



Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success



Jess Isden*, Carmen Panayi¹, Caroline Dingle², Joah Madden

Centre for Research in Animal Behaviour, College of Life and Environmental Sciences, University of Exeter, Exeter, U.K.

ARTICLE INFO

Article history:

Received 12 March 2013
Initial acceptance 8 April 2013
Final acceptance 16 July 2013
Available online 29 August 2013
MS. number: 13-00228R

Keywords:

cognitive performance
free-living
mate choice
Ptilonorhynchus maculatus
reproductive success
sexual selection
spotted bowerbird

Individuals exhibiting a high level of cognitive ability may also exhibit more elaborate traits and so gain higher levels of mating success. This suggests that selection may act on cognitive performance through mate choice. Studies investigating this relationship have tended to focus on single cognitive tasks, or tasks that are closely related to existing natural behaviours, and individuals are frequently tested in captive conditions. This can introduce test artefacts and may tell us more about selection on specific display behaviours that we imagine being particularly cognitively complex, rather than a general cognitive ability. We tested free-living male spotted bowerbirds, *Ptilonorhynchus maculatus*, that exhibit elaborate sexual displays which appear to be cognitively demanding. We describe a method for testing individuals in the wild, without the need for constraint or captivity. We looked for evidence of a general cognitive ability in males by assaying their performance in a series of novel tasks reflecting their natural bower-building behaviour (bower maintenance) or capturing more abstract measures of cognitive ability (colour and shape discrimination, reversal learning, spatial memory and motor skills). We related performance in these tasks to their mating success. An individual's performance in one task was a relatively poor predictor of performance in any other task. However, an individual's performance across tasks could be summarized by a principal component which explained a level of total variance above which has previously been accepted as evidence of a general cognitive ability. We found no relationships between an individual's overall performance, or performance in any single task, and mating success. Our results highlight the need for further investigation of whether selection on cognition in bowerbirds is exerted through mate choice. We offer this as an example of how classic cognitive tasks can be transferred to the wild, thus overcoming some limitations of captive cognitive testing.

© 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

The evolution of enhanced general cognitive abilities poses a challenge to biologists. To understand how selection pressures may be acting on cognitive traits, individual cognitive differences must be related to measures of fitness variation (Shumway 2008; Sol 2009; Morand-Ferron et al. 2011; Cole et al. 2012; Cauchard et al. 2013). One promising, yet little explored, context in which cognitive performance may have fitness consequences is via sexual selection (Boogert et al. 2011b). Selection may act through female choice for complex displays which are cognitively costly to produce (Madden et al. 2011). For example, many female songbirds choose mates based on song elements with clear cognitive components, such as

repertoire size and song complexity (Reid et al. 2005; Pfaff et al. 2007), and in several manakin species females choose males based on challenging coordinated dance displays (Trainer et al. 2002; DuVal 2007). Females may benefit from such choice because high cognitive ability may come at a metabolic cost of increased neural processing, with only high-quality males able to bear such a cost (Miller 2000; Nowicki et al. 2002). Cognitive-based signals, such as birdsong, may inform females about the developmental, social and individual learning ability of males (Boogert et al. 2008; Holveck et al. 2008; Riebel et al. 2012). Alternatively, if cognitive abilities are positively correlated across domains then female selection on cognitive traits may confer benefits in other contexts, such as foraging ability or predator avoidance.

Positive covariance between cognitive abilities has been demonstrated in humans, in which this general ability (referred to as *g*) is described as being both heritable and an honest indicator of fitness (Jensen 1998; Miller 2000; Plomin & Spinath 2002; Deary et al. 2010). It has also been demonstrated in mice, *Mus musculus* (Matzel et al. 2003; Galsworthy et al. 2005), rats, *Rattus norvegicus*

* Correspondence: J. Isden, Centre for Research in Animal Behaviour, College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4QG, U.K.

E-mail address: jj214@exeter.ac.uk (J. Isden).

¹ C. Panayi is now at Behavioural Ecology Group, Department of Zoology, University of Cambridge, Cambridge, U.K.

² C. Dingle is now at Department of Earth Sciences, University of Hong Kong, Hong Kong.

(Anderson 1993), cottontop tamarins, *Saguinus oedipus* (Banerjee et al. 2009), honeybees, *Apis mellifera* (Chandra et al. 2000), bumblebees, *Bombus terrestris* (Muller & Chittka 2012) and pigeons, *Columba livia* (Bouchard et al. 2007). However, few studies relate measures of *g* to fitness differences and the expression of sexual traits; instead, the focus has been on describing relationships between a trait and a single measure of performance in a specific cognitive task. For example, in male siskins, *Carduelis spinus*, plumage brightness was correlated with performance in a novel foraging task demonstrating insight (Mateos-Gonzalez et al. 2011), in male guppies, *Poecilia reticulata*, the expression of orange patch coloration was correlated with algal searching ability (Karino et al. 2007), in male zebra finches, *Taeniopygia guttata*, song complexity correlated with a novel foraging task demonstrating problem-solving ability (Boogert et al. 2008) and song bout length in European starlings, *Sturnus vulgaris*, influenced by early rearing conditions, was indicative of spatial learning ability (Farrell et al. 2012). Inferring selection pressure on general cognitive ability by considering only a single measure of performance risks overlooking important elements of such relationships. In those few studies in which multiple cognitive measures have been assayed, links between sexual traits and an individual's general cognitive performance are less clear. For example, in male song sparrows, *Melospiza melodia*, song repertoire correlated positively with performance in an inhibitory control task, but not with other cognitive measures (Boogert et al. 2011a). Species that exhibit multiple cognitive elements in their sexual display, perhaps manifested in multitrait displays, offer improved opportunities for exploring such selection pressures. Females may pay attention to multiple traits because each trait signals a different aspect of male quality, or because using combinations of traits helps to reduce mate choice error (Møller & Pomiankowski 1993; Candolin 2003).

Bowerbirds exhibit multitrait displays comprising elements likely to depend on a range of different cognitive abilities, presenting females with an opportunity to select for general cognitive performance. Males of 17 species construct and decorate elaborate display sites, bowers, which serve as targets of female choice (Marshall 1954; Borgia et al. 1985; Frith & Frith 2004). They construct technically intricate display courts (Borgia 1985), requiring fine-scale motor skills. They collect and arrange decorations (Diamond 1987; Borgia 1995), categorizing them by colour (Endler & Day 2006) and paying particular attention to those that are good predictors of mating success (Madden 2003a, b), requiring discriminatory and classification skills. Male great bowerbirds, *Ptilonorhynchus nuchalis*, create a forced perspective to enhance the audience view of their bower display (Endler et al. 2010), suggesting advanced perceptual skills. Display is not limited to bower construction; males perform courtship dances which can be adjusted according to female response (Patricelli et al. 2002, 2006), and which can include vocal mimicry (Loffredo & Borgia 1986; Frith & McGuire 1996; Coleman et al. 2007), requiring memory, learning and further motor skills. Males show flexibility in their display behaviours; they appear to improve their display through learning (Madden 2008), resolve trade-offs between improved signalling to females and increased male marauding (Madden 2002) and are able to compensate for the loss of one signal by enhancing another (Bravery & Goldizen 2007). If multiple traits, such as those exhibited by male bowerbirds, signal individual general cognitive ability we may expect female selection preferences to reflect male performance across a suite of cognitive tasks.

A relationship between cognitive performance and mating success has previously been demonstrated in the congeneric satin bowerbird, *Ptilonorhynchus violaceus*. The speed and degree to which males solved two novel problem-solving tasks was positively

correlated with mating success (Keagy et al. 2009). Measures of other traits thought to require high levels of cognitive performance (vocal mimicry and bower restoration behaviour) also predicted mating success individually or in conjunction with one another (Keagy et al. 2011, 2012). However, intercorrelations between performances in tasks were low (Keagy et al. 2009, 2011), and while multiple cognitive display traits provided a more accurate prediction of overall cognitive ability, the authors suggested that these multiple traits may also be used to signal different aspects of male quality rather than just indicate a general cognitive ability (Keagy et al. 2012). However, it is not clear which cognitive processes were being measured, and how the different tests related to one another in terms of exploring different cognitive domains or repeatedly testing the same cognitive domain (e.g. the two novel tasks were assumed to reflect problem solving). Neither is it clear how discrete selection on cognitive performance in these tasks relates to more conventionally defined selection on the behaviours of bower building or vocalizations.

We investigated whether individual male spotted bowerbirds, *Ptilonorhynchus maculatus*, differed in their specific or general cognitive abilities across a range of problem-solving and cognitive tasks, and whether their individual or overall performance in tasks correlated with their mating success. We repeated one of the novel problem-solving tasks previously presented to satin bowerbirds (Keagy et al. 2009), to permit comparison across species. In addition, we avoided the confound of testing cognitive performance in natural behaviours (such as vocalizations and bower construction) or behaviours closely linked to natural behaviours (bower maintenance and removal of disliked objects; Keagy et al. 2009, 2011, 2012) which may be subject to strong direct selection without reflecting a broader cognitive ability across contexts. Instead, we implemented a series of classic psychological cognitive tasks, with a proven history of use in the laboratory, to test specific cognitive traits apparently underpinning, but discrete from, bower-building behaviour. These included the ability to learn a novel motor task, colour and shape discrimination, colour reversal (as a measure of behavioural flexibility) and spatial memory.

METHODS

General Field Methods

Data were collected from a population of wild, individually marked spotted bowerbirds in Taunton National Park (Scientific) in central Queensland, Australia (23.54989S and 149.24088E; see Miles & Madden 2002 for a detailed description of the study site). Bowerbirds offer an ideal opportunity for testing cognitive performance in the wild. Male bowerbirds maintain bowers for several months over the breeding season, and spend a significant proportion (up to 70%) of daylight hours tending their bowers (Frith & Frith 2004). Each bower has a single male owner, allowing repeated trials on the same individual, and their regular presence in a specific location is reasonably predictable. Therefore, all tests were carried out on free-living individuals that were not brought into captivity. Males also show relatively low levels of neophobia, interact with novel items willingly and are motivated to gain food rewards.

Fieldwork and cognitive testing were conducted during two breeding seasons, July 2010–January 2011 (subsequently referred to as the 2010 breeding season) and August 2011–February 2012 (referred to as the 2011 breeding season). At the beginning of each season bowers were located and owners identified with unique combinations of coloured leg bands. Bowens were spaced approximately 1 km apart (Miles & Madden 2002). Once located, remote motion-sensing cameras (StealthCam I590, Grand Prairie, TX,

U.S.A.) were placed at bowers for the duration of the breeding season. Camera recording hours differed minimally between males depending on the date/time cameras were deployed, and because of rare camera failures in the field (maximum 3 days).

Measuring Mating Success

We measured an individual's mating success by calculating copulation rates for the two seasons during which testing took place. Females may make multiple visits to bowers during the breeding season (Uy et al. 2000), and copulations occur in the bower avenue (Borgia 1985; Frith & Frith 2004). Spotted bowerbirds are monomorphic, and we were not able to distinguish females in the field. Therefore, we used the total number of copulations per male captured from camera data as a measure of reproductive success. Copulations were easily recognizable behaviours and observed male mating success has been shown to be a reliable predictor of reproductive success in satin bowerbirds (Reynolds et al. 2007). The number of copulations each male obtained was summed, and the dates of the first and last copulations across the study population were used to define the copulation season. Copulation rates for each individual were calculated as the number of copulations witnessed at the bower divided by the total number of camera recording hours at the bower during the copulation season. Bowers had the same owners in 2010 and 2011, and reproductive skew, calculated according to Pamillo & Crozier (1996), was similar in both seasons: 0.48 and 0.52, respectively (a score of zero indicates no skew and 1 indicates all copulations are gained by a single male). However, copulation rates were not significantly correlated between seasons ($r_S = 0.25$, $N = 13$, $P = 0.42$).

Measuring Cognitive Performance

We deployed six different cognitive tasks, designed to capture a measure of individual performance across separate types of cognitive domains (Table 1). The first task (1) was the barrier removal task, which replicated and extended the novel problem-solving task previously presented to male satin bowerbirds (Keagy et al. 2009), and represented a task that was based on natural male bower maintenance and restoration behaviour. In the next set of tasks (2–6), we presented males with a novel task apparatus, a pokebox, which was used to test five different potential cognitive abilities male bowerbirds may be expected to exhibit, but using an abstract paradigm separated from their natural behaviours.

All tasks were conducted at bowers where male behaviour could be monitored remotely. Not all males were presented with all tasks.

Table 1
Summary of the six cognitive tasks

Task	Apparatus	Season	N	What the task demonstrated
Barrier removal	Transparent barrier	2010	19	Problem-solving ability
Novel motor task	Pokebox	2010–2011	14	Motor skills in a novel task
Colour discrimination	Pokebox	2011	12	Discrimination based on colour
Colour reversal	Pokebox	2011	12	Behavioural flexibility
Shape discrimination	Pokebox	2011	11	Discrimination based on shape
Spatial memory	Pokebox	2011	11	Memory for spatial location of rewards

Cognitive tasks were presented over two consecutive breeding seasons. Tasks were divided by the type of cognitive domain they tested and the apparatus used to carry out testing.

The barrier removal tasks were conducted with 19 males during the 2010 season; however, not all these males were available for testing during 2011. The pokebox tasks were carried out in 2011 with 14 males, of which 13 had been previously tested in the barrier removal tasks. Of these 14, two were lost (presumably predated) during the test period in 2011. Thus, the total number of males that were presented with all tasks was 11.

When bowers were located at the start of the season, a Velcro-covered board (250 × 150 mm and 3 mm thick, made of plywood) was fixed to the ground on the outer edge of the bower using 75 mm nails, to which the test apparatus could be rapidly attached. This prevented males removing the apparatus and ensured it was consistently presented at a specific location. Tasks were presented during two sessions each day: morning (dawn to midday) and afternoon (1500 hours to sunset). They were not presented during the middle of the day, when birds are less active at their bowers (Sparfeld 2012). All tasks were filmed using Samsung SMX-C20 camcorders in the absence of an observer to reduce any external influence on male behaviour.

Barrier removal task

Males were presented with a transparent plastic barrier (10 cm diameter × 11 cm high clear plastic beaker) underneath which objects could be placed. This barrier was placed 25 cm from the entrance to the bower avenue. We presented male spotted bowerbirds with three different trials in a randomized order: an aversive object trial, a desirable object trial and a control trial. The aversive object trial was a replication of the task presented by Keagy et al. (2009) and tested the ability and motivation of males to remove disliked objects (three 1 cm³ yellow blocks) from their bower by removing them from underneath the barrier. The desirable object trial tested exactly the same mechanism (problem solving via barrier removal) but tested whether motivation differed with desirable objects (two green glass chips and one decoration taken from the bower avenue, typically a *Solanum* spp. fruit; see Madden 2003b). The control trial addressed a key limitation of Keagy et al. (2009), where the male's reaction towards the barrier itself was not considered. If males consider the barrier alone to be an object with which they wish to interact (either a disliked object that they want to remove, or a desirable object they want to display) they may be motivated to move it, and this could be seen as a simple bower maintenance task requiring little problem-solving ability, rather than a response to a perceived problem (gaining access to covered objects) that requires solving. Males were scored on the time taken to gain access to the first object underneath the barrier; males that were faster at solving the trial were deemed to be better problem-solvers. To 'solve' the control trial males had to move the barrier one diameter length (10 cm) from its original location, which would indicate a motivation towards removing it or adding it to their display.

'Solving' a barrier removal trial may be simply explained by variation in persistence, rather than in cognitive ability. Males that pecked at the barrier at a faster rate may increase their chances of gaining access to the objects in a faster time, yet this may not represent an enhanced cognitive ability. Therefore, we counted the pecks made to the barrier and used this measure to investigate whether males solving the trial in a shorter amount of time were simply more persistent in their interactions with the task apparatus.

Nineteen males were presented with each of the three trials (aversive, desirable and control) once between August and December 2010, in a randomized order and with a minimum of 30 days between trials. Trials were videoed for 3.5 h, after which the barrier and objects were removed. Males were scored on both time attentive to trial (cumulative time male spent interacting with

barrier (within 20 cm of the barrier and oriented towards it) until solved) and total elapsed time (total time from first attentive until solved).

Novel motor task

We explored how fast 14 males learned to perform the novel motor task of opening a pokebox to gain access to a food reward (Appendix Fig. A1). The pokebox was a medium-density fibre-board, 15 × 15 cm and 3 cm high box with 12 wells (diameter 25 mm) drilled around the outside edge. A matching lid (2 mm plywood) was fixed to the box. In between the box and the lid a sheet of paper could be inserted, which prevented direct access to and hid the contents of the wells. Males were trained to peck through a plain white paper lid to gain access to food reward items (fragments of green grapes) using a systematic shaping procedure (Table 2; Boogert et al. 2008), which guided males through four stages of training, each of which increased in difficulty. Males were required to pass each stage of training before they could progress to the next stage and were scored on the total number of trials taken to pass stages 2–4. The first stage of training was considered to be habituation to the novel equipment, and was excluded from the final score given. The minimum number of trials required to pass each stage was two; therefore males required a minimum of six trials in total to complete this task. Males were presented with up to five trials in the morning session and three in the afternoon session. Pokeboxes were reset every 45 min, although the actual retention time between trials was determined by the male's presence at the bower; trials conducted when the male did not attend his bower were discounted. Resetting was quick (2–3 min), caused minimal disturbance to the males, and involved swapping the current pokebox with a preset box that had been prepared out of sight from the males.

Colour discrimination

Fourteen males were presented with a colour discrimination task. Six wells on the pokebox were covered with a paper lid of one colour and contained a food reward (grape fragment). The other six wells were covered with a second colour and contained reward cues (crushed grapes) but access to the reward was blocked by a

wooden plug. As bowerbirds show strong colour preferences, we chose two neutral colours with the same greyscale value to control for preferences towards pecking light/dark. The rewarded colour was randomized between males. We tested how quickly males learned to discriminate the colours, only pecking at rewarded wells. Males passed the colour discrimination task if they pecked at all six rewarded wells before pecking an unrewarded well on two consecutive trials. No males pecked at only rewarded wells on their first trial.

For this and all subsequent pokebox trials, male performance was scored on the cumulative number of trials taken to reach a pass criterion. The maximum number of trials presented was 35; after this males showed a significant reduction in their motivation to engage with the apparatus. Some trials were stopped sooner if males showed decreased motivation, for example because of a lack of positive reinforcement. Males that failed to reach the pass criterion were given scores of the maximum number of trials to allow their inclusion in analyses.

Colour reversal

Immediately following the colour discrimination task, males were presented with a reversal task, in which the previously rewarded colour became the unrewarded, blocked colour. Reversal tasks are considered to provide a measure of behavioural flexibility (Boogert et al. 2010; Tebbich et al. 2010). Males were required to reach the same pass criterion as the colour discrimination tasks. Thirteen males were presented with this task, as one male was lost from the population (presumed predated) before this task commenced.

Shape discrimination

Twelve males were presented with a shape discrimination task (a second male was lost before the start of this task). Half of the wells were displayed with blue circles and the other six were displayed with blue triangles. As with the colour discrimination task, one shape covered rewarded wells while the other shape covered blocked wells. The rewarding shape was randomized between males. Males were required to reach the same pass criterion as in the colour discrimination tasks.

Spatial memory

Twelve males were presented with a spatial memory task. Eight wells were used for testing, with the four corner wells left uncovered and empty. Two adjacent wells on one side of the box were consistently rewarded, with the remaining three pairs of wells unrewarded and blocked. The pokebox was placed in the same location, ensuring that the spatial position of the rewarded holes relative to the bower was constant. All wells were covered with plain white paper lids, and boxes were switched between trials to ensure that males could not use inadvertent cues to aid solving the task.

Males passed this task when they correctly chose the two rewarded wells before pecking any unrewarded wells in two consecutive trials.

Motivation checks

To measure motivation in the barrier removal task, the time taken to move objects more than 20 cm from their original position under the barrier once access had been gained was measured (see Keagy et al. 2009). All males immediately (within 1–3 s) removed the objects >20 cm, and thus all showed high motivation in this task.

Motivation in the pokebox trials was checked by presenting males twice with a pokebox with all 12 wells rewarded and covered with plain white lids. This was identical to the final stage in the

Table 2

The four stages of the systematic shaping procedure used to train males to open a pokebox

Stage	Training
1	Habituation to Equipment All pokebox wells were open and each contained one fragment of green grape (reward). One fragment of grape and two decorations were placed on top of the pokebox to draw the male's attention to the apparatus
2	Paper Lid Pokebox presented with a reward in every well, and with paper lid added. Six holes fully opened (paper torn open so that reward is easily obtainable) by experimenter and six partially opened (paper torn down centre, so that food can be seen but not obtained without further ripping of the paper by the male)
3	Closed Holes Pokebox presented with a reward in every well, with eight holes fully closed (complete intact paper lid) and four holes partially opened
4	Final Test Pokebox presented with a reward in every well, with all holes closed

Each stage in the procedure was passed when all 12 pieces of grape were taken from all wells on two consecutive trials. Only stages 2–4 were counted in the novel motor task analysis, as stage 1 was considered as a habituation stage in which males were encouraged to interact with the novel item.

shaping procedure, and was presented following completion of the colour reversal and spatial memory tasks. These trials served to reinforce the association between opening wells and receiving a reward, and to check whether males had remained motivated to engage with the task. All males passed these trials, indicating that despite being unrewarded in previous cognitive tests, males had not habituated to the presence of the apparatus and were still motivated to engage with the pokebox.

Statistical Analysis

Individual variation in task performance

For the barrier task we looked for differences in a male's ability to solve each of the three trials presented using a Cochran's Q nonparametric test for dichotomous data, and further investigated these results with pairwise McNemar tests between each of the tasks. When considering the ability of males to solve the tasks, we looked for correlations between the three measures taken: time attentive to task, total time elapsed and number of pecks made to barrier. For the pokebox cognitive tasks we used the number of trials males required to reach the pass criterion as a score of individual performance (Boogert et al. 2008, 2011a).

Relationship between individual performances in different tasks

We explored how a male's performance in one task related to his performance in another task. First, we explored simple relationships between performances in pairs of tasks using Spearman rank correlations. Second, we explored whether variation in the cognitive performance could be explained by a single underlying factor (analogous to g), by conducting a principal components analysis (PCA) on scores from the 11 birds that had been presented with all tasks (these included solvers and non-solvers). To allow for the inclusion of males that failed to solve tasks, and to normalize the data where possible, we calculated the inverse of our response variables by taking the maximum performance score per trial and dividing this by each male's performance score. In this way, males that failed to solve a task were given a score of zero, with higher scores indicating greater ability. We conducted a PCA with an unrotated factor solution and extracted individual composite scores from the first and second components with eigenvalues >1 .

Relationship between cognitive performance and mating success

Spearman rank correlations were used to see whether male performances in each task correlated with mating success, both for the year in which the task was carried out, and for his average mating success across both years of testing. We then tested whether individual PCA composite scores were correlated with a male's mating success, both in each year of testing and with average mating success across both years. We also took an alternative measure of cognitive performance by averaging the relative performance of each male on each cognitive task with which he was presented (see Keagy et al. 2011), and related this score to measures of mating success.

Finally, we implemented a linear mixed model to explore how performance scores and male mating success were related, given the variation within males in their relative mating success across the two seasons measured. Since mating success for each male was not significantly correlated across seasons, we entered both seasons as a repeated measure in the mixed model, with PC1 composite scores as fixed effects, and season and bird identity as random effects. Re-running the analyses controlling for male bower ownership, a proxy for age, did not qualitatively alter any of the results we report (see Appendix). All analyses were carried out in SPSS version 19 (SPSS Inc., Chicago, IL, U.S.A.).

Ethical Note

Permission to work with the population of wild spotted bowerbirds in Taunton National Park (Scientific) was granted by the Queensland Government Environmental Protection Agency (Permit Number WITK0615290). Ethics approval was granted by the University of Queensland (Animal Ethics Approval Certificate SBMS/285/09). Birds were caught in mist nets and ringed with a unique combination of coloured bands and a metal Australian Bird and Bat Banding Scheme band (ABBBS). Captured birds were held in cloth bags and processed immediately. Capture and banding was carried out by J.R.M. and C.D. (ABBBS Authority Number 2323). All birds were free-living and could choose whether to interact with the task apparatus. We used rewards rather than punishments as motivation. All equipment was removed from bowers at the end of the test period. No males abandoned bowers as a result of our testing and of those tested in 2010, all returned the following season in 2011 to reassert their ownership at the same bower.

RESULTS

Individual Variation in Task Performance

Barrier removal task

Males did not solve the three barrier trials equally well (Cochran's Q : $\chi^2 = 14.53$, $N = 19$, $P < 0.001$). Of the 19 males, 14 (74%) solved the aversion trial, and males were more likely to solve this trial than the control trial (pairwise McNemar tests: control–aversion: $N = 19$, $P < 0.01$). Nine males (47%) solved the desirable objects trial, and males were more likely to solve this trial than the control trial (pairwise McNemar tests: control–desirable: $N = 19$, $P = 0.04$). Only two of the 19 (11%) males solved the control trial.

When we considered the aversion trial only (for which we had the largest sample size of problem-solvers), the time that males that solved the task spent attentive was strongly related to the total elapsed time ($r_s = 0.80$, $N = 14$, $P < 0.001$). Males varied widely in the time they took to solve this trial (mean time attentive to trial \pm SD = 92.7 ± 76.7 s, range 19–305 s). The number of pecks that males (solvers and nonsolvers) made to the barrier was positively correlated with the time spent attentive to trial ($R^2 = 0.88$, $N = 19$, $P < 0.001$; Fig. 1). This relationship held when only solvers were included in the analysis ($R^2 = 0.85$, $N = 14$, $P < 0.001$).

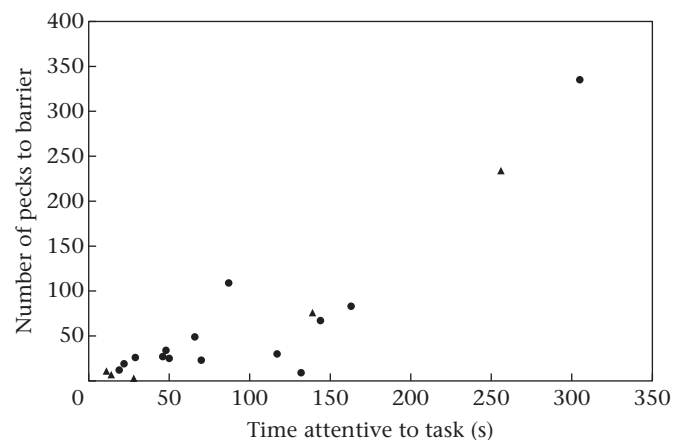


Figure 1. Relationship between time attentive to task and number of pecks made to the barrier in the aversion trials for all males. Solvers are indicated by circles; males that failed to solve are indicated by triangles.

Pokebox tasks

Males varied in their ability to learn the novel motor task of opening paper-covered wells ($N = 14$, mean \pm SD to pass = 8.35 ± 2.82 , range 6–15). Five males passed the motor task with the minimum number of trials required. All males passed the colour discrimination task ($N = 14$, mean \pm SD = 5.93 ± 2.56 , range 4–13) but only half solved the reversal task ($N = 13$, solved = 7: mean \pm SD = 20.86 ± 4.78 , range 14–35, 35 being the maximum number of trials given). Twelve males were presented with a shape discrimination task; three failed to solve this task and those that passed took, on average, more trials than in the colour discrimination task ($N = 12$, mean \pm SD = 9.78 ± 4.21 , range 5–35). The spatial memory task was also presented to 12 males and had the lowest completion rate and the largest variance between solvers ($N = 12$, mean \pm SD = 12.75 ± 9.67 , range 4–35). Males that were unable to solve this task tended to peck repeatedly at nonrewarded holes, leading to a lack of positive reinforcement.

Relationships Between Individual Performance in Different Tasks

Bivariate relationships

Performances across pairs of tasks were generally positively correlated; the spatial memory task showed negative correlations with some tasks (Table 3). No correlations were significant after a Bonferroni correction for multiple comparisons was applied. When we controlled for male tenure at bowers, there was no qualitative change in these results (see Appendix Table A1).

Principal components analysis

Two components were extracted with eigenvalues >1 (Table 4). Male performances in all tasks loaded positively onto the first component, which captured over 44% of the total variance. Performance in the barrier and colour reversal tasks loaded on the second component, which explained a further 23% of the variance. The spatial memory task loaded strongly on the negative pole of the second component, with the motor task and colour discrimination showing weaker negative associations with this PC.

Relationships Between Cognitive Performance and Mating Success

We found no relationships between an individual's performance in any of the cognitive and problem-solving tasks and his mating success. There were no significant relationships between each of the individual trials and measures of mating success (Table 5). We

Table 3
Spearman rank correlations between performances in cognitive tasks

	Barrier task	Motor task	Colour discrimination	Colour reversal	Shape discrimination
Motor task	$r_s=0.00$ $P=0.99$ $N=13$				
Colour discrimination	$r_s=0.13$ $P=0.67$ $N=13$	$r_s=0.43$ $P=0.12$ $N=14$			
Colour reversal	$r_s=0.25$ $P=0.44$ $N=12$	$r_s=0.06$ $P=0.84$ $N=13$	$r_s=0.44$ $P=0.13$ $N=13$		
Shape discrimination	$r_s=0.33$ $P=0.32$ $N=11$	$r_s=0.41$ $P=0.19$ $N=12$	$r_s=0.60$ $P=0.04$ $N=12$	$r_s=0.60$ $P=0.04$ $N=12$	
Spatial memory	$r_s=-0.07$ $P=0.83$ $N=11$	$r_s=0.18$ $P=0.47$ $N=12$	$r_s=0.41$ $P=0.19$ $N=12$	$r_s=-0.22$ $P=0.50$ $N=12$	$r_s=0.36$ $P=0.24$ $N=12$

Bonferroni correction: α level of significance = 0.003. Bold indicates tasks showing a trend towards a positive correlation. N reduces in some trials owing to the loss of male owners during the breeding season.

Table 4
Results from the unrotated principal components analysis

Task	Component 1	Component 2
Barrier task	0.16	0.57
Motor task	0.67	-0.26
Colour discrimination	0.80	-0.09
Colour reversal	0.58	0.66
Shape discrimination	0.89	0.25
Spatial memory	0.63	-0.72
Eigenvalue	2.65	1.42
% Variance explained	44.12	23.62

Results are based on inversely transformed performance scores in the barrier and pokebox tasks, showing the two components extracted with eigenvalues >1 and percentage of total variance in performance explained.

also found no relationship between mating success and composite scores on the first and second principal components of the PCA (Pearson correlations between task composite scores and average mating success: PC1: $R^2 = -0.04$, $N = 11$, $P = 0.91$; Fig. 2; PC2: $R^2 = -0.01$, $N = 11$, $P = 0.78$). Additionally, there was no relationship between an alternative measure of cognitive ability, the average of each male's rank performance on each cognitive task completed, and mating success in the year of testing ($r_s = 0.13$, $N = 13$, $P = 0.68$). Finally, we found no overall relationship between PC1 scores and mating success scores when adjusting for season and male identity ($F_{1,10} = 0.01$, $P = 0.91$).

DISCUSSION

In this paper we describe a method that enables the cognitive testing of wild individuals over extended trials, without the need for constraint or captivity. We presented a series of novel tasks that tested a range of cognitive domains, including problem solving, novel motor skills, colour and shape discrimination, behavioural flexibility and simple, local spatial abilities. Male spotted bowerbirds differed in their ability to solve these tasks, and performance in any one of these tasks was a relatively poor predictor of performance in any of the other tasks. We found weak, nonsignificant positive correlations between individual performances, which, in part, mirrors results gained from the congeneric satin bowerbird (Keagy et al. 2011). Few species have been subject to an in-depth battery of cognitive testing with an emphasis on quantifying within-species individual variation (Thornton & Lukas 2012), but in those species that have, this positive covariation has been summarized by a single factor and has been described as analogous to human g (Chandra et al. 2000; Plomin & Spinath 2002; Matzel et al. 2003; Banerjee et al. 2009). Although the PCA extracted more than one principal component with an eigenvalue >1 , all tasks loaded positively onto this component which captured over 44% of the total variance in performance. This is above levels that have previously been accepted as evidence for g in humans (ca. 40%; Plomin & Spinath 2002) and in mice (ca. 30%; Matzel et al. 2003), and is also higher than has been found in satin bowerbirds (28–33%; Keagy et al. 2011). Thus, it could be concluded that male spotted bowerbirds exhibit individual differences in cognitive performance that operate within a general cognitive structure across domains: a general intelligence. Such domain-general intelligence may be important for tackling nonrecurrent problems, which are evolutionarily novel in nature (Chiappe & MacDonald 2005).

The first set of tasks (barrier removal) tested naturalistic behaviours with assumed cognitive domains. Males were more motivated to interact with the barrier when there were objects (aversive or desirable) underneath, suggesting that the presence of the barrier did not pose a problem in itself. Therefore, we can be confident that this task reflected a male's capacity to remove a

Table 5
Correlations between individual task performances and mating success

Trial	Year	Mating success in same year			Average mating success across years		
		Correlation coefficient, r_s	N	P	Correlation coefficient, r_s	N	P
Barrier: time attentive	2010	0.20	17	0.47	−0.05	18	0.83
Barrier: time elapsed		0.19	17	0.48	−0.11	18	0.65
Motor task	2011	0.24	13	0.42	0.42	14	0.14
Colour discrimination	2011	−0.26	13	0.40	−0.25	14	0.39
Colour reversal	2011	0.15	13	0.63	0.27	13	0.38
Shape discrimination	2011	0.17	12	0.59	0.07	12	0.84
Spatial memory	2011	0.34	12	0.27	−0.19	12	0.56

Spearman rank correlations are shown for both the individual year in which males were tested, and for mean mating success over both years.

barrier to gain access to novel objects, with the highest motivation being to remove unwanted aversive objects. A similar proportion of males solved the aversive object tasks as had been found in satin bowerbirds (Keagy et al. 2009). Males that pecked the barrier more times were not faster solvers, indicating that solving this task was not simply a product of persistence and vigour.

As with many problem-solving tasks, it can be difficult to identify the specific cognitive ability being tested, or to rule out alternative, noncognitive explanations for success (Thornton & Lukas 2012). Males may have been able to solve such tasks through luck, for example, by inadvertently tipping the barrier against debris. The fact that this problem-solving task loaded positively, albeit weakly, onto the first component suggests that it may align with general cognitive performance across domains. We suggest further evidence is required on this potentially important, yet so far unverified, relationship between problem-solving tasks based on maximizing ecological validity and more abstract, domain-specific cognitive tasks with clear psychological definitions. Such evidence could help confirm the tentative relationship we present here.

Our subsequent five tasks aimed to provide a measure of cognitive ability based on paradigms generally accepted within cognitive psychology. Males varied widely in their success in solving these tasks in the wild. The majority of males were able to solve the colour and shape discrimination tasks; however, surprisingly, many failed to pass the spatial memory and shape discrimination tasks. Male song sparrows required 40+ exposures of a similar reversal task (Boogert et al. 2011a), suggesting that the lack of performance seen in spotted bowerbirds may be caused by the limited number of trials presented. Alternatively, the failure of males to pass this and other tasks may be an unintended consequence of our presenting them to free-living animals. Reversal

tasks are considered to measure behavioural flexibility (Bond et al. 2007; Tebbich et al. 2010; Boogert et al. 2011a; Leal & Powell 2012) and we expected male bowerbirds to exhibit a high level of behavioural flexibility based on the complex nature of their display behaviours and their inhabiting fluctuating environments. However, we detected no such ability. One reason may be because wild male bowerbirds were more easily able to switch to an alternative choice strategy, for example by searching for reward resources elsewhere in their environment. Under constrained laboratory conditions individuals presented with a cognitive experimental apparatus are often presented with the task in isolation, preventing the opportunity to switch to an alternative. Arguably, switching in itself is a demonstration of behavioural flexibility, but our tasks were not designed to detect it in this context.

One further explanation why males failed to solve some of the tasks may be our inability to control motivation in the wild. Male bowerbirds continually engaged with the task apparatus and showed high levels of motivation throughout the study period but we could not control their individual motivation level for each task on any given day. However, motivation is rarely standardized in laboratory conditions either; starvation periods may increase, but are unlikely to equalize, motivation and may also increase stress which can affect performance (Kolss & Kawecki 2008; Lupien et al. 2009). Increasing motivation artificially through starvation and restricting behavioural responses to a single task may not accurately reflect interindividual variation, and as Thornton & Lukas (2012) pointed out, it may be difficult to envisage how abilities that are manifested only under artificial conditions are selected for in nature. This highlights a potential important limitation of relying solely on captive studies to draw evolutionary explanations, and calls for the further development of cognitive tests to be transferred to the wild to complement conclusions drawn from captivity.

We found no relationships between a male's performance on any single problem-solving or cognitive task and his mating success, nor between composite measures of performance (the principal components and individual average rank score across tasks) and mating success. We are reticent about drawing strong conclusions from our data set considering the relatively limited number of tasks (six) that we set the males and, because of the nature of conducting such tests in the wild, our sample sizes for all tasks were limited, and as such suffer from low statistical power. We had the largest sample size in our barrier tasks, with the number of individuals tested being similar to the number of male satin bowerbirds tested in the previous study (Keagy et al. 2009). However, our lack of relationship with mating success contrasts with the satins, which is surprising, as the complex nature of the spotted bowerbird display when compared to the satin's, coupled with the associated relative difference in brain size (Madden 2001), suggests a stronger dependence on cognitive performance for the construction of the spotted bowerbird's display. Similarly, the results from composite measures of performance differ in part from those found with satin

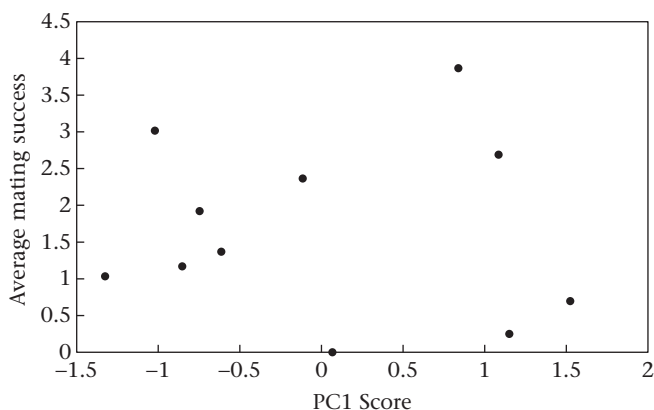


Figure 2. Relationship between individual composite scores on the first principal component and average mating success across both years of testing.

bowerbirds, for which low intercorrelations between tasks initially suggested independence between cognitive domains, yet an integrated measure of performance across cognitive tasks predicted mating success (Keagy et al. 2011, 2012). We repeated our analyses controlling for male bower tenure, and found no significant impact of this on our results, supporting previous results on problem solving in satin bowerbirds. We used male bower tenure as a proxy for male age; male tenure is arguably a more reliable indicator of male experience, as males may differ in the age at which they gain bower ownership and thus the amount of experience gained within similar age brackets. However, although male age has been shown to influence certain aspects of male display and mating success in bowerbirds, performance in novel cognitive tasks may not be intrinsically linked to age and/or experience in species that already delay display until maturity (Collis & Borgia 1992; Keagy et al. 2009, 2012). In both the satin and spotted bowerbird studies results rely on relatively small sample sizes and thus are susceptible to noise, but the lack of consistency between performances in two very similar tasks may indicate meaningful differences between congeneric species.

There are several explanations for why a lack of a positive relationship between cognitive performance and mating success may be a true reflection of mate choice decisions in spotted bowerbirds. In contrast to satin bowerbirds, we found no correlation between mating success measured in the 2 consecutive years of our study, suggesting there is variation in intramale display quality and/or female mate preferences over time. Such variation in mating success may be better explained by noncognitive factors, such as a male's social status and/or opportunities for learning and experience (Collis & Borgia 1992) or with changes in male physical attributes, such as parasite load (Borgia & Collis 1989). Alternatively, this lack of relationship may reflect variable female preferences for males; females may differ in their choices of mates in ways that are not directionally aligned with male quality (Cotton et al. 2006). Low-quality females may actively choose lower quality males (Riebel et al. 2010), or have weaker mate preferences than high-quality females (Cotton et al. 2006), and preferences may change as females age (Coleman et al. 2004). Variable or assortative female choice may confound any directional selection for cognitive traits.

Relationships between sexually selected traits and cognitive performance may not always be direct; in guppies, females showed a preference for males with an enhanced rate of learning, but this was not related to well-described sexually selected traits in this species (body size and orange patch saturation), and the mechanism by which females gain such information remains unknown (Shohet & Watt 2009). Similarly, cognitive ability may be indirectly reflected in display traits via its influence on other behavioural mechanisms, such as foraging ability (Boogert et al. 2011b).

An additional explanation for a lack of relationship may be because the construction of a high-quality bower, known to be an important target in female choice (Borgia 1985; Borgia & Mueller 1992; Lenz 1994), relies on singular cognitive skills that are not transferable across even quite conceptually similar tasks. Specific traits may be independently selected without a requirement for overall intelligence (for example, face perception ability in humans may be determined by specific cognitive specialist genes that are not necessarily related to any general cognitive measure; Zhu et al. 2010). Alternatively, the complex and multifaceted nature of bowers could suggest that successful bower building can be achieved through numerous combinations of skills; for example, little is known about the degree to which bower building is socially learned (Madden 2008). Evidence in satin bowerbirds suggests that multiple display traits may indicate one integrative measure of overall cognitive ability to females and/or different aspects of male

quality (Keagy et al. 2012) although the exact nature of these associations remains unclear.

Finally, inferior individuals may be more likely to adopt innovative behaviour; Cole & Quinn (2012) found that in great tits, *Parus major*, competitive ability was negatively correlated with novel problem-solving ability, and Thornton & Lukas (2012) raised the interesting notion that perhaps individuals that are low achievers are the ones that innovate more to compete with superior competitors, thus confounding any effects of selection for such traits.

We employed a range of cognitive tasks with which male bower owners were repeatedly motivated to engage in the wild. We based our tasks on natural behaviours that males appear to exhibit, but decoupled the specific tasks from the natural expression of these behaviours in the wild, allowing for a more rigorous exploration of defined cognitive traits. We found little support for the suggestion that enhanced cognition is selected for through mate choice, but accept there are limitations to the conclusions we can draw from this limited data set, and encourage further exploration of these concepts. We hope that the methods described here will inspire others to develop opportunities for exploring the link between cognitive performance across domains in a range of contexts. We expect the increasing number of studies testing the relationship between cognitive performance and fitness outcomes will create more opportunities to refine the methods used and generate a deeper understanding of the evolution of cognitive differences within species in both males and females and the selective forces operating on them.

Acknowledgments

We are especially grateful to John Wyland and the Queensland Parks and Wildlife Service for permission and assistance at Taunton National Park, and to Anne Goldizen at the University of Queensland. We also thank Janka Sparfeld and Amy Munro-Faure for assistance with data collection, and two anonymous referees for comments. Metal bands were provided by the Australian Bird and Bat Banding Scheme (ABBBS). J.R.M. and C.D. were funded by a BBSRC grant to J.R.M. J.I. was funded by an EGF studentship from the University of Exeter.

References

- Anderson, B. 1993. Evidence from the rat for a general factor that underlies cognitive performance and that relates to brain size: intelligence? *Neuroscience Letters*, **153**, 98–102.
- Banerjee, K., Chabris, C. F., Johnson, V. E., Lee, J. J., Tsao, F. & Hauser, M. D. 2009. General intelligence in another primate: individual differences across cognitive task performance in a New World monkey. *PLoS One*, **4**, e5883.
- Bond, A. B., Kamil, A. C. & Balda, R. P. 2007. Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*, **121**, 372–379.
- Boogert, N. J., Anderson, R. C., Peters, S., Searcy, W. A. & Nowicki, S. 2011a. Song repertoire size in male song sparrows correlates with detour reaching, but not with other cognitive measures. *Animal Behaviour*, **81**, 1209–1216.
- Boogert, N. J., Fawcett, T. W. & Lefebvre, L. 2011b. Mate choice for cognitive traits: a review of the evidence in nonhuman vertebrates. *Behavioral Ecology*, **22**, 447–459.
- Boogert, N. J., Giraldeau, L.-A. & Lefebvre, L. 2008. Song complexity correlates with learning ability in zebra finch males. *Animal Behaviour*, **76**, 1735–1741.
- Boogert, N. J., Monceau, K. & Lefebvre, L. 2010. A field test of behavioural flexibility in Zenaida doves (*Zenaida aurita*). *Behavioural Processes*, **85**, 135–141.
- Borgia, G. 1985. Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behaviour*, **33**, 266–271.
- Borgia, G. 1993. The cost of display in the non-resource-based mating system of the satin bowerbird. *American Naturalist*, **141**, 729–743.
- Borgia, G. 1995. Complex male display and female choice in the spotted bowerbird: specialized functions for different bower decorations. *Animal Behaviour*, **49**, 1291–1301.
- Borgia, G. & Collis, K. 1989. Female choice for parasite-free male satin bowerbirds and the evolution of bright male plumage. *Behavioral Ecology and Sociobiology*, **25**, 445–453.

- Borgia, G. & Mueller, U.** 1992. Bower destruction, decoration stealing and female choice in the spotted bowerbird *Chlamydera maculata*. *Emu*, **92**, 11–18.
- Borgia, G., Pruett-Jones, S. G. & Pruett-Jones, M. A.** 1985. The evolution of bower-building and the assessment of male quality. *Zeitschrift für Tierpsychologie*, **67**, 225–236.
- Bouchard, J., Goodyer, W. & Lefebvre, L.** 2007. Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Animal Cognition*, **10**, 259–266.
- Bravery, B. D. & Goldizen, A. W.** 2007. Male satin bowerbirds (*Ptilonorhynchus violaceus*) compensate for sexual signal loss by enhancing multiple display features. *Naturwissenschaften*, **94**, 473–476.
- Candolin, U.** 2003. The use of multiple cues in mate choice. *Biological Reviews*, **78**, 575–595.
- Cauchard, L., Boogert, N. J., Lefebvre, L., Dubois, F. & Doligez, B.** 2013. Problem-solving performance is correlated with reproductive success in a wild bird population. *Animal Behaviour*, **85**, 19–26.
- Chandra, S. B. C., Hosler, J. S. & Smith, B. H.** 2000. Heritable variation for latent inhibition and its correlation with reversal learning in honeybees (*Apis mellifera*). *Journal of Comparative Psychology*, **114**, 86–97.
- Chiappe, D. & MacDonald, K.** 2005. The evolution of domain-general mechanisms in intelligence and learning. *The Journal of General Psychology*, **132**, 5–40.
- Cole, E. F. & Quinn, J. L.** 2012. Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B*, **279**, 1168–1175.
- Cole, E. F., Morand-Ferron, J., Hinks, A. E. & Quinn, J. L.** 2012. Cognitive ability influences reproductive life history variation in the wild. *Current Biology*, **22**, 1808–1812.
- Coleman, S. W., Patricelli, G. L. & Borgia, G.** 2004. Variable female preferences drive complex male displays. *Nature*, **428**, 742–745.
- Coleman, S. W., Patricelli, G. L., Coyle, B., Siani, J. & Borgia, G.** 2007. Female preferences drive the evolution of mimetic accuracy in male sexual displays. *Biology Letters*, **3**, 463–466.
- Collis, K. & Borgia, G.** 1992. Age-related effects of testosterone, plumage, and experience on aggression and social-dominance in juvenile male satin bowerbirds (*Ptilonorhynchus violaceus*). *The Auk*, **109**, 422–434.
- Cotton, S., Small, J. & Pomiankowski, A.** 2006. Sexual selection and condition-dependent mate preferences. *Current Biology*, **16**, 755–765.
- Deary, I. J., Penke, L. & Johnson, W.** 2010. The neuroscience of human intelligence differences. *Nature Reviews Neuroscience*, **11**, 201–211.
- Diamond, J.** 1987. Bower building and decoration by the bowerbird *Amblyornis inornatus*. *Ethology*, **74**, 177–204.
- DuVal, E. H.** 2007. Adaptive advantages of cooperative courtship for subordinate male lance tailed manakins. *The American Naturalist*, **169**, 423–432.
- Endler, J. A. & Day, L. B.** 2006. Ornament colour selection, visual contrast and the shape of colour preference functions in great bowerbirds, *Chlamydera nuchalis*. *Animal Behaviour*, **72**, 1405–1416.
- Endler, J. A., Endler, L. C. & Doerr, N. R.** 2010. Great bowerbirds create theaters with forced perspective when seen by their audience. *Current Biology*, **20**, 1679–1684.
- Farrell, T. M., Weaver, K., An, Y.-S. & MacDougall-Shackleton, S. A.** 2012. Song bout length is indicative of spatial learning in European starlings. *Behavioral Ecology*, **23**, 101–111.
- Frith, C. B. & Frith, D. W.** 2004. *The Bowerbirds: Ptilonorhynchidae*. New York: Oxford University Press.
- Frith, C. B. & McGuire, M.** 1996. Visual evidence of vocal avian mimicry by male tooth-billed bowerbirds *Scenopoeetes tictirostris* (Ptilonorhynchidae). *Emu*, **96**, 12–16.
- Galsworthy, M. J., Paya-Cano, J. L., Liu, L., Monleón, S., Gregoryan, G., Fernandes, C., Schalkwyk, L. C. & Plomin, R.** 2005. Assessing reliability, heritability and general cognitive ability in a battery of cognitive tasks for laboratory mice. *Behavior Genetics*, **35**, 675–692.
- Holveck, M.-J., de Castro, A. C. V., Lachlan, R. F., ten Cate, C. & Riebel, K.** 2008. Accuracy of song syntax learning and singing consistency signal early condition in zebra finches. *Behavioral Ecology*, **19**, 1267–1281.
- Jensen, A. R.** 1998. *The g Factor: the Science of Mental Ability*. London: Praeger.
- Karino, K., Shinjo, S. & Sato, A.** 2007. Algal-searching ability in laboratory experiments reflects orange spot coloration of the male guppy in the wild. *Behaviour*, **144**, 101–114.
- Keagy, J., Savard, J. F. & Borgia, G.** 2009. Male satin bowerbird problem-solving ability predicts mating success. *Animal Behaviour*, **78**, 809–817.
- Keagy, J., Savard, J. F. & Borgia, G.** 2011. Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, *Ptilonorhynchus violaceus*. *Animal Behaviour*, **81**, 1063–1070.
- Keagy, J., Savard, J. F. & Borgia, G.** 2012. Cognitive ability and the evolution of multiple behavioral display traits. *Behavioral Ecology*, **23**, 448–456.
- Kolss, M. & Kaweckí, T. J.** 2008. Reduced learning ability as a consequence of evolutionary adaptation to nutritional stress in *Drosophila melanogaster*. *Ecological Entomology*, **33**, 583–588.
- Leal, M. & Powell, B. J.** 2012. Behavioural flexibility and problem-solving in a tropical lizard. *Biology Letters*, **8**, 28–30.
- Lenz, N.** 1994. Mating-behavior and sexual competition in the regent bowerbird *Sericulus chrysocephalus*. *Emu*, **94**, 263–272.
- Loffredo, C. A. & Borgia, G.** 1986. Male courtship vocalizations as cues for mate choice in the satin bowerbird (*Ptilonorhynchus violaceus*). *The Auk*, **103**, 189–195.
- Lupien, S. J., McEwen, B. S., Gunnar, M. R. & Heim, C.** 2009. Effects of stress throughout the lifespan on the brain, behaviour and cognition. *Nature Reviews Neuroscience*, **10**, 434–445.
- Madden, J.** 2001. Sex, bowers and brains. *Proceedings of the Royal Society B*, **268**, 833–838.
- Madden, J. R.** 2002. Bower decorations attract females but provoke other male spotted bowerbirds: bower owners resolve this trade-off. *Proceedings of the Royal Society B*, **269**, 1347–1351.
- Madden, J. R.** 2003a. Bower decorations are good predictors of mating success in the spotted bowerbird. *Behavioral Ecology and Sociobiology*, **53**, 269–277.
- Madden, J. R.** 2003b. Male spotted bowerbirds preferentially choose, arrange and proffer objects that are good predictors of mating success. *Behavioral Ecology and Sociobiology*, **53**, 263–268.
- Madden, J. R.** 2008. Do bowerbirds exhibit cultures? *Animal Cognition*, **11**, 1–12.
- Madden, J. R., Isden, J. & Dingle, C.** 2011. Commentary on review by Boogert et al.: some problems facing females. *Behavioral Ecology*, **22**, 461–462.
- Marshall, A. J.** 1954. *Bower-birds: Their Displays and Breeding Cycles; a Preliminary Statement*. Oxford: Clarendon Press.
- Mateos-Gonzalez, F., Quesada, J. & Senar, J. C.** 2011. Sexy birds are superior at solving a foraging problem. *Biology Letters*, **7**, 668–669.
- Matzel, L. D., Han, Y. R., Grossman, H., Karnik, M. S., Patel, D., Scott, N., Specht, S. M. & Gandhi, C. C.** 2003. Individual differences in the expression of a 'general' learning ability in mice. *Journal of Neuroscience*, **23**, 6423–6433.
- Miles, A. J. & Madden, J. R.** 2002. Bower location by the spotted bowerbird (*Chlamydera maculata*). *Emu*, **102**, 187–193.
- Miller, G.** 2000. Sexual selection for indicators of intelligence. *Novartis Foundation Symposium*, **233**, 260–270.
- Møller, A. P. & Pomiankowski, A.** 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology*, **32**, 167–176.
- Morand-Ferron, J., Cole, E. F., Rawles, J. E. C. & Quinn, J. L.** 2011. Who are the innovators? A field experiment with 2 passerine species. *Behavioral Ecology*, **22**, 1241–1248.
- Muller, H. & Chittka, L.** 2012. Consistent interindividual differences in discrimination performance by bumblebees in colour, shape and odour learning tasks (Hymenoptera: Apidae: *Bombus terrestris*). *Entomologia Generalis*, **34**, 1–8.
- Nowicki, S., Searcy, W. & Peters, S.** 2002. Brain development, song learning and mate choice in birds: a review and experimental test of the 'nutritional stress hypothesis'. *Journal of Comparative Physiology A*, **188**, 1003–1014.
- Pamilo, P. & Crozier, R. H.** 1996. Reproductive skew simplified. *Oikos*, **75**, 533–535.
- Patricelli, G. L., Uy, J. A. C., Walsh, G. & Borgia, G.** 2002. Male displays adjusted to female's response: macho courtship by the satin bowerbird is tempered to avoid frightening the female. *Nature*, **415**, 279–280.
- Patricelli, G. L., Coleman, S. W. & Borgia, G.** 2006. Male satin bowerbirds, *Ptilonorhynchus violaceus*, adjust their display intensity in response to female startling: an experiment with robotic females. *Animal Behaviour*, **71**, 49–59.
- Pfaff, J. A., Zanette, L., MacDougall-Shackleton, S. A. & MacDougall-Shackleton, E. A.** 2007. Song repertoire size varies with HVC volume and is indicative of male quality in song sparrows (*Melospiza melodia*). *Proceedings of the Royal Society B*, **274**, 2035–2040.
- Plomin, R. & Spinath, F. M.** 2002. Genetics and general cognitive ability (g). *Trends in Cognitive Sciences*, **6**, 169–176.
- Reid, J. M., Arcese, P., Cassidy, A. L. E. V., Hiebert, S. M., Smith, J. N. M., Stoddard, P. K., Marr, A. B. & Keller, L. F.** 2005. Fitness correlates of song repertoire size in free living song sparrows (*Melospiza melodia*). *The American Naturalist*, **165**, 299–310.
- Reynolds, S. M., Dryer, K., Bollback, J., Uy, J. A. C., Patricelli, G. L., Robson, T., Borgia, G. & Braun, M. J.** 2007. Behavioral paternity predicts genetic paternity in satin bowerbirds (*Ptilonorhynchus violaceus*), a species with a non-resource-based mating system. *The Auk*, **124**, 857–867.
- Riebel, K., Holveck, M.-J., Verhulst, S. & Fawcett, T.** 2010. Are high-quality mates always attractive? State-dependent mate preferences in birds and humans. *Communicative and Integrative Biology*, **3**, 271–273.
- Riebel, K., Spierings, M. J., Holveck, M.-J. & Verhulst, S.** 2012. Phenotypic plasticity of avian social-learning strategies. *Animal Behaviour*, **84**, 1533–1539.
- Shohet, A. J. & Watt, P. J.** 2009. Female guppies *Poecilia reticulata* prefer males that can learn fast. *Journal of Fish Biology*, **75**, 1323–1330.
- Shumway, C. A.** 2008. Habitat complexity, brain, and behavior. *Brain, Behavior and Evolution*, **72**, 123–134.
- Sol, D.** 2009. Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters*, **5**, 130–133.
- Sparfeld, J. M.** 2012. *Temporal patterns in the display behaviour of male spotted bowerbirds, Ptilonorhynchus maculata, and the influence of light on display frequency, prop use and mating success*. M.Sc. thesis. University of Potsdam.
- Tebich, S., Sterelny, K. & Teschke, I.** 2010. The tale of the finch: adaptive radiation and behavioural flexibility. *Philosophical Transactions of the Royal Society B*, **365**, 1099–1109.
- Thornton, A. & Lukas, D.** 2012. Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philosophical Transactions of the Royal Society B*, **367**, 2773–2783.
- Trainer, J. M., McDonald, D. B. & Learn, W. A.** 2002. The development of coordinated singing in cooperatively displaying long-tailed manakins. *Behavioral Ecology*, **13**, 65–69.
- Uy, J. A. C., Patricelli, G. L. & Borgia, G.** 2000. Dynamic mate-searching tactic allows female satin bowerbirds *Ptilonorhynchus violaceus* to reduce searching. *Proceedings of the Royal Society B*, **267**, 251–256.
- Zhu, Q., Song, Y., Hu, S., Li, X., Tian, M., Zhen, Z., Dong, Q., Kanwisher, N. & Liu, J.** 2010. Heritability of the specific cognitive ability of face perception. *Current Biology*, **20**, 137–142.

APPENDIX

Measuring Male Tenure at Bowers

Male bowerbirds are known to hold tenures at bowers for over a decade and tenure is assumed to be a reliable proxy for male age (Borgia 1993; Frith & Frith 2004). Male age data were not available for our study population; however, data on bower ownership collected since 1998 allow us to estimate male tenure at bowers and adjust scores accordingly. Males were rank ordered based on the known number of years in which they were bower holders. Ranks for males were then adjusted upwards according to whether they were owners at the start and/or end of the study period (see Borgia 1993). Males that were estab-

lished as owners at the start of the study or males that retained ownership of their bower until the end of the breeding season in 2011 were given a one-rank increase. Males that were owners at both were given a two-rank increase.

Statistical Analysis and Results

Partial correlations between tasks were carried that controlled for male tenure. There was little qualitative change in the coefficients compared to when tenure was not controlled for (Table A1). We repeated the linear mixed model with tenure included as a fixed effect, and again found no significant relationship with mating success and cognitive performance ($F_{2, 9} = 0.01$, $P = 0.92$).



Figure A1. The experimental set-up for pokebox cognitive tasks: (a) a male bowerbird completing a colour discrimination task, (b) a male completing a shape discrimination task and (c) showing the general positioning of the pokebox on the outer limit of the bower (the bower avenue can be seen positioned between two white snail shell piles, which usually delimit the outer boundaries of decorations).

Table A1

Nonparametric partial correlations between rank performances in cognitive tasks

	Barrier task	Motor task	Colour discrimination	Colour reversal	Shape discrimination
Motor task	$r_s=0.41$ $P=0.36$ $df=5$				
Colour discrimination	$r_s=0.59$ $P=0.16$ $df=5$	$r_s=0.50$ $P=0.25$ $df=5$			
Colour reversal	$r_s=0.53$ $P=0.22$ $df=5$	$r_s=0.29$ $P=0.53$ $df=5$	$r_s=-0.11$ $P=0.82$ $df=5$		
Shape discrimination	$r_s=0.27$ $P=0.56$ $df=5$	$r_s=0.54$ $P=0.21$ $df=5$	$r_s=0.47$ $P=0.90$ $df=5$	$r_s=-0.22$ $P=0.64$ $df=5$	
Spatial memory	$r_s=0.14$ $P=0.76$ $df=5$	$r_s=0.47$ $P=0.29$ $df=5$	$r_s=0.69$ $P=0.09$ $df=5$	$r_s=-0.45$ $P=0.28$ $df=5$	$r_s=-0.75$ $P=0.05$ $df=5$

Partial correlations controlling for male tenure at bowers (as a proxy for age). Bonferroni correction for multiple correlations: α level of significance = 0.003.