

Original Article

# Cognitive ability and the evolution of multiple behavioral display traits

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Males of many species have multiple behavioral display traits. Females may be able to use these multiple behavioral display traits together to evaluate a male's overall cognitive ability, which may be related to his genetic quality. It is also possible that individual behavioral display traits indicate unique aspects of male quality possibly related to cognitive performance. We tested predictions of these 2 hypotheses in satin bowerbirds, *Ptilonorhynchus violaceus*, a species with a large number of behavioral display traits involved in mate choice. We calculated 2 integrative measures of male performance on 6 cognitive tasks. An aggregate measure of male display quality (produced from 4 behavioral display traits) was correlated with one of these measures of overall cognitive ability and with mating success. Multiple behavioral display traits used together, rather than individually, more accurately predicted this measure of overall cognitive ability. In addition, we found some support for the hypothesis that separate display traits may indicate different aspects of male quality. One display trait indicated male age and possibly survivability. These results suggest that multiple behavioral display traits may have evolved in part because of the large variety of information they can convey about male quality. *Key words:* cognition, cognitive evolution, mating success, multicomponent traits, *Ptilonorhynchus violaceus*, satin bowerbird, sexual selection. [*Behav Ecol* 23:448–456 (2012)]

## INTRODUCTION

Cognition is commonly defined as neuronal processes concerned with acquisition, processing, retention, and use of information (Dukas 2004; Shettleworth 2010). Since Darwin there has been great interest in both cognition (Darwin 1871, 1872) and sexual selection (Darwin 1871), although the connection between these 2 topics has not received much attention (for a recent review, see Boogert, Fawcett, et al. 2011). One notable exception is the study of bird song learning, a cognitive trait (Shettleworth 2010) known to be under sexual selection (Hasselquist et al. 1996; Ballentine et al. 2004; Coleman et al. 2007). For example, DeVoogd (2004) suggested that female birds that select individual males with greater song complexity are likely choosing males who are better at a number of cognitive behaviors due to a correlation between the size of the song control nuclei and the forebrain (a brain region that controls a number of complex cognitive functions). The finding that individual male birds with more complex songs are also better at solving a novel foraging problem supports this hypothesis (Boogert et al. 2008). However, song is not the only behavioral display trait that likely has a cognitive component. For example, many species have intricate and often interactive “dances” (Prum 1994; Patricelli et al. 2002; Duval 2007; Scholes 2008), construction of display courts (Borgia 1985; Andersson 1991; Uy and Endler 2004), and collection of objects from the environment (Borgia 1985; Diamond 1986; Soler et al. 1996; Wojcieszek et al. 2007; Doerr

2010). The specific examples cited here likely reflect varying degrees of interplay between information processing, learning, memory, and decision making, all hallmarks of cognitive traits.

In addition, many species have more than one behavioral display trait. There is a long history in the sexual selection literature of attempting to explain multiple display traits in general (reviewed most recently in Candolin 2003). Two influential hypotheses were suggested by Møller and Pomiankowski (1993). The “redundant signals hypothesis” suggests that multiple traits offer redundant and complementary information about one aspect of male quality. Each display trait has a certain degree of error associated with how well it correlates with male quality, and so by using multiple display traits together, females get a more accurate measure of male quality (Møller and Pomiankowski 1993; see also Johnstone 1996 who calls it the “back-up signals hypothesis”). The “multiple messages hypothesis” suggests that each display trait offers information about a unique aspect of male quality (Møller and Pomiankowski 1993; Johnstone 1996). These hypotheses are often presented as alternatives, when they are really ends of a continuum of possibilities. If traits that indicate different aspects of male quality (i.e., multiple messages) are correlated with overall quality, they could also serve as redundant signals to females (Candolin 2003). This set of hypotheses offer a useful framework for understanding how females might use multiple behavioral display traits in mate choice.

In this study, we use satin bowerbirds, which have a history of use as a model system for understanding the evolution of multiple display traits (e.g., Patricelli et al. 2003; Coleman et al. 2004; Robson et al. 2005). Satin bowerbirds have a non-resource based mating system with a large skew in male mating success (Borgia 1985). We consider how multiple behavioral display traits may act to inform females in 2 different ways. First, we test the hypothesis that they may act together to give females an accurate indicator of a male's

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Received 13 September 2011; revised 16 November 2011; accepted 19 November 2011.

overall cognitive ability. Male cognitive ability has been suggested to be a good indicator of genetic quality due to the large number of genes that are required for the growth and maintenance of the brain, making it especially vulnerable to high mutation load (Miller 2000; Prokosch et al. 2005; Arden et al. 2009; Boogert, Fawcett, et al. 2011; Keagy et al. 2011). In addition, if there are fitness advantages to better cognitive ability and these are heritable, females choosing males with better cognitive ability are likely to have offspring with these same advantages (Keagy et al. 2009, 2011). Second, each behavioral display trait may provide some unique information to females about a specific aspect of the male's quality. We chose to focus on age and parasitism for this second part of the study because these data were readily available, and these 2 variables can have important effects on cognitive performance and behavioral displays. First, if individual cognitive abilities (or behavioral display traits) improve over time through learning, they can accurately reflect age, which may be an indicator of survivability in certain situations (Manning 1985; Kokko and Lindstrom 1996; Brooks and Kemp 2001), assuming individuals are continuously tested in competitive circumstances (i.e., they cannot cheat by "sitting out" of mating competition during certain years to avoid the costs of such competition). Second, parasites have important effects on individual fitness and infection with parasites may differentially impact some cognitive functions while having no effect on others (Nokes et al. 1992; Kavaliers et al. 1995).

We focus on 4 behavioral display traits that may have at least some cognitive component in satin bowerbirds. Male bowerbirds build a stick bower on the ground that females visit for courtship and copulation (Borgia 1985). These bower sites are >100 m apart and visually isolated from each other (Borgia 1985). Bower building has been suggested to be a cognitively complex task (Madden 2001). It is common to describe 4 aspects of bowers: bower symmetry, stick size, stick density, and overall quality of construction (Borgia 1985, also Wojcieszek et al. 2007, but with some modifications). We focus on symmetry and stick size here. One of the other variables, overall quality of construction, takes into account symmetry, stick size, and stick density and so is not independent of them. In addition, the correlation between symmetry and stick size tends to be lower than between the other variables (Keagy J, Savard J-F, and Borgia G, unpublished data). More importantly, symmetry and stick size probably reflect very different aspects of bower building skill. Differences in stick size most likely are due to differences in ability to locate the smallest sticks (bowers preferred by females have smaller sticks, Borgia 1985). It would be much more speculative to say how males create symmetrical bowers, but symmetry could be influenced by male perception of symmetry and/or ability to conditionally follow simple building "rules" that result in symmetrical bowers. Males preferentially decorate their bowers with blue objects (Borgia et al. 1987; Borgia and Keagy 2006) that females find attractive (Borgia 1985; Coleman et al. 2004). Blue objects are rare in the environment (Borgia et al. 1987), and the number of the preferred blue decorations (feathers from rosellas, *Platycercus elegans* and *P. eximius*) is mostly a function of the ability of males to steal them from other male bowers and is thus an honest indicator of male quality (Borgia and Gore 1986). In addition, the fact that males tend to steal preferentially from neighbors with large caches of decorations and that many stealing events are reciprocal (Borgia and Gore 1986) suggests males are able to remember bower locations, which should not be surprising because females also have this ability (Uy et al. 2000, 2001). The functions of nonblue decorations (e.g., snail shells, yellow leaves, cicada exuviae) are less well understood, but some of them are also rare and/or clumped in distribution, and they tend to be less often the focus of stealing events (Keagy J, Savard

J-F, and Borgia G, unpublished data), suggesting that their numbers may be affected by skill in finding them. All 4 of these display traits have previously been shown to predict mating success: bower symmetry (Borgia 1985), bower stick size (Borgia 1985), number of blue decorations (Borgia 1985; Coleman et al. 2004), and number of other decorations (Borgia 1985).

In a recent study, we were able to assess male performance on 6 distinct cognitive tasks in nature (Keagy et al. 2011; MATERIALS AND METHODS). We used male scores on these cognitive tasks to construct 2 integrative measures of cognitive ability, both of which strongly predicted mating success, an important fitness component (Keagy et al. 2011). As in that study, we do not propose that animal cognition is as simple as a single metric. However, reducing our cognition variable set this way does allow us the opportunity for further analysis that has led to insights not otherwise possible. For example, we have tended to not find correlations between male display traits such as the ones used in this study and performance on individual cognitive tasks. In this current study, we test: 1) whether multiple behavioral display traits could be used together to predict integrative measures of cognitive ability and 2) whether different behavioral display traits might differentially indicate unique aspects of male quality.

## MATERIALS AND METHODS

### Study site and data collection

This study was conducted in 2004 and 2005 at Wallaby Creek (28°28'S, 152°25'E), New South Wales, Australia. All bower holders were individually identifiable by a unique combination of 3 colored plastic bands on each leg. All behaviors at 21 bowers were recorded throughout the mating season (31 October 2004–21 December 2004 and 27 October 2005–19 December 2005) using an automated video monitoring system. Field assistants recorded daily counts of all decorations and twice-daily qualitative scores of bower stick size and bower symmetry (1–4 with 0.5 increments, 1 being smallest sticks or most symmetrical, respectively), and these were averaged across the mating season (Borgia 1985). Individual birds were selectively caught in baited traps (2004: 46.78 ± 16.4 days, 2005: 46.13 ± 4.70 days prior to the start of the mating season [mean ± standard deviation, SD]) and examined for parasites. The louse *Myrsidea ptilonorhynchi* is the only abundant ectoparasite found on satin bowerbirds at Wallaby Creek (Borgia and Collis 1989). The nits of this parasite are common only in areas around the eyes where birds cannot preen and are counted visually (Borgia and Collis 1989; Borgia et al. 2004). There has been uninterrupted monitoring of this field site since 1995, providing us detailed age information for birds (Keagy et al. 2009, 2011). Males in this study were between 8 and 20 years old in 2004 (mean ± SD, age = 11 ± 3.48 years). We use the number of copulations a male receives on our complete video record as a measure of his mating success (Borgia 1985), and paternity analyses indicate that this is an accurate measure of male reproductive success (Reynolds et al. 2007). 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 license 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.).

### Measures of cognitive ability

We were able to assess 21 males on their performance on 6 distinct cognitive tasks that have been validated previously

(Keagy et al. 2009, 2011, with brief descriptions below): 1) ability to remove a clear barrier covering target objects, 2) ability to conceal an immovable undesirable object, 3) mimetic repertoire size, 4) stick placement skill, 5) flexible response to a novel bower manipulation, and 6) use of a behavioral “tool” for creating symmetrical bowers. Tasks 1 and 2 were problem solving tests originally described by Keagy et al. (2009) that take advantage of an intense male motivation to remove red objects from the bower platform (Morrison-Scott 1937; Borgia et al. 1987; Borgia and Keagy 2006). Task 1 involved quantifying the time it took males to remove a clear container (>50% the size of the male) placed over 3 red objects. Despite the apparent simplicity of this problem, 33% of males failed to solve it. For task 2, the red object they were motivated to remove was superglued to a long screw and fixed into the bower platform and ground below so that it could not be physically moved. Males could only solve this problem if they exercised inhibitory control (a complex cognitive ability, Taylor et al. 2007; Boogert, Anderson, et al. 2011) and instead of trying to lift the red object, covered it with other objects. We took digital photographs after 24 h and calculated the proportion of the red object covered using ImageJ software (v.1.34i, National Institutes of Health, Bethesda, MD). Task 3 used methods from Coleman et al. (2007) to calculate the average number of species mimicked by each male using courtships between unique male–female dyads. This procedure controlled for repeated interactions between a male and the same female influencing his behavior toward her. The average number of species a male mimics is very similar to his total repertoire size (Pearson correlation:  $r = 0.71$ ,  $t_{19} = 4.39$ ,  $P = 0.0003$ ). Tasks 4–6 were recorded after a novel bower manipulation in which we completely destroyed only one wall. Task 4 was measured as the amount of time it took males to place 100 sticks. This task was almost entirely affected by a male’s ability to efficiently manipulate sticks (Keagy et al. 2011), a skill which is heavily influenced by motor coordination that is refined through a 7-year period of improvement during which juveniles practice building bowers (Vellenga 1970; Collis and Borgia 1993) and engage in social learning (Madden 2008). Task 5, flexible response to the novel bower manipulation, 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 1985) 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 (which is what males do under normal circumstances, Keagy J, unpublished data). Flexibility is a hallmark of many definitions of animal intelligence (Roth and Dicke 2005) The final variable was a measure of male use of a behavioral tool for creating symmetrical bowers, called “templating.” 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, place the stick in an identical position in the opposite wall. Males who template tend to have more symmetrical bowers ( $r = 0.58$ ,  $t_{18} = 3.02$ ,  $P = 0.007$ ). Previous work has shown that differences in performance on any of these tasks cannot be explained by differences in age, size (either mass or skeletal), or motivation (Keagy et al. 2011).

### Measuring motivation

In general, studies of cognition attempt to increase motivation of their subjects by either withholding food for a set period of time before testing individuals or using preferred treats. This procedure only increases motivation level but does not control

for individual differences in motivation level unless all individuals reach some kind of motivational ceiling (for an alternative method, see Roth et al. 2010). We took a different approach. With our problem-solving tests, males were highly motivated due to their intense dislike for red objects at their bowers (Morrison-Scott 1937; Borgia et al. 1987; Borgia and Keagy 2006). More importantly, we could directly estimate male motivational level by presenting males with the simple task of moving the same red objects 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 male problem solving performance (it was not, Keagy et al. 2009, 2011). For the variables measured following the one-wall destruction experiment, we measured the latency between our one-wall destruction and when each male started to rebuild (Keagy et al. 2011). If male performance on these 3 tasks was simply a reflection of male motivation to build or activity level, we would expect positive correlations between latency to build and the cognitive measures (there were none, Keagy et al. 2011). 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. Therefore, despite using tasks that utilized different motivational systems than is typical (i.e., food), we are confident that motivation of subjects was high and that the variation that did exist in motivation was quantified and did not predict male performance on any of the cognitive tasks (Keagy et al. 2011).

### Statistical analysis

We constructed our first integrative measure of cognitive ability by using scores from the first unrotated principal component from a principle component analysis of standardized data ( $z$ -transformed values) of the 6 cognitive tasks (Keagy et al. 2011). This methodology has a long history of being used in psychology to quantify general intelligence (Spearman 1904; Plomin 2001; Galsworthy et al. 2005). While  $g$  in humans is commonly quantified this way, there is abundant additional evidence for its existence, such as large covariances between different cognitive tests (the “positive manifold”), high repeatability, large correlations with other measures of intelligence, and high heritability (Plomin 2001; Deary et al. 2010), although there is still disagreement regarding what exactly these data imply. In a previous study, we found little support for such a singular general cognitive ability (Keagy et al. 2011). There was little covariation between the different cognitive tests and more than one large principal component. However, the first principal component did explain 27.5% of the variation in cognitive test performance, and males with higher values of this variable had significantly higher mating success. We refer to this variable as SB- $g$  (where “SB” stands for “satin bowerbird”) to acknowledge that it was quantified in an analogous way as human  $g$  but to recognize that it differs from human  $g$  in several important ways. Another way to quantify general cognitive ability in humans is through the use of IQ tests. These are additive measures of scores from tests of multiple cognitive abilities (Plomin 2001) that are often scaled to have certain statistical characteristics. This variable tends to be correlated with  $g$  in humans (Plomin 2001). Previously, we calculated an alternative integrative measure of cognitive ability that was the average of each male’s relative performance on each of the cognitive tasks (with a rank of 1 being worst at that task, Keagy et al. 2011). Because of its mathematical similarity to human IQ, we refer to it here as SB-IQ. Both of these abbreviations are used to simplify discussion of these variables, not to imply that cognition is the same

**Table 1**  
Principal components analysis of display trait variables

Display trait ( <i>n</i> = 21)	Loading
Rank bower stick size	0.87
Rank bower symmetry	0.66
Rank blue decorations	0.79
Rank nonblue decorations	0.68
Eigenvalue	2.27
% Variance	56.9

The first principal component explained the majority of the variance in these 4 display traits. All 4 traits loaded highly and with similar magnitudes on this component. When raw data are used instead of ranked data, the resulting PCA is very similar. For example, there is also only one major PC and the scores of this PC and the one in the table above are highly correlated ( $r = 0.93$ ,  $t_{19} = 11.03$ ,  $P \ll 0.0001$ ).

in bowerbirds as in humans or to imply that cognition is as simple as one variable. Both methods of integrating information across multiple variables have common usage in studies of behavioral ecology and evolution. Cognitive tasks 2 and 3 were assessed in 2004 and cognitive tasks 1 and 4–6 were assessed in 2005. One male had his bower completely destroyed by a neighboring male during the observation period for cognitive tasks 4–6, and so we were not able to assign him scores of SB-g or SB-IQ (see also Keagy et al. 2011).

We calculated 2 composite measures of display quality using bower stick size, bower symmetry, number of blue decorations, and number of nonblue decorations. These 2 measures of display quality reflect different assumptions in how females might use display traits together during mate choice. First, it is possible that females are simply choosing males who are on average better at multiple aspects of behavioral display. We ranked males for each display trait and then calculated the average across all display traits. A common statistical method for creating a composite variable is to use principal components analysis of the variable set of interest, which implicitly assumes that covariation between traits is important to females. We used the first principal component of this analysis as our third measure of display quality (Table 1). There were 2 years of data available for bower stick size, bower symmetry, number of blue decorations, and number of nonblue decorations, and there were significant interyear correlations for these variables (bower stick size:  $r = 0.48$ ,  $t_{19} = 2.40$ ,  $P = 0.027$ ; bower symmetry:  $r = 0.58$ ,  $t_{19} = 3.07$ ,  $P = 0.006$ ; number of blue decorations:  $r = 0.83$ ,  $t_{19} = 6.43$ ,  $P \ll 0.0001$ ; number of nonblue decorations:  $r = 0.87$ ,  $t_{19} = 7.52$ ,  $P \ll 0.0001$ ). Therefore, before ranking males, we first averaged values for these variables for each male across both of these years in all analyses except for those involving parasites (the pattern of parasite infection varied widely across years). Mating success was rank transformed because of the strongly skewed distribution of copulations among male satin bowerbirds; this makes the distribution of mating success more normal (Keagy et al. 2009, 2011). Using log transformations results in qualitatively similar results. We then averaged male relative mating success across years (Keagy et al. 2011); there was a trend for rank mating success to be correlated across years ( $r = 0.41$ ,  $t_{19} = 1.94$ ,  $P = 0.07$ ).

All analyses were done using Statistica 6.0 (Statsoft Inc., Tulsa, OK). We used regression analysis to test the hypothesis that aggregate measures of male display quality predicted overall cognitive ability and mating success. In addition, the structural equation modeling module in Statistica was used to perform a path analysis which modeled the relationships between cognitive ability, mating success, and display quality.

We also used regression analysis to assess how well individual display traits predicted overall cognitive ability, parasitism, age, and mating success. We examined the relationships between display traits using Pearson's correlations. Residuals were analyzed for normality and no additional transformations were required. All statistical tests are 2 tailed.

## RESULTS

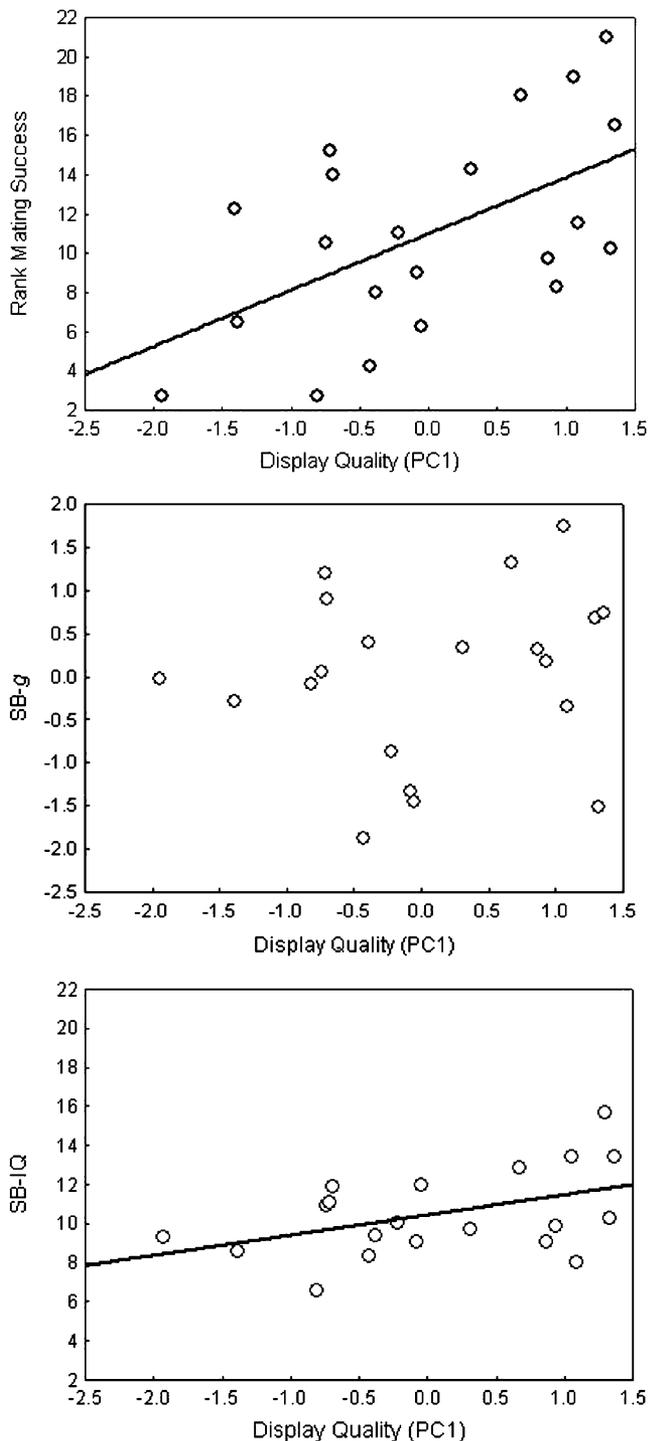
We created 2 composite measures of display quality that reflect different assumptions in how females might use display traits together to choose males: 1) the arithmetic average and 2) first principal component (PC1) of the rank scores of the display traits. These 2 measures of display quality were highly correlated ( $r > 0.99$ ,  $t_{19} = 94.68$ ,  $P \ll 0.0001$ ). Therefore, to reduce redundancy, we conducted all analyses using only the PC1 measure of male display as it provides a very good description of the total variation in all the display traits measured (Table 1). Display quality did not predict SB-g but did predict SB-IQ and mating success (Figure 1). We investigated the relationship between mating success, cognitive ability, and display quality further using path analysis. This analysis revealed that while SB-g only has a significant relationship with mating success, there is a significant relationship between SB-IQ and both display quality and mating success (Figure 2).

We tested whether overall cognitive ability could be better estimated through using multiple display traits than using these traits individually. None of the individual display traits significantly predicted SB-IQ or SB-g (Table 2). This result gives some support to the hypothesis that females using multiple traits can more accurately measure an aspect of male quality, in this case, SB-IQ. In addition, if there is some redundancy in the information that each display trait conveys, all of the traits should be intercorrelated. We found mixed support for this hypothesis, suggesting that some traits are more redundant than others (Table 3).

Next, we tested whether variation in display traits might predict different aspects of male quality. We first considered whether age, which can be an indicator of survivability, was associated with variation in individual display traits. Only number of nonblue decorations was associated with age (positively, Figure 3). Of the different types of nonblue decorations, snail shells (which make up a mean  $\pm$  standard error of  $26 \pm 3\%$  of nonblue decorations) stand out as the only nonblue decoration type significantly associated with age (Table 4). This association could result from at least 2 mechanisms. First males may accumulate snails over time, as they do not degrade for many years. Another possibility is that males are better at finding these decorations as they get older. In addition, these 2 possibilities are not mutually exclusive. We then assessed whether parasitism was indicated by variation in individual display traits and found no consistent relationship (Table 5). The significant relationship between age and nonblue decorations (snails) gives some support to the hypothesis that females can use individual traits to assess different aspects of male quality.

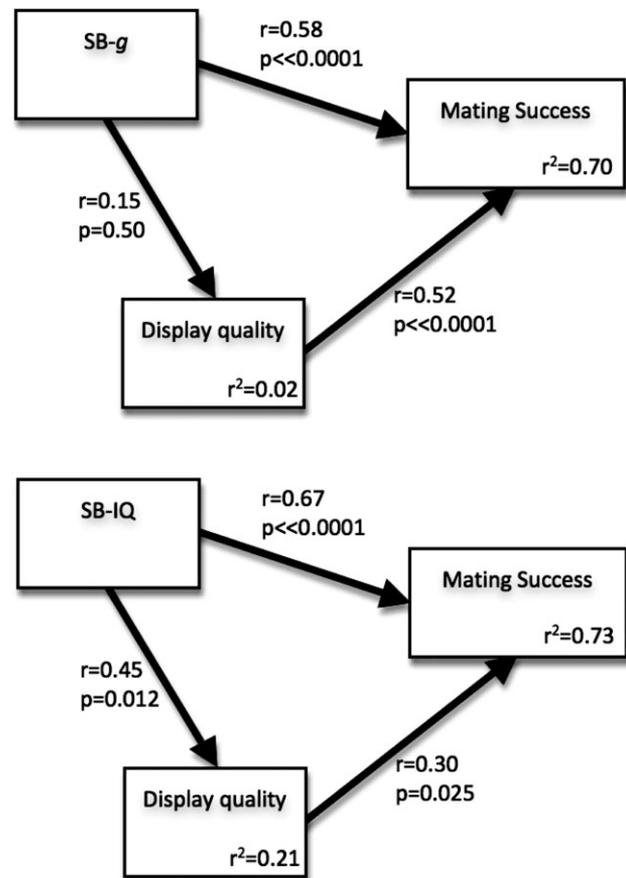
## DISCUSSION

In this study, we constructed 2 integrative measures of performance on 6 cognitive tasks, first, a measure which best describes covariation in cognitive performance, which we call SB-g, and second, a measure describing average performance on these tasks, which we call SB-IQ. In addition we constructed 2 composite measures of 4 display traits that reflected different assumptions in how females might use display traits together to choose males with better overall cognitive ability. These 2 measures of display quality were highly correlated. While these composite measures of display quality did not



**Figure 1**  
Display quality strongly predicts reproductive success ( $r^2 = 0.31$ ,  $F_{1,19} = 8.54$ ,  $P = 0.009$ ). It also marginally predicts one measure of overall cognitive ability, SB-IQ ( $r^2 = 0.21$ ,  $F_{1,18} = 4.69$ ,  $P = 0.044$ ), but not the other, SB-g ( $r^2 = 0.02$ ,  $F_{1,18} = 0.42$ ,  $P = 0.52$ ).

predict SB-g, we did find that display quality predicted SB-IQ. Thus display could indicate to females at least one measure of male overall cognitive ability. The major difference between these 2 measures is that SB-g is influenced primarily by covariation between performance on the 6 cognitive tasks, whereas SB-IQ weights performance on all the cognitive tasks equally.



**Figure 2**  
Path analysis of relationships between measures of overall cognitive ability (SB-g and SB-IQ), an aggregate measure of display quality, and mating success. Above each arrow is the partial regression coefficient (and its significance), which describes how well the variable at the start of the arrow (predictor variable) explains the variable pointed to by the arrowhead (response variable), given the effect of other pathways leading to that response variable. This is why there are different values for the pathway between display quality and mating success depending on which measure of overall cognitive ability is included in the model. That pathway describes the extent to which display quality predicts mating success, controlling for the effect of SB-g or SB-IQ on mating success (as in a multiple regression). The  $r^2$  values indicate the variance in that variable explained by the variables pointing to it. Importantly, this analysis provides a way of understanding to what extent the large positive relationship between cognitive ability and mating success (Keagy et al. 2011) can be explained through cognitive ability's hypothesized impact on display quality. This analysis demonstrates that SB-g does not influence mating success through its impact on display quality as measured in this study. However, SB-IQ has 2 different significant pathways to mating success: one indirect through its influence on display and the other direct. The significant direct pathway from both SB-g and SB-IQ probably represents other unmeasured display traits. Numerical results given here are from a model using the PC1 of display traits (bower symmetry, bower stick size, number of blue decorations, and number of nonblue decorations) as the measure of display quality.

However, this still does not satisfactorily explain our previous finding of a highly significant relationship between male scores on SB-g and SB-IQ and their attractiveness to females (Keagy et al. 2011). Our path analysis in this current study gives some insight into why this is the case, although it also raises new questions. The highly significant direct path to mating success in both path analyses suggests that there are additional traits to those that we measured that females use to choose cognitively

**Table 2.**  
**Tests of the redundant signals hypothesis**

Display trait	SB-g	SB-IQ
Rank bower stick size	$r^2 = 0.03$ , $F_{1,18} = 0.58$ , $P = 0.45$ (+)	$r^2 = 0.18$ , $F_{1,18} = 4.15$ , $P = 0.06$ (+)
Rank bower symmetry	$r^2 = 0.12$ , $F_{1,18} = 2.50$ , $P = 0.13$ (-)	$r^2 = 0.11$ , $F_{1,18} = 2.32$ , $P = 0.14$ (+)
Rank blue decorations	$r^2 = 0.07$ , $F_{1,18} = 1.33$ , $P = 0.26$ (+)	$r^2 = 0.07$ , $F_{1,18} = 1.39$ , $P = 0.25$ (+)
Rank nonblue decorations	$r^2 = 0.10$ , $F_{1,18} = 2.01$ , $P = 0.17$ (+)	$r^2 = 0.09$ , $F_{1,18} = 1.73$ , $P = 0.20$ (+)

Individual display traits predict SB-IQ less well than a composite of these display traits (the PC1). They do not predict SB-g, in the same way that the PC1 of these display traits did not (see Figure 1). (+) and (-) refer to a positive or negative relationship, respectively, but note that none of these relationships are significantly different from zero.

superior males. This should not be too surprising because we already know of other traits in bowerbirds that are associated with mating success and that are cognitive in nature, such as responding effectively to female signals of comfort (Patricelli et al. 2002, 2003) and mimetic accuracy (Coleman et al. 2007). Unfortunately, in the present study, we were not able to get measures of these variables. Regardless, we think that this, paired with our result that individual display traits do not explain SB-g or SB-IQ, suggests that females are choosing males with better cognitive abilities through the use of many different display traits.

We found a highly significant association between number of nonblue decorations and age. In this case, males who had more decorations were older, and it is likely that this relationship was driven by older males tending to have more snail shells. Age is thought to indicate superior survivability (Manning 1985; Kokko and Lindstrom 1996), and although this idea has been controversial in the past (Hansen and Price 1995), it has received new support (reviewed in Brooks and Kemp 2001). Age would only be an effective indicator if males are not able to avoid potentially difficult or costly life-history stages and still perform effective displays. In bowerbirds, male displays appear to involve a complex learning process over a long juvenile period (Vellenga 1970; Collis and Borgia 1993), and males who stop maintaining a bower site never regain a bower site in the future (Keagy J, Savard J-F, and Borgia G, unpublished data), making such avoidance unlikely for males with fully developed displays.

Given the large number of empirical studies demonstrating that parasitism can negatively impact a cognitive behavioral display trait, bird song (Buchanan et al. 1999; Spencer et al. 2005; Gilman et al. 2007; Bischoff et al. 2009) as well as other cognitive abilities (Nokes et al. 1992; Kavaliers et al. 1995; Gegear et al. 2006), it may seem surprising that there were no consistent negative relationships between parasitism and bowerbird display traits. It could be argued that this is due to a lack of power to detect these differences. However, using a larger data set, we have also been unable to find a significant relationship between parasitism and display traits (4 years of data, 14–23 males each year, Keagy J, Savard J-F, and Borgia G, unpublished data). In addition, there are a number of biological reasons to suspect that parasitism may not have a large influence on

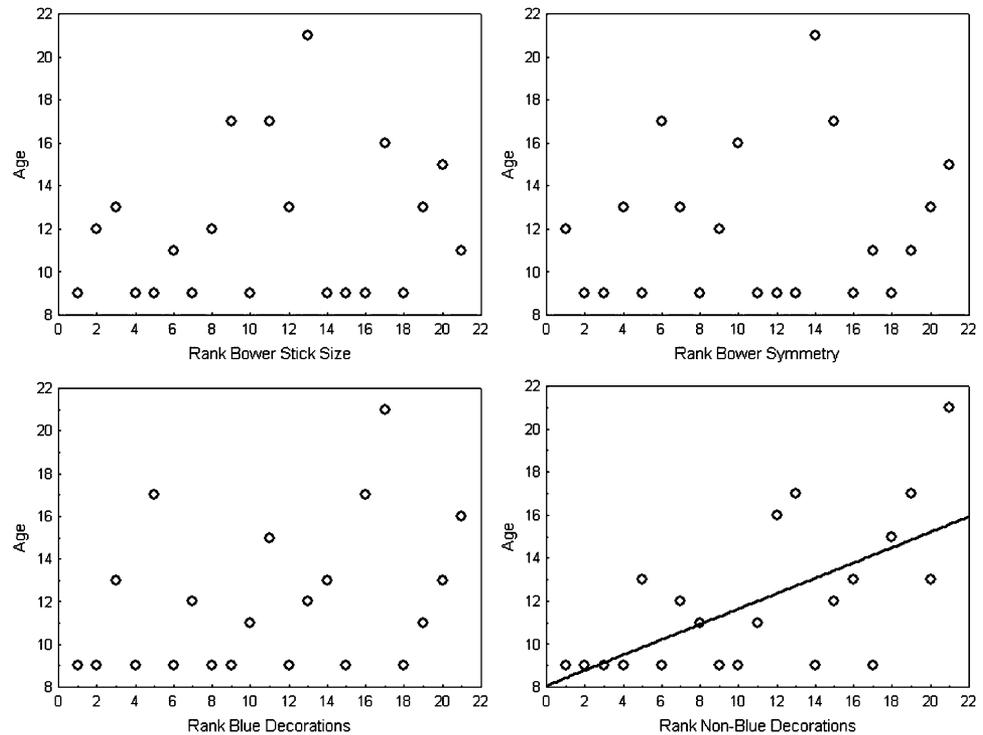
display in this system. First, adult male bower holders tend to have very low numbers of parasites (Borgia 1986; Borgia and Collis 1989; Borgia et al. 2004). Hence, the detrimental effect of parasitism is likely to be low. However, parasites are probably not benign. There is evidence that there is a survival cost to very high numbers of parasites (Borgia and Collis 1989). Second, adult male bower holders also tend to have had low numbers of parasites as juveniles (Borgia et al. 2004) when they learn their displays (Vellenga 1970; Collis and Borgia 1993; Coleman 2005) and when they are most likely to be negatively impacted by parasitism's effect on brain development. Males that do have large numbers of parasites as juveniles, while often surviving to adulthood, are not able to secure ownership of bower sites (Borgia et al. 2004). Thus, those males that may be most impacted by parasitism during development are the same males who do not end up being able to have displays in the future.

Behavioral display traits may be different from morphological display traits (e.g., plumage color) because of their reliance on the brain for their expression. It has been suggested that displays of motor ability, either vigor or skill, are especially good indicators of genetic quality because they are the result of the combined expression of most or all of the functional genome (Borgia 1979, 2006; Byers et al. 2010). However, this should be true of many behavioral traits, particularly where learning and practice appear to play a role in display trait development. Direct evidence for this hypothesis has recently been demonstrated with the sequencing of the zebra finch genome, and the finding that production of bird song relies on the expression of an extremely large number of genes (Warren et al. 2010). While several of the display traits we focused on in this study are unique to bowerbirds, they represent the expression of cognitive abilities probably shared among many animal species. For example, it may be possible that analogous displays involving similar cognitive abilities can be found in cichlids that build sand display arenas (McKaye et al. 1990), birds that build nests that have been cooped as signals of male quality (Quader 2005), and in bird species where males bring particular materials to the nest (Soler et al. 1996; Gwinner 1997). Species such as these are good candidates for further exploration of the relationship between cognition and sexual selection.

**Table 3**  
**Relationship between behavioral display traits**

<i>n</i> = 21	Rank bower stick size	Rank bower symmetry	Rank blue decorations	Rank nonblue decorations
Rank bower stick size				
Rank bower symmetry	$r = 0.61$ , $P = 0.003$			
Rank blue decorations	$r = 0.55$ , $P = 0.009$	$r = 0.25$ , $P = 0.27$		
Rank nonblue decorations	$r = 0.39$ , $P = 0.08$	$r = 0.17$ , $P = 0.46$	$r = 0.53$ , $P = 0.013$	

Several of the traits are at least marginally significantly correlated with each other, although only the relationship between bower stick size and bower symmetry is significant after correcting for multiple comparisons (adjusted alpha = 0.008).



**Figure 3**

Tests of the multiple messages hypothesis: Age. Older males have relatively more nonblue decorations ( $r^2 = 0.41$ ,  $F_{1,19} = 12.98$ ,  $P = 0.002$ , still significant at adjusted alpha of 0.017), and so nonblue decorations may indicate a male's ability to survive. The other display traits did not predict age (bower stick size:  $r^2 = 0.04$ ,  $F_{1,19} = 0.71$ ,  $P = 0.41$ ; bower symmetry:  $r^2 = 0.02$ ,  $F_{1,19} = 0.44$ ,  $P = 0.51$ ; blue decorations:  $r^2 = 0.13$ ,  $F_{1,19} = 2.94$ ,  $P = 0.10$ ).

A more indirect way in which cognitive ability might be reflected in display has been discussed in detail by Boogert, Fawcett, et al. (2011). They explain that condition-dependent display traits may reflect individuals' cognitive abilities or at least their foraging ability. Given the importance of foraging ability on fitness and overall condition, this mechanism seems plausible. In addition, there are some recent studies demonstrating evidence for this hypothesis (Karino et al. 2007; Mateos-Gonzalez et al. 2011). This indirect mechanism is not mutually exclusive with the more direct mechanism of behavioral traits indicating cognitive ability. To some extent, whether one mechanism is more likely than the other may depend on how many morphological display traits relative to behavioral ones a species has. For example, there are morphological aspects of bowerbirds that may function as display traits (e.g., the amount of blue in their plumage, Savard et al. 2011), but almost all of the known display traits of bowerbirds are behavioral. More study regarding the relative importance of these 2 mechanisms is an important future direction.

Explaining the existence of multiple display traits has been an active area of sexual selection research (reviewed in Candolin 2003 which has been cited 302 times according to Web of Science on 12 September 2011). Two influential hypotheses

that are especially relevant to this study and our findings are the redundant signals hypothesis that multiple traits offer redundant and complementary information about one aspect of male quality and the multiple messages hypothesis that each display trait offers information about a unique aspect of male quality (Møller and Pomiankowski 1993; Johnstone 1996). Our findings that a composite measure of display quality predicted one integrative measure of cognitive ability, SB-IQ, better than individual display traits is consistent with the redundant signals hypothesis. Also, our finding of an association between one display trait and a unique aspect of male quality is consistent with the multiple messages hypothesis (Møller and Pomiankowski 1993; Johnstone 1996). These hypotheses have tended to be pitted against one another as alternatives, and the potential dual nature of multiple behavioral display traits has rarely been recognized (Candolin 2003). The special nature of behavioral display traits may make it even more likely that individual behavioral display traits could indicate unique aspects of male quality while

**Table 4**

**Relationship between age and nonblue decorations (all relationships were positive)**

Nonblue decoration type	Age
Rank yellow leaves	$r^2 = 0.19$ , $F_{1,19} = 4.51$ , $P = 0.047$
Rank snail shells	$r^2 = 0.40$ , $F_{1,19} = 12.82$ , $P = 0.002$
Rank yellow blossoms	$r^2 = 0.13$ , $F_{1,19} = 2.85$ , $P = 0.11$
Rank cicadas	$r^2 = 0.12$ , $F_{1,19} = 2.61$ , $P = 0.12$
Rank man-made objects	$r^2 = 0.00$ , $F_{1,19} = 0.01$ , $P = 0.91$
Rank other natural objects	$r^2 = 0.08$ , $F_{1,19} = 1.62$ , $P = 0.22$

Only snail shells significantly predicted age after Bonferroni correction for multiple comparisons (adjusted alpha = 0.008).

**Table 5**

**Tests of the multiple messages hypothesis: parasitism**

Display trait	Parasites
Rank bower stick size (in year x)	2004: $r^2 = 0.00$ , $F_{1,7} = 0.00$ , $P = 0.97$ (-) 2005: $r^2 = 0.03$ , $F_{1,6} = 0.20$ , $P = 0.67$ (-)
Rank bower symmetry (in year x)	2004: $r^2 = 0.00$ , $F_{1,7} = 0.02$ , $P = 0.89$ (+) 2005: $r^2 = 0.13$ , $F_{1,6} = 0.87$ , $P = 0.39$ (-)
Rank blue decorations (in year x)	2004: $r^2 = 0.11$ , $F_{1,7} = 0.88$ , $P = 0.38$ (+) 2005: $r^2 = 0.00$ , $F_{1,6} = 0.02$ , $P = 0.89$ (+)
Rank nonblue decorations (in year x)	2004: $r^2 = 0.00$ , $F_{1,7} = 0.01$ , $P = 0.94$ (-) 2005: $r^2 = 0.55$ , $F_{1,6} = 7.26$ , $P = 0.036$ (+)

There is no evidence for display traits consistently predicting parasite numbers. (+) and (-) refer to a positive or negative relationship, respectively, but note that none of these relationships are significantly different from zero after Bonferroni correction (adjusted alpha = 0.013).

together indicating overall male quality. In fact, females may have been selected to use multiple behavioral display traits in part because of this feature. Therefore, females may be able to use multiple behavioral display traits as if they were a sort of sexually selected intelligence test of males.

We expect exploration of the relationship between cognitive ability and sexual selection in other animal species to generate a more comprehensive understanding of how cognition affects and is affected by the mate selection process. For example, in this particular study, we have some evidence that males with better displays have better overall cognitive ability, although this possibility clearly needs additional study. The idea that females could use multiple display traits in their assessment of male quality highlights how female cognitive ability could be important in determining the form sexual selection takes. In bowerbirds, there is a large body of evidence suggesting cognition is important to females making good mating decisions (Uy et al. 2000, 2001; Patricelli et al. 2004; Coleman 2005). In addition, DeVoogd (2004) pointed out that the neural processing associated with decoding and assessing song will likely be as sophisticated as that associated with accurate motor acquisition and production, and this has been backed up by some neurological studies (Leitner and Catchpole 2002). Learning also seems to be an important component in determining female preferences (Lauay et al. 2004; Kozak and Boughman 2009). This strong role for cognition is important because it suggests the potential for much more flexibility in mate choice than is often assumed in models of sexual selection (e.g., sensory bias: Ryan and Rand 1990). Thus, a more pointed focus on the role of cognition in display and mate choice will lead to a much better understanding of the processes involved in sexual selection.

## FUNDING

National Science Foundation (0518844 to G.B.). J.K. received additional support from a Hockmeyer Fellowship at the University of Maryland.

The authors wish to thank the Australian Bird and Bat Banding Scheme (ABBBS), New South Wales National Parks Services, B. Buttemer at the University of Wollongong, and the Kennedy, Bell, and Mulcahy families for assistance in Australia. C. Long helped supervise the field crew. G. Gareau, B. Kennedy, D. Obenshein, L. Parker, L. Plenderleith, M. South, and J. Spence assisted with the field experiments. Experiments were done with the approval of the Institutional Animal Care and Use Committee of the University of Maryland and University of Wollongong Animal Ethics Committee. A large number of undergraduates assisted with collecting data from videos, especially G. Bryant, A. Fishbein, K. Sheikh, M. Smith, and M. Sumpter. S. Brauth, K. Carleton, W. Hodos, K. Thompson, G. Wilkinson, and 2 anonymous reviewers provided valuable comments.

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