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Bower paint removal leads to reduced female visits, suggesting bower paint functions as a chemical signal

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The multifaceted courtship display of male satin bowerbirds, *Ptilonorhynchus violaceus*, involves several elements that have been studied in detail. However, one of their most unique display elements, bower painting, has received relatively little attention despite males' large investment of time in this behaviour. Male bowerbirds chew plant material and apply the resulting mixture of masticated vegetation and male saliva or 'bower paint' to a chest-high band inside their bower walls. Searching females taste this paint, suggesting that paint may be a chemosensory signal. We used both behavioural observations and experimental approaches to examine predictions made by two hypotheses for the function of bower paint. We measured natural variation in paint quantity to investigate whether quantity of paint at bowers is related to other male display traits, male mating success and male physical condition. We also investigated whether males and females are affected by experimental removal of bower paint. Additionally, we assessed male response to paint transplants from other individuals. We found a significant correlation between the amount of paint and a composite estimate of several other measures known to indicate bower and decoration display quality. Also, males whose bowers underwent experimental removal of paint had fewer females return for second courtships and copulations than did control males. This result provides the first experimental evidence that females respond to bower paint. These findings establish that bower paint is a trait that affects mate-searching decisions by females and demonstrates that the quantity of bower paint is important in attracting females.

Complex, multifaceted displays in the context of mating are common, especially in polygynous species and birds (Møller & Pomiankowski 1993; Andersson 1994). These displays can involve auditory, chemical, visual or tactile components and may provide searching females with various types of information including species, sex, individual identity, relatedness or quality (e.g. Kotiaho et al. 1996; Lindstrom & Lundstrom 2000; Reusch et al. 2001; Boogert et al. 2008). Often though, the exact information provided by a behaviour or potential signal is unknown. If these behaviours are suspected of being used in the context of mating, it is important to examine these traits in order to investigate their role in sexual display and mate choice.

The sexual display of satin bowerbirds, *Ptilonorhynchus violaceus*, contains several components that have been studied at length. Although it is one of the most unusual behaviours related to male display, bower painting has received relatively little attention. Bower painting involves males masticating vegetation and applying this 'paint' by touching their bills to the sticks on the inner bower walls (Fig. 1a). Males primarily masticate dried, hoop pine needles (*Araucaria cunninghamii*) to create bower paint (Robson et al. 2005; R. E. Hicks, personal observation). The paint is similar in colour to the bower sticks and is applied in a chest-high band on the inner bower walls, making the paint in satin bowerbirds difficult to assess visually except when in close proximity to the bower (Fig. 1b). Bower-holding males spend a substantial amount of time painting their bowers (Bravery et al. 2006), and male painting rate predicts mating success (Robson et al. 2005). Often, non-bower-holding males and juvenile males paint on bowers belonging to other males they visit (R. E. Hicks, personal observation). Some females that visit bowers during the mating season sample or 'taste' this paint by nipping at and swallowing it (Bravery et al. 2006). Because the paint is created from dried plant material and is sampled in small amounts, it is unlikely that the paint provides any nutritional value to females. Instead, this sampling suggests that bower paint may be a chemosensory signal that is utilized in mate assessment.

A female may gain various types of information from assessing the chemical composition of paint that may help her find more suitable mates. The use of chemical signals in mate choice has been

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Figure 1. (a) Male satin bowerbird painting with hoop pine (*Araucaria cunninghamii*). (b). Image of painted bower sticks.

demonstrated in several taxa, and studies have demonstrated that females can use chemical cues to gain information about aspects of male quality (e.g. physical condition: Martin et al. 2007; Giaquinto et al. 2010; genetic heterozygosity: Charpentier et al. 2008; sperm fertility: Ruther et al. 2009) and genetic compatibility (e.g. Aeschlimann et al. 2003; Charpentier et al. 2010; Conrad et al. 2010; Setchell et al. 2011; reviewed in: Setchell & Huchard 2010). Evidence for the use of chemical signals in birds is less extensive, perhaps because the importance of the olfactory sense in this group historically has been marginalized. Recent studies investigating the use of chemical signals in birds have revealed that this sensory modality plays a larger role in communication than previously thought (Steiger et al. 2008; reviewed in: Rajchard 2007). Studies have shown that, in birds, olfaction can be utilized in several contexts such as foraging (Nevitt 1999; Mardon et al. 2010), navigation (Holland et al. 2009; Gagliardo et al. 2011), kin recognition/inbreeding avoidance (Krause et al. 2012; Bonadonna & Sanz-Aguilar 2012), nest recognition (Bonadonna et al. 2004; Caspers & Krause 2010), species recognition (Hagelin et al. 2003; Bonadonna & Mardon 2010) and predator avoidance/parasite defence (Shawkey et al. 2003; Zidar & Løvlie 2012) among others (reviewed in: Campagna et al. 2012). Furthermore, there is evidence that chemical signals may be important in mate choice and mate recognition in birds (Hagelin 2007; Jouventin et al. 2007; Hirao et al. 2009; Mardon & Bonadonna 2009).

Satin bowerbirds are an ideal model for studying the use of complex displays in female choice as they exhibit a non-resource-based mating system, suggesting that females choose males based on genetic benefits (e.g. Trivers 1972; Zahavi 1975). The sexual display of male satin bowerbirds is multifaceted, involving the formation of a bower, gathering and arranging of decorations, and dynamic courtship displays consisting of diverse vocalizations and choreographed movements (e.g. Borgia 1985b; Loffredo & Borgia 1986; Patricelli et al. 2002; Coleman et al. 2004, 2007). Furthermore, several of these display traits are correlated with male mating success, including number of blue decorations, quality of bower construction and bower stick density (e.g. Borgia 1985b). Satin bowerbirds exhibit a mate-searching process in which most females narrow down their pool of potential mates throughout the season, visiting male bowers for first courtships and returning for second courtships before finally deciding to copulate with a male (Uy et al. 2001). Because experimental evidence demonstrates that the alteration of certain male display traits can affect these female search patterns (Coleman et al. 2004), it is not surprising that males assess their own displays and invest substantial time in maintenance of displays; males rapidly rebuild bower walls that were destroyed by competing males (Borgia 1985a), they remove inappropriate items from their bower platform while seeking out highly desired objects as decorations (Borgia & Keagy 2006), and they adjust the intensity of their courtship displays depending on female comfort level (Patricelli et al. 2004).

In this study, we used several tests to examine two hypotheses for the function of bower paint. First, the 'paint quality hypothesis' proposes that females assess bower paint by evaluating the paint's composition, which may provide information about the bower owner such as genetic compatibility or quality. The 'paint quality hypothesis' predicts that males should recognize and respond to 'foreign' paint (i.e. the paint of other males) on their bowers by painting over or removing foreign paint. However, the degree to which a male responds to foreign paint may vary depending on what type of information is provided by the paint's composition. For instance, if paint composition reflects male quality, we predicted that males would show a greater response to foreign paint from lower-quality males than from higher-quality males. On the other hand, if paint composition reflects male genetic composition, we predicted that all males, regardless of the quality of the paint donor, would respond similarly to foreign paint. We tested these predictions using an experiment in which painted sticks were transplanted among adult male bowers. Because assessing female response to these transplants was impractical, we instead assessed how males responded to the experimental addition of foreign paint. This kind of test is appropriate in species like bowerbirds, in which males construct off-body displays to attract females, and hence where the males' behaviour should be a good indicator of female preferences (Borgia & Keagy 2006).

Second, the 'paint quantity hypothesis' proposes that females utilize bower paint in mate choice decisions by assessing paint quantity. As with several other male display traits, there is substantial variation in the quantity of paint on male bowers (R. E. Hicks, personal observation). It is possible that this variation in paint quantity reflects differences in male quality, as has been demonstrated with other display traits such as quality of bower construction and number of particular bower decorations (Borgia 1985b). Males that have more paint may be of higher genetic quality, as they must be able to invest more time and effort into maintaining this display trait. The 'paint quantity hypothesis'

predicts that the quantity of bower paint should correlate with male quality, with male mating success, and with the quality of other display traits known to be important in mate choice. We tested these predictions using comprehensive observational data, which was collected over the course of an entire mating season. The 'paint quantity hypothesis' also predicts that, in response to a reduction in paint quantity, males should increase painting effort in order to replace the lost paint. Similarly, the 'paint quantity hypothesis' predicts that females should also respond to paint reduction by choosing not to receive courtships or copulations from males whose paint has been reduced. We tested these two predictions using a bower washing experiment in which paint was repeatedly removed from bowers during the peak mating season. This is the first study to use an experimental approach to examine how bower paint may affect female behaviour and the first to propose and test multiple hypotheses for the function of bower paint.

METHODS

Bird Banding and Behavioural Monitoring

This research was conducted at Wallaby Creek, New South Wales, Australia in 2008 and 2009. Prior to the start of the mating season, birds were caught at baited traps and banded with a unique combination of three colour bands and a numbered metal band (Borgia 1985b). In our study population, all bower-holding adult males and most females are banded, allowing for accurate identification of individuals from video recordings. Birds were also scored for plumage characteristics, which allowed for the determination of sex and approximate age of most individuals (Vellenga 1980). In addition, mass, number of ectoparasites and tarsus length were also measured (Borgia 1986; Borgia & Collis 1989). We calculated an index of body condition using: mass/(mean tarsus length)^3.

Behavioural monitoring of all bower sites was performed throughout the mating season for 29 adult bowers in 2008 and for 30 adult bowers in 2009 (34 different males across these 2 years). Automatic video-monitoring systems triggered by infrared detectors (Borgia 1995b) recorded all behaviours that occurred at bowers between 31 October and 20 December in 2008 (ca. 2176 h) and between 25 October and 19 December in 2009 (ca. 3832 h). The camera set-ups were checked at least twice daily to assure that all behaviours were captured. This set-up allows for a comprehensive record of male mating success for all bower-owning males in the population, a measure that provides an accurate estimate of male reproductive success in our system (Reynolds et al. 2007). Counts of decorations and assessment of bower quality made during each bower visit were used to calculate season averages. To assess overall bower quality, bowers were evaluated for symmetry of structure, stick size, stick density and overall quality of construction, where bowers of the highest quality were symmetrical, and had fine straight sticks, densely placed sticks and thick curved walls (Borgia 1985b).

Ethical Note

Care was taken to minimize disturbance and adverse effects to birds during experimentation and handling. Satin bowerbirds were captured using baited traps and removed immediately (Borgia 1986; Borgia & Collis 1989). Traps were continuously monitored by a researcher approximately 20 m away between 0530 and 1200 hours, except during heavy rains. Traps were accessible to birds only during these observation times. The captured birds were colour-banded, weighed, measured for wing and tarsus length, had plumage characteristics scored, and released immediately (Borgia 1986; Borgia & Collis 1989). Birds in our study population have been handled frequently in previous years, and most readily return to the traps after release (Collis & Borgia 1993). These procedures were approved by the Institutional Animal Care and Use Committee of the University of Maryland (protocol R-08-79).

Paint Quantity Measurements

In 2009, we randomly assigned adult males to one of four bower sample locations: northeast wall; southeast wall; northwest wall; southwest wall. For each bower, we assessed the quantity of bower paint by taking two measurements. First, we measured the length (cm) of paint on the 10 consecutively placed sticks within the assigned sample location. Second, we scored the thickness of bower paint from 1 to 3 in half-point intervals (1 = thin; 3 = thick). An observer visually examined the 10 consecutively placed sticks within the sample location, then scored the overall thickness of the bower paint. Prior to data collection, the observer performed a blind test to ensure repeatability of paint thickness scores. When multiple measures of paint thickness and length were taken, averages were calculated. These two measures of paint quantity were significantly correlated (Spearman rank correlation: $r_S = 0.452$, $N = 29$, $P = 0.014$). To investigate whether quantity of paint is correlated with other bower display traits, we performed principal component analysis to create a summary variable for four bower and decoration display traits that have been shown to be important in mate choice (i.e. bower stick density, quality of bower construction, number of blue feather decorations and number of snail shell decorations). We performed principal component analysis on these four variables and used the first principal component, PC1 (which explained 66.4% of the total variance), as an index for overall bower and decoration display quality (Table 1).

Paint Removal Experiment

We performed a paint removal experiment to determine how males and females respond to removal of bower paint. Using measurements of bower quality and number of blue blossom decorations (two indicators of mating success), we made paired comparisons of adult bower-owning males to maximize similarity in these display traits (Borgia 1985b). Within each dyad, the bower of one male (washed male) was randomly selected to receive the paint removal treatment, where we removed paint by spraying sticks with 500 ml of water and gently brushing away visible paint for approximately 5 min. Following the protocol used in Bravery et al. (2006), we used a clear plastic sheet with a 2 cm grid to measure the amount of paint on bower walls before and after the wash treatment to confirm that paint was indeed removed. We found that bower washing removed over 99.5% of visible paint on bower walls. The bower of the other male (control male) in the dyad received the control treatment, where the unpainted sticks on the outer bower walls were washed for approximately 5 min with 500 ml of water, leaving the paint on the inner bower walls undisturbed. Because males paint more frequently in the morning (Bravery et al. 2006), nearly all paint removal and control

Table 1
Factor loadings for the first principal component from a principal component analysis of four bower display traits in satin bowerbirds

Variable	Loading
Bower density	0.880
Quality of bower construction	0.830
Number of blue feathers	0.830
Number of snails	0.710

treatments were performed between 0600 and 10 000 hours Australian Eastern Daylight Time (AEDT). In a similar experiment performed by Bravery et al. (2006), males showed no response to bower washing, but it was unclear whether this lack of response was due to paint removal being performed only once. Therefore, in the present study, bower washing was repeated daily from 9 November to 15 December 2008. To identify the sex of birds that received courtships at washed and control bowers, we used plumage characteristics of courted birds (Vellenga 1980) and a list of known females in the population based on behavioural data (e.g. receiving copulations) from our video records from previous seasons and during the years of this study.

To examine female response to paint removal, we first categorized females based on the type of visit they made to each male (i.e. females that visited a male only once for a first courtship (first courtship), females that visited a male more than once (return courtship) and females that copulated with a male (copulation)). Next, we counted the total number of females that visited washed and control males for first courtships, return courtships or copulations. If females respond to paint removal, we predicted an association between type of male visited (control or washed) and type of female visit, with washed males having fewer females visiting for return courtships and copulations than controls. To assess male response to paint removal, we compared painting rate of control and washed males over 2 days during the paint removal experiment.

Paint Transplant Experiment

We performed a paint transplant experiment between 1 November and 12 December 2009 to assess how males respond to transplants of another male's paint into his bower. Adult males received a transplant of painted sticks between 0600 and 1000 hours AEDT. First, male bowers were paired based on their proximity to one another to minimize paint degradation during transfer. Within each pair, one bower was assigned the donor and the other was assigned the recipient. Recipient bowers were then randomly designated a treatment location on either the east or west bower walls. During transplants, 10 sticks with the most and freshest paint were selected from the inside walls of the donor bower and transplanted to the assigned treatment location within the recipient bower. To control for handling of sticks, the 10 sticks in the area opposite the treatment location (i.e. the control location) were pulled out and immediately replaced, making sure not to disturb paint on these sticks. Following the transplants, we measured the length of paint in control and treatment locations to confirm that there was no difference in the length of paint on the donated sticks in the treatment location and on the sticks in the control location (Wilcoxon signed-ranks test: $Z = 0.395$, $N = 23$, $P = 0.693$).

To determine male response to paint transplants, we analysed how males behaved during the first painting bout following the transplant. In particular, we noted whether males manipulated or removed transferred sticks containing paint from another individual. We also noted whether males placed their first paint stroke on the treatment wall to determine whether males preferentially placed their first paint stroke in the section of the bower containing foreign paint. Finally, we compared the number of paint strokes applied on sticks in the treatment location to the number of paint strokes applied on sticks in the control location. This comparison is only informative if there is naturally no asymmetry in bower painting behaviour. To test this assumption, we measured the size of east and west walls and the proportion of east and west walls covered in paint, using a clear plastic sheet with a 2 cm grid held up to the inside bower walls (see protocol in: Bravery et al. 2006). We also counted the number of paint strokes applied to east and west walls during normal painting bouts. Analysis of these measurements demonstrated that there was no asymmetry in the size of east and west walls (Wilcoxon signed-ranks test: $Z = 0.723$, $N = 26$, $P = 0.469$), in the amount of paint on east and west walls ($Z = 1.373$, $N = 26$, $P = 0.170$) or in the number of paint strokes applied to east and west walls ($Z = 0.538$, $N = 26$, $P = 0.590$).

Statistical Analyses

Number of paint strokes, one measure of male painting effort, was collected using JWatcher v.1.0 software (http://www.jwatcher.ucla.edu). Post hoc calculations of effect sizes and their associated 95% confidence intervals were performed for tests with $N < 23$. Confidence intervals for the Spearman rank correlation were determined using the Fisher transformation. The effect size for the Mann–Whitney U test and the Wilcoxon signed-ranks test was determined using Cliff's delta and was analysed in R v.2.15.1 (R Foundation for Statistical Computing, Vienna, Austria). All other data were analysed using Statistica v.6.0 (Statsoft Inc., Tulsa, OK, U.S.A.). All tests are two tailed.

RESULTS

Relationship of Paint Quantity with Mating Success and Bower Display

Because quantity of paint on sampled sticks was correlated with several other bower display traits important to mate choice (Table 2), we calculated PC1 as a summary variable for these other display traits and as an index of overall bower and decoration display quality. PC1 was highly correlated with length of bower paint (Spearman rank correlation: $r_S = 0.574$, $N = 29$, $P = 0.001$) and thickness of bower paint ($r_S = 0.465$, $N = 29$, $P = 0.011$; Fig. 2a, b). However, there was no significant correlation between mating success and length of paint ($r_S = 0.228$, $N = 29$, $P = 0.234$) or thickness of paint ($r_S = 0.021$, $N = 29$, $P = 0.914$).

Female Response to Paint Removal

We tested whether females were affected by the repeated reduction in paint quantity at male bowers. There was a significant association between type of male visited (i.e. control or washed male) and type of female visit (i.e. first courtship, return courtship or copulation), with fewer females returning for second courtships with washed males compared to control males (chi-square test: $\chi^2_1 = 8.89$, $P = 0.003$) and fewer females copulating with washed males than control males (chi-square test: $\chi^2_1 = 7.10$, $P = 0.008$; Fig. 3).

Male Response to Paint Removal

We also tested whether males adjust their painting effort in response to paint removal. We found no difference in painting rate

Table 2
Spearman rank correlations between the two measures of bower paint quantity and four other male display traits in satin bowerbirds

Display trait (N=29)	Paint length		Paint thickness	
	r_S	P	r_S	P
Stick density	0.466	0.011	0.558	0.002
Quality of bower construction	0.39	0.035	0.360	0.055
Feathers	0.620	0.000	0.491	0.007
Snails	0.419	0.024	0.194	0.313

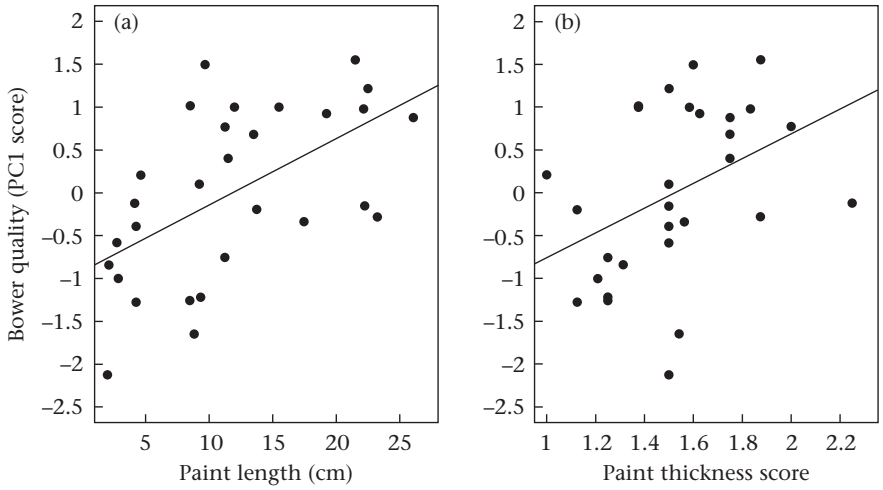

Figure 2. (a) Relationship between paint length and overall bower and decoration display quality of satin bowerbird bowers as indicated by PC1. (b) Relationship between paint thickness and overall bower and decoration display quality as indicated by PC1. A higher PC1 score indicates better bower and decoration display quality.

between control males and washed males (Wilcoxon signed-ranks test: $Z = 0.175$, $N = 14$, $P = 0.862$, Cliff's delta $= -0.214$, 95% CI: -0.652, 0.330).

Relationship of Paint Quantity with Male Quality

We tested whether the quantity of paint was related to male physical condition, one aspect of male quality. The 'paint quantity hypothesis' posits that paint quantity is related to measures of male condition, but we found no correlation between male condition and paint length (Spearman rank correlation: condition index: $r_S = -0.102$, $N = 12$, $P = 0.753$, 95% CI: 0.639, 0.501; parasites: $r_S = -0.294$, $N = 12$, $P = 0.353$, 95% CI: -0.742, 0.337) or between male condition and paint thickness (condition index: $r_S = -0.299$, $N = 12$, $P = 0.346$, 95% CI: -0.745, 0.332; parasites: $r_S = -0.110$, $N = 12$, $P = 0.735$, 95% CI: -0.643, 0.495).

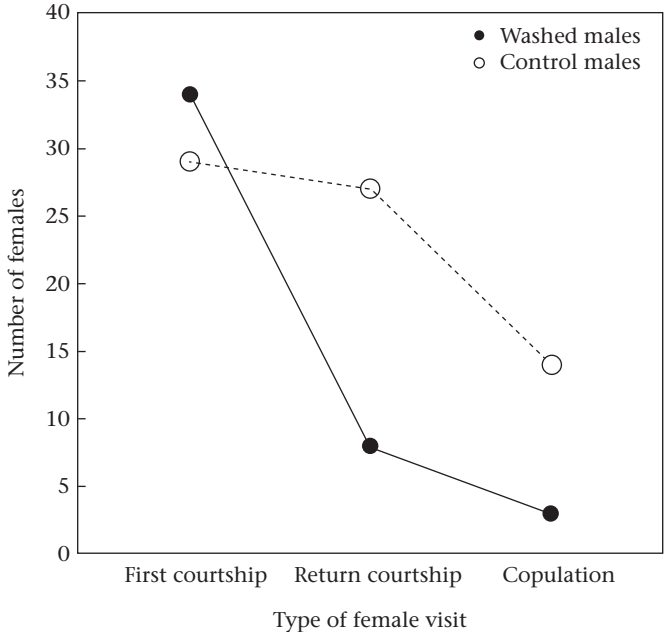

Figure 3. Association between type of female visit and type of male bower visited (i.e. control or washed) during bower paint removal experiment.

Male Response to Paint Transplant

We tested whether males respond to paint from another individual by determining how they reacted when donated paint was transferred to one of their bower walls. We found no difference in the amount that males painted on the wall where paint was transferred versus the control wall (Wilcoxon signed-ranks test: $Z = -0.213$, $N = 23$, $P = 0.416$). Also, males did not place their first paint stroke on the wall with transplanted sticks more often than expected by chance ($\chi^2_1 = 0.044$, $P = 0.835$). Furthermore, none of the 23 males that received paint transplants removed or repositioned transplanted sticks. Additionally, males that received paint transplants from lower-quality individuals and those that received paint transplants from higher-quality individuals did not differ in the degree to which they painted over transplanted paint (Mann–Whitney U test: $U = 33.5$, $N_1 = 12$, $N_2 = 9$, $P = 0.148$, Cliff's delta $= 0.380$, 95% CI: -0.143, 0.737).

DISCUSSION

Several lines of evidence from this study indicate an important role of bower paint in female mate choice. In particular, our results confirmed two of the predictions made by the paint quantity hypothesis. First, we found that females preferentially returned to and copulated with males from control bowers, confirming our prediction that males experiencing a daily reduction in the quantity of bower paint have fewer returning visitors and fewer mates (Fig. 3). This result also provides the first experimental evidence that females use paint in the mate-searching process and in mate selection. Also, we found that paint length and paint thickness were significantly correlated with overall bower and decoration display quality (i.e. PC1), confirming another prediction made by the paint quantity hypothesis (Fig. 2a, b). This result suggests that the quantity of bower paint and the traits that explain PC1 (i.e. quality of bower construction, bower stick density, number of blue feathers and number of snail shells) may provide similar information to searching females.

Despite this evidence that paint quantity is important to mate choice, we detected no correlation between paint quantity and male mating success. We believe this may occur if females assess paint during first courtships in order to decide which males to return to for second courtships and, consequently, which males to retain in their pool of potential mates. However, these returning

females may use other display traits in their later decision to return for further courtship and mating (see Coleman et al. 2004). The display traits that females assess during these return courtships may be the same bower and decoration traits represented by PC1 (i.e. bower stick density, quality of bower construction and number of blue feather and snail shell decorations), as these traits are highly correlated with mating success (Borgia 1985b). The value of bower and decoration traits as predictors of male mating success may change as courtship and the mating season progress. For instance, early in the mating season, bower and decoration traits are often degraded due to higher stealing and destruction rates (see Borgia 1985a; Borgia & Gore 1986; R. E. Hicks, personal observation). Furthermore, because painting rates are higher earlier in the mating season (Bravery et al. 2006) and because females sample paint more in the earlier stages of the mate-searching process (Cendes 2009), paint may play a particularly important role early in the season when other traits are less reliable.

Considering this, females may assess paint early in the season in order to decide which bowers to return to for second courtships, since bower and decoration display traits may be less informative at this time. Later in the season, during return courtships, females may assess bower and decoration displays in order to decide with whom to copulate. Thus, bower paint may be a signal involved in the sequential assessment of display traits; this sequential assessment of multiple display traits has been demonstrated in spotted bowerbirds, *Chlamydera maculata*, and in other taxa (e.g. Borgia 1995a; Gibson 1996; Shine & Mason 2001; Leonard & Hedrick 2010). This pattern would explain why we found a strong correlation between paint length and PC1, but no significant correlation between paint length and male mating success.

Given this explanation, however, males might still be expected to respond to a reduction in quantity of bower paint, but males in our study did not adjust their painting effort in response to paint removal. It is possible that males may already invest the maximal amount of time in painting and therefore were unable to respond to paint removal by increasing the rate at which they painted. Similarly, we would also expect the quantity of bower paint to be correlated with measures of male condition and quality, but this was not the case. It is likely though that we were unable to detect an effect because of relatively small sample sizes for these two tests.

Finally, we found that males did not respond to transplants of painted sticks from other individuals, a result consistent with findings from Bravery et al. (2006), but inconsistent with our predictions of the paint quality hypothesis. If paint composition reflects male genetic composition, then all males should have responded to paint transplants regardless of the quality of the donor male. Alternatively, if paint composition indicates male quality, then males that received paint transplants from individuals of lower quality should have responded more to transplanted paint than males receiving transplants from higher-quality individuals. We found no evidence of either pattern and were therefore unable to verify this prediction of the paint quality hypothesis. It is possible that the absence of a male response to transplanted paint could result if males cannot detect the foreign paint. This might occur for several reasons, including males not sampling their own paint or a low probability of finding the sticks containing foreign paint. Although the tests we performed did not confirm our predictions of the paint quality hypothesis, we cannot rule out the possibility that females sample paint to assess its composition. In fact, the observation that females sample paint by nibbling and swallowing it does suggest that females may be able to assess paint composition. Chemical analysis of bower paint will be necessary, however, to determine whether paint composition provides information about the male and to examine the paint quality hypothesis more comprehensively. In particular, determining whether the chemical composition of paint could reflect variation in male quality or could serve as an individual-specific signal would provide further insights into the function of bower paint.

Using several approaches and a comprehensive record of mate-searching behaviour and mating success, we tested multiple predictions of the paint quantity hypothesis and the paint quality hypothesis. Our results did not verify our predictions of the paint quality hypothesis, although further analyses are needed to test this hypothesis more rigorously and to determine whether females gain information about a male by assessing the chemical composition of his paint. Alternatively, our results support the paint quantity hypothesis by confirming two of its predictions. We provide the first experimental evidence that female search patterns are strongly influenced by bower paint; paint removal affected mate-searching females' return visits to male bowers, establishing that paint is involved in the mate-searching process.

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