $F_{1,23} = 0.20$, $P = 0.66$; time attentive to task: $R^2 = 0.00$, $F_{1,\ 23} = 0.23$, $P = 0.88$), nor did it explain male mating success in 2005, the year in which this problem was presented ($R^2 = 0.01$, $F_{1,23} = 0.33$, $P = 0.57$). A partial correlation analysis removing this small effect of age from both variables gave further evidence of a significant association between problem-solving ability and mating success (total elapsed time: $R^2 = 0.29$, $t_{22} = -2.97$, $P = 0.004$; time attentive to task: $R^2 = 0.26$, $t_{22} = -2.78$, $P = 0.005$). We measured motivation as the time that males took to move one of three red objects far enough from their bower to not be visible on video (>20 cm). Males tended to do this quickly (mean ± SD = 14.75 ± 7.86 s, range 4–28 s), implying that the males were highly motivated to move the red objects. Most of the variance in time was determined by the latency to move the red object rather than the time spent carrying the object. This motivation measure did not explain the speed at which males solved the barrier problem (total elapsed time: $R^2 = 0.01$, $F_{1,14} = 0.09$, $P = 0.77$; time attentive to task: $R^2 = 0.08$, $F_{1,14} = 1.22$, $P = 0.29$). In addition, we performed a multiple regression analysis in which motivation and age were used to explain problem-solving ability. Neither the model nor the individual components of the model significantly explained problem-solving ability (total elapsed time: $R^2 = 0.12$, $F_{2,13} = 0.86$, $P = 0.44$, $b_{\text{age}} = 0.37$, $P = 0.22$, $b_{\text{motivation}} = 0.08$, $P = 0.80$; time attentive to task: $R^2 = 0.25$, $F_{2,13} = 2.17$, $P = 0.15$, $b_{\text{age}} = 0.46$, $P = 0.11$, $b_{\text{motivation}} = 0.48$, $P = 0.10$). The lack of a significant relationship between problem-solving ability and either age or motivation, the two most likely alternative explanations for our observed results, is consistent with the hypothesis that male ability to solve the barrier problem was influenced primarily by cognitive ability.

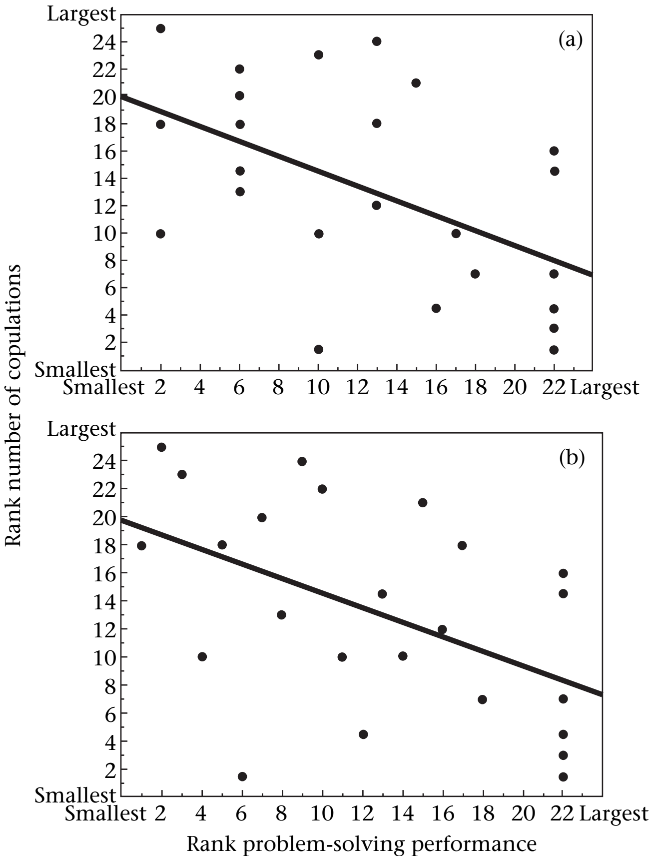

Figure 4. Relation between problem-solving performance (less time = better performance = smaller rank) and mating success (more copulations = larger rank) of male bowerbirds: (a) total elapsed time: $R^2 = 0.29$, $F_{1,23} = 9.43$, $P = 0.003$; (b) time attentive to task: $R^2 = 0.27$, $F_{1,23} = 8.31$, $P = 0.004$. 'Total elapsed time' was measured as the time since the male first encountered the problem until he solved it by removing the barrier. 'Time attentive to task' was measured as the number of seconds the male spent within 20 cm of the problem either oriented towards or touching it. Males that did not solve the experiment were given the largest rank (most time).

Red Coverage Experiment

Male bowerbirds covered red tiles significantly more than they did blue tiles (Wilcoxon signed-ranks test: $T = 174$, $N = 33$, $P = 0.029$) and they tended to cover red tiles more than they did green tiles ($T = 196$, $P = 0.066$). This result is consistent with satin bowerbird colour preferences (i.e. blue preference > green > red) and suggests that males were reacting to the problem by covering the undesirable red tile most. However, the amount of the red tile covered was not significantly related to male mating success ($R^2 = 0.02$, $F_{1,31} = 0.79$, $P = 0.19$). Male age did not explain the amount of the red tile covered ($R^2 = 0.03$, $F_{1,31=}0.91$, $P = 0.35$), but it did predict male mating success in 2004, the year that this problem was presented, with older males having more copulations ($R^2 = 0.27$, $F_{1,31} = 11.71$, $P = 0.002$). We performed a partial correlation analysis to determine the relationship between problem-solving ability and mating success independent of age effects, and we found a significant association between problem-solving ability and mating success ($R^2 = 0.09$, $t_{30} = 1.68$, $P = 0.05$).

Tiles were placed in a triangle, with two of the tiles close to the bower walls and the third tile further from the bower walls near the middle of the display platform and directly in front of the bower entrance (Fig. 3). There was a significant difference in the variation in coverage of the red tile depending on its position (adjacent to the bower versus away from the bower; Levene's test: $F_{1,31} = 4.36$, $P = 0.045$), with more variation in the group of males with the red tile in the position away from the bower. When considering only the males with the red tile in the away position, the amount of red tile coverage significantly predicted mating success (effect of age not removed: $R^2 = 0.43$, $F_{1,8} = 5.98$, $P = 0.02$; effect of age removed: $R^2 = 0.77$, $t_7 = 4.83$, $P = 0.0009$). We had detailed position data available for movements of nine males on their bower platforms (not during the experiment) and found that during courtship, males do not appear to spend more time within 10 cm of one tile position relative to another (position 1 = close to left bower wall, position 2 = close to right bower wall, position 3 = middle of display platform; paired *t* tests: 1 versus 2: $t_8 = 0.58$, $P = 0.58$; 1 versus 3: $t_8 = -0.95$, $P = 0.37$; 2 versus 3: $t_8 = -1.19$, $P = 0.27$). This suggests that variation in red coverage based on tile position is not explained by variation in incidental disturbance of decorations caused by male movement on the bower platform. We had detailed information on the number of decorations within 10 cm of each tile position within a week of the experiment for 26 males and found that decoration numbers did not vary by position (paired *t* tests: 1 versus 2: $t_{25} = 0.00$, $P = 1.00$; 1 versus 3: $t_{25} = 0.37$, $P = 0.71$; 2 versus 3: $t_{25} = 0.37$, $P = 0.71$). This suggests that variation in decoration position and availability does not explain variation in red coverage based on red tile position.

We measured motivational level by determining how far males moved the same red tiles when they were not fixed in the ground. This measure of motivation did not explain the amount of coverage of red tiles by males (all males: $R^2 = 0.03$, $F_{1,22} = 0.61$, $P = 0.44$; males with red in the away position: $R^2 = 0.00$, $F_{1,6} = 0.01$, $P = 0.93$). In addition, we performed a multiple regression analysis in which motivation and age were used to explain problem-solving ability. Neither the model nor the individual components of the model significantly explained problem-solving ability (all males: $R^2 = 0.12$, $F_{2,18} = 1.21$, $P = 0.32$, $b_{age} = -0.34$, $P = 0.20$, $P_{motivation} = -0.01$, $P = 0.96$; males with red in the away position: $R^2 = 0.30$, $F_{2,2} = 0.42$, $P = 0.70$, $b_{age} = -0.50$, $P = 0.58$, $b_{motivation} = -0.07$, $P = 0.93$). The lack of a significant relationship in these comparisons is consistent with the hypothesis that the males' ability to solve the red coverage problem was driven primarily by cognitive performance.

Relationship between Problem-solving Tests

Twenty males were presented both problem-solving tests (barrier experiment in 2005; red coverage experiment in 2004). There was no correlation between scores on the two problems (Pearson correlation: total elapsed time × red coverage: $R = -0.04$, $P = 0.88$; time attentive to task × red coverage: $R = -0.17$, $P = 0.46$). We performed a canonical correlation analysis to determine the overall correlation between problem-solving ability on both tests and mating success in both years. We found a strong positive relationship between problem-solving ability and mating success (using total elapsed time as barrier problem-solving ability: canonical $R = 0.74$, $\chi^2_4 = 15.46$, $P = 0.002$; using time attentive to task as barrier problem-solving ability: canonical $R = 0.71$, $\chi^2_4 = 14.05$, $P = 0.004$; Table 1). This relationship was even stronger when age was factored out of all variables (using total elapsed time as barrier problem-solving ability: canonical $R = 0.78$, $\chi^2_4 = 18.47$, $P = 0.0005$; using time attentive to task as barrier problem-solving ability: canonical $R = 0.74$, $\chi^2_4 = 16.90$, $P = 0.001$).

Table 1
Factor structure (loadings) of first canonical variates from canonical correlation analysis*

Variable	Factor structure (loading)
Analysis 1†	
Problem-solving ability	
Barrier removal (rank total elapsed time)	−0.70
Red coverage	0.74
Mating success	
Rank number of copulations 2004	0.49
Rank number of copulations 2005	0.99
Analysis 2†	
Problem-solving ability	
Barrier removal (rank time attentive to task)	−0.76
Red coverage	0.77
Mating success	
Rank number of copulations 2004	0.50
Rank number of copulations 2005	0.99

* The canonical correlation analysis was done twice, once using 'total elapsed time' as a measure of problem-solving ability on the barrier experiment and once using 'time attentive to task'. The barrier experiment was conducted in 2005 and the red coverage experiment was conducted in 2004.

† The factor structure supports the predicted relationships between problem-solving ability and mating success, as also shown in the univariate analyses.

Direct Effects of Problem-solving Experiments on Female Mating Decisions

For females to make mate choice decisions based directly on male performance on the problem-solving tests, they would have had to visit bowers during the experiments. However, few females visited bowers during the problem-solving tests (mean ± SD barrier: 0.64 ± 0.81; red coverage: 0.97 ± 1.19). The number of visits by females during testing was less than 2% of the total number of visits to bowers during the entire mating season. The number of females present at bowers during testing was less than 10% of the total number of mate-shopping females.

DISCUSSION

This is the first study to show evidence of a positive relationship between male problem-solving ability and mating success. The results from our canonical correlation analysis revealed that although the problem-solving tests were very different from each other and scores on each were not statistically significantly correlated, there was a common cognitive factor that was positively associated with mating success. This is analogous to the situation in humans where the intelligence factor, *g*, is a latent variable formed from a factor analysis of multiple abilities (e.g. verbal ability, mathematical ability, etc.) that are not always statistically significantly correlated. The general intelligence factor, *g*, was first described by Spearman (1904) and has since been shown to be one of the most heritable and repeatable of all human behavioural traits (Brody 1992; Mackintosh 1998; Deary 2000). Furthermore, we were able to quantify age and motivational level, and we found that neither variable explained problem-solving scores.

Given that it is unlikely that females were directly influenced by our experiments, the association between problem-solving ability and mating success could result from two other mechanisms. First, females may actively select mates based on traits that are correlated with problem-solving ability. For example, a recent study found that the ability of male zebra finches, *Taeniopygia guttata*, to learn a foraging task was related to song complexity (Boogert et al. 2008), a trait known to influence mate choice in this species and others (e.g. Hasselquist et al. 1996; Byers 2007; Coleman et al. 2007). Female bowerbirds may attend to male behavioural display traits that have a strong cognitive component and are related to mating success, such as vocal mimicry of other species of birds (Loffredo & Borgia 1986; Coleman et al. 2007) or quality of bower construction (Borgia 1985b). Female bowerbirds may have evolved to choose males with better cognitive performance because of good genes benefits associated with mating with males that have better cognitive abilities. Second, males that are better problem-solvers may be better able to influence females to choose them as mates. For example, in satin bowerbirds, males that respond to female signals of comfort are preferred as mates (Patricelli et al. 2002, 2006). These mechanisms are not mutually exclusive, and each mechanism would result in females tending to select males with traits that are correlated with problem-solving ability. This correlated effect could also lead to the evolution of increased cognitive performance through sexual selection.

The actual patterns of cognitive evolution resulting from sexual selection on male cognitive performance are unclear. One prediction is that species with more intense sexual selection, such as polygynous species, should have enhanced cognitive abilities because of more intense selection for males with better cognitive performance. The degree to which this pattern is seen in a given taxon may vary for many reasons. First, costs associated with more complex or bigger brains (metabolic costs: Aiello & Wheeler 1995; Isler & van Schaik 2006b; life-history costs: Foley & Lee 1991;

developmental costs: Barrickman et al. 2008) may limit the extent to which evolution of cognitive performance is possible. Second, higher cognitive performance can have additional fitness advantages to males, which could have diverse effects on the realized strength of sexual selection in some species. For example, in socially monogamous species, males with better cognitive abilities may be better at provisioning young and this could increase the number of offspring that those males have relative to other males (Isler & van Schaik 2006a, 2008). For these reasons, patterns of cognitive elaboration may not be predictable simply by the level of reproductive skew or other measures of the strength of sexual selection.

Continued sexual selection on males for increased cognitive performance could lead to sexual dimorphism in cognitive abilities. For example, sexual dimorphism in spatial cognitive abilities has been demonstrated in rodents (Galea et al. 1996; Jonasson 2005), with males having better spatial abilities presumably because they search for females. Costs may limit the elaboration of such cognitive abilities in the sex that is not under sexual selection. Sexual dimorphism in cognitive abilities could also evolve because of different selective forces on males and females, with specific abilities being emphasized in each sex (Lindenfors et al. 2007). This type of sexual dimorphism may not occur if there is also selection on females for similar types of increased cognitive abilities so that they can make better mate choice decisions. For example, female canaries with more developed HVCs are better able to discriminate between male songs (Leitner & Catchpole 2002), and males with more developed HVCs have more complex songs (Nottebohm et al. 1981).

The cognitive performance hypothesis has similarities to the nutritional stress hypothesis (NSH) (Nowicki et al. 1998, 2002), or the more general developmental stress hypothesis (DSH) (Buchanan et al. 2003). These hypotheses suggest that a single cognitive trait, birdsong, indicates male quality to females because of a connection between a male's ability to buffer developmental stress and the quality of the brain tissue that influences song production as an adult. The NSH and DSH received initial experimental (Nowicki et al. 2002; Buchanan et al. 2003; Spencer et al. 2005; MacDonald et al. 2006) and recent theoretical support (Ritchie et al. 2008). However, studies imposing naturally occurring levels of stress on young birds have mixed support for these hypotheses (for: Soma et al. 2009; against: Gil et al. 2006). Also, in long-lived species, it would be difficult for females to distinguish between high-quality males that show some effects of stress because they developed in bad years and poor-quality males that developed during good years and suffered little stress (Borgia 2006). The cognitive performance hypothesis differs from the NSH and DSH in three important respects. First, it suggests that cognitive abilities in general, rather than only birdsong, influence reproductive success. Second, it can operate under a wider range of conditions because it is not restricted to those situations where early developmental stress is important, as are the NSH and DSH. Third, because it is not dependent on stressful conditions to produce phenotypic effects, it avoids the problem of separating environmental and genetic effects in mating systems where females may be choosing the latter. The cognitive performance hypothesis is more widely applicable than the NSH or the DSH, and it has great relevance for understanding the evolution of cognition through sexual selection.

In summary, we conducted the first test of the hypothesis that males with higher general cognitive performance have higher mating success. Our results indicate that male general cognitive ability is an important and previously unconsidered factor in determining male mating success. It is possible that bowerbirds evolved enhanced cognitive performance because of sexual selection, but whether sexual selection is currently driving further evolution of male cognitive abilities depends on many factors, including the relative current costs and benefits of better cognitive abilities and the heritability of cognitive performance differences. Our results suggest that cognitive performance is important to male reproductive success, but we also suggest that there are many sexually selected advantages to females in having well-functioning brains, especially given the complexity of female mate choice in many species.

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