Male satin bowerbird problem-solving ability predicts mating success

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Mate choice and mate attraction are important behaviours influencing the evolution of elaborate traits. It is possible that male general cognitive performance plays an important role in sexual attractiveness, but there has been no direct test of this hypothesis. Satin bowerbirds, *Ptilonorhynchus violaceus*, are an excellent species for testing this hypothesis because their complex male courtship, including use of decorations of certain colours, suggests a selective advantage to individuals with superior cognitive abilities. We used males' strong aversion to red objects on their bowers to design two unique problem-solving tests. We presented males with these problems to test the hypothesis that males that are better problem-solvers have higher mating success. We confirmed this prediction and demonstrate that neither age nor motivational level significantly influenced problem-solving scores. Our findings suggest that general cognitive performance is related to male mating success. This is the first evidence that individuals with better problem-solving abilities are more sexually attractive.
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Since Darwin there has been great interest in both sexual selection (Darwin 1871) and mental processes (Darwin 1871, 1872), both of which have important effects on fitness. Perhaps because many evolutionary biologists have underappreciated the significance of mental processes in nonhuman organisms, their influence on fitness, in conjunction with that of sexual selection, has received scant attention. Recently, the greater appreciation that cognitive performance can affect fitness (Shultz et al. 2005; Sol et al. 2005, 2007, 2008; Roth & Pravosudov 2009), the obvious large investments in tissue associated with cognition (Aiello & Wheeler 1995) and the high level of complex behavioural interactions in sexual displays (e.g. Balsby & Dabelsteen 2002; Patricelli et al. 2002) all suggest there may be important effects of cognition on sexual display and mate choice (see also Miller 2001; DeVoogd 2004). Here we test the 'cognitive performance hypothesis', which suggests a positive relationship between general cognitive performance and reproductive success. We assess general cognitive performance using problem-solving tests, an accepted measure of general cognitive ability (Roth & Dicke 2005). This hypothesis has not been directly tested in any species.

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

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

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

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

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

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

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

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

METHODS

Study System

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