
COGNITIVELY DRIVEN CO-OPTION AND THE EVOLUTION OF COMPLEX SEXUAL DISPLAYS IN BOWERBIRDS

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INTRODUCTION

Two of Darwin's greatest contributions were his work on sexual selection (Darwin, 1871) and on the evolution of mental processes (Darwin, 1872). Currently, sexual selection is among the most studied topics in evolutionary and behavioral biology (Andersson and Simmons, 2006; Cronin, 1991), but there has been little consideration of how mental ability affects sexual selection (Miller, 2001; Ryan *et al.*, 2009; Boogert *et al.*, 2011). This issue was addressed in the debate between Darwin and Wallace over the adequacy of females to carry out choice needed to produce sexually dimorphic traits in male birds. And while Darwin prevailed in his view that female choice was critical in the evolution of male sexual signals, there remained a widely held view that most species, with the exception of primates, had very limited cognitive ability (Herrick, 1924). Then, starting around 30 years ago, a number of studies showed unexpectedly high levels of mental development in other animals, particularly in birds. Generally, cognitive ability as we use the term here, refers to the ability of individuals to use mental processes to solve problems that under natural conditions leads to increased fitness. Various studies have shown a role for cognition in spatial memory (Kamil and Balda, 1985; Bennett, 1993; Healy and Hurly, 1995; Pravosudov and Clayton, 2002), food theft (Bugnyar and Kotrschal, 2002), vocal ability (Pepperberg, 1999), tool-making (Jones and Kamil,

Animal Signaling and Function: An Integrative Approach, First Edition.

Edited by Duncan J. Irschick, Mark Briffa, and Jeffrey Podos.

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1973; Taylor *et al.*, 2007), string-pulling (Werdenich and Huber, 2006), and many other contexts. Recent neuroanatomical studies have shown that birds have relatively large brains for their body size (Jarvis *et al.*, 2005). Emery and Clayton (2004) suggested that the particularly large-brained New Caledonian crow may be similar to chimpanzees in cognitive ability.

Despite these studies, there has been an almost inexplicable lag in developing the seemingly obvious connection between cognitive ability and sexual selection. It would seem that the ability to perform relatively sophisticated cognitive processing would be beneficial for the very important fitness-affecting role of enhancing reproduction through sexual selection. This may be especially so in lekking species (those with nonresource-based (NRB) mating systems) that commonly show large skews in male reproduction (see Höglund and Alatalo, 1995; Widemo and Owens, 1995; Johnstone and Earn, 1999; Wiley, 1991). With these large skews in mating success, even small differences in male performance can be amplified into very large fitness effects.

Evidence of significant cognitive capabilities in various species suggests that they might often be applied in mate choice and display where they can have a large effect on fitness. In this chapter, we identify instances where females and males appear to use cognitive abilities in mate choice and display (see also Boogert *et al.*, 2011). This includes complex patterns of mate searching and assessment by females, complex courtship communication between the sexes that allows males to adjust courtship to the needs of individual females, and for males, the acquisition of learned complex displays from other males, innovation of new types of display behavior, and age-related improvement in the quality of display.

Most current sexual selection models assume little or no complex cognitive ability affecting male display or female choice (Lande, 1981; Zahavi, 1975, 1977; Hamilton and Zuk, 1982; Ryan and Rand, 1993; Kokko *et al.*, 2002; Borgia, 1979). This may be attractive to evolutionary theoreticians because it allows their models to be applied across a wide variety of species, including those with very limited cognitive abilities. This approach replicates some of the issues raised in the Darwin–Wallace controversy in the sense that females are often perceived to have limited ability to make adaptive adjustments when choosing mates, and male use of cognitive ability to enhance attractiveness to females is not considered. Limitations on female ability to choose sires that provide high fitness for their offspring has led to the conclusion that mate choice does not result in adaptive outcomes (e.g., Kirkpatrick, 1987), which remains a commonly held view (e.g., Dawkins and Guilford, 1996; Prum, 2010). Several widely cited models are dependent on the constraint of low female mental ability and how it restricts them in profitably discriminating among males. For example, in their chase-away model, Holland and Rice (1998) argue that males evolve highly elaborate displays as part of selection to overcome repeated episodes of initial female attraction and then resistance to their display. Males are suggested to repeatedly overcome the adaptive choice behavior of females due to the inability of females to reject increasingly large and otherwise maladaptive displays. Cognitively capable females should have more options

for overcoming male manipulations that might otherwise repeatedly override their interests, even when engaged with males who are also cognitively capable. The ability to make cognitively based mating decisions suggests that females have multiple options for mate choice and can express context-dependent preferences and decisions, rather than being locked into particular nonadaptive preferences, such as those suggested to evolve as side effects of other evolutionary processes (e.g., Ryan and Rand, 1990; Rodd *et al.*, 2002).

There is now increasing evidence for behavioral flexibility in male display (King *et al.*, 1996; Patricelli *et al.*, 2002) and female choice (e.g., Morris *et al.*, 2003; Kodric-Brown and Nicoletto, 2001; Coleman *et al.*, 2004; Hebets, 2003) across a variety of species. This flexibility is consistent with adaptive mate choice influenced by cognitive processes, and does not support some popular models that require genetic correlations between a particular male trait and its corresponding female preference (e.g., runaway, Lande, 1981; some versions of good genes, Pomiankowski, 1988, or those that claim to integrate these two kinds of models, Kokko *et al.*, 2002). In the past 30 years, there has been relatively little progress on the critical question of the relative importance of competing sexual selection models (Andersson, 1994; Cronin, 1991; Borgia, 2006). Establishing the important role for cognition in sexual selection offers the possibility of breaking this impasse by identifying models that are and are not compatible with cognitively dependent mate choice and display. This should lead to consideration of models tuned to the cognitive capacity of the set of species under study. We need to begin evaluating the connection between cognition and sexual selection, exploring how different elements of male display might be used to indicate general or possibly more specific male cognitive capabilities, and how cognition influences the evolution of sexual displays.

Females may choose males with greater cognitive ability for a variety of reasons. For example, (i) Cognitive ability may be a heritable good genes trait that allows choosing females to produce cognitively superior offspring. Offspring with higher cognitive ability may live longer by avoiding predation, finding more food, gaining better territories, or avoiding parasites. In addition, their sons may have better sexual displays (Airey *et al.*, 2000a) and their daughters may exhibit more effective mate choice (Leitner and Catchpole, 2002) by better discriminating between males and spending less time mate-searching for high-quality males. (ii) In species with male parental care, males with better cognitive performance may be better at provisioning offspring (Isler and van Schaik, 2006, 2008). (iii) Males may be able to use their cognitive abilities to attract or coerce females into copulating with them in ways that may not be beneficial for females, but increase their own reproductive success. (iv) If females vary in their requirements for sexual display depending on their age (Coleman *et al.*, 2004) or level of experience (Hebets, 2003), then cognitively capable males may respond better to their diverse needs. (v) Cognitively superior males may be better at acquiring and manipulating display sites that enhance mating success, such as courts with better lighting (Gomez and Théry, 2004), that are safer from predators, or which are located near higher concentrations

of receptive females (see Bradbury, 1981). There are many other reasons why individuals with superior cognitive abilities might perform better in sexual selection.

A variety of studies have sought to demonstrate a relationship between cognition and sexual display. Comparative studies investigating the relationship between brain size and display trait elaboration show inconsistent results, with some finding a positive relationship between total brain size and trait size (e.g., Madden, 2001; but see Day *et al.*, 2005), a negative relationship (Pitnick *et al.*, 2006), or no relationship (Garamszegi *et al.*, 2005a, 2005b; Spencer *et al.*, 2005). Iwaniuk and Hurd (2005) and Healy and Rowe (2007) are critical of this approach, pointing out that numerous factors that affect brain size are not controlled in these studies. Additionally, brain size is a coarse measure of cognitive ability, which can be affected by morphological traits other than size. Highly detailed information on comparative brain anatomy and its relation to brain function, which is not yet available for most species, is necessary if neuroanatomical comparisons are to meaningfully address the relationship between cognitive ability and sexual selection.

Recent studies have shown that within-species differences in song complexity are correlated with the size of the key song control nucleus (HVC) (Spencer *et al.*, 2005; also see Nottebohm *et al.*, 1981; Canady *et al.*, 1984; Airey *et al.*, 2000b; Nowicki *et al.*, 2000, 2002). Additional evidence that the quality of male display is related to brain function comes from tests of the nutritional stress (Nowicki *et al.*, 2002) and developmental stress hypotheses (Buchanan *et al.*, 1999, 2003). In these studies, young birds either were fed highly restricted diets or were exposed to parasites and, compared to controls, had smaller song control nuclei and sang lower quality songs. These studies show a clear relationship between characteristics of particular brain structures and male ability to produce vocal displays. A more direct approach for assessing cognitive ability has been to measure it using tests of problem-solving ability (PSA) (Roth and Dicke, 2005). Boogert *et al.* (2008) assessed male performance on problem-solving tests involving foraging skills and found that scores from these tests were positively related to male vocal ability. In the only test relating cognitive ability directly to male reproductive success, we found (Keagy *et al.*, 2009, 2011) in two different PSA tests that in male satin bowerbirds (*Ptilonorhynchus violaceus*) cognitive ability was associated with male mating success.

COGNITION, CO-OPTION, AND COMPLEX DISPLAY

Biologists have long been interested in the causes of sexual display trait complexity and elaboration (Darwin, 1872; Fisher, 1915, 1930; Andersson, 1994; and many others). Here we argue that two elements, co-option and cognition, can greatly affect the evolution of these complex displays. As modern evolutionary biology has shown, co-option is an important ingredient for the evolution of complex adaptations. Co-option involves expressing already-evolved traits under novel conditions that may allow for new functions. This rapid evolution can shortcut the gradual process of building complex adaptations that might otherwise require many small

changes over time. Co-option can have particularly dramatic effects when cognition directs this process, and it allows individuals to rapidly bring together different, already-evolved component traits to form novel complex adaptations.

Cognition can play a major role in co-option events because it can speed up the acquisition and assembly of traits, bypassing the slower process of genetic evolution. This can occur because cognitive processes like learning and the ability to anticipate future needs (i) do not require genetic change and allow acquisition of new traits within one generation, (ii) allow individuals to preferentially acquire traits that they recognize as functioning well in other contexts or individuals, and (iii) can integrate different acquired component traits to produce a high level of function.

Cognitive acquisition of traits through co-option has been used to explain rapid and dramatic human cultural evolution (Alexander, 1981) and to a more limited extent considered for primates (van Schaik *et al.*, 1999; Tomasello, 1999). It has received less attention in the discussion of the behavior of other animals (but see Bugnyar and Kotrschal, 2002; Sasvari and Hegyi, 1998), and in particular, in the literature on sexual selection (Koksal and Domjan, 1998). As noted above, there has been relatively little progress in understanding the evolution of complex elaborate displays. We propose that in relatively large-brained animals such as passerine birds (Emery and Clayton, 2004), cognition may play an important role in the development of sexual display, by driving the co-option of existing behavioral elements and the assembly of these elements into novel complex displays. There is likely high overlap in the perceptual abilities and preferences of males and females, and males appear to assess elements of their own display (see below). We suggest that a high level of male cognitive ability may allow males to anticipate how females will react to display innovations and to use this information in crafting more effective displays.

The behavioral displays of bowerbirds (Family Ptilonorhynchidae) are among the most elaborate sexual displays of any species, and these displays provide an excellent model for considering the role of how cognition and co-option might shape these displays. In bowerbirds, there are many instances where cognition and co-option working separately and, at other times, together appear to have shaped aspects of male display behavior and related female responses, and we review some of these cases. Satin bowerbirds (*P. violaceus*) have received particular attention in studies of male display and female choice. Courtship and mating occur at their display sites called *bowers*. The bower structure is made of sticks with an adjacent decorated display court. Because courtship and mating occur at the bower, we have been able to position automated video cameras to monitor the bower, providing a complete record of all behavior of marked individuals at bowers through the mating season (Borgia, 1995a). Analysis of these detailed records has shown a consistent pattern in which males and females appear to use their cognitive abilities in ways that influence male mating success.

Male satin bowerbirds locate display sites on an exploded lek where individual males build and maintain decorated stick bowers separated by more than 100 m, and court and mate with visiting females (Borgia, 1985a; Uy *et al.*, 2001a; Hansell,

2009). The display court on the north end of the bower is predominantly decorated with blue objects placed on a carpet of yellow straw and leaves. Decorations are collected from the surrounding habitat or stolen from other males (Borgia and Gore, 1986; Hunter and Dwyer, 1997; Wojcieszek *et al.*, 2007). Male mating success is affected by multiple display elements including bower decorations (Borgia, 1985a, 1993; Coleman *et al.*, 2004), bower quality (Borgia, 1985a), vocal display (Loffredo and Borgia, 1986; Coleman *et al.*, 2007), and dancing display (Patricelli *et al.*, 2002, 2003, 2004, 2006). Several other aspects of display may also be important, including the holding of specific types of bower decorations in males' beaks during courtship (Borgia, unpublished data) and the painting of bower walls with masticated plant fiber by males (Bravery *et al.*, 2006; Cendes, 2009; Hicks *et al.*, 2013).

Other bowerbird species show many similarities with satin bowerbirds, but there are also significant differences. Males of most polygynous bowerbird species build bowers; exceptions are toothbilled (*Scenopoeetes dentirostris*) and Archbold's bowerbirds (*Amblyornis (Archboldia) papuensis*) that display on cleared courts with no bower, and the monogamous catbirds that do not have either courts or bowers (see Borgia, 1995b). Satin bowerbirds belong to one clade of bowerbirds that erect two-walled bowers made of sticks with a display court at one or both ends (Kusmierski *et al.*, 1997). Some of these bowers are raised up on tall stick platforms (fawn breasted (*Chlamydera cerviniventris*) and yellow-breasted (*Chlamydera lauterbachii*) bowerbirds). The other clade includes maypole builders that build a stick maypole around a sapling surrounded by a display court. In some species (streaked (*Amblyornis subalaris*) and Vogelkop (*Amblyornis inornatus*)) a hut-like roof is built over part of the court (see Gillard, 1969; Cooper and Forshaw, 1979; Frith and Frith, 2004). Males of all court clearing species display to visiting females with dancing displays. These species display decorations collected from the habitat on their courts and sometimes on the bower. Species differ in color, number, and types of objects used as decorations.

Bowerbirds have all of the attributes that Emery (2006) suggests are associated with high intelligence species. We believe that evidence from highly detailed studies of bowerbird courtship offers a unique set of information supporting a large role for cognition affecting mate choice in bowerbirds. When we started this research, we expected to test sexual selection models that relied on genetic correlations such as runaway and some good genes models. It became obvious that bowerbirds have many traits indicating a high level of cognitive involvement, for example, learning in display trait acquisition (Collis and Borgia, 1993) and complex decision-making (Uy *et al.*, 2001a, 2001b; Patricelli *et al.*, 2002), suggesting that the co-evolutionary genetic models that dominate much of sexual selection theory do not adequately explain sexual behavior in satin and other bowerbird species. Instead, models dependent on a high level of cognitive ability and co-option seem more appropriate. Here we review observations of bowerbird display that support this view.

Cognition can affect the acquisition and utilization of bowerbird display elements in several ways. Some of these mechanisms are (i) learning, (ii) innovation, (iii) flexibility, and (iv) anticipation. Each of these requires, at least for traits

expressed in bowerbirds, a reasonably sophisticated mental framework for their successful operation. In the following sections, we discuss how these mechanisms may be involved in male display and female mate choice. Most of these observations have been obtained from our video camera system that has provided highly detailed records of male and female behavior at bowers. We also include some anecdotal results that reflect extraordinary cases that are not suited to statistical analysis, but give important insights into the cognitive capabilities of some exceptional individuals (see Lefebvre *et al.*, 2004).

DELAYED MALE MATURITY, MALE–MALE COURTSHIP, AND DISPLAY TRAIT ACQUISITION

Male sexual maturity is delayed in bowerbirds, and this period appears to provide an opportunity for learning complex elements of sexual displays. A progressive pattern of age-related plumage changes in male satin bowerbirds appears to affect interactions among males at display sites. At 5 years old, their neck and upper chest plumage changes from mottled yellow to dark green and their beak changes from black to yellow (Vellenga, 1980). At age 7, males produce a blue-black plumage and around this age attempt to acquire a permanent display site where they build a bower. Male satin bowerbirds produce sperm when they are 5 years old. Young males build temporary, poorly constructed practice bowers where they court other young males (Collis and Borgia, 1993). Before the start of the mating season, these males often visit adult, bower-holding males who court them. Adult males who had decorations experimentally added to their bowers were preferred for visits by young males, suggesting that these young males may use decorations, as do females, for identifying adult males with high-quality displays (Coleman, 2005). Such males might serve as more effective tutors for young males.

Young males implanted with testosterone up to 4 years before their natural transition to adult plumage changed to adult plumage at their next molt (Collis and Borgia, 1993). These implanted males constructed low quality bowers, suggesting that their normal delayed maturation is necessary to allow them to learn bower building and other aspects of display. The specialized plumage of older juvenile males may allow them to attract less threat from adult males than if they had the adult male plumage. This may improve their opportunity to learn displays when they are courted at adult males' bowers.

Young males visiting adult male bowers and receiving courtship appear to learn the content of display (Collis and Borgia, 1993). For example, as part of their vocal displays, male satin bowerbirds mimic up to five other species, and males with higher-quality mimicry (Loffredo and Borgia, 1986; Coleman *et al.*, 2007) and more species mimicked (Coleman *et al.*, 2007), obtain more matings. The complexity of these displays and their mimetic nature leave little doubt that they are learned as might be the initial portion of the courtship vocalization that involves buzzes similar to those of cicadas, a food source for young birds (Donaghey, 1996). The delayed maturation of young males that visit the bowers of adult males, and

courtship involving learned components are consistent with the hypothesis of cultural transmission of male display traits (Collis and Borgia, 1993; Loffredo and Borgia, 1986; Coleman *et al.*, 2007; see also Madden, 2008) and a critical role for cognition in the acquisition and effective display of these traits.

Adult male satin bowerbirds often display to empty bowers and, before the mating season, to young males. Since successful males courting females must be able to adjust their display in response to signals from female courtship partners (see next section), males receiving courtship may be useful surrogates providing feedback to courting males on how to modulate their display in response to the receiver's reactions. These courtships appear to be important to courting males because of the high frequency of these male–male courtships, and the use of calls, including begging calls, to attract other males to receive same-sex displays. Once the mating season starts and there is the potential for interference with male–female courtships by visiting males, adult male bower owner behavior changes and visiting males are no longer tolerated at bowers. This reversal in the behavior by bower-holding males appears to be a beneficial cognitive adaptation for improving display quality while reducing costly side effects during the mating season.

FEMALE SIGNALING TO AFFECT MALE DISPLAY INTENSITY: AN INNOVATION THAT IMPROVES COURTSHIP SUCCESS

Female bowerbirds are attracted to intense male courtship displays that contain elements similar to male aggressive displays that can be threatening to females (Borgia and Presgraves, 1998; Patricelli *et al.*, 2002, 2004). In satin bowerbirds, females signal their level of comfort with display to the courting male. Females may make multiple visits to a male's bower, and females comfortable with the male's display commonly return for additional courtship and move into a deeper crouch. As females assess potential mates, female tolerance for intense display increases during successive courtships with preferred males. Females then signal their readiness for copulation (Patricelli *et al.*, 2002, 2004). Other females, less comfortable with a male's display, lower into a crouch more slowly or not at all, or if already in a crouch, may rise up rapidly showing a “startle” response. Female crouching is inversely related to the frequency of female startling during courtship and thus signals the degree of display intensity that females will tolerate from a male without startling (Patricelli *et al.*, 2002). Female age and condition affect the level of female comfort (Coleman *et al.*, 2004). To test the hypothesis that successful males reduce the intensity of their courtship displays after females indicate their discomfort, we used robotic female bowerbirds that mimicked female behavior in the bower. Supporting this hypothesis, males displayed with significantly lower intensity toward robots when they crouched at a lower rate (Patricelli *et al.*, 2002) and when the female robot startled (Patricelli *et al.*, 2006) in experimental treatments, compared to treatments with faster crouching and no startling. Thus, female signals help direct males to produce displays of appropriate intensity. Males able to respond by adjusting display intensity relative to the level of female comfort with the male's display are attractive to a wider range of females and thus gain a mating advantage from

their ability to respond to female signals (Patricelli *et al.*, 2002). Females benefit from this communication by receiving displays at an intensity they are willing to tolerate, thus reducing startles and the possible disruption of courtship, and allowing them to more effectively choose their mate (Patricelli *et al.*, 2004).

An additional cognitive component in bowerbird intersexual communication signals by females is suggested by age-related changes in female preferences for components of male courtship display in mate choice. All age classes of female satin bowerbirds use bower decorations in early assessment of males in initial courtship visits to bowers, but in later courtship visits, older females select males based on male dancing and vocal elements of courtship display. Younger females appear to be more threatened by the high intensity male courtships and base mate choice more on bower decorations than courtship displays (Coleman *et al.*, 2004). When bower decorations were manipulated by placing an increased number of blue plastic squares on bowers, this had a greater effect on the mating decisions by young females than their older counterparts (Coleman *et al.*, 2004). Cognitive ability appears important because young females must learn not to be threatened by intense male courtship displays, and how to use these displays in choosing mates.

Cognition affects male ability to react to female signals of comfort and this has an important effect on male mating success (Patricelli *et al.*, 2002, 2004, 2006). The intensive practice by males both before sexual maturity and as adults in displays with other males may allow fine tuning of male ability to read the reactions of courtship partners. The large amount of time and effort devoted to attracting same-sex courtship partners and displaying to them suggests that the refinement of courtship abilities is important in male success in courtships with females. The significant age-related change in female response to male display suggests that learning and cognitive ability affect female ability to respond to male display.

MATE SEARCHING AND FLEXIBILITY IN ADAPTIVE DECISION-MAKING

Mate searching is a critical process for females attempting to maximize the fitness benefits of mate choice. Females can apply their cognitive abilities to mate searching to enhance its benefits by allowing them to locate high-quality mates while limiting the costs of mate searching. Using time and date information on video tapes of female visitation at bowers, we (Uy *et al.*, 2000, 2001a, 2001b) reconstructed female satin bowerbird mate-searching patterns. We found that females commonly repeatedly visited bowers and sampled courtships of multiple males before mating. Females tended to have two distinct sampling bouts, the first involving a larger set of males with some rejected before nest building, followed by a second bout during which a mate was chosen from a more limited set of males. Females varied in the number of males sampled, with some visiting the bower of only one male. Some of this variation can be explained by differences among females in past experience with males. Females who chose males attractive to a large number of other females (top males) typically mated with that same male in the following year, sampling relatively few other males. Females who had mated with less attractive males typically rejected these males as mates the next year. These females searched among a relatively large set of males, usually finding a mate of higher quality than

their previous mate (Uy *et al.*, 2000). Females mated to top males who died sampled more males the next year. These results indicate that the loss of attractive mates forces females to increase their search and provides evidence that past experience in sampling males shapes subsequent mate-searching behavior (Uy *et al.*, 2001b). This suggests that the cognitive ability of females can provide adaptive flexibility in mate-searching tactics that allows females to obtain higher-quality mates while limiting their search costs. Previous mate-searching models had not considered the effect of long-term memory on female flexibility in mate-searching tactics that is clearly dependent on having the cognitive capability to make complex fitness-enhancing decisions.

FEMALE UNCERTAINTY AND FLEXIBILITY IN ACTIVE MATE ASSESSMENT

Female assessment of male display behavior is often difficult to quantify because females often passively view male display. However, if females actively sample aspects of male display, this can provide valuable information about how females assess male display components. In satin bowerbirds, active and quantifiable female sampling behavior is associated with the assessment of paint males apply to their bower walls. Males paint their bowers by applying masticated vegetation to the sticks on the inside of their bower walls, and females sample paint by nipping at the painted bower wall. The intensity of female sampling of paint can be related to the stage of courtship females are involved in and other characteristics of females that relate to their mate choice decision process. Females sample more in early courtship visits to males (Bravery *et al.*, 2006; Cendes, 2009). This suggests that paint sampling is more common when females are less certain about which male they will choose. Cendes (2009) tested this hypothesis by using three different measures of female uncertainty and then relating them to the degree of paint sampling. First, she found that the proportion of visits with paint sampling by females is positively correlated with the number of males visited and number of visits to males. Second, females mating with multiple males had visits with a high level of paint sampling. Third, paint sampling was positively related to the proportion of switches between males visited. Thus, paint sampling is higher among females who need additional information to resolve mate choice decisions. These cognitively based adaptive adjustments in paint sampling should allow females to improve their assessment of males in mate choice. Also, it may allow females to make up for deficiencies in male display, such as when bower decorations are scarce (see Bravery *et al.*, 2006).

LONG-TERM AGE-RELATED IMPROVEMENT IN DECORATION DISPLAY: SYMMETRICAL DECORATION DISPLAYS ON OLDER MALES' BOWERS

One of the most attractive features of bowerbird display to human observers involves elaborate patterns of bower decoration. Some bowers have spectacular decoration displays, like a spotted bowerbird (*Chlamydera maculata*) bower we

found near the home of a stained glass artisan. The male bower owner collected fragments of stained glass and laid them out in a beautiful symmetrical design on the display court with white sheep vertebrae (bones) near the bower encircled by neatly laid out arcs of orange and blue glass that covered an area 4 m wide. This marked male disappeared between mating seasons and was replaced by a different and probably younger, less experienced male the next year. The colored glass decorations the former owner used were still present, but the new bower owner created a far less elaborate display with the colored decorations mixed in a pile with white vertebrae near the bower. The new male's failure to artfully display those colorful decorations may be due to it having less experience in bower decoration display. This hypothesis is supported by observations of increased complexity of bower decoration displays in cases where we have monitored individual males at bowers for 10 or more years. These males have a more colorful set of decorations, often with a high degree of symmetry in the placement of these decorations. These examples suggest that it may take years for males to develop the skills and obtain the materials to produce these displays. Often males "try out" locations for new decorations, changing their position over days and sometimes weeks. This suggests that developing complex displays is a cognitive process in which birds are sensitive to small changes in the placement of decorations on their display courts. With decoration displays composed of thousands of decorations, a male bower owner must make numerous decisions about which decorations to include in his display and where on the court to place them. Successful spotted and great bowerbirds commonly sort decorations into piles of like-colored objects, with certain colors placed at particular locations around the bower (Borgia and Presgraves, 1998), for example, flat green glass near the bower entrance, small pieces of cubic auto window glass or sometimes small green fruits in the bowl located in the middle of the bower avenue, and red plastic next to the outside of the bower walls near the bower entrance. For these decoration types, males commonly add similar kinds of decorations to already existing piles. The symmetrical arrangement of different colors far out from the bower are far less common, and appears to require the benefit of prolonged decorating experience. We do not know if highly ornate symmetrical decoration displays result in increased male attractiveness to females. We hypothesize that it takes much of a male bird's lifetime to develop the ability to produce these elaborate displays. Interestingly, the decoration display itself can serve as a repository of the products of past decisions that the bird can manipulate and build upon with slight improvements that eventually lead to ornate displays. The ability to build symmetrical displays may result from the same sense of symmetry applied to bower building. Successful male bowerbirds tend to build more symmetrical bowers (Borgia, 1985a) and this may reflect a general preference for symmetry that is extended to these ornate decoration displays. The placement of decorations in patterns could be functional in aiding female mate searching. Patterned displays make bowers more recognizable from a distance as a designed display rather than an accidental grouping of bright objects. These patterns could also provide females information about the bower owner such as his age, based on the complexity of the display, and his identity, by indicating through a unique

display that the same male is present at the bower over successive years. Highly complex symmetrical displays might also indicate a male's cognitive ability.

ANTICIPATION OF MALE ROUTES DURING COURTSHIP: PATHS ON DISPLAY COURTS OF SPOTTED BOWERBIRDS

In most bowerbird species, males have specific paths around the bower that they travel on during courtship. Large decorations can potentially obstruct male movements along these paths as they court females. In spotted bowerbirds, males using numerous large sheep vertebrae, snail shells, or stones as decorations leave paths clear of large decorations near the bower where they travel during courtship. Bower owners may carpet these paths with flat stones, a stick mat, or leave them bare. Beside the path, vertebrae may be stacked into piles three high, providing a white background (see Figure 4.1) for courting males to display their lilac crests. The narrow, neatly sculpted pathway between the bower wall and piles of vertebrae leaves few other options for movement during courtship near the bower. As with other aspects of decoration display, there are clear cognitive aspects to the patterning of these display elements. When we placed vertebrae or other large decorations on the path, they were quickly cleared away (Borgia, personal observation). These behaviors suggest that males anticipate the movements they will make during courtship and clear objects that might impede their display.

One method males use to advantageously place decorations in positions that will not interfere with courtship is through practice courtship displays. Practice displays to empty bowers or to visiting males are common among a variety of



Figure 4.1. A wall of sheep vertebrae is positioned as a backdrop for males displaying in front of the bower. (See *insert* for color representation of this figure.)

bowerbird species. In satin bowerbirds, males often begin practice displays and then suddenly stop, and then rearrange decorations on the bower. Thus, by rehearsing their display movements, males can identify problems with the position of display items and reposition them for a more effective display. Movement of decorations on display courts also occurs independently of practice courtships (see Borgia *et al.*, 1987; Borgia and Keagy, 2006). Male bowerbirds are able to use a great diversity of objects, including many novel man-made objects, and choose those of appropriate size, shape, and color for different functions on the bower, placing them in appropriate positions, often in piles of similar color or type of decorations (Borgia, 1995a; Uy and Borgia, 2000; Doerr, 2010). This suggests attention to fine detail in developing their decoration display and the ability to classify objects by color and other features.

A different explanation for the positioning of decorations on display courts has been offered by Endler *et al.* (2010) and Kelley and Endler (2012). They suggest that male great bowerbirds use the placement of decorations of different size to create a forced perspective optical illusion that may keep female attention longer during courtship, for example by causing the displaying male to look larger to her. Anderson (2012) points out that Kelley and Endler (2012) fail to consider the effects of other display elements that could account for a positive relationship between decoration gradients and mating success. Our own analysis of their data fails to support their conclusion that the proposed illusion was related to male mating success (Borgia *et al.*, 2012) and in the populations we observe, we see little evidence of the linear gradations of decoration size they describe, necessary to create the proposed optical illusion (see Figure 4.2). An alternative hypothesis that explains why decoration displays often show a stepwise pattern of size change is that smaller decorations on the display court near the bower allow the male to display near the bower entrance and larger decorations placed farther away are less likely to impede male movement during courtship.

SOME OTHER POSSIBLE COGNITIVE DISPLAY-RELATED BEHAVIORS OF BOWERBIRDS

A variety of other studies have suggested a possible cognitive function affecting male display in bowerbirds. Mikami *et al.* (2010) found that great bowerbird bowers tend not to be affected by fire and they argue that males have learned to build them away from grassy spots that are likely to burn. However, there are a variety of reasons why males may not build bowers in grassy areas, including avoiding areas where predators may not be easily detected, or areas where it is difficult for females to see the bower. Each of these alternatives is also consistent with a role for cognition in bower site selection.

Madden (2002) suggests that less dominant, spotted bowerbird males remove decorations added to their bower in order to avoid destructions by more dominant males. Borgia (1993) tested for this effect in satin bowerbirds that have closer neighboring bowers and higher destruction rates and found no tendency for any males to remove preferred types of decorations from their bowers. Doerr (2010)



Figure 4.2. The bower of a great bowerbird near Mareena, Queensland. This bower is unusual because of its large size, the way the male positioned it within a set of thick branches, and the uneven slope on which it is built. The pattern of decorations seen here and in most other great bowerbird bowers we have seen does not show a size gradient of decorations necessary to create the forced perspective illusion. In this case, decorations arrayed at the front of the bower are approximately the same size. Moreover, because these decorations are on a downward slope, they cannot be seen by a female being courted in the bower avenue to produce a forced perspective illusion even if there were a size gradient. Thus, the decorations appear to function in attracting females to the bower before they arrive in the bower avenue. (See *insert for color representation of this figure.*)

found similar results studying great bowerbirds. Bravery *et al.* (2006) suggest that decoration removal leads to higher levels of painting to compensate for the loss of this component of display. However, males with fewer bower decorations to arrange may simply be using time that might have been used for bower decoration instead for bower building.

CONSTRUCTION OF SUCCESSIVE SCENES FOR FEMALES VISITING THE BOWER

The presence of two-walled bowers, like those of satin, great, and spotted bowerbirds, contributes greatly to the evolution of display complexity. Females commonly fly into the vicinity of a bower and may perch in a tree looking at the bower site from above, and if attracted by the decoration display, move toward

the bower and then enter into the bower for courtship. The bower creates a series of special display environments (scenes) that add to the complexity and design of bower displays. The bower owner can create scenes appropriate for engaging females at each particular stage of courtship and mating. Decorations of different colors, compositions, and sizes are placed in the most advantageous positions in each scene to appeal to the visiting female's preferences. Males orient bowers and decorations to enhance illumination of the display site at critical times when females are likely to visit. The narrow avenue between the bower walls where the female stands during courtship dictates her orientation and allows the male to affect what she sees as he courts her. Males of several species decorate courts with colors that contrast with the male's plumage that may enhance the visibility of males to females.

In spotted bowerbirds, decorations up to 2 m in front of the bower are used for long distance attraction of females to the bower (Borgia, 1995a). Red, pink, orange, and black (less commonly yellow and light blue) plastic and piles of white bones are placed beyond a bush that might hide the bower from above. As females move close to the bower entrance, a different set of decorations become visible inside the bower, in the central bowl, and lining the inner walls. These were hidden by the bower walls when she was outside the bower. The decorations in the bowl are typically smaller than those outside the bower and slightly smaller than those lining the bower walls. These often include small cubic pieces of fractured quartz or auto window glass (Figure 4.3) that glow like gems in sunlight (Borgia, 1995b), small green fruit (Madden, 2002, 2003), and the shiniest of the male's small metal



Figure 4.3. Shiny quartz rocks are positioned in the central avenue of a spotted bowerbird bower. (See *insert for color representation of this figure.*)

objects including coins and jewelry, with less shiny versions placed outside the bower. When we offered males silver foil balls of different sizes, males placed the small balls inside the bower but kept the larger balls on the bower platform, supporting the suggestion that small items are preferred for display in the central avenue. In addition, the bower walls often have small pieces of metal, pull tops, red thin wire and stems, and silver seed pods arrayed on them.

The number of bower decorations in the bower's bowl is a strong predictor of male courtship success (Borgia and Mueller, 1992; Borgia, 1995a; Madden, 2002, 2003). This is not surprising as the female in the bower looking out the entrance can see few other colorful decorations. The green and red decorations outside of the bower are nearly all out of sight, hidden by the bower walls and appear to function mostly in attracting the female to the bower.

Just as male bowerbirds may acquire vocal displays by receiving them from other males as if they are females, males building bowers often traverse the route traveled by females into the bower. Males share many of the same preferences for decorations and bower architecture with females (Borgia and Keagy, 2006; Borgia, 1985a). This allows them to view scenes in the same way that females do and to build and adjust them to match female preferences at each step. The sole exception to this process is that males cannot see their own dancing display, and for this they may need to rely on the reaction of other males and females to their courtship displays. Males may begin to learn courtship behavior, bower decoration, and building from other males on visits to bowers when they are young. An important cognitive component of these displays involves remembering the elements of display, including vocal mimicry, and learning how those receiving courtship react to particular elements of display behavior, for example, does the female move away from, or is she attracted, a particular display element?

COGNITIVE ASPECTS OF BOWER BUILDING: AGE-RELATED IMPROVEMENT IN CONSTRUCTION AND NOVEL TECHNIQUES FOR MAINTAINING SYMMETRY

Bowers have a variety of design features that suggest that male bowerbirds must learn to build. Typically in satin bowerbirds, the bowers of young males are poorly built, but as males mature, the bower becomes more refined. An important difference results from the sticks used in bower construction; mature male satin bowerbirds use sticks that are straighter, thinner, and less often forked compared to sticks used by young males (Borgia, 1985a). Mature males pack sticks together tightly, placing them more vertically and using bends in the sticks to curve the bower walls. Bowers of attractive males have a more sculptured appearance, with even curvature of bower walls with a slight widening toward the center, a slight narrowing on the inside near the bower entrance, and the top of the walls curving over the bower avenue. Stick lengths are more even, often placed so that the wall has a more even height both within the wall and between the two walls. The overall appearance of the mature male bower has a finer and tighter overall structure, with few if any sloppily placed sticks.

In satin bowerbirds, bower symmetry scores are consistently correlated with male mating success (Borgia, 1985a). These birds have a unique mechanism for rebuilding bowers that are asymmetrically damaged. When one bower wall is destroyed, males use a technique we call templating in rebuilding the destroyed wall. After choosing a stick they will use in the destroyed bower wall, they first place it in or against the standing wall while standing on the midline of the bower avenue parallel with the wall. Then, they remove the stick and using a mirrored pattern of movements they used to initially place that stick in the standing wall, they place it in the destroyed wall they are rebuilding. Males appear to be using the standing wall as a template to measure the position of the stick they will place in the destroyed wall, allowing them to build a new wall that is symmetrical with the remaining standing wall. Males who show more templating behavior have more symmetrical bowers (Keagy *et al.*, 2012).

The age-related pattern of differences we see in satin bowerbird bowers suggests that similar variation in bower construction seen in other species is also age-related. In spotted and great bowerbirds, bowers of individual males we have followed for 10 or more years are neater and more precisely built. In addition, these males place decorations in a small pile in a small bowl built of sticks woven into the avenue floor (Figure 4.4). In the fawn breasted bowerbird (*C. cerviniventris*), bowers vary greatly. Mature males build more precisely constructed bowers, using fine sticks closely packed. The bower itself is built on a platform of sticks reaching 20 cm tall with the bower and a short decorated display court built on top. More sloppily built bowers may have no or only a small stick platform under the bower. Bowers of mature male yellow-breasted bowerbirds (*C. lauterbachii*)



Figure 4.4. A spotted bowerbird bower with a sunken central stick bowl where preferred decorations are placed. (See *insert* for color representation of this figure.)

are also raised on stick platforms with two stick ramps running from the middle of the bower up toward the tiny court on each end of the bower. The end of the court is raised up to form a set of end walls unique to this species, creating four walls rather than the two common in all other species of this clade. These unique features are absent from the bowers of young males so that there is little or no platform that raises the bower, and there is no ramp or end walls, and these bowers show less detail, lacking fine sticks or sculpturing. An exception to the trend for bowers of young males to be built on lower platforms occurs in western bowerbirds (*C. guttata*) at Exmouth, Australia, where the neater bowers of older males are typically built close to the ground while those of young males are often built on large rounded piles of sticks. Other differences are that young males have raised bower avenues that abruptly drop off at the ends of the bower avenue. Also, unlike mature males, they fail to line the stick walls of their bowers with yellow straw, although when we placed straw we collected near their bowers, they placed it in the bower walls.

The recurrence of age-related differences in the quality of bower construction across bowerbird species suggests that there may be significant learning necessary for effective bower construction. This hypothesis is supported by observations of young male visitors placing sticks in bowers owned by older males, and young males building generally poor quality bowers with misaligned and forked sticks years before they are likely to attract and copulate with females.

Alternatively, young males may be capable of building high-quality bowers but choose not to because lower-quality bowers are suitable for their needs in practicing display with other males, so it may not be worth their extra effort. Borgia (1985b) also hypothesized that young males may not build high-quality bowers in order to reduce threat of bower destruction by more aggressive dominant males. Evidence against these hypotheses comes from an experiment in which we implanted young males with testosterone, causing them to moult into adult plumage. These males who held permanent bower sites much like untreated adults, built poor quality bowers, as if they were still in juvenile plumage, suggesting that testosterone implantation did not provide the skills needed to build high-quality bowers, (Collis and Borgia, 1993).

There is also significant variation in the quality of adult bowers, and while the very youngest adult males may have poorer quality bowers, some differences persist over years and seem not to be age-dependent. In addition, males develop different distinctive styles of bower building affecting bower length, verticality of sticks, degree of sculpturing and symmetry of walls, avenue width, avenue height, and other features that make individual bowers recognizable. Often males build bowers on sloping terrain that they are able to level with a stick platform or by incorporating limbs from shrubs into the bower wall, showing the adaptability of males in building bowers. In golden bowerbirds (*Prionodura newtoniana*), males typically find a pair of saplings spaced approximately 1 m apart connected with a cross branch. The male then builds a stick spire around each sapling and surrounds the ends of the cross branch with tightly woven sticks. In part, due to the irregular separation, size, and branching of these saplings, these bowers are quite variable in

shape and illustrate the ability of these males to adjust bower building to meet the conditions imposed by the available buttressing saplings in the area where they will locate their bower. We suspect that as learning is important in affecting male building abilities, differences in male cognitive ability may be indicated by the variation in quality and style of bower building. It is also possible that these individual stylistic differences represent adjustments by males to enhance their unique patterns of courtship and may be used by females to recognize males.

COGNITIVE FLEXIBILITY AND INNOVATION IN DISPLAY

Male spotted bowerbirds have variable courtship displays at different locations in New South Wales and Queensland, Australia. Males of most populations (e.g., Nyngan, NSW and Hughenden, Queensland) we have surveyed, court with wide ranging displays but as they approach the bower they position themselves near the end of one bower wall (see also Madden, 2006). However, in one population we studied north of Thallon, in southern Queensland, bowers were rotated 90° from the N-S direction seen in other locations, with the avenue built extra wide between thin straw walls. Males gave especially high intensity displays and courted females through the unique see-through side walls of the bower. Courted females in the bower positioned themselves perpendicular to the main axis of the bower avenue, facing one bower wall. These males produced loud and rapid “Skraa” calls, throwing decorations as they courted females (Borgia and Presgraves, 1998; Borgia and Mueller, 1992). Birds in other spotted bowerbird populations have more subdued displays, with females standing parallel to the bower walls inside the bower avenue, facing the front entrance of the bower, and males standing at the end of one bower wall as he courts her. By building the bower rotated by 90°, with courtship behind see-through straw walls, Thallon males create a protective barrier for females that physically separates them as he courts her with highly aggressive displays. This novel bower design allows males to give high intensity displays that are preferred by females while reducing the threatening aspects of the display to females (Borgia and Presgraves, 1998; Figure 4.5). To test the hypothesis that the bower wall functions to reduce threat to the courted female, we predicted that if one bower wall were destroyed, Thallon males would position themselves behind the remaining standing wall during courtship. When either the N or S wall was left standing, males consistently courted females with the standing wall between them (Borgia and Presgraves, 1998). In intact bowers, males tended to more often court from the N side, so to remove any bias males had for courting from one side of the bower, we rotated the bower 180°, thereby changing the position of the standing wall. We found that males adjusted to the new position of the wall, using it to separate them from females. In one case, the female stood outside the bower and the male courted her from within the bower, keeping the standing wall between them. Females also consistently moved behind the lone standing wall for courtship, suggesting that they could use the unusually positioned wall to mitigate threat from males. Males infrequently courted the female from the destroyed wall side of the bower, with no

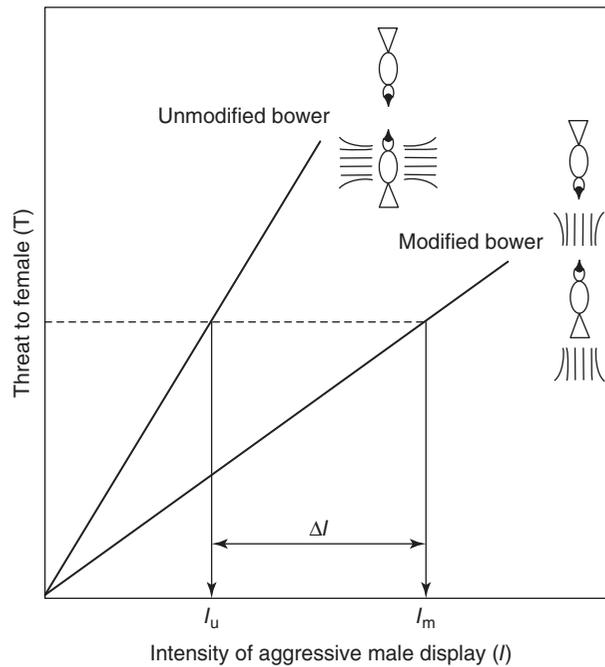


Figure 4.5. At Thallon in SE Queensland, male spotted bowerbirds have developed a special orientation and design to their bower. Unlike other spotted bowerbird populations and avenue builders, males court through a thin see-through wall that serves as a screen that appears to reduce threat to females from the males' especially intense display. This allows males to display at a much more intense level than males with unmodified bowers. (Figure taken from Borgia and Presgraves (1998).)

wall separating them from the female. In these cases, males significantly reduced display intensity (Borgia and Presgraves, 1998), showing that they were responsive to these unusual conditions. The flexible and highly appropriate reactions of males and females in this experiment suggest that they are cognizant of the threatening effect of male display or at least female reactions to it, and how the bower wall can be used to mitigate this threat. Males used this understanding to take up novel and effective courtship positions when bower walls were manipulated and then appropriately adjusted their display intensity when they did not have a protective wall present between them and the females they were courting. We did not anticipate that both sexes were capable of this high level of cognitive flexibility before conducting these experiments.

DECORATION STEALING: AN INNOVATION FOR DISPLAY TRAIT ACQUISITION

Male satin bowerbirds commonly use blue parrot feathers to decorate their bowers and the number of these feathers is positively related to male mating success (Borgia, 1985a; Patricelli *et al.*, 2004). Theft of feathers is critical for affecting

the number of feathers on a male's bower. The most active feather thieves were from areas where bowers were close together and they were involved in reciprocal stealing with males at adjacent bowers (Borgia and Gore, 1986). The occurrence of reciprocal stealing suggests that males may be able to identify males who steal from them and then go to their bowers to retrieve decorations. Studies of female movements in mate searching show that females search in a limited area for mates, thereby making nearby males competitors for females who search in that area (Uy *et al.*, 2000). The focus on nearby bowers for stealing is beneficial to the stealing male because it requires less time for them to be away from their bower and it permits them to take decorations from males who are their most likely direct sexual competitors. Stealing typically occurs when owners are not at bowers, so, for males to steal effectively, they need to be able to monitor their neighbors' behavior around bowers, and in the case of reciprocal stealing, past experience may cause males to direct extra effort toward males who are likely stealing threats. Male ability to successfully steal appears to require the ability to track their neighbors' behavior, determine who has stolen from them, and limit time away from their own bower so that they can protect their own decorations. Male cognitive ability may be important in affecting these tasks. Given what we know about how age affects male display behavior and bower building ability, it would be interesting to explore if male skills in stealing are affected by experience.

COOPERATING WITH RELATIVES FOR DISPLAY: AN INNOVATION TO REDUCE SEXUAL COMPETITION

Bower destruction is a common feature of male sexual competition in satin bowerbirds. Bowers are used by females in mate assessment (Borgia, 1985a) and are commonly destroyed by males' two nearest neighbors (Borgia, 1985b). As noted for feather stealing, females search in a limited locality for mates, so near neighbors are typically competing for the same females as mates. Unlike feather stealing, males do not directly enhance their own display when they destroy a neighbor's bower, although they do decrease the quality of display of their competitor/neighbor (Borgia, 1985b). Male dominance in aggression at feeding sites strongly predicted success in bower destructions and unlike feather stealing, there was little reciprocal bower destruction (Borgia, 1985b). Males in lekking species sometimes aggregate with their kin, suggesting that kin relationships can affect sexual display. One common suggestion is that kin may aid relatives in display. When this was tested in the intricate cooperative displays of long-tailed manakins, this was not supported (McDonald and Potts, 1994; Loiselle *et al.*, 2006), but it has been shown in turkeys (Krakauer, 2005). Bowerbirds differ from these species in that males display individually on widely separated display sites, which rules out direct cooperation in display. We found that satin bowerbird kin associated disproportionately as first or second nearest neighbors. We then tested the hypothesis that the presence of related neighbors mitigated the negative consequences of bower destruction. We found that males direct fewer bower destructions toward kin than equidistant

nonkin. Males with more relatives nearby also receive fewer bower destructions (Reynolds *et al.*, 2009). These results suggest that relatedness has a restraining effect on aggression and favors the close spatial association of related males. Male bower holders may repeatedly destroy the bowers of other less aggressive males and this behavior could affect the willingness of these victims to set up bowers in the neighborhood. The severe reduction in aggression in bower destruction seen by closely related males may facilitate close kin setting up bowers near their relatives. Male satin bowerbird cognitive ability may assist them in choosing which of their nearby neighbors' bowers to destroy and which others, owned by their relatives, not to destroy.

VOCAL MIMICRY: LEARNING AND INNOVATION IN USE OF CO-OPTED DISPLAYS

In satin bowerbirds, male courtship calls have two major components, first the aggressive “mechanical” portion in which males produce a whirring sound, followed by a trill accompanied by a rapid movement across the front of the bower while flashing their wings, and second, the “mimicry” portion of the call. Males mimic up to five species at our Wallaby Creek study site: Lewin's honeyeater (*Meliphaga lewinii*), laughing kookaburra (*Dacelo novaeguineae*), Australian raven (*Corvus coronoides*), sulphur-crested cockatoo (*Cacatua galerita*), and yellow-tailed black cockatoo (*Calyptorhynchus funereus*). Males show age-related improvement in the quality and completeness of mimetic calls, and males practice these calls as juveniles and adults, suggesting that learning is required to acquire these calls. Male age is related to the amount of practice, with younger males showing more and longer practice courtship bouts than older males. We found that both the mimetic and mechanical portions of the males' calls contributed to male courtship success (Loffredo and Borgia, 1986; Coleman *et al.*, 2007). Patricelli *et al.* (2004) found that, in satin bowerbirds, the mechanical portion of the display caused a higher level of discomfort in females, often causing females to startle, than the mimetic portions of male display. Male ability to modulate mechanical parts of the display in response to female discomfort was critical for their mating success. Coleman (2005) found that younger males induced a greater number of startles in male–male practice courtship displays. These results suggest that learning is important for the successful presentation of the mechanical calls at an intensity level that females or young males are comfortable viewing.

We hypothesize that male satin bowerbirds originally acquired mimetic calls by listening to model species. Now, however, because the same set of calls is used by males at Wallaby Creek and is also used in conspecific same-sex courtships of juvenile males by older males, it seems most likely that the calls are learned in these same-sex courtships. The alternative possibility that mimetic calls are genetically programmed is unlikely for several reasons. First, as passerine birds, bowerbirds are well-equipped to learn songs (e.g., Marler and Peters, 1981). Second, evolving the genetic programming to produce exact replicas of calls, some of which

are complex, from five different species, is unlikely. Third, the observation that mimetic calls improve with age and males spend a great deal of time practicing mimetic displays is more consistent with a learning hypothesis (extensive observation of other males might not be necessary if the calls were inherited primarily by genetic programming). Fourth, several other bowerbird species mimic unique situation-specific sounds that are clearly learned from the habitat, suggesting that vocal learning is a commonly used mechanism across bowerbirds.

Two steps are involved in the co-option model we apply to the evolution of mimetic displays in satin bowerbird mate choice. First, the male trait evolves because it provides an initial benefit to the male. We propose that males added mimicry to their courtship display because it calmed females after threatening mechanical calls, which are similar to aggressive calls. Studies of satin (e.g., Patricelli *et al.*, 2002; Coleman *et al.*, 2004) and spotted bowerbirds (Borgia and Presgraves, 1998) indicate that successful courtships involve a balance between intense display and threat-reducing elements. The alternation of intense mechanical elements and less intense mimicry appears to contribute to this balance. By interspersing melodic mimetic laughing kookaburra and Lewin's honeyeater calls between episodes of harsh mechanical calls, males may calm females and improve the likelihood that females will stay for additional courtship and copulation. Patricelli *et al.*'s (2004) observation that the broad band mechanical portion of the courtship song is more threatening and accounts for a large proportion of female startle behavior suggests that the mimicry portion is less threatening and could enhance female comfort with male display.

Once mimicry became incorporated as a regular aspect of male display, females appear to have secondarily co-opted these calls for use in mate assessment. Because the quality of male mimetic calls varies, females could use them to assess differences in male vocal ability and possibly differences in male genetic quality. Highly developed mimetic ability could indicate well-developed neural circuitry (Leitner and Catchpole, 2002; Nowicki *et al.*, 2000, 2002; Spencer *et al.*, 2005) that may indicate the overall genetic quality of males.

Mimicry is widespread in the bowerbird family and is commonly used by tooth-billed, spotted, and streaked bowerbirds, but they do not use it during courtship at bowers like satin bowerbirds. This suggests that mimicry was a preexisting capability in bowerbirds that was available for use in courtship by satin bowerbirds. Male spotted bowerbirds use relatively simple "Skraa" calls co-opted from their aggressive calls (Borgia and Coleman, 2000) as the predominant vocal display element during courtship. Male vocal mimicry of other species is more idiosyncratic and shows a great deal of individual variation in the models mimicked. For example, when we approach spotted bowerbird bowers, some males mimic cat meows, portions of kookaburra songs, and calls of goshawks and other species that seem to be mixed signals of threat and discomfort (see also Kelley and Healy, 2011). Tooth-billed bowerbird males produce long streams of calls from numerous other bird species and the sounds of car engines, creaking trees, cicadas, frogs, and so on (Chaffer, 1984; Iredale, 1950; Marshall, 1954; Frith and McGuire, 1996). Male streaked bowerbirds mimic complex acoustical scenes. In one case, a male started

with the mimicked sounds of a group of people talking as they moved through the forest with their machetes cutting bushes and dogs barking, and continued with the sound of machetes being used to fell a tree, complete with the rattle of shaking leaves after each blow, and eventually the sound of the tree falling and hitting the ground with a crash. Male Vogelkop bowerbirds (*A. inornatus*) in the Arfak Mountains are most like satin bowerbirds in regularly using mimicry during close courtship. Males display from the covered dark interior of their hut-like bower and vocally mimic the sounds of wing beating during courtship while their wings are held still. Spotted bowerbirds at Thallon, Queensland (see Borgia, 1995a) make a gurgling call during courtship that sounds like water in a stream running over stones that may or may not be mimicry. Male satin bowerbirds mimic ravens perhaps as a way of indicating a greater threat from a larger bird when attacked by groups of the cooperative breeding Australian bell miners (*Manorina melanophrys*). Bowerbirds clearly have the ability to mimic a large variety of sounds. While satin bowerbirds represent the only species that uses mimicry extensively in courtship, the numerous different contexts in which male bowerbirds use mimicry and the great diversity of sounds mimicked is consistent with the hypothesis that bowerbirds use cognitive processes to both learn the mimicry and then apply it in ways useful to them.

CO-OPTION MECHANISM

Co-option of preexisting male traits used in sexual display is widespread (Borgia, 2006). Some well-known examples include nests of weaverbirds (Lawes *et al.*, 2002) and sticklebacks (Barber *et al.*, 2001) that originally functioned in offspring rearing and are now also used in mate choice. The co-option process may start with an already existing male trait, for example, a neatly woven nest, that performs some nondisplay function and that can be assessed by females. If the male trait, for example, a well built nest, happens to be an effective indicator of male quality, then a female preference for that trait may evolve, resulting in co-option of the male trait and its use in male display. Co-option is also evident in several key aspects of bowerbird display.

Co-option is a critical and commonly unrecognized element in the acquisition of male display in a wide variety of species (Borgia, 2006). Initially it was proposed that aggressive displays were often borrowed for use in sexual display (Fisher, 1930; Borgia, 1979; Berglund and Rosenqvist, 2001; Berglund *et al.*, 1996; Borgia and Coleman, 2000). It was suggested that male aggressive signals are effective indicators of genome-wide good genes for fighting ability, and that females can use these same signals in mate choice to identify high-quality sires. Borgia and Coleman (2000) showed that the “Skraa” call that is used widely in bowerbirds as an aggressive call is also used as a courtship call in the bowerbird genus *Chlamydera*. This more limited distribution and the similarity of the call in the two contexts indicate that this call was co-opted for use in courtship from its previous use as an aggressive display. More recently, it has been recognized that many other preexisting male traits not associated with aggression can signal important information about males during courtship (Borgia, 2006).

The co-option of preexisting male traits resolves several difficult problems for sexual selection theory. For example, it explains how costly display traits might evolve. It is often argued that display traits must be costly to effectively indicate male quality (e.g., Zahavi, 1977; Grafen, 1990), but if there is a high cost to the trait, that reduces the net benefit of the trait (Borgia, 1979; Maynard Smith, 1978). However, if an expensive physical trait is already present, having evolved because of some other function, and it is then co-opted for a new function in sexual display, several problems related to trait cost-based honesty can be avoided. First, costs associated with the initial function of the trait can be effective in guaranteeing honesty related to the new trait function as a male quality indicator. Low quality males cannot pay for expensive traits, whether they evolved for sexual signaling or for a different original function. However, if this cost is already paid for, then the trait can be co-opted to serve as a mate choice signal that honestly distinguishes low- and high-quality males free of new added cost. This makes a co-opted signal more likely to evolve than a co-evolved trait and preference because of the greater net benefit (lower cost) to males and females of the co-opted trait. Second, the evolution of cost-based signals is complicated by the problem of low honesty for small inexpensive incipient signals in the early stages of display trait evolution. These signals are not likely to be effective in separating low- and high-quality males based on cost and as such signal evolution should be impeded. Co-option can bypass this problem by starting with an already enlarged and costly trait that allows only high-quality males to develop the displays preferred by females. While the reliability of all display traits may not always be cost-dependent (Borgia, 1993, 2006), co-option of existing traits may provide the best explanation for how expensive traits that use cost to ensure honesty can evolve.

Co-option models of sexual selection solve some additional issues in other common sexual selection models. First, they do not require difficult-to-initiate-and-maintain genetic correlations (Bakker and Pomiankowski, 1995) between male traits and female preferences that are required in many commonly considered models (e.g., Lande, 1981; Pomiankowski, 1988; Kokko *et al.*, 2002). If there is low genetic variation in either the male trait or female preference or females cannot effectively choose males with the appropriate trait, existing genetic correlations can be readily lost and may not be easily regenerated (Butlin, 1993). Co-option bypasses this problem because the male trait is already present and the female preference can evolve if females gain a benefit from choosing the male trait. Also, if the display trait and/or the female preference is learned, it is not clear that genetic correlations of the type needed to maintain the dynamic balance specified in these models can occur under all conditions. Second, in initial stages of co-evolutionary good genes models, it is necessary that both female preferences and male traits become simultaneously functional and operate with sufficient efficiency that there is net benefit for the choosing female. This is a much more difficult requirement than for a co-option model in which the fully developed male trait is already established and the female preference has time to evolve in the presence of the male trait. This less-complicated set of conditions with co-opted male traits should allow mate choice to more readily evolve than by co-evolutionary processes.

The multi-step process for co-option of existing male traits by females for mate choice may have occurred several times in bowerbirds. In the first step, a trait becomes established in males because it benefits males, but is not a product of selection by a direct female preference. For example, we hypothesize that in the evolution of bower decoration, males initially collected colorful objects to make their bowers more recognizable to mate-searching females as described by Parker's (1983) passive attraction hypothesis. Males who chose bright, distinctive, and rare colors of decorations for these displays produced a signal that was easier for females to recognize as a male display site in the clutter of the forest floor. Next, as males vied for limited distinctive decorations, male ability to collect and display these decorations, including stealing and defending them from one another (Borgia and Gore, 1986), coincidentally provided an indicator of differences in male physical and cognitive ability. Then, females that happened to evolve an active preference for males with more decorations could obtain high-quality mates, causing the preference to spread. Similarly, bowers originally evolved to reduce threat of forced copulation to females (see Borgia, 1995b). Male bowers differed in the quality of construction, reflecting differences in male motor and neurological quality. Females who attended to these differences in mate assessment effectively co-opted the bower for a secondary function in mate choice. This co-option process explains the dual function of traits like bowers and decorations and provides a relatively simple stepwise process by which complex signal systems can evolve without the need for genetic correlations difficult to develop and maintain. Other traits for which there may have been co-option in bowerbirds are mimetic calls used initially as a calming element in male display and then, as females recognized differences in male call quality, as a basis for female choice of mates (see section "Vocal Mimicry: Learning and Innovation in Use of Co-opted Displays"). Thus, several major components of satin bowerbird display appear to be co-opted from other preexisting traits that initially did not evolve through mate choice.

COGNITION IN DISPLAY TRAIT ACQUISITION

The co-option of complex bowerbird displays often appears to be dependent on cognitive ability. For females to discriminate among males based on decoration numbers, they have to recognize at least qualitative and perhaps quantitative differences in decoration numbers (Borgia, 1985a; Coleman *et al.*, 2004), remember those differences as they move to separated bowers (Uy *et al.*, 2000, 2001a, 2001b) and then select the most decorated among those visited (Patricelli *et al.*, 2003, 2004; Borgia and Mueller, 1992; Uy *et al.*, 2000; Madden, 2002). For this to occur, that females must have had the necessary cognitive abilities before their complex pattern of decoration choice evolved. Male courtship adjustments in response to female discomfort in courtship (Patricelli *et al.*, 2002) suggest that males are able to appropriately perceive and respond to female behavior in the bower. Males may relate female behaviors to their own experiences resulting from courtship directed at them by other males (Collis and Borgia, 1993) and use this experience to appropriately modify their own display behavior.

Male bowerbirds appear to anticipate female reactions to novel display traits they produce. In several situations described already, males in the absence of females adjust their displays to match those preferred by females. This ability may have been important in the past integration of novel elements into male display. For example, male satin bowerbirds may have tried out different mimicked calls and learned to use those that calmed females after inserting them into their courtship display. But also intriguing is the possibility that when male satin bowerbirds initially chose calls to mimic during courtship, they found certain calls of other species calming to them and they anticipated that they would have a similar effect on females, and thus incorporated them into their displays. Male ability to anticipate female reactions based on shared reactions and experiences could be a potentially important mechanism for streamlining the evolution of complex displays. This could make the co-option process more effective in producing advantageous new displays.

In bowerbirds, a group with the most intensively studied pattern of sexual display, cognition appears to play a key role in the operation, acquisition, and assessment of these displays. Given that cognition is rarely mentioned in conjunction with sexual selection in most species and in NRB species in particular, there is a large discrepancy between what we have found and some of the most commonly cited models for sexual selection. This work suggests that a new set of models based on cognitively directed co-option that more directly considers cognitive processes in display trait evolution need to be developed. We believe that these models will more accurately describe how new behavioral signals are acquired and preferences evolve. This view sees females as sophisticated decision makers able to make complex fitness-enhancing mating decisions, and males as using their cognitive processes to creatively construct highly effective new displays.

REFERENCES

- Alexander, R.D. (1981) *Darwinism and Human Affairs*, University of Washington Press, Seattle.
- Airey, D.C., Castillo-Juarez, H., Casella, G., Pollak, E.J., and DeVoogd, T.J. (2000a) Variation in the volume of zebra finch song control nuclei is heritable: developmental and evolutionary implications. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **267**, 2099–2104.
- Airey, L.C., Buchanan, K.L., Szekely, T., Catchpole, C.K., and Devoogd, T.J. (2000b) Song, sexual selection, and a song control nucleus (HVC) in the brains of European sedge warblers. *Journal of Neurobiology*, **44**, 1–6.
- Anderson, B.L. (2012) Bird-brained illusionists. *Science*, **335**, 292–293.
- Andersson, M. (1994) *Sexual Selection*, Princeton University Press, Princeton, New Jersey.
- Andersson, M. and Simmons, L.W. (2006) Sexual selection and mate choice. *Trends in Ecology and Evolution*, **21**, 296–302.
- Barber, I., Nairn, D., and Huntingford, F. (2001) Nests are ornaments: revealing construction by male sticklebacks. *Behavioral Ecology*, **12**, 390–396.

- Bakker, T.C.M. and Pomiankowski, A. (1995) The genetic basis of female mate preferences. *Journal of Evolutionary Biology*, **8**, 129–171.
- Bennett, A.T.D. (1993) Spatial memory in a food storing corvid. I. Near tall landmarks are primarily used. *Journal of Comparative Physiology A*, **173**, 193–207.
- Berglund, A. and Rosenqvist, G. (2001) Male pipefish prefer dominant over attractive females. *Behavioral Ecology*, **12**, 402–406.
- Berglund, A., Bisazza, A., and Pilastro, A. (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society of London*, **58**, 385–399.
- Boogert, N.J., Giraldeau, L.A., and Lefebvre, L. (2008) Song complexity correlates with learning ability in zebra finch males. *Animal Behaviour*, **76**, 1735–1741.
- Boogert, N.J., Fawcett, T.W., and Lefebvre, L. (2011) Mate choice for cognitive traits: a review of the evidence in nonhuman vertebrates. *Behavioral Ecology*, **22**, 447–459.
- Borgia, G. (1979) Sexual selection and the evolution of mating systems, in *Sexual Selection and Reproductive Competition* (eds M.S. Blum and N.A. Blum), Academic Press, New York, pp. 19–80.
- Borgia, G. (1985a) Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behaviour*, **33**, 266–271.
- Borgia, G. (1985b) Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhynchus violaceus*). *Behavioral Ecology and Sociobiology*, **18**, 91–100.
- 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. (1995a) Complex male display and female choice in the spotted bowerbird: specialized functions for different bower decorations. *Animal Behaviour*, **49**, 1291–1301.
- Borgia, G. (1995b) Why do bowerbirds build bowers? *American Scientist*, **83**, 542–547.
- Borgia, G. (2006) Preexisting male traits are important in the evolution of elaborated male display. *Advances in the Study of Behavior*, **36**, 249–302.
- Borgia, G. and Coleman, S.W. (2000) Co-option of male courtship signals from aggressive display in bowerbirds. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **267**, 1735–1740.
- Borgia, G. and Gore, M.A. (1986) Feather stealing in the satin bowerbird (*Ptilonorhynchus violaceus*): male competition and the quality of display. *Animal Behaviour*, **34**, 727–738.
- Borgia, G. and Keagy, J. (2006) An inverse relationship between decoration and food colour preferences in satin bowerbirds does not support the sensory drive hypothesis. *Animal Behaviour*, **72**, 1125–1133.
- Borgia, G., Coyle, B., and Keagy, J. (2012) Comment on “Illusions Promote Mating Success in Great Bowerbirds”. *Science*, **337** (6092), 292.
- Borgia, G. and Mueller, U. (1992) Bower destruction, decoration stealing, and female choice in the spotted bowerbird (*Chlamydera maculata*). *Emu*, **92**, 11–18.
- Borgia, G. and Presgraves, D.C. (1998) Coevolution of elaborated male display traits in the spotted bowerbird: an experimental test of the threat reduction hypothesis. *Animal Behaviour*, **56**, 1121–1128.

- Borgia, G., Kaatz, I., and Condit, R. (1987) Flower choice and the decoration of the bower of the satin bowerbird (*Ptilonorhynchus violaceus*): a test of hypotheses for the evolution of display. *Animal Behaviour*, **35**, 129–139.
- Bradbury, J.W. (1981) The evolution of leks, in *Natural Selection and Social Behavior* (eds R.D. Alexander and D.W. Tinkle), Chiron Press, New York, pp. 138–169.
- Bravery, B.D., Nicholls, J.A., and Goldizen, A.W. (2006) Patterns of painting in satin bowerbirds *Ptilonorhynchus violaceus* and males' responses to changes in their paint. *Journal of Avian Biology*, **37**, 77–83.
- Buchanan, K.L., Catchpole, C.K., Lewis, J.W., and Lodge, A. (1999) Song as an indicator of parasitism in the sedge warbler. *Animal Behaviour*, **57**, 307–314.
- Buchanan, K.L., Spencer, K.A., Goldsmith, A.R., and Catchpole, C.K. (2003) Song as an honest signal of past developmental stress in the European starling (*Sturnus vulgaris*). *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **270**, 1149–1156.
- Bugnyar, T. and Kotrschal, K. (2002) Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? *Animal Behaviour*, **64**, 185–195.
- Butlin, R.K. (1993) A comment on the evidence for a genetic correlation between the sexes in *Drosophila melanogaster*. *Animal Behaviour*, **45**, 403–404.
- Canady, R.A., Kroodsma, D.E., and Nottebohm, F. (1984) Population differences in complexity of a learned skill are correlated with the brain space involved. *Proceedings of the National Academy of Sciences of the United States of America*, **81**, 6232–6234.
- Cendes, L. (2009) Active female sampling of male display predicts female uncertainty in mate choice. Master's thesis. Department of Biology, University of Maryland, College Park, MD USA.
- Chaffer, N. (1984) *In Quest of Bowerbirds*, Rigby, Melbourne.
- Coleman, S.W., Patricelli, G.L., and Borgia, G. (2004) Variable female preferences drive complex male displays. *Nature*, **428**, 742–745.
- Coleman, S.W. (2005) Variable female preferences and the evolution of complex male displays in the satin bowerbird (*Ptilonorhynchus violaceus*). Doctor of Philosophy Dissertation. Behavior, Ecology, Evolution, and Systematics Program, University of Maryland, College Park, MD USA.
- Coleman, S.W., Patricelli, G.L., Coyle, B., Siani, J., and Borgia, G. (2007) A new role for vocal mimicry: the most attractive males are the best mimics. *Biology Letters*, **3**, 463–466.
- Collis, K. and Borgia, G. (1993) The costs of male display and delayed plumage maturation in the satin bowerbird (*Ptilonorhynchus violaceus*). *Ethology*, **94**, 59–71.
- Cronin, H. (1991) *The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today*, Cambridge University Press, Cambridge.
- Cooper, W.T. and Forshaw, J.M. (1979) *The Birds of Paradise and Bowerbirds*, David R. Godine, Boston.
- Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*, D. Appleton Company, New York.
- Darwin, C. (1872) *The Expression of the Emotions in Man and Animals*, D. Appleton Company, New York.
- Dawkins, M.S. and Guilford, T. (1996) Sensory bias and the adaptiveness of female choice. *American Naturalist*, **148**, 937–942.

- Day, L.B., Westcott, D.A., and Olster, D.H. (2005) Evolution of bower complexity and cerebellum size in bowerbirds. *Brain, Behavior and Evolution*, **66**, 62–72.
- Doerr, N.R. (2010) Decoration supplementation and male–male competition in the great bowerbird (*Ptilonorhynchus nuchalis*): a test of the social control hypothesis. *Behavioral Ecology and Sociobiology*, **64**, 1887–1896.
- Donaghey, R. (1996) Satin bowerbird, Regent Bowerbird, in *Finches, Bowerbirds and Other Passerines of Australia* (ed R. Strahan), Harper Collins Publishers, Sydney.
- Emery, N.J. (2006) Cognitive ornithology: the evolution of avian intelligence. *Philosophical Transactions of the Royal Society of London, Series B*, **361**, 23–43.
- Emery, N.J. and Clayton, N.S. (2004) The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, **306**, 1903–1907.
- Endler, J.A., Endler, L.C., and Doerr, N.R. (2010) Great Bowerbirds create theaters with forced perspective when seen by their audience. *Current Biology*, **20**, 1679–1684.
- Fisher, R.A. (1915) The evolution of sexual preference. *Eugenics Review*, **7**, 184–192.
- Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Clarendon Press, Oxford.
- Frith, C.B. and Mcguire, M. (1996) Visual evidence of vocal avian mimicry by male Tooth-Billed Bowerbirds *Scenopoeetes dentirostris* (Ptilonorhynchidae). *Emu*, **1**, 12–16.
- Frith, C.B. and Frith, D.W. (2004) *The Bowerbirds: Ptilonorhynchidae*, Oxford University Press, Oxford.
- Garamszegi, L.Z., Eens, M., Erritzoe, J., and Møller, A.P. (2005a) Sexually size dimorphic brains and song complexity in passerine birds. *Behavioral Ecology*, **16**, 335–345.
- Garamszegi, L.Z., Eens, M., Erritzoe, J., and Møller, A.P. (2005b) Sperm competition and sexually size dimorphic brains in birds. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **272**, 159–166.
- Gillard, E.T. (1969) *The Birds of Paradise and Bowerbirds*, Weidenfeld and Nicholson, London.
- Gomez, D. and Théry, M. (2004) Influence of ambient light on the evolution of colour signals: comparative analysis of a Neotropical rainforest bird community. *Ecology Letters*, **7**, 279–284.
- Grafen, A. (1990) Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.
- Hamilton, W.D. and Zuk, M. (1982) Heritable true fitness and bright birds: a role for parasites. *Science*, **218**, 384–387.
- Hansell, M. (2009) *Built by Animals: The Natural History of Animal Architecture*, Oxford University Press, Oxford.
- Healy, S.D. and Rowe, C. (2007) A critique of comparative studies of brain size. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **274**, 453–464.
- Healy, S.D. and Hurly, T.A. (1995) Spatial memory in rufous hummingbirds (*Selasphorus rufus*): a field test. *Animal Learning and Behavior*, **23**, 63–68.
- Hebets, E.A. (2003) Subadult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 13390–13395.
- Herrick, C.J. (1924) *Neurological Foundations of Animal Behaviour*, Hafner, New York.

- Hicks, R.E., Larned, A., and Borgia, G. (2013) Bower paint removal leads to reduced female visits, suggesting bower paint functions as a chemical signal. *Animal Behaviour*, **85**, 1209–1215.
- Höglund, J. and Alatalo, R.V. (1995) *Leks*, Princeton University Press, Princeton, New Jersey.
- Holland, B. and Rice, W.R. (1998) Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution*, **52**, 1–7.
- Hunter, C.P. and Dwyer, P.D. (1997) The value of objects to satin bowerbirds *Ptilonorhynchus violaceus*. *Emu*, **97**, 200–206.
- Iredale, T. (1950) *Birds of Paradise and Bowerbirds*, Georgian House, Melbourne.
- Isler, K. and van Schaik, C. (2006) Costs of encephalization: the energy trade-off hypothesis tested on birds. *Journal of Human Evolution*, **51**, 228–243.
- Isler, K. and van Schaik, C.P. (2008) Why are there so few smart mammals (but so many smart birds)? *Biology Letters*, **5**, 125–129.
- Iwaniuk, A.N. and Hurd, P.L. (2005) The evolution of cerebrotypes in birds. *Brain, Behavior and Evolution*, **65**, 215–230.
- Jarvis, E.D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., Paxinos, G., Perkel, D.J., Shimizu, T., Striedter, G., Wild, J.M., Ball, G.F., Dugas-Ford, J., Durand, S.E., Hough, G.E., Husband, S., Kubikova, L., Lee, D.W., Mello, C.V., Powers, A., Siang, C., Smulders, T.V., Wada, K., White, S.A., Yamamoto, K., Yu, J., Reiner, A., and Butler, A.B. (2005) Opinion: Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience*, **6**, 151–159.
- Johnstone, R. and Earn, D.J. (1999) Imperfect female choice and male mating skew on leks of different sizes. *Behavioral Ecology and Sociobiology*, **45**, 277–281.
- Jones, T.B. and Kamil, A.C. (1973) Tool-making and tool-using in the northern blue jay. *Science*, **180**, 1076–1078.
- Kamil, A. and Balda, R. (1985) Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology and Animal Behavioral Processes*, **11**, 95–111.
- Keagy, J., Savard, J.-F., and Borgia, G. (2009) Male satin bowerbird problem-solving ability predicts mating success. *Animal Behaviour*, **78**, 809–817.
- Keagy, J., Savard, J.-F., and 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., and Borgia, G. (2012) Cognitive ability and the evolution of multiple behavioral display traits. *Behavioral Ecology*, **23**, 448–456.
- Kelley, L.A. and Healy, S.D. (2011) The mimetic repertoire of the spotted bowerbird *Ptilonorhynchus maculatus*. *Naturwissenschaften*, **98**, 501–507.
- Kelley, L. and Endler, J. (2012) Illusions promote mating success in great bowerbirds. *Science*, **335**, 335–338.
- King, A.P., Freeberg, T.M., and West, M.J. (1996) Social experience affects the process and outcome of vocal ontogeny in two populations of cowbirds (*Molothrus ater*). *Journal of Comparative Psychology*, **110**, 276–285.
- Kirkpatrick, M. (1987) Sexual selection by female choice in polygynous animals. *Annual Review of Ecology and Systematics*, **18**, 43–70.

- Kodric-Brown, A. and Nicoletto, P.F. (2001) Age and experience affect female choice in the guppy (*Poecilia reticulata*). *American Naturalist*, **157**, 316–323.
- Kokko, H., Brooks, R., McNamara, J.M., and Houston, A.I. (2002) The sexual selection continuum. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **269**, 1331–1340.
- Koksal, F. and Domjan, M. (1998) Observational conditioning of sexual behavior in the domesticated quail. *Animal Learning and Behavior*, **26**, 427–432.
- Krakauer, A.H. (2005) Kin selection and cooperative courtship in wild turkeys. *Nature*, **434**, 69–72.
- Kusmiński, R., Borgia, G., Uy, A., and Crozier, R. (1997) Molecular information on bowerbird phylogeny and the evolution of exaggerated male characters. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **264**, 307–313.
- Lande, R. (1981) Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America*, **78**, 3721–3725.
- Lawes, M., Slotow, R., and Andersson, S. (2002) Male nest building but not display behaviour directly influences mating success in the polygynous Red Bishop, *Euplectes orix*. *Ostrich*, **73**, 87–91.
- Leitner, S. and Catchpole, C.K. (2002) Female canaries that respond and discriminate more between male songs of different quality have a larger song control nucleus (HVC) in the brain. *Journal of Neurobiology*, **52**, 294–301.
- Lefebvre, L., Reader, S.M., and Sol, D. (2004) Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution*, **63**, 233–246.
- Loffredo, C.A. and Borgia, G. (1986) Male courtship vocalizations as cues for mate choice in the satin bowerbird (*Ptilonorhynchus violaceus*). *Auk*, **103**, 189–195.
- Loiselle, B.A., Ryder, T.B., Duraes, R., Tori, W., Blake, J.G., and Parker, P.G. (2006) Kin selection does not explain male aggregation at leks of 4 manakin species. *Behavioral Ecology*, **18**, 287–291.
- Madden, J.R. (2001) Sex, bowers and brains. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **268**, 833–838.
- Madden, J. (2002) Bower decorations attract females but provoke other male spotted bowerbirds: bower owners resolve this trade-off. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **269**, 1347–1351.
- Madden, J.R. (2003) Bower decorations are good predictors of mating success in the spotted bowerbird. *Behavioral Ecology and Sociobiology*, **53**, 269–277.
- Madden, J.R. (2006) Interpopulation differences exhibited by Spotted Bowerbirds *Chlamydera maculata* across a suite of male traits and female preferences. *Ibis*, **148**, 425–435.
- Madden, J.R. (2008) Do bowerbirds exhibit culture? *Animal Cognition*, **11**, 1–12.
- Marler, P. and Peters, S. (1981) Sparrows learn adult song and more from memory. *Science*, **213**, 780–782.
- Maynard Smith, J. (1978) *The Evolution of Sex*, Cambridge University Press, Cambridge.
- McDonald, D.B. and Potts, W.K. (1994) Cooperative display and relatedness among males in a lek-mating bird. *Science*, **266**, 1030–1032.
- Marshall, A.J. (1954) *Bower-Birds: Their Displays and Breeding Cycles*, Clarendon Press, Oxford.

- Mikami, O.K., Katsuno, Y., Yamashita, D.M., Noske, R., and Eguch, K. (2010) Bowers of the Great Bowerbird (*Chlamydera nuchalis*) remained unburned after fire: is this an adaptation to fire? *Journal of Ethology*, **28**, 15–20.
- Miller, G. (2001) *The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature*, Anchor Books, New York.
- Morris, M.R., Nicoletto, P.F., and Hesselman, E. (2003) A polymorphism in female preference for a polymorphic male trait in the swordtail fish *Xiphophorus cortezi*. *Animal Behaviour*, **65**, 45–52.
- Nottebohm, F., Kasparian, S., and Pandazis, C. (1981) Brain space for a learned task. *Brain Research*, **213**, 99–109.
- Nowicki, S., Hasselquist, D., Bensch, S., and Peters, S. (2000) Nestling growth and song repertoire sire in great reed warblers: evidence for song learning as an indicator mechanism in mate choice. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **267**, 2419–2424.
- Nowicki, S., Searcy, W.A., and 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.
- Parker, G.A. (1983) Mate quality and mating decisions, in *Mate Choice* (ed P. Bateson), Cambridge University Press, Cambridge, pp. 141–166.
- Patricelli, G.L., Uy, J.A.C., Walsh, G., and Borgia, G. (2002) Male displays adjusted to female’s response. *Nature*, **415**, 279–280.
- Patricelli, G.L., Uy, J.A.C., and Borgia, G. (2003) Multiple male traits interact: attractive bower decorations facilitate attractive behavioural displays in satin bowerbirds. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **270**, 2389–2395.
- Patricelli, G.L., Uy, J.A.C., and Borgia, G. (2004) Female signals enhance the efficiency of mate assessment in satin bower-birds (*Ptilonorhynchus violaceus*). *Behavioral Ecology*, **15**, 297–304.
- Patricelli, G.L., Coleman, S.W., and 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.
- Pepperberg, I.M. (1999) *The Alex Studies: Cognitive and Communicative Abilities of Grey Parrots*, Harvard University Press, Cambridge, MA.
- Pitnick, S., Jones, K.E., and Wilkinson, G.S. (2006) Mating system and brain size in bats. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **273**, 719–724.
- Pomiankowski, A.N. (1988) The evolution of mate preferences for male genetic quality. *Oxford Surveys in Evolutionary Biology*, **5**, 136–184.
- Pravosudov, V.V. and Clayton, N.S. (2002) A test of the adaptive specialization hypothesis: population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). *Behavioral Neuroscience*, **116**, 515–522.
- Prum, R.O. (2010) The Lande–Kirpatrick mechanism is the null model of evolution by intersexual selection: implications for meaning, honesty, and design in intersexual signals. *Evolution*, **64**, 3085–3100. doi: 10.1111/j.1558-5646
- Reynolds, S.M., Christman, M.C., Uy, J.A.C., Patricelli, G.L., Braun, M.J., and Borgia, G. (2009) Lekking satin bowerbird males aggregate with relatives to mitigate aggression. *Behavioral Ecology*, **20**, 410–415.

- Rodd, F.H., Hughes, K.A., Grether, G., and Baril, C. (2002) A possible non-sexual origin of a mate preference: are male guppies mimicking fruit? *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **269**, 475–481.
- Roth, G. and Dicke, U. (2005) Evolution of the brain and intelligence. *Trends in Cognitive Sciences*, **9**, 250–257.
- Ryan, M.J. and Rand, A.S. (1990) The sensory basis of sexual selection for complex calls in the tungara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution*, **44**, 305–314.
- Ryan, M.J. and Rand, A.S. (1993) Sexual selection and signal evolution: the ghost of biases past. *Philosophical Transactions of the Royal Society, Series B*, **340**, 187–195.
- Ryan, M.J., Akre, K.L., and Kirkpatrick, M. (2009) Cognitive mate choice, in *Cognitive Ecology II* (eds R. Dukas and J.M. Ratcliffe), University of Chicago Press, Chicago, pp. 137–155.
- Sasvari, L. and Hegyi, Z. (1998) How mixed-species foraging flocks develop in response to benefits from observational learning. *Animal Behaviour*, **55**, 1461–1469.
- Spencer, K.A., Buchanan, K.L., Leitner, S., Goldsmith, A.R., and Catchpole, C.K. (2005) Parasites affect song complexity and neural development in a songbird. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **272**, 2037–2043.
- Taylor, A.H., Hunt, G.R., Holzhaider, J.C., and Gray, R.D. (2007) Spontaneous metatool use by New Caledonian crows. *Current Biology*, **17**, 1504–1507.
- Tomasello, M. (1999) Emulation learning and cultural learning. *Behavioural and Brain Sciences*, **21**, 703–704.
- Uy, J.A.C. and Borgia, G. (2000) Sexual selection drives rapid divergence in bowerbird display traits. *Evolution*, **54**, 273–278.
- Uy, J.A.C., Patricelli, G.L., and Borgia, G. (2000) Dynamic mate-searching tactic allows female satin bowerbirds *Ptilonorhynchus violaceus* to reduce searching. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **267**, 251–256.
- Uy, J.A.C., Patricelli, G.L., and Borgia, G. (2001a) Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. *American Naturalist*, **158**, 530–542.
- Uy, J.A.C., Patricelli, G.L., and Borgia, G. (2001b) Loss of preferred mates forces female satin bowerbirds (*Ptilonorhynchus violaceus*) to increase mate searching. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **268**, 633–638.
- van Schaik, C.P., Deaner, R.O., and Merrill, M.Y. (1999) The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, **36**, 719–741.
- Vellenga, R.E. (1980) Moults of the satin bowerbird *Ptilonorhynchus violaceus*. *Emu*, **80**, 49–54.
- Werdenich, D. and Huber, L. (2006) A case of quick problem solving in birds: string pulling in keas, *Nestor notabilis*. *Animal Behaviour*, **71**, 855–863.
- Widemo, F. and Owens, I.P.F. (1995) Lek size, male mating skew and the evolution of lekking. *Nature*, **373**, 148–151.
- Wiley, R.H. (1991) Lekking in birds and mammals: behavioral and evolutionary issues. *Advances in the Study of Behavior*, **20**, 201–291.

- Wojcieszek, J.M., Nicholls, J.A., and Goldizen, A.W. (2007) Stealing behavior and the maintenance of a visual display in the satin bowerbird. *Behavioral Ecology*, **18**, 689–695.
- Zahavi, A. (1975) Mate selection – selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.
- Zahavi, A. (1977) Cost of honesty – (further remarks on handicap principle). *Journal of Theoretical Biology*, **67**, 603–605.