Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, *Ptilonorhynchus violaceus*

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Many animal species have complex cognitive abilities previously assumed to be limited to humans. Explanations for how these abilities evolved have focused on ways in which cognitive performance may influence survival, such as solving ecological problems or navigating complex social environments. However, sexual selection (differences in the reproductive success of individuals) can also lead to the evolution of complex traits. This could occur, for example, if females prefer males with better cognitive ability. A common assumption of models of female choice for male cognitive ability is that performance scores on different cognitive tasks are intercorrelated. In the present study, we evaluated performance of male satin bowerbirds on six cognitive tasks. Although we found little intercorrelation amongst males' performance scores of these tasks, males with better scores for two integrative measures of these cognitive tasks had higher mating success, which is a good indicator of reproductive success in this species. In addition, a multiple regression analysis suggested that performance on most cognitive tasks independently predicted mating success. Our results point to an important link between sexual selection and cognitive ability that has not been well appreciated and appears to be quite complex.

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Cognition is commonly defined as neuronal processes concerned with acquisition, processing, retention and use of information (Dukas 2004; Shettleworth 2010). Many species have complex cognitive abilities that were once considered to be limited to humans (Tomasello & Call 1997; Shettleworth 2010). These well-developed cognitive abilities are thought to have evolved for a variety of reasons including solving ecological problems (Pravosudov & Clayton 2002; Sol et al. 2007; Cnotka et al. 2008) or navigating complex social environments (Byrne & Whiten 1988; Dunbar 1998; Bond et al. 2003; Holekamp et al. 2007). Mate choice and mate attraction are significant behaviours that also have large impacts on fitness and influence the evolution of elaborate traits (Darwin 1871; Andersson 1994). However, there has been much less attention on the possible connection between cognitive performance (shorthand for 'performance on one or more cognitive tasks') and sexual selection. This should be surprising given the potentially large fitness benefits of mating with individuals with better cognitive performance and the behavioural and possibly cognitive complexity of many sexual displays (e.g. cooperative and highly coordinated sexual displays of several manakin species (Pipridae): Prum 1994; elaborate construction and decoration of bowers in bowerbirds: Frith & Frith 2004).

A few recent studies have demonstrated that individuals that are better at certain cognitive tasks are sexually preferred (bowerbirds: Keagy et al. 2009; guppies: Shohet & Watt 2009) or have more elaborate sexually selected signals (zebra finches: Boogert et al. 2008; guppies: Karino et al. 2005, 2007). Females may preferentially choose males with better cognitive performance for a number of reasons (reviewed by Keagy et al. 2009). The most commonly considered are that a female receives either direct benefits from males that use their cognitive abilities to better provide for the female and/or offspring (Isler & van Schaik 2006, 2008) or indirect genetic benefits from heritable differences in male quality related to male cognitive ability (Airey et al. 2000). These two possibilities are not mutually exclusive, however, if the cognitive trait(s) that allow an individual to be a better provider are heritable. In fact, heritability of cognitive ability has been demonstrated in a number of species (mice: Galsworthy et al. 2005; humans: Plomin 2001; Deary et al. 2006; fish: Karino et al. 2005). Thus, offspring of a male that performs well at a cognitive task could inherit the ability to do well at that same task.

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It has also been suggested that individuals that perform well at one cognitive task are preferred by females because they are better at cognitive tasks in general, which can result in both direct and/or indirect benefits for females (DeVoogd 2004; Boogert et al. 2008; Keagy et al. 2009). This particular scenario is only possible, however, if there are intercorrelations between cognitive traits. In humans, this 'positive manifold' has often been observed in large batteries of cognitive tests (Plomin 2001), although a statistical reduction of these data to a single metric, g, has been controversial because of the widely accepted view that human intelligence is more complex than this (Brody 2000). Animal cognition research has tended to focus on 'cognitive modules', often rejecting suggestions of an analogue to human 'intelligence' (Shettleworth 2010). However, Lefebvre (2010) recently suggested that there are some general processes involved in animal cognition. Evidence for a general cognitive ability has been found in mice (Galsworthy et al. 2002, 2005; Matzel et al. 2003; but see Locurto et al. 2003) and tamarins (Banerjee et al. 2009). The statistical technique usually used to construct g (principal components analysis; Spearman 1904; Plomin 2001; Locurto et al. 2003) does have widespread use in studies of behavioural ecology and evolution, where it is used to create composite measures from sets of variables. While we acknowledge that animal cognition is not as simple as a single metric, principal components analysis does give us a tool to examine the degree to which performance on different cognitive tasks are intercorrelated. Even more interestingly, it offers us an opportunity to determine whether common variation in cognitive traits is related to male mating success.

Satin bowerbirds offered us the opportunity to test the hypotheses that there is covariation between male performance on cognitive tasks and that this covariation is associated with male reproductive success. Several aspects of satin bowerbird biology make them ideal for this study. First, males have a large set of behaviours that appear to have a considerable cognitive component (Madden 2008; Keagy et al. 2009). Second, males build and defend display sites called bowers (Borgia 1985b), providing specific locations where we could present individual males with a number of distinct cognitive tasks. In addition, these sites are not within visual range of each other (at least >100 m apart) and males are not tolerated at neighbouring bowers, making it very unlikely that individuals could have observed others completing tasks. Third, our use of video cameras triggered by infrared detectors at these sites (Borgia 1985b) allowed us to record all behaviour at bowers during daylight hours (this resulted in roughly 5000 h of video per 2-month mating season). This allowed us to record in detail male performance on cognitive tasks. In addition, this camera system permitted us to detect every copulation in our population (even with very rare camera malfunctions, we estimate that we captured >99% of copulations), which provides an extremely accurate measure of mating success (Borgia 1985b). This measure is known from paternity analyses to be a good proxy for reproductive success in our study population (Reynolds et al. 2007).

From our population of approximately 30 adult breeding males, we were able to assess 21 of them on their performance on six different cognitive tasks. The first two tasks were previously validated methods of assessing problem-solving ability in satin bowerbirds: (1) ability to remove a clear barrier covering target objects and (2) ability to conceal an immovable undesirable object (Keagy et al. 2009). The third task was mimetic repertoire size during courtship of females. Birdsong, and mimetic ability in particular, is widely accepted as a learned behaviour with later song production from memory (Beecher & Brenowitz 2005) and as such is a cognitive trait. The last three tasks were variables recorded after destroying one of the two walls of each male's bower, a novel situation that we have not observed to occur in nature, although

other types of bower destruction are done by neighbouring males (Borgia 1985a). Bower building has been suggested to be a cognitively complex task (Madden 2001), and comparative analyses of a number of bowerbird species have suggested a link between bower complexity and brain size (Madden 2001) or at least cerebellar size (Day et al. 2005). The cerebellum is thought to influence observational and experiential learning of procedural tasks (Leggio et al. 2000; Graziano et al. 2002) and the ability to learn to associate a particular context with a specific motor sequence that is later recalled and used (Trach 1996). The first variable we assessed after the one-wall bower destruction was bower-rebuilding efficiency, measured as the handling time of sticks. This variable is heavily influenced by motor coordination that is refined through a 7-year period of improvement during which juveniles practise building bowers (Vellenga 1970; Collis & Borgia 1993) and engage in social learning (Madden 2008). The second variable, flexibility in bower rebuilding, was measured as the proportion of sticks that males placed where the destroyed wall had been. This variable is more akin to problem-solving ability because males that react flexibly and appropriately to the problem of creating a symmetrical bower (which females prefer; Borgia 1985b) when one wall is missing, should place most of the sticks where the destroyed wall was, rather than inflexibly placing half of the sticks in each side. The final variable was a measure of male use of a behavioural 'tool' for creating symmetrical bowers, called 'templating'.

We chose these tasks to maximize ecological validity and the range of cognitive complexity and modality. This is important to meet the goal of constructing a variable that reflects variation in neurophysiological quality (and perhaps ultimately genetic quality), which is a common interpretation of the g factor (Miller 2000; Plomin 2001; Banerjee et al. 2009). We anticipate that there may be some disagreement regarding the cognitive nature of these tasks because some of them have not been used before. However, all six of these tasks fit the common definition of cognition given above.

In general, studies of cognition rely on food rewards to ensure sufficient motivation of subjects, either starving individuals for a set period of time before testing or using highly preferred food treats. Note, however, that this procedure does not control for individual differences in motivational level (see Roth et al. 2010 for a way in which this has been done). We took a different approach. For our problem-solving tests we took advantage of male bowerbirds' intense dislike for red objects at their bowers (Morrison-Scott 1937; Borgia et al. 1987; Borgia & Keagy 2006) to design problem-solving tests that males were highly motivated to complete (Keagy et al. 2009). In addition, we could estimate male motivational level by presenting males with the simple task of moving a small red object away from the bower (i.e. no obstacle to its removal) and then seeing whether male propensity to move this object was a good predictor of problem-solving performance (Keagy et al. 2009). For the variables measured following the one-wall destruction experiment, we knew that all males were motivated to build bowers by virtue of them having built bowers in the first place (there is strong competition for bower sites) and their constant maintenance behaviour. However, as a more rigorous measure of their motivation to rebuild, we measured the latency between our one-wall destruction and when the male started to rebuild. Although we did not have a direct method for assessing motivational level for mimicry, mimetic repertoire size has been widely accepted as a cognitive trait. In addition, males were recorded mimicking to females, which means their motivational level would be expected to be high. In conclusion, individual motivation to perform these cognitive tasks should have been high and, in most cases, we had actual measurements directly related to motivational level to evaluate statistically the effect of motivation on task performance.

Consistent with other studies (Spearman 1904; Plomin 2001; Galsworthy et al. 2005), we constructed *g* using scores from the first unrotated principal component from a principle component analysis of the six cognitive tasks. We also examined the other factors that explained a large proportion of the variance in cognitive task scores (eigenvalues > 1) and the correlation matrix to see how well the data fit a model of a general cognitive ability and intercorrelation of task performance scores. In addition, we calculated an additive measure of cognitive ability analogous to human IQ (Plomin 2001) by determining the average rank score of each male across all tasks. We tested the hypothesis that males with better cognitive ability had higher mating success using these two integrative measures of cognitive ability. Finally, we examined through a multiple regression analysis how performance on each cognitive task independently predicted mating success.

METHODS

Study Site and Data Collection

This study was conducted in 2004 and 2005 at Wallaby Creek (28°28′S, 152°25′E), NSW, Australia. All bower holders could be identified by a unique combination of three coloured plastic bands on each leg. All behaviours at 21 bowers were monitored throughout the mating season (31 October 2004–21 December 2004 and 27 October 2005–19 December 2005) using an automated video-monitoring system. There has been uninterrupted monitoring of our field site since 1995, providing us detailed age information for birds. Males in this study were between 8 and 20 years old in 2004 (mean ± SD age = 11 ± 3.48 years). 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.K.), 2539 (J.-F.S.) and 946 (G.B.).

Problem-solving Tests (Tasks 1–2)

Males have strong preferences for decorations of particular colours collected from the environment (Borgia et al. 1987; Borgia & Keagy 2006) that are rare (Borgia et al. 1987) and attractive to females (Borgia 1985b; Coleman et al. 2004). Males have an intense dislike for red objects at their bowers (Morrison-Scott 1937; Borgia et al. 1987; Borgia & Keagy 2006), but not in other contexts (e.g. foraging: Borgia & Keagy 2006). We used this behaviour to design problem-solving tests that males were highly motivated to complete (Keagy et al. 2009). Detailed validation of these methods is described elsewhere (Keagy et al. 2009). Briefly, in 2004 we super-glued a red square tile to a long screw and fixed the tile into the bower platform and ground below so that it could not be physically removed. We took digital photographs after 24 h and calculated the proportion of the red tile covered (task 1: red coverage) using ImageJ software (v.1.34i, National Institutes of Health, Bethesda, MD, U.S.A.). In 2005 we placed a clear container (>50% the size of the male) over three red objects and quantified the time for each male to remove the container (task 2: barrier problem). Versions of this particular task have been used in other tests of problem-solving ability (e.g. Roth et al. 2010). For many males we were able to quantify their motivation to solve these two problems using the same red objects in situations where there was no obstacle to their removal (Keagy et al. 2009). Males responded

rapidly to tests presented at their bowers, and only the bower owner attempted to solve the tests presented at his bower.

Mimetic Repertoire Size (Task 3)

Using automated camcorders equipped with omnidirectional microphones suspended 1 m above bowers, we recorded all male courtship vocalizations during the mating season of 2004. We used Raven Pro 1.3 (Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.) to visualize and analyse sound recordings. Individual males in our study population mimic up to five sympatric bird species: laughing kookaburra, *Dacelo novaeguineae*; Lewin's honeyeater, *Meliphaga lewinii*; Australian raven, *Corvus coronoides*; sulphur-crested cockatoo, *Cacatua galerita*; and yellow-tailed black cockatoo, *Calyptorhynchus funereus* (Coleman et al. 2007). We calculated the average number of species mimicked for all males using courtships between unique male–female dyads. This procedure controlled for repeated interactions between a male and the same female influencing his behaviour towards her. Number of courtships available for analysis was not correlated with mimetic repertoire size (Pearson correlation: $r_{19} = 0.08$, $P = 0.73$), suggesting that additional data would not qualitatively change our results.

Bower Rebuilding (Tasks 4–6)

We destroyed one wall of each male's bower once during the mating season of 2005. Destructions were spread over a 3-week period after the peak in female copulations had occurred, to reduce any direct effects on female mate searching. The wall that was destroyed was randomly chosen such that half of the bowers had the eastern wall destroyed and half had the western wall destroyed. Bowers were destroyed in the morning (0636–0955 hours Australian Eastern Daylight Time; mean ± SD time = 0803 ± 0101 hours), as this is the time when males are most active. Destructions were done by lifting up one entire wall from the bower platform, pulling the sticks apart and laying them flat on the ground near where the wall had been. For rebuilding, males used sticks from the destroyed wall as well as from the bower platform (in other words, males travelled short and roughly equal distances for the sticks used to build during our observation periods). We recorded all rebuilding behaviour on video and determined the total time that males took to place 100 sticks (task 4: handling time), the proportion of those sticks placed in the destroyed wall (task 5: building flexibility) and the proportion of sticks placed using a behavioural 'tool' called 'templating' (task 6: templating). Males that had longer handling times had greater difficulty manipulating sticks, were more likely to drop sticks as they were being placed, had to try multiple times to get a stick placed properly, and/or moved a stick multiple times to different locations before making a final decision on where it should be placed (J.K., personal observation). Males that placed more sticks in the missing wall were reacting more appropriately to the novel situation of only one wall being completely destroyed and the problem of creating a symmetrical bower, which is preferred by females (Borgia 1985b). The fact that males on average placed a significantly greater proportion of sticks in the destroyed side (mean ± SD: $0.70 ± 0.10$; $t_{19} = 9.14$, $P << 0.0001$), suggests that males tended to react to this problem in a flexible and appropriate manner, adding support for this variable being used as a cognitive measure. During templating, males pick up a stick and stand on the midline of the bower avenue. They then place the stick into or against one wall and, without letting go of the stick, pull it away from that wall, and, using an exact reversal of movements, they place the stick in an identical position in the opposite wall. In addition to these measures of cognitive performance, we recorded the time between the

Table 1
Correlation matrix of cognition variables

	Task 1: red coverage	Task 2: barrier problem	Task 3: mimetic repertoire size	Task 4: handling time	Task 5: building flexibility	Task 6: templating
Task 1: red coverage						
Task 2: barrier problem	$(-)$ $r_{19}=-0.18$ $P=0.43$					
Task 3: mimetic repertoire size	$(+)$ $r_{19}=0.18$ $P=0.42$	$(-)$ $r_{19}=0.40$ $P=0.07$				
Task 4: handling time	$(-)$ $r_{18}=-0.16$ $P=0.51$	$(+)$ $r_{18}=0.16$ $P=0.49$	$(-)$ $r_{18}=-0.11$ $P=0.66$			
Task 5: building flexibility	$(+)$ $r_{18}=0.27$ $P=0.25$	$(-)$ $r_{18}=0.09$ $P=0.70$	$(+)$ $r_{18}=-0.10$ $P=0.66$	$(-)$ $r_{18}=0.16$ $P=0.50$		
Task 6: templating	$(+)$ $r_{18}=-0.18$ $P=0.46$	$(-)$ $r_{18}=0.11$ $P=0.66$	$(+)$ $r_{18}=-0.08$ $P=0.74$	$(-)$ $r_{18}=0.45$ $P=0.045$	$(+)$ $r_{18}=-0.12$ $P=0.62$	

$(+)$ and $(-)$ refer to a hypothesized positive and negative correlation, respectively, under the hypothesis that skill in one cognitive task correlates with skill on another cognitive task.

destruction of the wall and the time that the male began to rebuild the wall using video time stamps. This is a measure of male motivation to rebuild, with males that have longer latencies to build being less motivated to build. Males always began rebuilding the same day their bower wall was destroyed (mean $\pm$ SD time to begin rebuilding $= 39.35 \pm 85.68$ min, range 3–398 min).

Statistical Analyses

Data were analysed using Statistica 6.0 (Statsoft Inc., Tulsa, OK, U.S.A.). We used Pearson correlations to test for associations between variables. We performed a principal components analysis to determine how well covariance between cognitive traits fit a model of a single general factor of cognitive ability. We constructed g using scores from the first unrotated principal component from this analysis (Plomin 2001; Locurto et al. 2003). We also conducted factor rotations (e.g. varimax) to determine the robustness of conclusions based on the original principal components analysis. These analyses were done on standardized data (z-transformed values) because of the very different units and variances of the cognitive variables. As an alternative measure of cognitive ability analogous to IQ, we took the average of each male's relative performance on each of the cognitive tasks (with a rank of 1 being worst at that task). Multiple regression analysis was used to test whether different cognitive tasks independently predicted mating success.

Residuals of analyses were examined for normality and, when appropriate, variables were transformed to create distributions that were sufficiently normal. Mating success for each year was rank-transformed because of the strongly skewed distribution of copulations amongst male satin bowerbirds (Keagy et al. 2009). Results were similar when we used log transformations. Rank mating success measures from each year were then averaged to create a single mating success variable. Alternative methods to combine these variables (e.g. PCA) did not qualitatively change our results. Rank mating success between years was relatively repeatable (for these two years: $r_{19}=0.41$, $P=0.07$). Results reported here were qualitatively the same when analyses were redone by year (data available by request). Time to solve the barrier problem was rank-transformed so that males that did not solve the problem could be included in the analysis (with the worst rank). One male had his bower completely destroyed by a neighbouring male during the observation period and was not included in analyses involving cognitive tasks 4–6 because of missing data. All statistical tests are two tailed.

RESULTS

There was little support for intercorrelation of cognitive tasks, or a singular general cognitive ability. There was a lack of statistically significant correlations among the different cognitive tasks (Table 1), suggesting that there may be a large degree of independence between the cognitive abilities involved in each. In addition, there were three principal components with eigenvalues greater than 1, rather than a single factor effectively describing covariation between cognitive traits (Table 2). These principal components described 27.5%, 23.5% and 20.7% of the variation in performance on the cognitive tasks, respectively. However, males with higher scores of the first principal component did have higher mating success ($r_{18}=0.66$, $P=0.002$; Fig. 1a). This suggests that covariation between different cognitive abilities, even if small, is related to some variable or set of variables important to females (which might even be cognitive in nature). This does not seem to be an outcome simply because of the statistical method we used. For example, when we conducted a factor rotation, the results were very similar, with scores from the first principal component still correlated with mating success ($r_{18}=0.58$, $P=0.008$). In addition, males that were on average better at all cognitive tasks had higher mating success ($r_{18}=0.81$, $P<<0.0001$; Fig. 1b) and higher scores of g ($r_{18}=0.50$, $P=0.023$; Fig. 1c). Average rank score on cognitive tests is analogous in many ways to the additive measure of human intelligence called IQ, which correlates reasonably well with g (Plomin 2001).

Factor loadings of cognitive tasks on g (correlations between performance on cognitive tasks and scores of g) tended to be in the

Table 2
Principal components analysis of performance on six cognitive tasks

Cognitive task ($N=20$)	PC1	PC2	PC3
1. Red coverage	0.57	0.21	0.49
2. Time to remove barrier	-0.31	0.80	-0.06
3. Mimetic repertoire size	0.19	0.84	-0.24
4. Handling time	-0.76	0.07	0.42
5. Building flexibility	0.12	0.13	0.87
6. Templating	-0.78	0.00	0.05
Eigenvalue	1.65	1.41	1.24
% Variance	27.5	23.5	20.7
Correlation with mating success	$r_{18}=0.66$ $P=0.002$	$r_{18}=0.07$ $P=0.78$	$r_{18}=0.12$ $P=0.62$

Displayed here are the unrotated component loadings, eigenvalues, percentage of total variance in cognitive performance explained by each component (with eigenvalue >1), and the relationship between scores on each component and mating success.
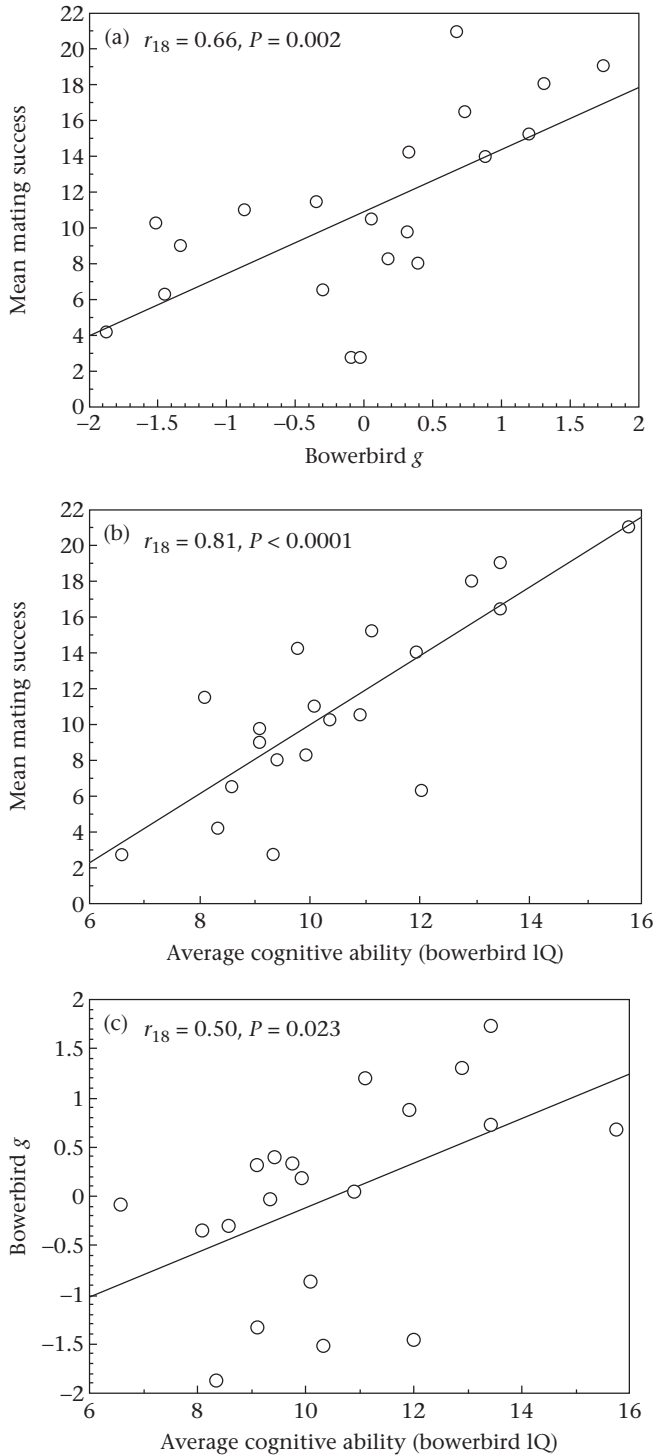
Figure 1. Relation between mating success in male bowerbirds and two integrative measures of performance on six cognitive tasks: (a) first principal component scores of performance (Bowerbird *g*) and (b) average rank performance (Bowerbird IQ). (c) Relation between Bowerbird *g* and Bowerbird IQ.

predicted direction (Table 2). Templating was the exception, and the strong negative loading on *g* paired with a positive correlation between templating and building time (males that templated more had longer handling times: $r_{18} = 0.45$, $P = 0.045$) suggests a possible trade-off between the two measures. If this were true, we would predict that males better able to resolve this trade-off would be preferred by females This is what we found; residuals of the
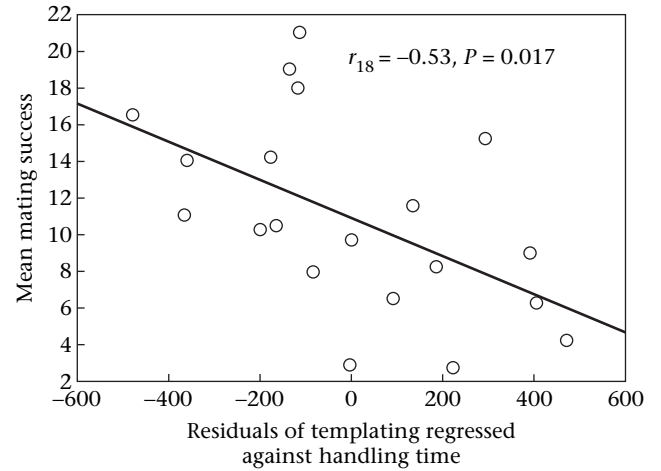

Figure 2. Relation between mating success in male bowerbirds and ability to resolve the trade-off between templating and handling time.

regression between handling time and templating were negatively correlated with mating success ($r_{18} = -0.53$, $P = 0.017$; Fig. 2).

Females could not have directly assessed male performance on most of the cognitive tasks because female visits were rare (on average <1 female visit/bower) during our cognitive task trials. Mimetic repertoire size was the exception, however, because we assessed it during courtship. We constructed another measure of *g* without this variable to ensure that we were not biasing our analysis in a way that would make a significant relationship between *g* and mating success more likely. Males with better scores of *g* (calculated without repertoire size) also had higher mating success ($r_{18} = 0.63$, $P = 0.003$) and this *g* explained 33% of the variance in the five cognitive traits we measured. The two measures of *g* were significantly correlated ($r_{18} = 0.99$, $P \ll 0.0001$). Similarly, when we recalculated male average rank score on all cognitive tests (bowerbird 'IQ') without mimetic repertoire size, we still found a significant relationship between this summary measure of cognitive ability and mating success ($r_{18} = 0.67$, $P = 0.001$). The two measures of IQ were also significantly correlated ($r_{18} = 0.89$, $P \ll 0.0001$).

We tested the extent to which these different cognitive tasks could independently predict male mating success using a multiple regression analysis. This model revealed that better performance on most cognitive tasks was independently associated with higher mating success (Table 3). Red coverage and templating were the exceptions, although there were trends with these variables in the expected directions.

We examined a number of variables that could have influenced male performance on the cognitive tasks. First we tested whether age might have influenced male performance. For example, older males may be better at handling sticks because of more practise.

Table 3
Independent contribution of cognitive tasks to mating success

Cognitive task (N=20)	β	t_{13}	P
1. Red coverage	+0.27 (+)	1.87	0.08
2. Barrier problem	−0.49 (−)	−3.26	0.006
3. Mimetic repertoire size	+0.47 (+)	3.13	0.008
4. Handling time	−0.52 (−)	−3.49	0.004
5. Building flexibility	+0.33 (+)	2.34	0.036
6. Templating	+0.24 (+)	1.65	0.12

Performance on most cognitive tasks also independently predicted mating success. In addition, the overall multiple regression model predicting male mating success was significant ($r^2 = 0.79$, $F_{6,13} = 8.26$, $N = 20$, $P = 0.008$). (+) and (−) refer to hypothesized positive and negative relationships, respectively.

However, age did not explain cognitive performance, measured either by the separate cognitive tasks or our summary variables of overall cognitive ability (Supplementary Material, Table S1). The lack of an influence of age on cognitive performance makes sense for at least two reasons. First, adult male bowerbirds experience a 7-year juvenile period of development where they practise extensively skills similar to those needed to perform well on our cognitive tasks (Vellenga 1970; Collis & Borgia 1993). Improvement appears to be relatively steep early during this period and then tapers off (J.K., J.-F.S. & G.B., personal observations). Similarly, in humans g is one of the most stable behavioural traits after childhood (Plomin 2001). We also had measures of motivation to perform the problem-solving tests (tasks 1–2) and to rebuild (which may have influenced tasks 4–6). Consistent with our previous results (Keagy et al. 2009) we found no effect of motivation on male problem-solving performance (barrier problem: $r_{12} = 0.38$, $P = 0.18$; red coverage: $r_9 = -0.02$, $P = 0.94$). In addition, the time it took males to begin building after bower destruction was not related to handling time ($r_{17} = 0.05$, $P = 0.84$), proportion of sticks placed in the destroyed wall ($r_{17} = 0.08$, $P = 0.76$), or templating ($r_{17} = -0.08$, $P = 0.73$), suggesting that male latency to build or activity level was not related to male performance on tasks related to rebuilding. It is also conceivable that male size could have influenced performance on at least some of the cognitive tasks (e.g. ability to solve the barrier problem or handle sticks). However, this was not the case (Supplementary Material, Table S2).

DISCUSSION

In this study we measured male performance on six cognitive tasks and found mixed results for the hypothesis that performance scores on cognitive tasks are intercorrelated. Our correlation matrix revealed no pattern of correlations between performance on different tasks. In addition, our principal components analysis found three factors with eigenvalues greater than 1. However, the first principal component explained a large amount of variance (28–33%) in the cognitive traits, which is only of a slightly lower magnitude than that reported in mice (22–41%: Galsworthy et al. 2005; 38%: Matzel et al. 2003) and humans (roughly 40%: Plomin 2001). In addition, scores of this factor were significantly positively associated with male mating success, a measure that is a strong predictor of reproductive success in this species (Reynolds et al. 2007). A likely explanation for these results is that covariation between performance on the cognitive tasks, although low, is correlated with a variable or set of variables that females are able to assess during mate searching. Furthermore, we found that a second integrative measure of male cognitive ability, average rank score on cognitive tasks, was also correlated with mating success, suggesting that the link between male general cognitive ability and male attractiveness is robust.

It has been suggested that general cognitive ability may be a reliable indicator of genetic quality (Prokosch et al. 2005; Arden et al. 2009). Also, general cognitive ability has been found to be highly heritable in mice (Galsworthy et al. 2005) and humans (Deary et al. 2006). Thus, the evolution of increased general cognitive ability could be possible through female choice for males with better cognitive ability, perhaps because of genetic benefits to females' offspring. This route for cognitive evolution has received very little attention (Miller 2000; Keagy et al. 2009), but may be widespread, as suggested by a number of other species with complex sexual displays that appear to involve an extensive cognitive component (e.g. cooperative and highly coordinated sexual displays of several manakin species: Prum 1994).

Attempts to measure batteries of cognitive tasks in animals have been rare because of their difficulty. Our study species, while

attractive because of our ability to get an accurate measure of mating success, presented some difficulties. For example, we had to design measures that could be assessed with wild individuals in their natural environment. We could not take individual males indoors for experimentation because removal of males results in their bower sites being taken over by other males and thus no future mating success measure for the removed males. In addition, this large and unnatural turnover in males would have unknown effects on future studies with this population. Because some of these measures do not have established laboratory history, we anticipate there will not be universal agreement that they measure cognitive ability. However, we have explained in detail why these tasks do correspond to the most widely accepted and used definitions of cognition. In addition, we designed these tasks to be ecologically valid and to ensure that all males were highly motivated to complete them. Furthermore, for all tasks except for mimicry (which has long been accepted as a cognitive trait) we had ways of assessing male motivational level and found that this variable did not explain male task performance. Cognitive test batteries of any sort in birds are not very well developed, and they will certainly undergo continual improvement. However, our study will hopefully encourage further work on the relationship between cognition and sexual selection both in the wild and in the laboratory.

Studies of cognitive abilities together, rather than in isolation, are important to fully understand cognitive evolution, especially if comparative study of the structure of cognition (e.g. the extent to which there is a general cognitive ability) is ever going to be possible (Banerjee et al. 2009). Historically, there has been a debate about the extent to which different cognitive modules evolve independently from each other ('mosaic', Barton & Harvey 2000 versus 'concerted' evolution, Finlay & Darlington 1995). Distinct from this line of research has been the finding across multiple taxonomic groups that species counts of feeding innovations are associated with other measures thought to indicate aspects of cognitive ability (Lefebvre et al. 2002; Reader & Laland 2002; Deaner et al. 2006). This suggests that there may be general processes of cognition (Lefebvre 2010). The existence of independent cognitive units is not necessarily inconsistent with the presence of a general factor of cognitive ability, because cognitive modules clearly reside in the same brain and so all are influenced to some degree by a similar set of genetic and neurophysiological variables (Miller 2000; Plomin 2001; Banerjee et al. 2009). General cognitive ability is ultimately an individual trait, and we suggest that a compelling research approach will be to test individuals on batteries of cognitive tests in different species. These data (e.g. the extent to which performance on cognitive tasks are correlated as well as multivariate descriptions of the covariation between performance on different cognitive tasks) could then be compared (see also Banerjee et al. 2009).

Our multiple regression analysis suggested that performance on each cognitive task independently predicted mating success, although for two of these variables the relationship was not statistically significant. This suggests that sexual selection pressures on the underlying cognitive abilities used by each task differ. The relatively high amount of independence suggests that cognitive abilities involved in different tasks could also evolve independently. Of course, the extent to which sexual selection could actually result in evolutionary change of male cognitive abilities depends on many factors, including the relative current costs and benefits of better cognitive abilities and their heritability. For example, it has been suggested that in some species the high costs of brain tissue may trade off with costs of other tissues (Pitnick et al. 2006). Together the data from this study suggest further research is needed to understand the complex relationship between sexual selection and cognitive performance and that sexual selection should be considered as a potential force affecting cognitive evolution.

Although this study focused on variation in male cognitive performance, female cognitive ability is also likely to be an important factor in determining the course of sexual selection. For example, female bowerbirds remember information about mates from previous years (Uy et al. 2001) and human females can accurately assess male intelligence by watching their behaviour (Prokosch et al. 2009). Females may require a certain degree of cognitive ability to discriminate between males based on differences in their cognitive performance. In addition, female cognitive ability may be under selection if the benefits of distinguishing between males on the basis of cognitive ability are high. Indeed, given that general cognitive ability is heritable in the species tested thus far (Plomin 2001; Galsworthy et al. 2005; Deary et al. 2006), there should be many aspects of male cognitive ability that are shared with females even though their expression may differ. Thus it is possible to envision coevolution of cognitive ability in males and females, with cognitively superior males being preferred by females and cognitively superior females being more likely to effectively choose those males.

Supplementary Material

Supplementary material for this article is available in the online version at doi:10.1016/j.anbehav.2011.02.018.

Acknowledgments

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