ABSTRACT

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Males of many species have complex behavioral sexual displays and it is possible that these displays indicate aspects about male quality because of their relationship with cognitive ability. However, the relationship between behavioral display traits, cognitive ability, and reproductive success has received little attention. Satin bowerbirds, *Ptilonorhynchus violaceus*, are an excellent species for studying this relationship because their complex male courtship suggests a selective advantage to individuals with superior cognitive abilities. Here I show that cognitive performance can have important effects on mating success and the quality of behavioral displays. First, I present males with two novel problem solving tests and find that males who are better at solving these problems have higher mating success, establishing a link between male cognitive ability and sexual attractiveness. Second, I add four additional cognitive tests to expand the diversity of cognitive abilities tested and

construct two measures of general cognitive ability using these data: the scores from an analysis that best explains covariation among performance on the different cognitive tests (g), and the average rank score on these cognitive tests ("IQ"). I show that these measures of general cognitive ability, as well as the majority of the independent cognitive tests, are positively associated with mating success. Third, I construct a different composite measure of male cognitive ability using an analysis that determines the combination of cognitive traits that make males most successful in attracting females (f). I show that this measure is significantly associated with my measures of general cognitive ability, suggesting that evolution of cognitive ability in bowerbirds is possible if there is sufficient heritability. I construct three different aggregate measures of male display quality (produced from four behavioral display traits) and find that they are all associated with f and with mating success. Finally, I show some support for the hypothesis that separate display traits may indicate different aspects of male cognitive ability. These results suggest that behavioral display traits may have a special role in sexual selection because of their connection to cognitive ability. Overall, this research highlights the importance of considering the interrelationship between cognitive ability and sexual selection.

COGNITIVE PERFORMANCE AND THE EVOLUTION OF MULTIPLE
BEHAVIORAL DISPLAY TRAITS

By

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Preface

This dissertation contains a single introduction section, three chapters, and a concluding section. Chapter I is presented in the format in which it is published (*Animal Behaviour*. 2009. **78,** 809-817). Chapters II and III are presented in manuscript form. Each of the three chapters includes their own abstract, introduction, methods, results and discussion sections, followed by tables, figure captions and figures. A single bibliography section is at the end for references cited throughout the dissertation.

To my parents, Alan and Cindy Keagy, for their care and understanding.

Acknowledgements

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INTRODUCTION

Cognition, defined as neuronal processes concerned with the acquisition, processing, retention, and/or use of information (Shettleworth 1998; Dukas 2004), is widely assumed to have fitness benefits such as allowing animals to solve ecological problems (Pravosudov and Clayton 2002; Sol et al. 2007; Cnotka et al. 2008) or navigate complex social environments (Byrne and Whiten 1988; Dunbar 1998; Bond et al. 2003; Holekamp et al. 2007). However, sexual selection, differences in the reproductive success of individuals, also produces elaborate traits. The idea that sexual selection could influence cognitive evolution was originally hinted at by Darwin (1871) and has been elaborated on with respect to humans by some evolutionary psychologists (e.g. Miller 2000), but has not been considered in hypotheses regarding the evolution of cognition in non-human animals.

In a similar manner, studies of sexual selection have tended to not explicitly consider the role of cognition. For example, some models of sexual selection assume that females are unable to use sensory stimuli in a context-dependent fashion, a skill that is not cognitively complex (e.g. sensory exploitation: Ryan and Rand 1990). There are some important exceptions, such as studies that explicitly consider the implications of bird song being a sexually selected cognitive trait (e.g. Nowicki et al. 1998, 2002; Buchanan et al. 2003; Boogert et al. 2008), studies of spatial learning and memory in male meadow voles searching for females (Galea et al. 1996; Jonasson 2005; Spritzer et al. 2005), or studies on the role of intelligence in mate choice in

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humans (e.g. Li et al. 2002; Prokosch et al. 2009). Also there is increasing evidence for behavioral flexibility in male display (Travis and Woodward 1989; Patricelli et al. 2002, 2006) and female choice (Gong and Gibson 1996; Reynolds and Jones 1999; Kodric-Brown and Nicoletto 2001; Hebets 2003; Coleman et al. 2004). Despite this progress, a better and more explicit understanding of the relationship between sexual selection and cognition is needed.

It seems reasonable to think that cognition might have an important role in sexual selection given that in many species males use elaborate display traits that appear to have a cognitive component. These display traits are often used together and include things such as intricate and often interactive "dances" (Prum 1994; Patricelli et al. 2002; Duval 2007; Scholes 2008), construction of display courts (Borgia 1985a; McKaye et al. 1990; Andersson 1991; Uy and Endler 2004), and collection of objects from the environment (Borgia 1985a; Diamond 1986; Wojcieszek et al. 2007; Doerr 2010). Understanding why species have multiple display traits has been an important question in sexual selection (Møller and Pomiankowski 1993; Borgia 1995; Johnstone 1996; Andersson et al. 2002; Candolin 2003), but like other questions in this field, has not been explicitly examined with respect to the role of cognitive performance.

In this dissertation, I use satin bowerbirds, *Ptilonorhynchus violaceus*, to consider how females might choose males based on their cognitive abilities. Satin bowerbirds are uniquely suited for this type of study. First, a number of aspects of their exploded lek mating system makes detailed study of their behavior possible and eliminates many variables that would complicate interpretation of female choice.

Male display sites, called bowers, are located on the ground and widely separated in the forest (>100 m) (Borgia 1985a). This means that females must individually sample males, eliminating the confounding factor of simultaneous assessment of multiple males that can occur on traditional leks (Höglund and Alatalo 1995). In addition, females arrive at bowers and are courted individually, making female mate choice copying unlikely. Females typically sample a mean ± SE of 2.64 ±0.18 adjacent bowers per mating season (range 1–8; Uy et al. 2001). As is typical for other lek birds, males provide only sperm and readily mate with any willing female. In addition there is a large skew in male mating success, suggesting agreement among females about which males are of the highest quality (Borgia 1985a). Because male display sites are on the ground, we can use automated video cameras with time and date stamps to record an extensive record of all behaviors at bower sites (Borgia 1985a). In addition, all male bower holders and the majority of females are marked for identification. One consequence of this is a record of all copulations a male receives, which paternity analyses demonstrate is a good measure of male reproductive success (Reynolds et al. 2007).

Second, male satin bowerbirds have all the attributes Emery (2006) suggests are associated with species with high intelligence: an omnivorous generalist diet (Frith and Frith 2004; Borgia and Keagy 2006), highly social (especially as juveniles: Vellenga 1970; Collis and Borgia 1993; but also in winter feeding flocks: Marshall 1954), large relative brain size (Madden 2001; cf. Day et al. 2005; Iwaniuk et al. 2005), innovative (Marshall 1954; Frith and Frith 2004), long developmental period (6-7 years to maturity: Marshall 1954; Vellenga 1980), extended longevity (males in

this study were 7-21 years old), and use of variable habitat (Frith and Frith 2004). Additionally, males have traits suggesting that they use cognition in sexual display. Bowerbirds are well known for their construction of stick structures called bowers where females sit during courtship. There is great individual variation in the quality and form of these structures, and this variation appears to have been coopted by females for mate choice (Borgia 1985a). In addition, males decorate the area directly in front of the bower with objects collected from the environment from a very specific palette of colors (Morrison-Scott 1937; Borgia 1985a; Borgia and Keagy 2006), which are preferred by females (Borgia 1985a; Coleman et al. 2004). These decorations are often acquired from neighboring males that are not within view of each other (Borgia 1985b; Borgia and Gore 1986; Pruett-Jones and Pruett-Jones 1994; Hunter and Dwyer 1997), which implies a mental map of bower locations. Males also react to female signals during intense elements of their courtship and adjust their display accordingly (Patricelli et al. 2002, 2006). Immediately following the intense elements of courtship, males stand relatively still and accurately mimic up to five species of birds during courtship (Loffredo and Borgia 1986; Coleman et al. 2007). During their prolonged juvenile period males engage in practice displays with other males and over the course of several years improve their display performance (Vellenga 1970; Collis and Borgia 1993). All of this suggests an important role for cognition in the sexual display of this species.

The major objective for this work is to examine the relationship between male cognitive ability and sexual selection in satin bowerbirds. I begin this investigation in Chapter I by assessing male problem solving ability. I presented males with two novel

problems to test the hypothesis that males that are better problem solvers have higher

mating success. These problems were designed to take advantage of males' strong

aversion to red objects on their bower platforms, which they immediately attempt to

remove (Morrison-Scott 1937; Borgia et al. 1987; Borgia and Keagy 2006). This

behavior 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. I show that males who were better problem solvers did have

higher mating success. In addition, I demonstrate that neither age nor motivational

level significantly explains variation in problem solving scores, strengthening the

conclusion that variation in problem solving tests is primarily a reflection of cognitive

performance. This represents the first evidence of a relationship between a measure of

general cognitive ability and mating success.

In Chapter II, I borrow from techniques primarily used in research on human

cognition to examine more closely the relationship between general cognitive ability

and mating success. These techniques utilize data on a number of different cognitive

tests, and here I use six cognitive tests that vary widely in the degree of their

cognitive complexity and are influenced to different degrees by problem solving

ability, motor ability, and vocal ability. First, I calculate the scores of the first factor

of a principle components analysis of this data. This variable is called g by

psychologists and is widely used in human psychology research (Mackintosh 1998;

Plomin 2001), at least three independent labs studying mice (Locurto et al. 2003; Matzel et al. 2003; Galsworthy et al. 2005) and recently in tamarins (Banerjee et al. 2009). Second, I calculate male average rank performance on all of the cognitive tasks, which is analogous to how human IQ is calculated (a transformation of a total score calculated from tests across multiple cognitive modalities (Mackintosh 1998; Plomin 2001)). I show that both of these measures are positively associated with mating success. In addition, four of the six cognitive tasks I use to construct my measures of general cognitive ability independently predict mating success, while the others do not, suggesting differing selection pressures on particular cognitive traits. These results suggest a much more important relationship between cognition and sexual selection than has previously been appreciated.

In Chapter III, I switch focus to test the hypothesis that male behavioral display traits have an important role in indicating male cognitive ability to females choosing mates. In this chapter, I use two statistical measures of male overall cognitive ability, 1) scores from an analysis that best explains covariation among six different cognitive tests (this is *g* from Chapter II) and 2) scores from an analysis that determines the combination of cognitive traits that made males most successful in attracting females (I call this *f*). I find that these two measures are significantly correlated, suggesting that evolution of cognitive ability in bowerbirds is possible if there is sufficient heritability. In addition, I construct three different aggregate measures of male display quality (produced from four different behavioral display traits) that differ in the assumptions made about how females use multiple behavioral display traits. I find that these measures of display quality are correlated with one

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measure of overall cognitive ability, f, and with mating success. I show that multiple behavioral display traits used together, rather than individually, more accurately predict this measure of overall cognitive ability. Finally, I find some support for the hypothesis that separate display traits may indicate different aspects of male cognitive ability. These results suggest that there is a relationship between male behavioral display, cognitive ability, and attractiveness to females, such that females who mate with males with attractive displays are selecting males with better cognitive ability.

CHAPTER I

Male satin bowerbird problem solving ability predicts mating success

ABSTRACT

Mate choice and mate attraction are important behaviors that influence 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 colors, suggests a selective advantage to individuals with superior cognitive abilities. I used males' strong aversion to red objects on their bowers to design two unique problem solving tests. I presented males with these problems to test the hypothesis that males that are better problem solvers have higher mating success. I confirmed this prediction and demonstrate that neither age nor motivational level significantly influenced problem solving scores. My 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.

INTRODUCTION

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 behavioral 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 I test the 'cognitive performance hypothesis' that suggests a positive relationship between general cognitive performance and reproductive success. I 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 (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 behavioral 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 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

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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 behavioral 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 overall brain size, but did correlate with the size of the HVC, an important song control nucleus (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 behavioral 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). I 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 behavioral traits that suggest cognitive performance may be important in their sexual display: they build a stick bower on the ground

where courtship occurs (Borgia 1985a), they react to female signals during courtship and adjust their display accordingly (Patricelli et al. 2002), they steal from and destroy neighboring bowers that are not within view of each other, which implies a mental map of bower locations (Borgia 1985b; 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 1985a), which indicates strong sexual selection. This measure of mating success is obtained from automated monitoring of bowers where copulations occur (Borgia 1985a; 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, I evaluated the hypothesis that there was a positive relationship between problem solving ability and mating success. Second, I 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, I 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, I was interested in understanding not only how problem solving scores relate to mating success, but also how age and motivational level influence problem solving scores.

I 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 behavior 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.

I 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 behavior that probably requires little cognitive ability to complete and

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therefore should only be influenced by differences in motivation. Both motivation and cognitive ability could affect performance on novel problem solving tests such as mine that involve more complicated solutions than simply picking up and moving an object. Therefore, I tested for an association between my 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 (Figure 1).

METHODS

Study System

This study was conducted in 2004 and 2005 at Wallaby Creek (28º28'S, 152º25'E), NSW, Australia (Borgia 1985a). Males court females at bowers that are at least 100 m apart (Borgia 1985b), and females visit a mean ± 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 1985a). 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. 1987), suggesting that the number of blue objects on a

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male's bower is a measure of male quality. Male bowerbirds have highly specific color preferences and actively remove red objects on or near their bower platform (Morrison-Scott 1937; Borgia et al. 1987; Borgia & Keagy 2006). This behavior may be related to the use of specific color 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). I 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 colored plastic bands on each leg (Borgia 1985a). I monitored bowers throughout the mating season using an automated video-monitoring system to provide a complete record of behavior at these bowers. I 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 this field site since 1995, providing me 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 license 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 (Figure 2). I videotaped all behaviors for 24 h and then

removed the experimental apparatus. As a measure of problem solving ability, I

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': I recorded 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.

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, I observed males covering screws inserted into their platforms, which led me 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 (Figure 3). I predicted that the tiles would be covered in order of color 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, I randomly assigned the three colored squares to one of six possible configurations.   After 24 h, I 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.). I used the area of the red tile that was covered as a measure of problem solving ability. To measure motivation, I presented males with a red tile that was not fixed into the ground. I did not record the time that males took to move the red tile, but I did record the distance that they moved the red tile after 4 h. I used this distance as my measure of motivation and assumed that males that were more motivated to move red objects would move the red tile further from their bower. I 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.

Statistical Analyses

Data were analyzed using Statistica 6.0 (Statsoft Inc., Tulsa, OK, U.S.A.). I used regression analysis to test the hypothesis that problem solving ability predicts mating success. In addition, I 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 I 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), I performed a partial correlation analysis that removed the effect of age, however small, from both variables.

My data set consists of performance scores on two problem solving tests presented in different years, along with each year's associated mating success scores. I used canonical correlation analysis (James & McCulloch 1990; Bond & Diamond 2005) to analyze 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 analyzed 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 my mating success data resulted in distributions that were sufficiently normal and nearly identical to those

achieved through log transformations. I 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 I 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 my 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

I measured the time that males took to solve the barrier problem in two ways.

First, I 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: $R^2=0.29$, $F_{1,23}=9.43$,

$P=0.003$; Figure 4a). For the second measure ('time attentive to task'), I 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; Figure 4b). These two measures were highly correlated (Pearson correlation: R^2=0.84, t_{23}=11.08, P<<0.0001).

I 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). I 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, I 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_{age}=0.37, P=0.22, $b_{motivation}$=0.08, P=0.80; time attentive to task: R^2=0.25, $F_{2, 13}$=2.17, P=0.15, b_{age}=0.46, P=0.11, $b_{motivation}$=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 my observed results, is consistent with the hypothesis that male ability to solve the barrier problem was influenced primarily by cognitive ability.

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 color 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 ($R^2=0.27$, $F_{1, 31}=11.71$, $P=0.002$). I performed a partial correlation analysis to determine the relationship between problem solving ability and mating success independent of age effects, and I 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 (Figure 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). I 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. I 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.

I 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, I 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 x red coverage: R=-0.04, P=0.88; time attentive to task x red coverage: R=-0.17, P=0.46). I performed a canonical correlation analysis to determine the overall correlation between problem solving ability on both tests and mating success in both years. I 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, χ^2_4=15.46, $P =$ 0.002; using time attentive to task as barrier problem solving ability: canonical R=0.71, χ^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, χ^2_4=18.47, $P = 0.0005$; using time attentive to task as barrier problem solving ability: canonical R=0.74, χ^2_4=16.90, $P = 0.001$).

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 my 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 behavioral traits (Brody 1992; Mackintosh 1998; Deary 2000). Furthermore, I was able to quantify age and motivational level, and I found that neither variable explained problem solving scores.

Given that it is unlikely that females were directly influenced by my 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 behavioral display traits that have a strong cognitive component 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 1985a). 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, bird song, 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 bird song, 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, I conducted the first test of the hypothesis that males with higher general cognitive performance have higher mating success. My 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. My results suggest that cognitive performance is important to male reproductive success, but I 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.

TABLES

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 the other 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.

FIGURE CAPTIONS

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.

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.

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%.

Figure 4. Relationship 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).

FIGURES

Figure 1
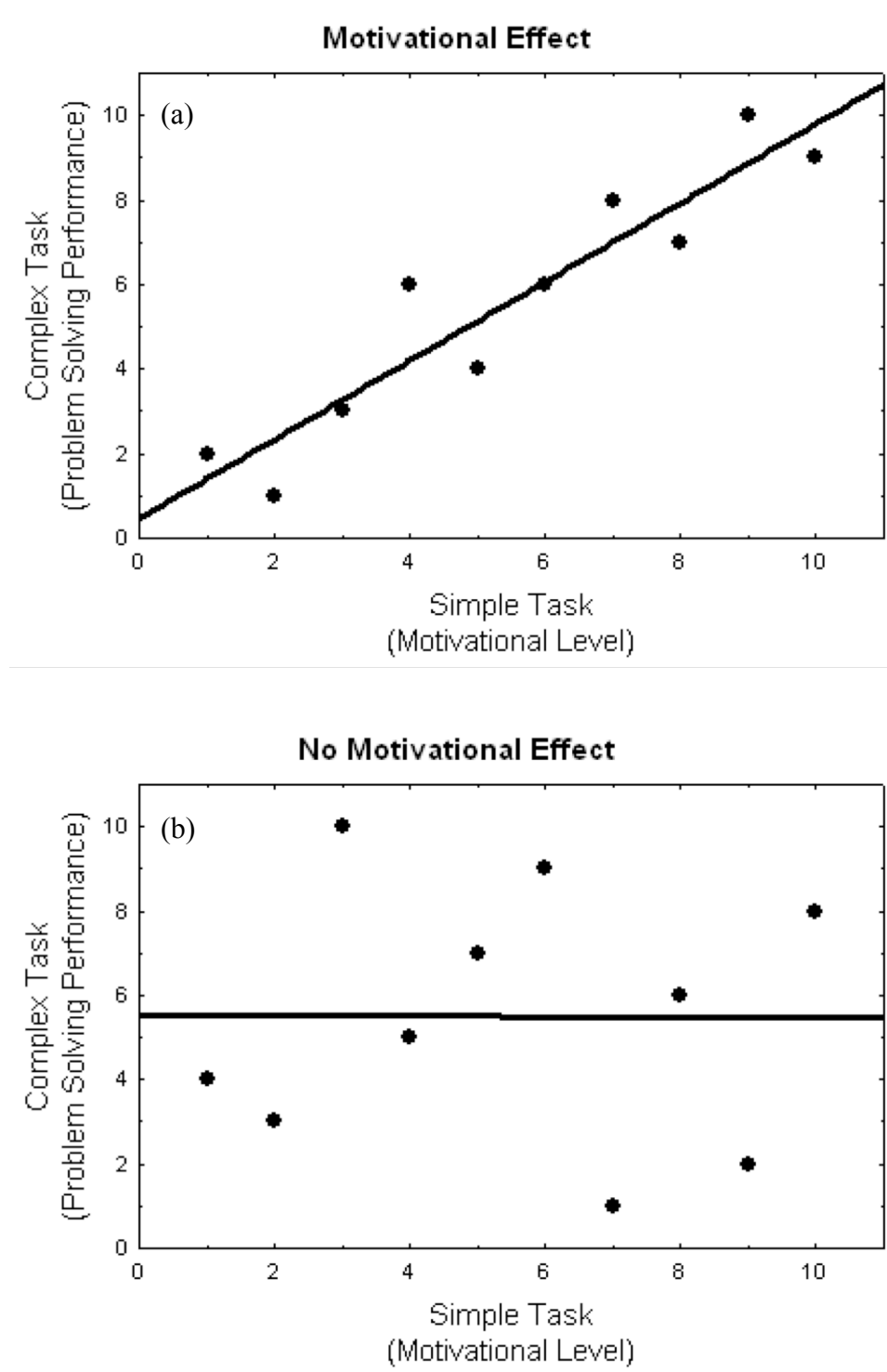
Figure 2

Figure 3

Figure 4
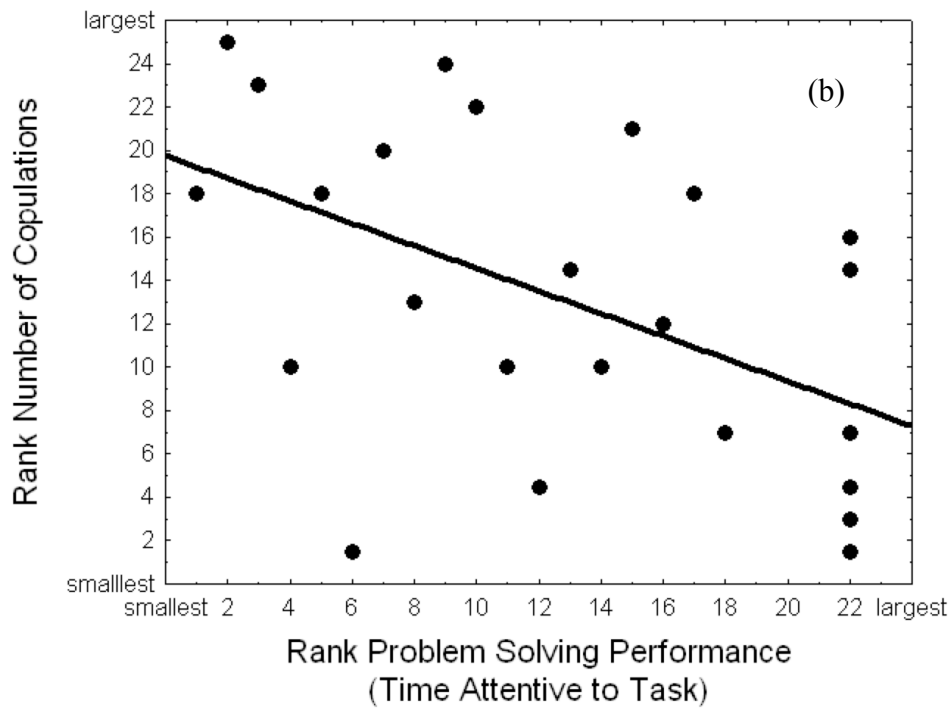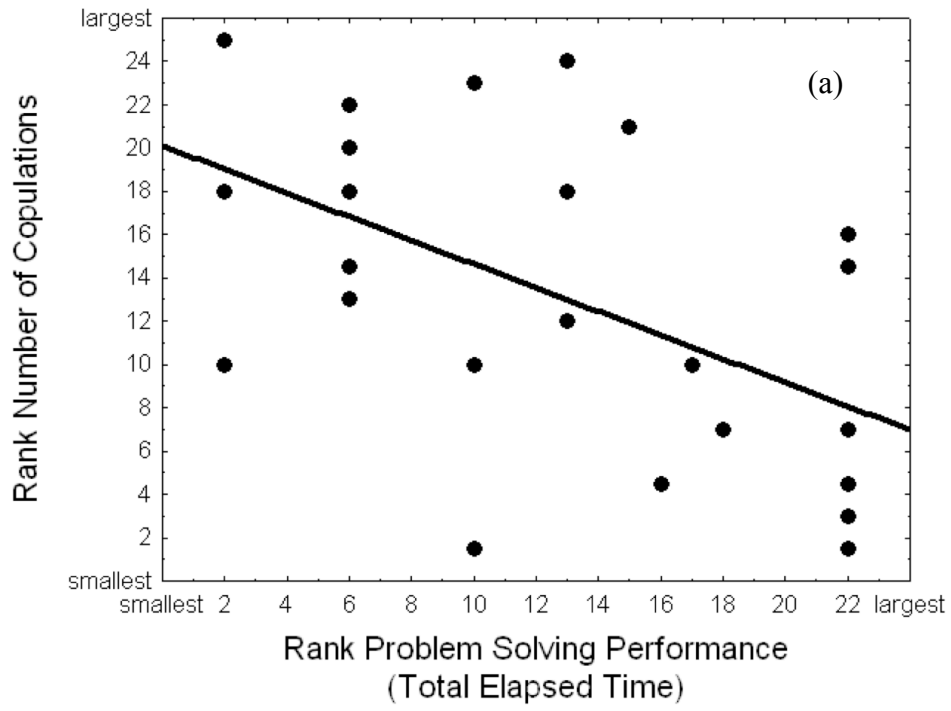
CHAPTER II

General cognitive ability predicts male mating success in satin bowerbirds

ABSTRACT

Many species have been shown to possess 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. Here I use performance on six different cognitive tasks to calculate two different measures of general cognitive ability. I show that male satin bowerbirds (*Ptilonorhynchus violaceus*) with better scores of general cognitive ability have higher mating success, which is known in this species to be a good indicator of reproductive success. In addition, four of the six cognitive tasks I used to construct my measures of general cognitive ability independently predicted mating success, while the others did not, suggesting differing selection pressures on particular cognitive traits. My results point to an important link between sexual selection and cognitive ability.

INTRODUCTION

Many species have complex cognitive abilities that were once considered to be limited to humans (Tomasello and Call 1997; Shettleworth 1998). These well-developed cognitive capabilities are thought to have evolved for a variety of reasons including solving ecological problems (Pravosudov and Clayton 2002; Sol et al. 2007; Cnotka et al. 2008) or navigating complex social environments (Byrne and Whiten 1988; Dunbar 1998; Bond et al. 2003; Holekamp et al. 2007). Mate choice and mate attraction are significant behaviors that also have large impacts on fitness and influence the evolution of elaborate traits (Darwin 1871; Andersson 1994). However, there has been little consideration of the possible connection between general cognitive ability and sexual selection. This should be surprising given the behavioral complexity of many sexual displays (e.g. Prum 1994; Frith and Frith 2004) and the potentially large fitness benefits of mating with individuals with better cognitive performance (e.g. discussed in relation to bird song by DeVoogd 2004).

It has been suggested that individuals with better cognitive performance have higher reproductive success (Miller 2000; Keagy et al. 2009). This may occur for several reasons, but one of the most discussed is a female preference for cognitively superior males who confer genetic benefits to their offspring (Keagy et al. 2009; Prokosch et al. 2009). General cognitive ability may be an especially good indicator of genetic quality for several reasons. First, results of a number of studies are consistent with the hypothesis that increased cognitive performance has fitness benefits (e.g. Dukas and Duan 2000; Sol et al. 2007; Roth et al. in press). Therefore, it has been proposed that cognitive performance should reflect aspects of genetic

quality such as survivability (DeVoogd 2004; Boogert et al. 2008). Second, it has

been pointed out that a large number of genes likely influence cognitive performance,

resulting in this trait representing a large integrated sample of the genome (Miller

2000). Direct evidence for this hypothesis has recently been demonstrated with the

sequencing of the zebra finch genome and the finding that learning and production of

bird song relies on the expression of an extremely large number of genes (Warren et

al. 2010). Third, in the species studied thus far (mice and humans) general cognitive

ability has been found to be highly heritable (Plomin 2001; Galsworthy et al. 2005;

Deary et al. 2006).

In humans, general cognitive ability, commonly referred to as intelligence, is

often measured using the scores of a statistical construct called g, which best explains

variation in performance on multiple cognitive tasks (Spearman 1904; Plomin 2001).

In addition, standard intelligence tests tend to be associated with g and also test

performance across a variety of cognitive domains (Prokosch et al. 2005). A link

between fitness and general cognitive ability has received some support in humans

(Prokosch et al. 2005; Arden et al. 2009). Also, human females are capable of

accurately assessing male intelligence by watching male behavior and rate more

intelligent males as more attractive (Prokosch et al. 2009). However, it is not clear

whether this attractiveness ranking translates directly into male reproductive success.

Outside of humans, the construction and use of g as a measure of general

cognitive ability has only been attempted in laboratory settings with mice (e.g. Matzel

et al. 2003; Galsworthy et al. 2005) and tamarins (Banerjee et al. 2009), and it has not

been used in non-human animal studies of sexual selection. However, the statistical

technique used to construct *g*, principal component analysis (Spearman 1904; Plomin 2001; Galsworthy et al. 2005), does have widespread use in studies of behavioral ecology and evolution where it is used to create composite measures from sets of variables. Instead of calculating *g* or some other composite variable, problem solving ability has been used as a proxy for general cognitive ability in at least two sexual selection studies of animals. These studies showed that problem solving ability predicts song complexity (Boogert et al. 2008), a sexually selected trait, and mating success (Keagy et al. 2009). However, a relationship between sexual selection and general cognitive ability would be demonstrated more definitively by assessing general cognitive ability using a more encompassing measure, such as *g*, and then testing whether individuals with better scores on that measure have higher reproductive success.

Satin bowerbirds offered me the opportunity to construct two measures of general cognitive ability with individuals in nature and then test whether males with better scores of general cognitive ability have higher mating success, a good proxy for reproductive success in this species (Reynolds et al. 2007). Several aspects of satin bowerbird biology make them ideal for this study. First, males have a large set of behaviors that appear to have a considerable cognitive component (Madden 2008; Keagy et al. 2009). Second, males build and defend display sites called bowers (Borgia 1985a), which means I had specific locations where I could present individual males with a number of distinct cognitive tasks, without interference from other males. Using automated video monitoring of these sites (Borgia 1985a), I could record performance on cognitive tasks by free-living individuals. Third, bowerbirds

have a non-resource based mating system where females receive only sperm from males. Automated video monitoring of bowers allows me to record every copulation in this population, resulting in an extremely accurate measure of mating success (Borgia 1985a). Results from genetic paternity tests match observed copulations on videos (Reynolds et al. 2007) and confirm that this measure of mating success is a true reflection of female choice for males.

I video monitored 21 males and assessed their performance on six different cognitive tasks: 1) ability to remove a clear barrier covering target objects, 2) ability to conceal an immovable undesirable object, 3) bower rebuilding efficiency, 4) flexibility in bower rebuilding, 5) use of a behavioral "tool" for creating symmetrical bowers, and 6) mimetic repertoire size (described in detail in Table 2 and Methods). I chose these tasks because they seemed likely to be within the behavioral repertoire of this species, and the tasks seemed to vary widely in the degree of their cognitive complexity. In addition, the tasks I presented allowed me to evaluate male performance on a number of different cognitive abilities, including problem solving ability, motor ability, and vocal ability, with some tasks assessing some combination of these abilities. This is important to meet the goal of constructing a variable that reflects variation in neurophysiological quality (and ultimately genetic quality), which is a common interpretation of the g factor (Miller 2000; Plomin 2001; Banerjee et al. 2009). Consistent with other studies (Spearman 1904; Plomin 2001; Galsworthy et al. 2005), I constructed g using scores from the first unrotated principal component from a principle component analysis of the six cognitive tasks. In addition, I used an

additive measure of cognitive ability analogous to human IQ (Plomin 2001) by

determining the average rank score of each male across all tasks.

METHODS

Study site and data collection

This study was conducted in 2004 and 2005 at Wallaby Creek (28º 28' S, 152º

25' E), NSW, Australia. All bower holders could be identified by a unique

combination of three colored plastic bands on each leg. All behaviors 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 me detailed age information for birds.

(i) Problem solving tests (cognitive tasks 1-2)

Males have strong preferences for decorations of particular colors collected

from the environment (Borgia et al. 1987; Borgia and Keagy 2006) that are attractive

to females (Borgia 1985a; Coleman et al. 2004). Males have an intense dislike for red

objects at their bowers (Morrison-Scott 1937; Borgia et al. 1987; Borgia and Keagy

2006), and I used this behavior to design problem solving tests that males were highly

motivated to complete (Keagy et al. 2009). Detailed methods are described elsewhere

(Keagy et al. 2009, see also Chapter I). Briefly, in 2005 I placed a clear container

over three red objects and quantified the time for each male to remove the container

(task 1 - barrier problem). Versions of this particular experiment have been used in other tests of problem solving ability (e.g. Roth et al. in press). In 2004 I super-glued a red square tile to a long screw and fixed the tile into the bower platform and ground below. I took digital photographs after 24 hours and calculated the proportion of the red tile covered (task 2 - red coverage) using Image J (v. 1.34i National Institutes of Health, Washington D.C.). In addition, for many males I was able to measure their motivation to solve these two problems by using the time it took males to move the same red objects when they were unconstrained. Males in this study are the subset of males that were presented both problem solving tests in a previous study (Keagy et al. 2009, see also Chapter I). Using these males, I performed univariate analyses comparing problem solving ability to mating success during the year each test was presented. Consistent with my previously reported results, I found that males that removed the barrier faster had higher mating success (r^2=0.28, $F_{1,19}$=7.27, P=0.014, n=21) and males that covered the red tile more had higher mating success (r^2=0.20, $F_{1,19}$=4.67, P=0.044, n=21).

(ii) Bower rebuilding (cognitive tasks 3-5)

I destroyed one wall of each male's bower once during the mating season of 2005. 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. I recorded all rebuilding behavior on video and determined the total time males took to place 100 sticks (task 3 - handling time), the proportion of those sticks placed in the destroyed wall (task 4 - proportion destroyed wall), and the proportion of sticks placed using a

behavioral "tool" called "templating" (task 5 - templating). Handling time is a reflection primarily of motor ability, but this ability is refined through a period of improvement during which juveniles practice building bowers (Vellenga 1970; Collis and Borgia 1993) and may even engage in social learning (Madden 2008). Males who had longer handling time 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. Keagy, personal observation). While bower destructions are commonly carried out by neighboring males (Borgia 1985b), destructions in which one wall is completely destroyed and the other is completely untouched have not been observed (J. Keagy, J-F Savard, and G. Borgia, personal observations). Males who place more sticks in the missing wall were reacting more appropriately to this novel situation and the problem of creating a symmetrical bower, which is preferred by females (Borgia 1985a). During templating, males pick up a stick they will use for rebuilding the destroyed bower wall while standing on the midline of the bower avenue. They then place the stick into the standing wall and, without letting go of the stick, pull it out of that wall and, using an exact reversal of movements, place that stick in an identical position in the formerly destroyed wall they are rebuilding. In addition to these measures of cognitive performance, I recorded using video time stamps the time between the destruction and time to begin building. This is a rough measure of male bower maintenance activity level and motivation to rebuild.

(iii) Mimetic repertoire size (cognitive task 6)

Using automated camcorders equipped with omnidirectional microphones suspended 1m above bowers, I recorded all male courtship vocalizations during the mating season of 2004. I used Raven Pro 1.3 (Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A) to visualize and analyze 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). I calculated the average number of species mimicked for all 21 males using courtships between unique male-female dyads. Number of courtships available for analysis was not correlated with mimetic repertoire size (R=0.08, P=0.73, N=21), suggesting that additional data would not qualitatively change my results.

Statistical analyses

Data were analyzed using Statistica 6.0 (Statsoft Inc., Tulsa, OK, U.S.A.). I constructed *g* using scores from the first unrotated principal component from a principal component analysis of the cognitive tasks. As an alternative measure of cognitive ability analogous to IQ, I 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). I used regression analysis in situations where one variable was hypothesized to

predict another and Pearson correlations to test for associations between variables without an *a priori* hypothesized direction of causality. Multiple regression analysis was used to test whether different cognitive tasks were independently under sexual selection.

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 among male satin bowerbirds (Keagy et al. 2009). Results were similar when I 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 my results. 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 neighboring male during the observation period and was not included in this analysis because of missing data for cognitive tasks 3-5. All statistical tests are two tailed.

RESULTS

As predicted, males with better scores of *g* had higher mating success (r^2=0.41, $F_{1,18}$=12.71, P=0.002, n=20; Figure 5). This measure of *g* explained 28% of the variance in the six cognitive traits I measured. Factor loadings of cognitive tasks on *g* (correlations between performance on cognitive tasks and scores of *g*) were in the predicted direction with one exception (Table 3). Further support for my

assessment of g being a measure of general cognitive ability is that males who were on average better at all cognitive tasks had higher scores of g ($r=0.50$, $t_{18}=2.43$, $P=0.026$, $n=20$, Figure 6). This is analogous to the situation in humans where an additive measure of cognitive ability, IQ, correlates reasonably well with g (Plomin 2001). This alternative measure of general cognitive ability also predicted mating success ($r^2=0.66$, $F_{1,18}=34.71$, $P\ll0.0001$, $n=20$; Figure 7).

Females could not have directly assessed male performance on most of the cognitive tasks because female visitation was rare during my assessment periods. Mimetic repertoire size is the exception, however, because I assessed it during courtship. I constructed another measure of g without this variable to ensure that I was not biasing my 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 ($r^2=0.38$, $F_{1,18}=11.19$, $P=0.004$, $n=20$) and this g explained 33% of the variance in the five cognitive traits I measured. The two measures of g were significantly correlated ($r=0.99$, $t_{18}=25.85$, $P\ll0.0001$, $n=20$). Similarly, when I recalculated male average rank score on all cognitive tests (bowerbird "IQ") without mimetic repertoire size, I still found a significant relationship between this measure of general cognitive ability and mating success ($r^2=0.45$, $F_{1,18}=14.65$, $P=0.001$, $n=20$). These two measures of bowerbid "IQ" were also significantly correlated ($r=0.80$, $t_{18}=8.59$, $P\ll0.0001$, $n=20$).

The existence of a general factor of cognitive ability is thought to be the result of variation in a similar set of genetic and neurophysiological variables (Miller 2000; Plomin 2001; Banerjee et al. 2009). I looked at whether there were correlations

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between different cognitive tasks to determine to what extent they were interrelated (Table 4). The lack of statistically significant correlations among the different cognitive tasks suggests independence between performance on the different cognitive tasks, a phenomenon often referred to as cognitive modularity. I tested whether these different cognitive tasks were independently under sexual selection using a multiple regression analysis. This model revealed that better performance on most cognitive tasks was independently associated with higher mating success, with the exception of red coverage and templating (Table 3). This is evidence that there are differing sexual selective pressures on particular cognitive traits.

Three factors that could have influenced male cognitive performance are age, motivation, and neophobia. Age did not explain cognitive performance, measured either by the separate cognitive tasks or my measures of g (Table 5). The lack of an influence of age on cognitive performance makes sense for at least two reasons. First, adult male bowerbirds experience a seven-year juvenile period of development where they practice extensively skills similar to those needed to perform well on my cognitive tasks (Vellenga 1970; Collis and Borgia 1993). Second, in humans, g is one of the most stable behavioral traits after childhood (Plomin 2001). Consistent with my previous results (Keagy et al. 2009) I found no effect of motivation (measured as time to move unconstrained target objects used in problem solving tests) on male problem solving performance (barrier problem: $r^2=0.14$, $F_{1,12}=1.99$, P=0.18, n=14, red coverage: $r^2=0.00$, $F_{1,9}=0.01$, P=0.94, n=11). In addition, the time it took males to begin building after my one-wall bower destruction was not related to handling time ($r^2=0.00$, $F_{1,17}=0.04$, P=0.84, n=19), suggesting that male latency to build or activity

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level was not related to male handling time. I did not have effective ways to measure motivation for the other cognitive tasks, but male bowerbirds tend to be very active in courtship and bower maintenance activities, which suggests that motivation may not be a large factor in controlling their behavior. Neophobia is unlikely to be a factor in my assessment of cognitive performance because only the problem solving tests involved novel objects. In addition, if there was variation in propensity to approach the novel objects used in the problem solving tests, this would have been reflected in my motivation measures and yet there was no relationship between these measures and problem solving ability. In other words, there is no reason to suspect that less neophobic individuals were better problem solvers.

DISCUSSION

In this study I measured male performance on six cognitive traits that represented a number of different cognitive abilities including problem solving ability, motor ability, and vocal ability. I used these data to construct two different measures of general cognitive ability. First, using a principle component analysis data, I constructed a statistical measure of general cognitive ability, g. Second, I calculated each male's average rank score on the cognitive tests, which is mathematically analogous to IQ scores (which is a transformation of a total score calculated from tests across multiple cognitive modalities). Using these two measures, I found that males with better general cognitive ability were preferred by females and had higher mating success, a measure that is a strong predictor of reproductive success in this species (Reynolds et al. 2007). It has been suggested that general

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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). This

indicates that the evolution of increased general cognitive ability is possible through

female choice for males with better cognitive ability, possibly because of genetic

benefits to her offspring. This possible route for cognitive evolution has received very

little attention (Miller 2000; Keagy et al. 2009), but may be widespread, as suggested

by the large number of species with complex sexual displays that appear to involve an

extensive cognitive component.

Attempts to measure general cognitive ability in animals have been very rare,

in part because of the difficulty of assessing individual differences on a battery of

different tasks. However, these studies are important if comparative study of the

evolution of general cognitive ability is ever going to be possible (Banerjee et al.

2009). Currently, this question can only be answered using proxies such as brain size

that may be inadequate at best in accurately capturing variation in general cognitive

ability between species (Healy and Rowe 2007). Intriguingly, my measure of g in

bowerbirds explained 28%-33% of the variance in the six cognitive traits I measured,

which is of a similar or slightly lower magnitude compared to that reported in mice

(22-41%: Galsworthy et al. 2005; 38%: Matzel et al. 2003) and humans (roughly

40%: Plomin 2001). Unlike these studies, however, I found a great deal of

independence between performance on individual cognitive tasks, which is

commonly referred to as modularity. The degree to which modularity occurs and

influences cognitive evolution is actively debated (Finlay and Darlington 1995;

Barton and Harvey 2000). Future research could shed light on whether there are differences between taxonomic groups in the relative independence of different aspects of cognition. For example, a recent study showed that variation in the brain regions of a diverse group of cichlid fishes shows a pattern of independent evolution and very little constraint (Gonzalez-Voyer et al. 2009). However, the existence of independent cognitive units is not necessarily inconsistent with the presence of a general factor of cognitive ability, because these modules clearly still 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).

My results and methodology should be applicable more generally because while the form of some of the cognitive tasks I measured may be bowerbird specific, they are likely influenced by cognitive abilities that are in some form shared by other species. For example, handling time of sticks (cognitive task 3) is a reflection primarily of motor ability, but is likely improved over the many years during which juveniles practice (Vellenga 1970; Collis and Borgia 1993). It has recently been suggested that sexual displays of motor ability may be an important component of courtship (Byers et al. 2010). In addition, Boogert et al. (2008) show a correlation between two cognitive traits in zebra finch males, song complexity and problem solving ability, which suggests the potential for studies of general cognitive ability in that species. I encourage further exploration of the relationship between general cognitive ability and sexual selection in other animals using adaptations of this technique appropriate to the species being studied.

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 behavior (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 co-evolution 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.

TABLES

Table 2. Description of cognitive tasks used to construct *g*, a measure of general cognitive ability.

Cognitive task	Description
1. Barrier problem	Time it took a male to move a clear plastic barrier before he could take three undesirable (red) objects from his bower. This is a previously documented technique for assessing problem solving ability (Keagy et al. 2009).
2. Red coverage	Proportion of an unmovable and undesirable (red) object a male was able to cover to remove it from view. This task required a male to first realize the undesirable object was immovable and then use the alternative strategy of concealing it with materials from the environment. This task requires a great deal of inhibitive control, which increases the difficulty of the problem (Taylor et al. 2007). This is a previously documented technique for assessing problem solving ability (Keagy et al. 2009).
3. Handling time	Time it took males to place 100 sticks after one bower wall was destroyed. This task is influenced by male ability to manipulate and place sticks properly and so assesses variation in male motor ability, but practice also appears to be important, at least in the initial development of this ability (Vellenga 1970; Collis and Borgia 1993).
4. Proportion destroyed wall	The proportion of sticks placed in the area left by the destroyed bower wall. This task assesses how well males react to the problem of having only one wall destroyed and the need to create a symmetrical bower, which is preferred by females (Borgia 1985a).
5. Templating	The proportion of sticks placed using a behavioral "tool" to create symmetrical bowers by using one wall as a template for the other.
6. Mimetic repertoire size	The average number of species males mimicked during courtship. This task reflects male ability to learn mimetic songs and later recall and produce them during courtship.

Table 3. Contribution of cognitive tasks to *g* and mating success.

Cognitive task (n=20)	Loading PCA	Multiple regression betas			
		ß	df	t	P
1. Barrier problem	-0.31 (-)	-0.49 (-)	13	-3.26	0.006
2. Red coverage	+0.57 (+)	+0.27	13	1.87	0.08
3. Handling time	-0.76 (-)	-0.52 (-)	13	-3.49	0.004
4. Proportion destroyed wall	+0.12 (+)	+0.33 (+)	13	2.34	0.036
5. Templating	-0.78 (+)	+0.24 (+)	13	1.65	0.12
6. Mimetic repertoire size	+0.19 (+)	+0.47 (+)	13	3.13	0.008

In general, performance on cognitive tasks correlated with *g* in the expected directions (loadings). Templating is the exception and the strong negative loading on *g*, paired with a tradeoff detected between templating and building efficiency (males who template more have longer handling times, $R=0.45$, $t_{18}=2.16$, $P=0.045$, $N=20$), suggests the possibility that males who template more may do so because of an inability to effectively use other methods to create symmetry. Performance on most cognitive tasks also independently predicted mating success. In addition, the overall multiple regression model predicting male mating success was significant ($r^2=0.79$, $F_{6,13}=8.26$, $P=0.008$, $n=20$). (+) and (-) refer to a hypothesized positive and negative relationship, respectively.

Table 4. Correlation matrix of cognition variables.

	Barrier problem	Red coverage	Handling time	Proportion destroyed wall	Templating	Mimetic repertoire size
	1	2	3	4	5	6
Barrier problem 1						
Red coverage 2	(-) r=-0.18 t_{19}=-0.80 P=0.43 n=21					
Handling time 3	(+) r=0.16 t_{18}=0.70 P=0.49 n=20	(-) r=-0.16 t_{18}=-0.67 P=0.51 n=20				
Proportion destroyed wall 4	(-) r=0.09 t_{18}=0.39 P=0.70 n=20	(+) r=0.27 t_{18}=-1.19 P=0.25 n=20	(-) r=0.16 t_{18}=0.68 P=0.50 n=20			
Templating 5	(-) r=0.11 t_{18}=0.45 P=0.66 n=20	(+) r=-0.18 t_{18}=-0.76 P=0.46 n=20	(-) r=0.45 t_{18}=2.16 P=0.045 n=20	(+) r=-0.12 t_{18}=-0.51 P=0.62 n=20		
Mimetic repertoire size 6	(-) r=0.40 t_{19}=1.93 P=0.07 n=21	(+) r=0.18 t_{19}=0.82 P=0.42 n=21	(-) r=-0.11 t_{18}=-0.45 P=0.66 n=20	(+) r=-0.10 t_{18}=-0.44 P=0.66 n=20	(+) r=-0.08 t_{18}=-0.34 P=0.74 n=20	

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

Table 5. Relationship between bowerbird cognition and age.

Cognitive task	Relationship with age				
	r^2	df	F	P	n
1. Barrier problem	0.01	1,19	0.23	0.64	21
2. Red coverage	0.01	1,19	0.13	0.72	21
3. Handling time	0.00	1,18	0.07	0.80	20
4. Proportion destroyed wall	0.04	1,18	0.68	0.42	20
5. Templating	0.00	1,18	0.01	0.91	20
6. Mimetic repertoire size	0.03	1,19	0.57	0.46	21
g (calculated using tasks 1-6)	0.00	1,18	0.05	0.83	20
g (calculated using tasks 1-5)	0.01	1,18	0.10	0.75	20
Bowerbird "IQ" (calculated using tasks 1-6)	0.01	1,18	0.14	0.71	20
Bowerbird "IQ" (calculated using tasks 1-5)	0.00	1,18	0.00	0.97	20

Age ranged from 8-20 years in 2004. The variation in performance on cognitive tasks or on scores of general cognitive ability could not be explained by differences in age.

FIGURE CAPTIONS

Figure 5. Relationship between g and mating success. This analysis revealed a significant relationship between g and mating success in satin bowerbirds ($r^2=0.41$, $F_{1,18}=12.71$, P=0.002, n=20).

Figure 6. Relationship between average rank performance across all cognitive tasks and g. Average rank performance across all cognitive tasks is an additive measure analogous to the additive measure of general cognitive ability in humans, IQ. The correlation between average rank performance on cognitive tasks and g lends further support to g being a measure of general cognitive ability (r=0.50, $t_{18}=2.43$, P=0.026, n=20).

Figure 7. Relationship between average rank performance (bowerbird "IQ") and mating success. This alternative measure of general cognitive ability also predicted mating success ($r^2=0.66$, $F_{1,18}=34.71$, P<<0.0001, n=20).

FIGURES

Figure 5
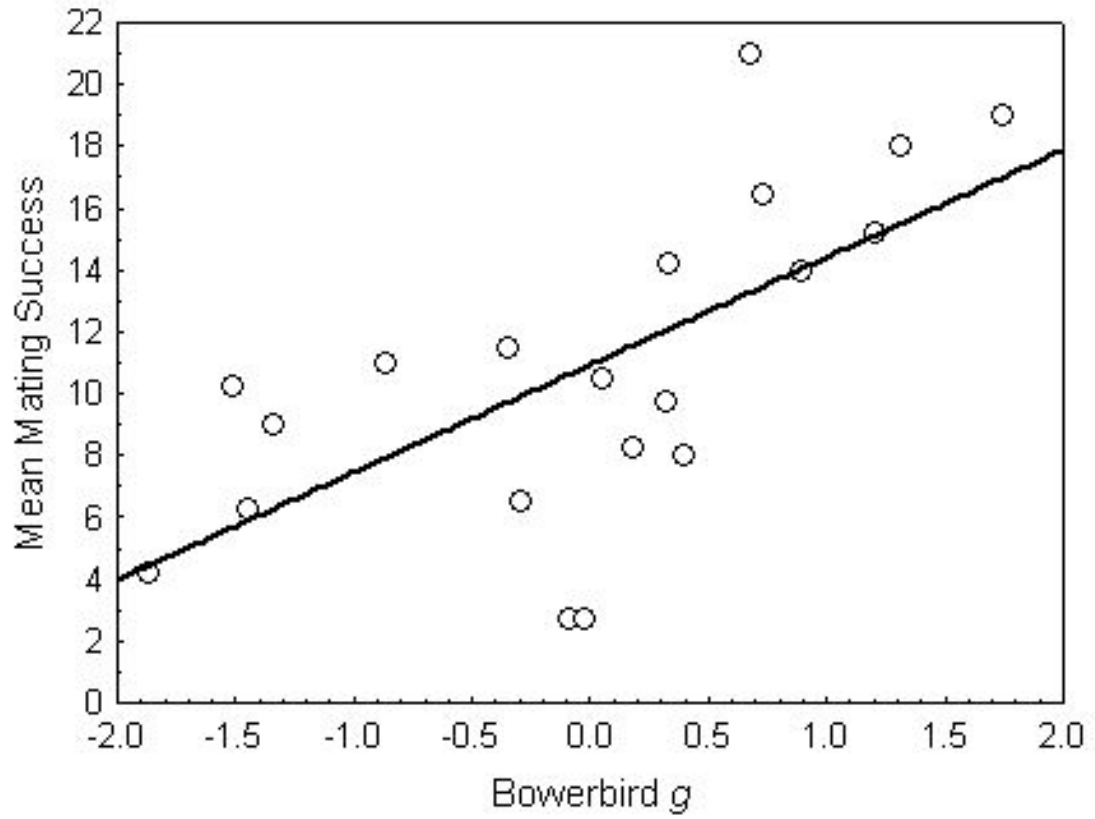
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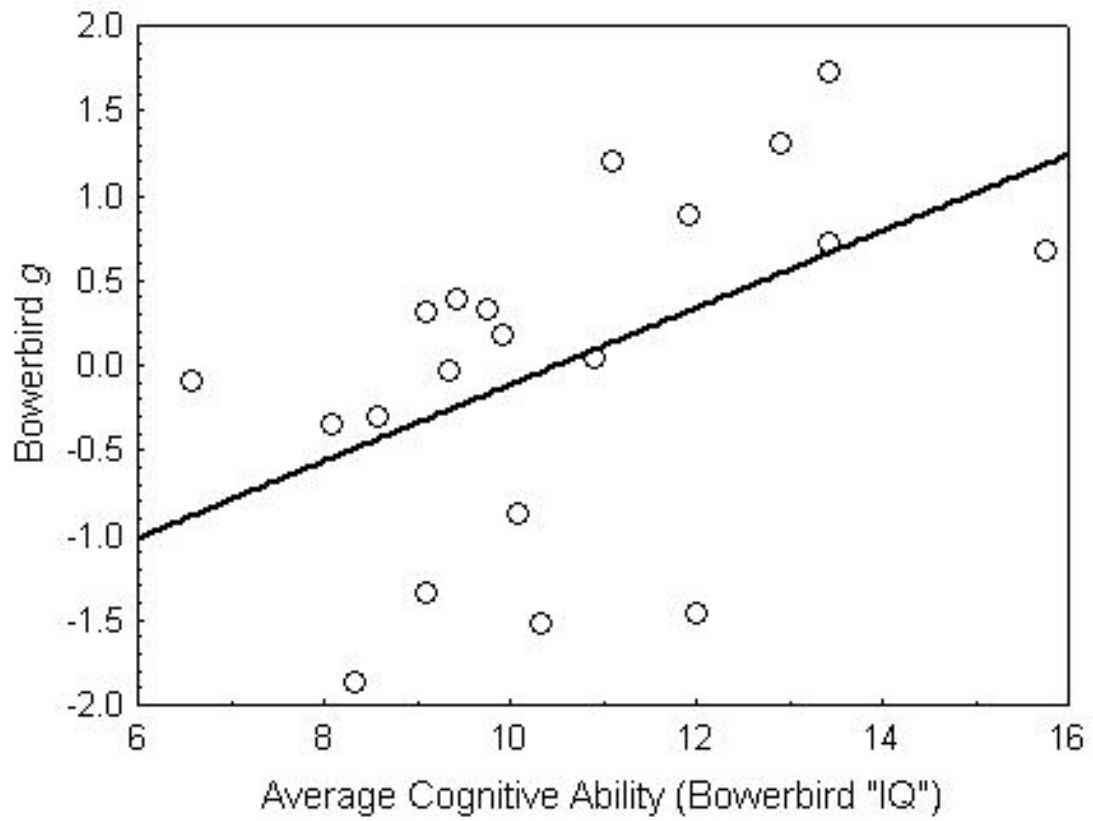
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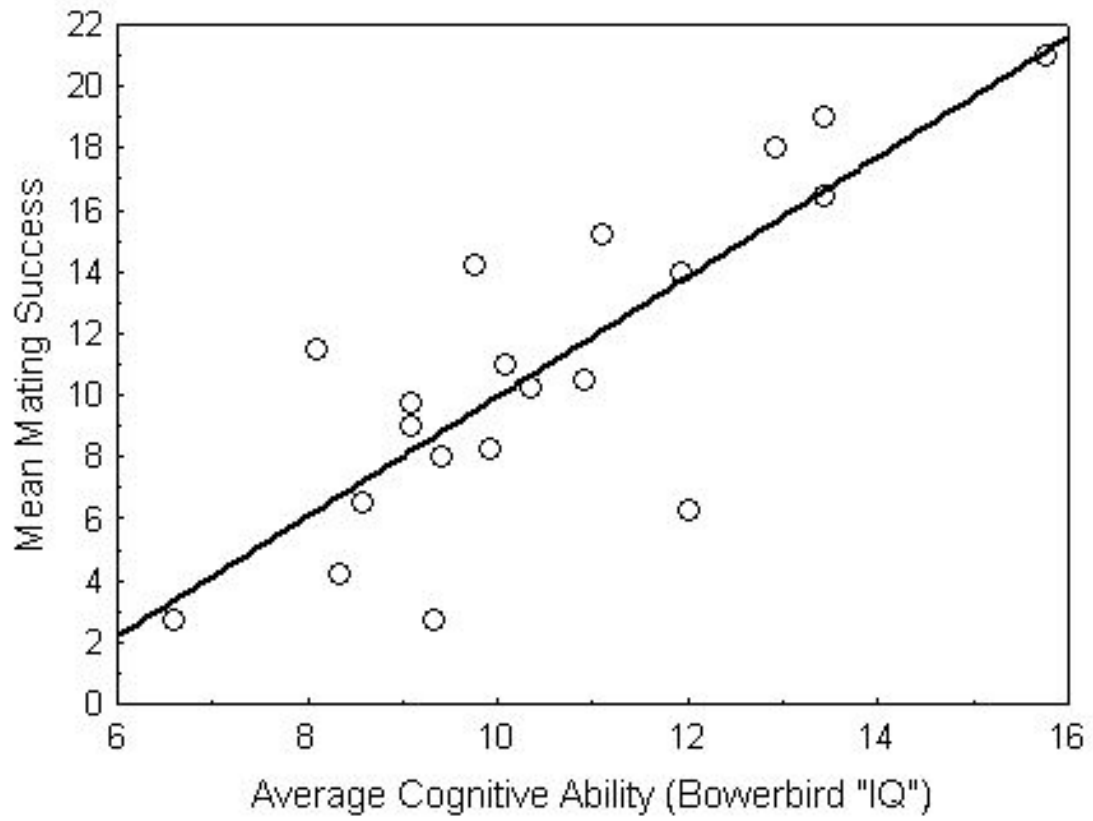
CHAPTER III

Cognitive ability and the evolution of multiple behavioral display traits

ABSTRACT

Males of many species have multiple behavioral display traits and the evolution of these traits may have been shaped in part by female selection for males with superior cognitive ability. Females may be able to use multiple behavioral display traits to evaluate a male's overall cognitive ability. It is also possible that individual behavioral display traits indicate unique aspects of male quality related to cognitive ability. I tested predictions of these two hypotheses in satin bowerbirds, *Ptilonorhynchus violaceus*, a species with a large number of behavioral display traits involved in mate choice. I used two statistical measures of male overall cognitive ability, the first used scores from an analysis that best explained covariation among six different cognitive tests (*g*) and the second used scores from an analysis that determined the combination of cognitive traits that made males most successful in attracting females (*f*). These two measures were significantly correlated, suggesting that evolution of cognitive ability in bowerbirds is possible if there is sufficient heritability. Three different aggregate measures of male display quality (produced from four behavioral display traits) were correlated with one measure of overall cognitive ability, *f*, and with mating success. Multiple behavioral display traits used together, rather than individually, more accurately predicted this measure of overall

cognitive ability. In addition, I found some support for the hypothesis that separate display traits may indicate different aspects of male cognitive ability. These results support the hypothesis that male behavioral display traits have an important role in indicating male cognitive ability to females choosing mates.

INTRODUCTION

Since Darwin there has been great interest in both sexual selection (1871) and cognition (1871, 1872), although the connection between these two topics has not received much attention. One notable exception is the study of bird song, a cognitive trait 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. The finding that individual male birds with more complex songs are also better at a foraging task supports this hypothesis (Boogert et al. 2008). However, song is not the only behavioral display trait that likely has a cognitive component. In addition, many species have multiple behavioral display traits. These other traits include intricate and often interactive "dances" (Prum 1994; Patricelli et al. 2002; Duval 2007; Scholes 2008), construction of display courts (Borgia 1985a; McKaye et al. 1990; Andersson 1991; Uy and Endler 2004), and collection of objects from the environment (Borgia 1985a; Diamond 1986; Soler et al. 1996; Wojcieszek et al. 2007; Doerr 2010). In this study I consider

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hypotheses about the function of these multiple behavioral display traits, focusing on how these displays are special because of their relationship to cognitive performance.

First, individual differences in behavioral display traits are likely influenced at least in part by common neurophysiological and ultimately genetic variation, as is thought to be the case for human cognitive abilities (Miller 2000; Plomin 2001; Banerjee et al. 2009). In humans this variation is considered to be responsible for the highly replicated finding of a statistical measure called g, created from the scores of the first factor from a principal components analysis of a large set of distinct cognitive tasks (reviewed in Plomin 2001). In addition, standard intelligence tests, which assess performance across a variety of cognitive domains in an additive way, tend to be associated with g (Plomin 2001; Prokosch et al. 2005). Also, it has been suggested that general cognitive ability may be an especially good indicator of genetic quality and thus useful as a mate choice criterion (Miller 2000). Supporting the hypothesis that general cognitive ability has a role in mate choice, human females rate more intelligent males as more attractive (Prokosch et al. 2009) and bowerbird females prefer to mate with males with better general cognitive ability (Keagy et al. 2009; Chapter II). In addition, a link between fitness and intelligence has received some support in humans (Prokosch et al. 2005; Arden et al. 2009). Just as g and intelligence tests are integrative measure of multiple behaviors, it is possible that females may be able to use multiple behavioral display traits in some way to assess male overall cognitive ability (Prokosch et al. 2009).

Second, individual behavioral display traits may also indicate unique information about male cognitive ability (and quality) to females. Cognitive function,

and also performance of many behaviors, can be influenced by a number of different factors, although less emphasis has been placed on studying these effects using behavioral display traits of animals. First, mutations can have differential effects on cognitive functions. For example, normal vocal learning in birds, which is under sexual selection, and language in humans, is disrupted by mutations in a gene called FOXP2, yet other cognitive abilities are not affected (Lai et al. 2001; MacDermot et al. 2005; Haesler et al. 2007). Second, individual cognitive abilities can change as a function of time in different ways. If an individual behavior continuously improves over time, it can accurately reflect age, which may be an indicator of genetic quality (Manning 1985; Kokko and Lindstrom 1996; Brooks and Kemp 2001) because older individuals who are continuously in competitive circumstances have repeatedly had their survivability tested. Third, parasites have important effects on individual fitness and infection with parasites may impair some cognitive functions while having no effect on others (Nokes et al. 1992; Kavaliers et al. 1995). Thus females assessing multiple behavioral display traits could be gaining information about multiple aspects of male quality because of a connection between behavioral performance and cognitive performance.

Therefore, multiple behavioral display traits may act to inform females in two different ways. First, they may act together to give females an accurate indicator of a male's overall cognitive ability (and possibly genetic quality). Second, each behavioral display trait may provide some unique information to females about a specific aspect of the male's quality. Møller and Pomiankowski (1993) suggested very similar hypotheses for explaining the evolution of multiple display traits in

general. 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.

Satin bowerbirds are a useful species for investigating questions about the evolution of multiple behavioral display traits. Male bowerbirds build a stick bower on the ground that females visit for courtship and copulation (Borgia 1985a). The quality of the bower construction appears to have been coopted for use in female mate assessment (Borgia 1985a). Males decorate their bowers with decorations of particular colors (Borgia et al. 1987; Borgia and Keagy 2006) that females find attractive (Borgia 1985a; Coleman et al. 2004). Blue objects are rare in the environment (Borgia et al. 1987) and the number of the preferred blue decorations is a function of the ability of males to steal them from other males and is thus an honest

indicator of male quality (Borgia and Gore 1986). During courtship a female stands

inside the bower and the male courts her with a dance that includes a series of loud

and aggressive displays followed by heterospecific mimicry (Loffredo and Borgia

1986; Coleman et al. 2007). I use continuous automated video monitoring of bowers

where copulations occur (Borgia 1985a) and paternity analyses indicate that this

monitoring allows me to get an accurate measure of male mating success that is a true

reflection of female choice for males (Reynolds et al. 2007).

In a recent study I was able to take advantage of this unique display behavior

to assess male performance on six distinct cognitive tasks in nature. I used male

scores on these cognitive tasks to construct a statistical measure of general cognitive

ability, g, and found that this measure strongly predicted mating success (Chapter II).

The validity of g, which is a statistical abstraction, has been questioned in the past,

but in humans at least there is a large body of evidence supporting it (Plomin 2001;

Prokosch et al. 2005; Deary et al. 2006). Part of the debate has centered on the fact

that statistical rotations of the vector creating g can result in different interpretations

of the importance of individual variables (Mackintosh 1998). I constructed a second

integrative measure of male cognitive ability using a canonical correlation analysis

comparing scores on the six cognitive tasks to mating success. This variable (which I

abbreviate as f for female choice or fitness vector) describes female selection on

overall male cognitive ability and weights the importance of male performance on

each cognitive task based on female choice. Supporting the use of f as a measure of

overall cognitive ability, scores of f are highly correlated with average male rank

performance across all cognitive tasks (see results), paralleling results with g (Chapter

II). Other rotations are of course possible, but this particular one has a clearly understandable biological meaning. This approach of calculating a linear combination of variables that best explains fitness has a long history of use in studies to describe selection on a group of traits (Lande and Arnold 1983).

In this study, I assessed male satin bowerbirds on six different cognitive tasks (see Methods and Chapter II) and four different behavioral display traits. These four behavioral display traits have been shown to individually predict mating success: mimetic repertoire size (Coleman et al. 2007), quality of bower construction (Borgia 1985a), number of blue decorations (Borgia 1985a; Coleman et al. 2004), and number of other decorations (Borgia 1985a). Using these data I consider hypotheses about the function of multiple behavioral display traits. I test whether use of multiple behavioral display traits predicts measures of overall cognitive ability, g and f, as well as mating success. In addition, I explore whether different behavioral display traits might differentially indicate unique aspects of male quality (in this study, age and parasitism).

METHODS

This study was conducted in 2004 and 2005 at Wallaby Creek (28º28'S, 152º25'E), NSW, Australia (Borgia 1985a). 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. Birds were individually identifiable on videos by leg bands (Borgia 1985a). Field assistants recorded daily counts of all decorations and twice-daily qualitative scores of bower

quality and these were averaged across the mating season (Borgia 1985a). Individual

birds were selectively caught in baited traps prior to the mating season. 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 me detailed age information for birds (Keagy et al.

2009; Chapter II). I use the number of copulations a male receives on my complete

video record as a measure of his mating success (Borgia 1985a) and paternity

analyses indicate that this is an accurate measure of male reproductive success

(Reynolds et al. 2007).

I was able to assess 21 males on their performance on six distinct cognitive

tasks (Chapter II): (1) ability to remove a clear barrier covering target objects, (2)

ability to conceal an immovable undesirable object, (3) bower rebuilding efficiency,

(4) flexibility in bower rebuilding, (5) use of a behavioral "tool" for creating

symmetrical bowers, and (6) mimetic repertoire size. Consistent with other studies

(Spearman 1904; Plomin 2001; Galsworthy et al. 2005), I constructed g using scores

from the first unrotated principal component from a principle component analysis of

the six cognitive tasks (see also Chapter II). I used the scores from the factor

produced by a canonical correlation analysis comparing performance on the six

cognitive tasks to mating success to construct a variable that best described female

selection on overall cognitive ability, and called this variable f. Cognitive tasks 2 and

6 were assessed in 2004, and cognitive tasks 1 and 3-5 were assessed in 2005. One

male had his bower completely destroyed by a neighboring male during the observation period for cognitive tasks 3-5 and so I was not able to assign him a score on overall cognitive ability.

I compared these two measures using a Pearson's correlation. In addition, I used a more sophisticated measure of the correlation between g and f by calculating the multivariate correlation between the vectors used to create g and f (the arccosine of the multivariate vector angle). This measure uses information about the weights of individual cognitive tasks on g and f rather than just the scores produced by these vectors. A significance value for this second analysis was achieved by performing a Monte Carlo permutation test with 10,000 replications where the mating success of each male was resampled without replacement and the first canonical factor (f) and its angle with the first principle component (g) were recalculated from this new dataset.

I calculated three composite measures of display quality using bower quality, number of blue decorations, number of non-blue decorations, and mimetic repertoire size. These three 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. I ranked males for each display trait and then calculated the average across all display traits. This measure assumes females are using display traits in an additive way. However, females may be more likely to pay attention to additional display traits of males who are especially good at one display trait (Candolin 2003). Therefore, my second measure of display quality was the geometric average of the ranks for each display trait. 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. I used the first principal component of this analysis as my third measure of display quality. There were two years of data available for bower quality, number of blue decorations, and number of non-blue decorations. Before ranking males, I averaged values for these variables for each male across both of these years in all analyses except for those involving parasites (parasite numbers varied widely across years). Values for bower quality, number of blue decorations, and number of non-blue decorations were significantly correlated across years (bower quality: $R=0.55$, $t_{19}=2.86$, $P=0.001$; number of blue decorations: $R=0.83$, $t_{19}=6.44$, $P<<0.0001$; number of non-blue decorations: $R=0.87$, $t_{19}=7.52$, $P<<0.0001$). Mating success was rank-transformed because of the strongly skewed distribution of copulations among male satin bowerbirds (Keagy et al. 2009). Using log transformations result in qualitatively similar results. I then averaged male relative mating success across years (Chapter II); there was a trend for rank mating success to be correlated across years ($R=0.41$, $t_{19}=1.94$, $P=0.07$).

The multivariate correlation analysis, including the Monte Carlo permutation test, was done in R (R Development Core Team 2009). All other analyses were done using Statistica 6.0 (Statsoft Inc., Tulsa, OK, U.S.A.). I used regression analysis to test the hypothesis that aggregate measures of male display quality predicted overall cognitive ability and mating success. I also used regression analysis to assess how well individual display traits predicted overall cognitive ability, parasitism, age, and mating success. I compared display traits to each other using Pearson's correlations.

Residuals were analyzed for normality and no additional transformations were required. All statistical tests are two tailed.

RESULTS

I used two measures of overall male cognitive ability: (1) the scores of the vector describing the greatest amount of variation in cognitive abilities, commonly referred to as general cognitive ability, or g, (2) scores of the vector describing the combination of cognitive abilities females found most attractive, which I call f. Supporting the use of these two variables as measures of overall cognitive ability, scores of f and g are highly correlated with the average of male rank scores of all the cognitive tasks, which is a measure analogous to human IQ (g vs. "IQ": $r=0.50$, $t_{18}=2.43$, $P=0.026$; f vs. "IQ": $r=0.89$, $t_{18}=8.22$, $p<<0.0001$; see also Chapter II). These two measures produce scores that are highly correlated ($r=0.74$, $t_{18}=4.65$, $P=0.0002$). Another measure of the correlation between two vectors is possible by calculating the arccosine of the angle created by the vectors. This method makes use of the additional information contained in the weights of each variable on the vector scores of f and g. This analysis also indicates that the direction of female choice (f) is similar to the direction of highest variation in cognitive ability (g) ($r=0.53$, bootstrap $p=0.033$). If the variation in cognitive ability is heritable, this suggests that the evolution of male cognitive ability is possible.

I used three composite measures of display quality that reflect different assumptions in how females might use display traits together to choose males with better overall cognitive ability. First, it is possible that females are simply choosing

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males who are on average better at multiple aspects of behavioral display. I ranked males for each display trait and then calculated the average across all display traits. Using average display quality in this way assumes females are using these traits in an additive way. It is also possible that females use display traits in a multiplicative way. In other words, females may be more likely to pay attention to additional display traits of males who are especially good at one display trait (Candolin 2003). Therefore, my second measure of display quality was the geometric average of the ranks for each display trait. 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. I used the first principal component of this analysis as my third measure of display quality. Regardless of the measure used, display quality predicted mating success and f, but not g (Table 6). In addition, these three measures of display quality were highly correlated (for all pairwise comparisons: $r > 0.99$, $p \ll 0.0001$, $n=21$). Path analysis shows that the positive relationship between f and display quality is not simply the result of f being constructed in a way that maximizes its correlation with mating success (Figure 8). If this were the case, I would not have expected all of the paths to be statistically significant. Because mimetic repertoire size was used in my measures of overall cognitive ability as well as display quality, these effects could be confounded. To remove this possible effect, I recalculated display quality without mimetic repertoire size and found similar results (Table 7).

I tested whether overall cognitive ability could be better estimated through using multiple display traits than using these traits individually. Although individual

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traits tended to predict f (but not g) not all of the relationships were statistically significant, and in all cases, individual traits did not predict f better than using multiple traits together (i.e. smaller R^2, Table 8). This result gives support to the hypothesis that females using multiple traits can more accurately measure an aspect of male quality, in this case, cognitive ability. In addition, if there is some redundancy in the information that each display trait conveys, all of the traits should be intercorrelated. I found mixed support for this hypothesis, suggesting that some traits are more redundant than others (Table 9).

Next, I tested whether variation in display traits might predict different aspects of male quality. I first considered whether age, which can be an indicator of survivability, was associated with variation in individual display traits. Only number of non-blue decorations was associated with age (positively, Figure 9). Of the different types of non-blue decorations, snail shells (which make up a mean±SE of 26±3% of non-blue decorations) stand out as the only non-blue decoration type significantly associated with age (Table 10). This association could result from at least two 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 two possibilities are not mutually exclusive. I then assessed whether parasitism was indicated by variation in individual display traits. Only mimetic repertoire size was associated with parasitism (negatively), after correcting for multiple comparisons (corrected alpha=0.013; Table 11). The significant relationship between age and non-blue decorations (snails) as well as between parasitism and mimetic repertoire size gives support to the

hypothesis that females can use individual traits to assess different aspects of male quality. Candolin (2003) states that 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. If I use females' judgments of male overall quality (i.e. male mating success) I can test this prediction. I found marginal support for this prediction (Table 12).

DISCUSSION

In this study I constructed two measures of overall cognitive ability, first, a measure which best describes covariation in cognitive performance, commonly referred to as general cognitive ability, or g, and second, a measure describing female selection on cognitive ability, which I call f. These two measures were highly correlated with each other. This suggests evolution of cognitive ability through sexual selection could occur if there is heritability of cognitive ability in bowerbirds, which is the case in mice (Galsworthy et al. 2005) and humans (Plomin 2001; Deary et al. 2006). In addition I constructed three composite measures of display quality that reflected different assumptions in how females might use display traits together to choose males with better overall cognitive ability. These three measures of display quality were highly correlated. While these composite measures of display quality did not predict the more traditional measure of general cognitive ability, g, I did find that display quality predicted f, a measure that relies on females to weight the importance of individual cognitive traits. Together these results suggest that females are judging males on cognitive ability through some number of display traits and there is a

correlation between their judgment of cognitive ability and my more abstract measure of cognitive ability, g, which resulted in my previous finding of g strongly associating with mating success (Chapter II).

My path analysis supports the assertion that constructing a measure of cognitive ability using information about female choice does not bias my analysis towards finding an association between f and display quality. If this were the case, I would not have found that every pathway in the analysis was statistically significant. The highly significant indirect path through display quality to mating success supports the hypothesis that females can use male display to choose males with better cognitive abilities. The highly significant direct path to mating success, as well as the lack of an association between display quality and g, suggests that there may be additional traits that females use to choose cognitively superior males. This shouldn't be too surprising since I 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 I was not able to get measures of these variables.

I found a highly significant association between mimetic repertoire size and parasite infection. Parasitism has often been implicated as a cause for cognitive deficits in species as diverse as humans (Nokes et al. 1992), bees (Gegear et al. 2005, 2006), mice (Kavaliers et al. 1995), and birds (Spencer et al. 2005). The fact that experimental removal can result in increases in cognitive performance (Nokes et al. 1992), suggests that parasites may draw away important resources needed for proper

cognitive function, either directly as part of the parasitism, or indirectly by activating the individual's immune system. My measure of mimetic repertoire size is not necessarily the total number of species an individual knows, but the average number of songs he produces during courtship. Parasitism could be interfering with either the recall of songs or the production of longer bouts of song. Mimicry is a highly specialized courtship specific behavior in this species and it is possible that the other display traits are more insulated from the effects of parasitism because they rely on behaviors that are also critical for survival and have evolved to be more resistant to the negative effects of parasitism. In addition, I found a highly significant association between number of non-blue decorations and age. In this case, males who had more decorations were older, and it is possible that this relationship is driven by male accumulation of snail shells over time. 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). In addition, 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), making such avoidance unlikely for males with fully developed displays.

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). 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). However, this should be true of many behavioral traits, particularly where learning and practice appear to play a role in display trait development. While several of the display traits I focused on in this study are unique to bowerbirds, they represent the expression of cognitive abilities probably shared among many animal species. Indeed it is possible that analogous displays of these same 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).

Explaining the existence of multiple display traits has been an active area of sexual selection research (Candolin 2003). Two influential hypotheses that seem especially relevant to this study and my 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). My finding that composite measures of display quality predicted one measure of overall cognitive ability, f, better than using display traits individually is consistent with the redundant signals hypothesis. Also, my finding of associations between two of the individual display traits and unique

aspects of male quality is consistent with the multiple messages hypothesis (Møller and Pomiankowski 1993; Johnstone 1996). 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 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, multiple behavioral display traits may act as a sort of sexually selected intelligence test.

I expect exploration of the relationship between general cognitive ability and sexual selection in other animal species generating a more comprehensive understanding of how cognition affects and is affected by the mate selection process. For example, in this particular study I have found that males who have better displays have better overall cognitive ability, at least in terms of how females weight the importance of individual cognitive traits. 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 exploitation: 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.

TABLES

Table 6. Display quality predicts one measure of overall cognitive ability, f, and reproductive success.

Aggregate Measure of Display Quality	g	f	Mating Success
Average display quality	r^2=0.08, $F_{1,18}$=1.51, p=0.23	r^2=0.30, $F_{1,18}$=7.90, p=0.012	r^2=0.44, $F_{1,19}$=14.79, p=0.001
Geometric average display quality	r^2=0.08, $F_{1,18}$=1.50, p=0.24	r^2=0.31, $F_{1,18}$=8.25, p=0.010	r^2=0.42, $F_{1,19}$=13.58, p=0.002
PC1 of display quality	r^2=0.08, $F_{1,18}$=1.57, p=0.23	r^2=0.30, $F_{1,18}$=7.66, p=0.013	r^2=0.43, $F_{1,19}$=14.50, p=0.001

Table 7. Display quality (calculated without mimetic repertoire size) predicts one

measure of overall cognitive ability, f, and mating success.

Aggregate Measure of Display Quality	g	f	Mating Success
Average display quality	$r^2=0.07$, $F_{1,18}=1.27$, $p=0.27$	$r^2=0.26$, $F_{1,18}=6.45$, $p=0.021$	$r^2=0.44$, $F_{1,19}=14.79$, $p=0.001$
Geometric average display quality	$r^2=0.06$, $F_{1,18}=1.24$, $p=0.28$	$r^2=0.25$, $F_{1,18}=6.16$, $p=0.023$	$r^2=0.42$, $F_{1,19}=13.89$, $p=0.001$
PC1 of display quality	$r^2=0.26$, $F_{1,18}=1.34$, $p=0.26$	$r^2=0.26$, $F_{1,18}=6.40$, $p=0.020$	$r^2=0.43$, $F_{1,19}=14.61$, $p=0.001$

Table 8. Tests of the redundant signals hypothesis. Individual traits predict *f* less well

than composite variables (see Table 6).

Display Trait	*g*	*f*
Rank bower quality	r^2=0.00, $F_{1,18}$=0.01, p=0.93	r^2=0.16, $F_{1,18}$=3.50, p=0.08
Rank blue decorations	r^2=0.07, $F_{1,18}$=1.33, p=0.26	r^2=0.16, $F_{1,18}$=3.48, p=0.08
Rank non-blue decorations	r^2=0.10, $F_{1,18}$=2.01, p=0.17	r^2=0.15, $F_{1,18}$=3.24 p=0.09
Rank mimetic repertoire size	r^2=0.05, $F_{1,18}$=0.97, p=0.34	r^2=0.19, $F_{1,18}$=4.30, p=0.05

Table 9: Relationship between behavioral display traits. The number of blue decorations correlates significantly with all the other behavioral display traits, but no other correlations are significant.

(n=21)	Rank bower quality	Rank blue decorations	Rank non-blue decorations	Rank mimetic repertoire size
Rank bower quality				
Rank blue decorations	r=0.45, p=0.043			
Rank non-blue decorations	r=0.34, p=0.13	r=0.53, p=0.013		
Rank mimetic repertoire size	r=0.25, p=0.28	r=0.52, p=0.016	r=0.26, p=0.25	

Table 10. Relationship between age and non-blue decorations.

Non-blue 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

Table 11. Tests of the multiple messages hypothesis: Parasitism. Males with fewer

parasites have relatively larger mimetic repertoire sizes.

Display Trait	Parasites
Rank bower quality (in year x)	2004: r^2=0.13, $F_{1,7}$=1.08, p=0.33
	2005: r^2=0.00, $F_{1,6}$=0.00, p=0.98
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 total (non-blue) 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
Rank mimetic repertoire size	2004: r^2=0.69, $F_{1,7}$=15.80, p=0.005

Table 12. Relationship between male overall quality (i.e. mating success) and quality of display traits. Candolin (2003) states that if traits that indicate different aspects of male quality (i.e. multiple messages) are correlated with overall quality, they could also serve as back-up signals to females. I used females' judgments of male overall quality (i.e. mating success) to test this prediction.

Display Trait	Male overall quality (mating success)
Rank bower quality	r^2=0.27, $F_{1,19}$=7.17, p=0.015
Rank blue decorations	r^2=0.26, $F_{1,19}$=6.84, p=0.017
Rank non-blue decorations	r^2=0.28, $F_{1,19}$=7.52, p=0.013
Rank mimetic repertoire size	r^2=0.15, $F_{1,19}$=3.23, p=0.09

FIGURE CAPTIONS

Figure 8. Path analysis of relationships between a measure of overall cognitive ability (*f*), an aggregate measure of display quality, and mating success. This analysis demonstrates that *f* has two different significant pathways to mating success, one indirect through its influence on display, and the other direct (which is probably actually through other unmeasured display traits). Results are given using the arithmetic average measure of display quality calculated with mimetic repertoire size (and in parentheses, without mimetic repertoire size). The short arrows with r^2 values indicate the variance explained by pathways leading to a given variable.

Figure 9. Tests of the multiple messages hypothesis: Age. Older males have relatively more non-blue decorations ($r^2=0.41$, $F_{1,19}=12.98$, $p=0.002$), and so non-blue decorations may indicate a male's ability to survive. The other display traits did not predict age (bower quality: $r^2=0.01$, $F_{1,19}=0.23$, $p=0.64$; blue decorations: $r^2=0.13$, $F_{1,19}=2.94$, $p=0.10$; mimetic repertoire size: $r^2=0.03$, $F_{1,19}=0.59$, $p=0.45$).
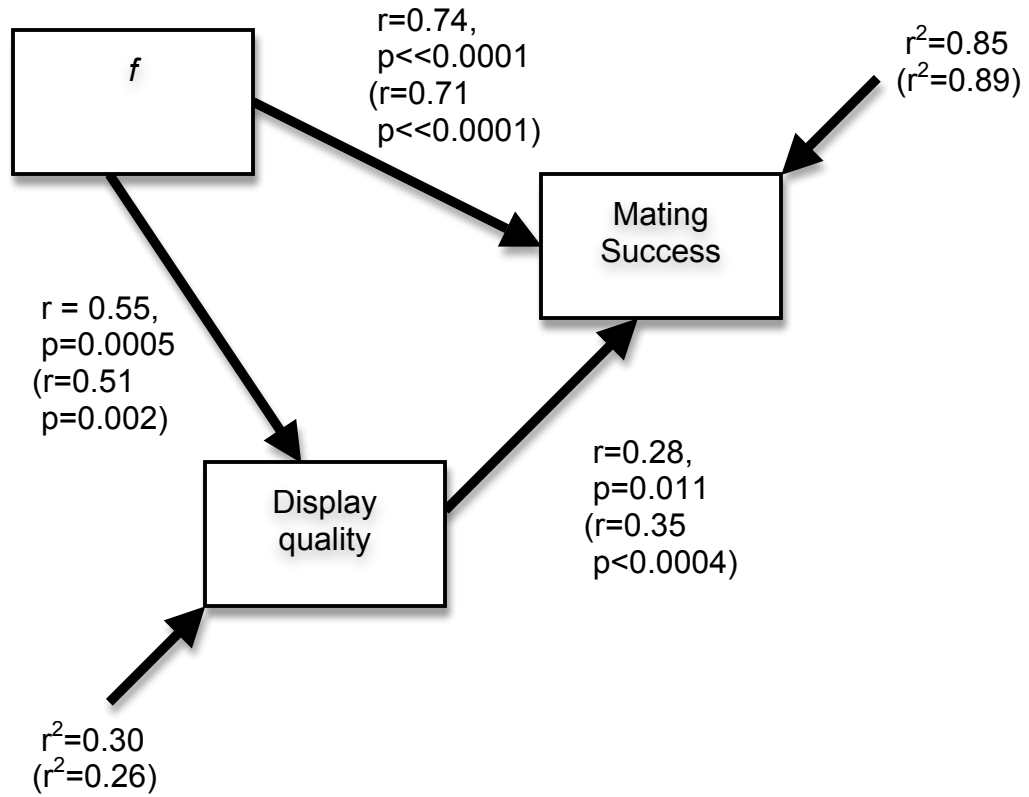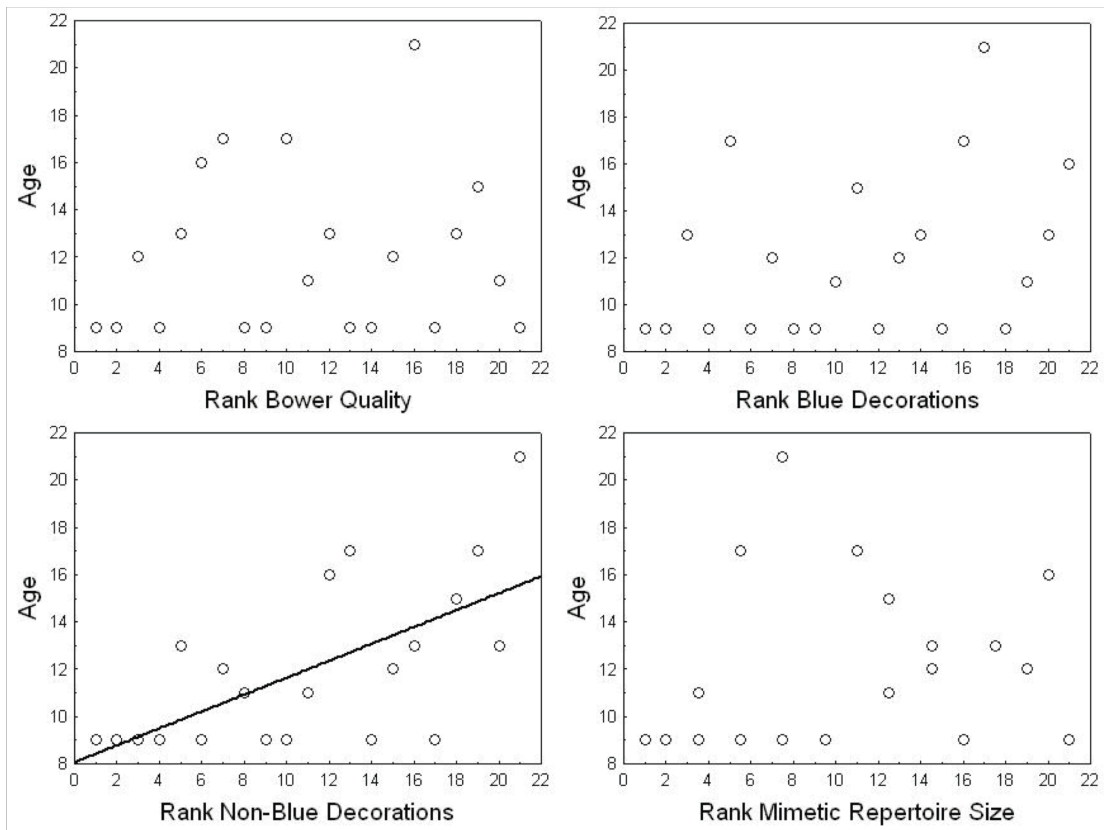
FIGURES

Figure 8

Figure 9.

CONCLUSION

OVERVIEW

In this dissertation I present data consistent with the hypothesis that cognitive ability has an important role in determining male attractiveness in satin bowerbirds, *Ptilonorhynchus violaceus*. In Chapter I, I show that males that perform better on problem solving tests have higher mating success. In Chapter II, I expand the number of cognitive tasks assessed to six, in an attempt to increase the diversity of cognitive abilities tested. I then summarize male performance across these six tasks using the first factor from a principle components analysis as well as average rank performance. I show that these integrative measures of male cognitive ability also predict mating success. In Chapter III, I examine the relationship between covariation in cognitive traits and female selection on this covariation to show that if there are heritable differences in cognitive ability, cognitive evolution could occur through sexual selection. In addition, males who have the combination of cognitive traits that females find most attractive have better displays and higher mating success, suggesting that females may be able to use male display traits to assess overall cognitive ability. I also show that individual male traits may indicate unique information about aspects of male quality. Together these results have several important implications. First, evolution of cognitive ability through sexual selection is not commonly considered, but my research suggests it could be possible. Second, my research clearly shows a relationship between measures of male cognitive ability and

male attractiveness. This is a relationship that has received almost no consideration in sexual selection research. Third, my research takes a unique approach in assessing performance on multiple cognitive tasks in the same individual animals, which is necessary if we are to ultimately understand the relationship between cognition and fitness (of which mating success is an important component).

CAVEATS

There are several aspects of my dissertation research that could be considered controversial, and I will describe briefly the potential issues I am aware of as well as explain why these issues do not ultimately change the conclusions of this study.

g *and IQ*

The statistical techniques I used to reduce data on male performance on the six cognitive tasks to a single number are ubiquitous in biological research. These summary variables have analogues in human psychology research and so I labeled them as such, *g* and IQ. This decision was made for two reasons, first to make it more obvious to the reader what I was measuring, and also to make explicit my assumption that human cognitive abilities have analogs in the animal world and must have an evolutionary history. However, using these labels also connects my research to a greater controversy in psychology about the nature of human intelligence and more especially, about its measurement.

The general intelligence factor, g, was first described by Spearman (1904) after an analysis of measures of sensory discriminative ability and academic performance in school children, which he found to be surprisingly positively correlated. He postulated that a general intelligence factor was responsible for the correlation between these cognitive traits and that any unexplained variance was related to specific factors influencing each test individually. Hence his theory of intelligence is now known as the "two-factor theory" of intelligence, where the second factor, s, is a summation of the influence of the specific factors (Mackintosh 1998; Brody 2000). However, Spearman (1904, 1927) did not impart much importance in this unexplained variance. Thurstone (1934, 1938) was an early opponent to this view of a singular general intelligence and proposed that there were multiple "group factors" describing different types of intelligence. These group factors can be extracted from the same correlation matrix as a general factor by putting different constraints on the statistical analysis used. In my research, I did not find evidence of clearly defined group factors; rather each cognitive task was not strongly correlated to any of the others (discussed further in the *Modularity* section). There have been a number of other theories proposed, including Cattel's (1963) distinction between fluid intelligence (*gf*) and crystallized intelligence (*gc*), Sternberg's triarchic theory of intelligence (1985, 1988) and Gardner's (1983) theory of multiple intelligences (including things not traditionally measured by intelligence tests such as kinesthetic and interpersonal abilities). The purpose of this section is not to discuss in detail all of the past and current theories of human intelligence, but to

demonstrate that there are many, and that the majority reject a unitary quantity that can describe individual intelligence.

Another issue with the use of *g* (and IQ) is that it tends to ignore other aspects of human intelligence that feature prominently in many of the modern models of intelligence. In other words, the test batteries used to calculate *g* (and IQ) tend to heavily test academic intelligence. Note however, that this is a departure from Spearman (1904) who used both academic measures and measures of sensory discrimination. In the end, any summary measure will be reflective of the tests used to create that variable. This has led to criticisms that intelligence tests are designed in a way that favor certain populations or groups of people. This is a familiar issue in animal cognition research, and is called "ecological validity". My tests had high ecological validity and also tested multiple cognitive abilities (including motor ability which can be thought of as analogous to the kinesthetic intelligence of Gardner (1983)).

Despite these issues, IQ and, to a lesser extent, *g*, are commonly calculated for use in studies attempting to easily quantify intelligence. It is clear now that a single number cannot summarize the complexity that is an individual's intelligence. However, the covariation found between disparate tasks likely has some real biological meaning. For example it has been suggested that *g* might represent processing speed (Mackintosh 1998) or variation in some other neurophysiological variable (Miller 2000; Plomin 2001; Banerjee et al. 2009). In addition, the relatively high heritability of *g* and IQ compared to many other traits suggests a strong genetic component to whatever underlies these measures, although there is clearly an

important environmental component as well (Brody 1992; Mackintosh 1998; Deary 2000).

Modularity

The modern conception of modularity of the mind was outlined by Fodor (1983, 2000). His idea is that various cognitive tasks are controlled by "modules" which are largely independent except for the fact that they tap into the same central higher-level processes. This differs from the account championed by evolutionary psychologists such as Cosmides and Tooby (1994) that modules are entirely independent of one another and have evolved to solve very specific problems (sometimes called the "massive modularity hypothesis" (Barrett & Kurzban 2006)). Evolutionary biologists have investigated a conceptually related issue of the extent to which distinct brain regions are constrained by development to evolve in size together. The "mosaic evolution hypothesis" proposes few constraints (Barton & Harvey 2000) versus the "concerted evolution hypothesis" (Finlay & Darlington 1995). Fodor's (1983, 2000) account of modularity is interesting because it offers an additional explanation for the covariation between different cognitive tasks that is the basis of *g*.

In Chapter II I find that the first principle component of an analysis of six cognitive tasks (*g*) explains roughly 30% of the covariation between these tasks and that there were no significant intercorrelations between individual traits. I suggest that these results are consistent with a high degree of modularity. There could be several objections to this interpretation. First, in humans *g* is the result of positive

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correlations between different cognitive tests. This is not the case in my study, so how can I call my measure *g*? I do not actually have sufficient power to detect anything other than very strong correlations between the cognitive traits I measure. Principle component analysis on the other hand is simply a description of the covariance matrix structure. This is a limitation of my current study, but could be improved upon in future experiments, most easily by using a species more amenable to lab experimentation and thus larger samples of individuals. Second, modularity predicts some degree of correlation between cognitive traits, so how can I argue that my lack of strong correlations suggests modularity? This objection ignores that the very concept of modules tapping into a central process allows for there to be variation in how much each module depends on that central processing. This variation would result in a continuum in the degree to which individual cognitive traits are correlated. My data are based on too few individuals to draw conclusions about what this means about modularity in general, but the contrast between my results and what is seen in humans offers an interesting comparison that I think should be followed with future study.

Am I Measuring A General *Cognitive Ability?*

There are at least three potential criticisms related to this question. First, some might argue that not all the tasks I presented male bowerbirds were cognitive in nature. I explained why I think all of the tasks were indeed related to cognition in Chapter II so I will not go into that same amount of detail here. However, the cognitive task that might be most controversial is handling time so I will give a few

further comments about it. Handling time is primarily a function of motor ability. Our observations with bowerbirds suggest that males experience motor learning during practice with building bowers, at least during their juvenile period when age-related improvement is most obvious. In addition, motor ability is a part of several modern theories of intelligence (for example it is similar to Gardner's (1983) kinesthetic intelligence). Thus I think there is ample reason to consider handling time a measure of cognitive ability. Second, all of these cognitive tasks are in some way related to male courtship display, although the problem solving tests are very tangentially related. This means that it could be said that I have only measured cognitive ability particular to male display. Future work could examine male cognitive ability in other contexts to test whether this is indeed true. Even if this is the case, it does not change my argument that cognitive ability is important in contributing to male attractiveness. In fact, if cognitive ability is important to attracting females, we might expect there to be disproportionate selection on those cognitive traits most important to display. Third, am I measuring something more specific such as a general problem solving ability? I find it difficult to believe that male mimetic repertoire size and even handling time could be described as problem solving ability. In fact I find it most fruitful to acknowledge that what I have is a statistical summary of multiple cognitive tasks, rather than speculating over the range and names of those abilities that I have tested. Certainly future work should expand on the types of cognitive tasks used. Tasks that explicitly test for memory, sensory discrimination, spatial cognitive ability, and learning speed would all be very valuable.

Heritability and Cognitive Evolution

Cognitive evolution is only possible if variation in cognitive ability is heritable. I currently do not have the capability for estimating heritability of cognitive ability in my species, although there is evidence for it in humans (Brody 1992; Mackintosh 1998; Deary 2000), mice (Galsworthy et al. 2005), and zebra finches (Airey et al. 2000). Related to this, I am unable to demonstrate at this time that offspring of males with better cognitive ability have "better genes" that allow them to also have better cognitive ability and survive well. In fact there are virtually no studies that show that individuals with better cognitive ability have higher survival (for possible exceptions see Hasselquist et al. 1996; Dukas & Duan 2000). For future work I propose conducting cognitive experiments with a laboratory species that still has a viable wild population (e.g. zebra finches) in order to establish easily repeatable techniques for assessing cognitive ability and estimates of its heritability. Then these same experiments could be conducted in the wild to assess survival of individuals and the realized heritability of variation in cognitive ability (there may be larger environmental effects in the wild compared to the sterile and "easy" lab environment). In addition, a question that I did not test at all in this dissertation was cognitive performance of females. This is an interesting question for reasons I allude to in the previous chapters. For example, female cognitive ability can determine the strength sexual selection takes (because of discriminative ability) and the models of sexual selection that are most likely (e.g. some models assume females cannot express context dependent preferences (sensory bias: Ryan & Rand 1990)). Also if the genes important for male cognitive ability are the same as those that are important

for female cognitive ability, this could result in coevolution of cognitive ability

through sexual selection processes.

FINAL THOUGHTS

None of the issues that I discussed above affect the overall conclusions of my

dissertation as stated at the beginning of this concluding section. These issues do

point out future directions and points for theoretical discussion as well as the

difficulties of understanding animal cognition when the study of human cognition is

itself an extremely contentious field. However, these difficulties are also in part due

to a lack of distinction between theory and empiricism (Mackintosh 1998). We

currently do not have the tools to easily distinguish between modern theories of

human intelligence, and there really are no substantive theories of animal intelligence.

However, what we can do is conduct empirical research with clearly defined

hypotheses, as I feel I have done here. Ultimately, while I will cause at least some

controversy because of my use of the labels of psychologists for the statistical

techniques I have used, these statistical techniques are sound and ubiquitous ways of

summarizing information that would be impossible to understand otherwise. I

conducted careful experimentation and objectively described the patterns in the data,

which strongly suggest male cognitive ability has an important role in attractiveness

to females. It may be in part because of the current and historical controversies in

human psychology research that virtually all animal cognition research focuses on

single cognitive traits at a time. However, such an approach that does not consider

how multiple cognitive traits might interact within individuals cannot fully inform us about the function and evolution of cognition.

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