ABSTRACT

Title of Document: REMOVAL OF BOWER PAINT REDUCES MATE SEARCHING FEMALES' RETURN VISITATION TO MALE BOWERS

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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 unusual behaviors, bower painting, has received little attention. Here, I propose two hypotheses for the function of paint and use multiple approaches to test predictions made by these hypotheses. First, I assessed how natural variation in paint quantity is related to other display traits, male mating success and male physical condition. Also, I used experimental methods including a paint removal and paint transfer experiment to investigate how birds responded to changes in the quantity and quality of bower paint. I found that males with more paint had better overall bower display quality and that fewer females returned to and copulated with males whose paint was removed. These results suggest that females may assess paint quantity during mate searching and demonstrate that paint influences male attractiveness.

REMOVAL OF BOWER PAINT REDUCES MATE SEARCHING FEMALES' RETURN VISITATION TO MALE BOWERS

By

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Thesis submitted to the Faculty of the Graduate School of the
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Advisory Committee:
Professor Gerald Borgia, Chair
Professor Steven Brauth
Professor Marjorie Reaka

Preface

This thesis contains a single chapter presented in manuscript form, including summary, introduction, methods, results, discussion and synthesis sections, followed by figure/table captions and figures/tables. A bibliography section is included at the end for references cited throughout the thesis.

Dedication

This thesis is dedicated to my parents, Kathryn T. Cryan-Hicks and Philip H. Hicks Jr. who inspire me with their love, support and value of education.

Acknowledgements

I would like to thank my thesis advisor, Gerald Borgia, for guidance and training throughout my thesis research. A special thanks to Archer Larned for assistance in collecting some of the data utilized in this thesis. I would also like to thank other past and present students in the Borgia lab for their insights and support: Jean-François Savard, Brian Coyle, Jason Keagy, Linda Cendes and Sheila Reynolds. Thanks also to my advisory committee for their time, consideration and helpful comments.

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SUMMARY

The multifaceted courtship display of male satin bowerbirds (*Ptilonorhynchus violaceus*) involves several elements that have been studied in detail including bower construction, decoration display and vocal mimicry. However, one of their most unique display elements, bower painting, has received relatively little attention despite males' large investment of time in this behavior. I used both behavioral observations and experimental approaches to examine predictions made by two hypotheses for the function of bower paint. I measured natural variation in paint quantity to investigate whether quantity of paint at bowers was related to other male display traits, male mating success and male physical condition. I also investigated how both males and females were affected by experimental removal of bower paint. Additionally, I assessed male response to paint transplants from other individuals. I found a significant correlation between 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 controls. This result provides the first experimental evidence that females respond to bower paint. I did not find evidence that males respond to the transfer of paint from another individual. These findings demonstrate that bower paint is a trait that affects mate-searching decisions by females and suggests that the quantity of bower paint may be important in attracting females.

INTRODUCTION

Complex, multi-faceted displays in the context of mating are common especially in polygynous species and in birds (Møller and 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. Reusch et al., 2001; Kotiaho et al.,1996; Lindstrom and Lundstrom, 2000; Boogert et al., 2008). Often though, the exact information provided by a behavior or potential signal is unknown. If these behaviors are suspected to be 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.

Satin bowerbirds (*Ptilonorhynchus violaceus*) are an ideal model for studying the use of complex displays in female choice. Bowerbirds exhibit a non-resource based mating system in which females acquire only sperm from males. Males do not provide material benefits such as parental care, suggesting that females choose males based on genetic benefits as in good genes selection, compatible genes selection or runaway selection (Zahavi, 1975; Trivers, 1972; Zeh and Zeh 1996; Fisher, 1930; Lande 1981). The sexual display of male satin bowerbirds is multi-faceted, 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, 1985*b*; Patricelli et al., 2002; Borgia and Loffredo, 1986, Coleman et al., 2007, Coleman et al., 2004). Although satin bowerbirds have a lek-like mating system, male bowers are typically separated by at least 100m, so single females search males individually. This eliminates confounding factors such as simultaneous assessment of multiple males or copying of mate choice by females. 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).

Several male display traits have been shown to correlate with mating success, including number of blue decorations, quality of bower construction, bower stick density and mimetic repertoire (e.g. Borgia, 1985*b*; Coleman et al., 2007). Experimental evidence also demonstrates that the alteration of certain male display traits can affect female search patterns, further establishing that these traits are important signals to females (Coleman et al., 2004). Therefore, it is not surprising that males assess their own displays and invest substantial time in maintenance of display; males rapidly rebuild bower walls that were destroyed by competing males, they remove inappropriate items from their bower platform while seeking out highly desired objects as decorations (Borgia and Keagy, 2006), and they adjust the intensity of their courtship display depending on female comfort level (Patricelli et al., 2004). Although several components of the mating display of satin bowerbirds have been studied at length, one of the most unusual behaviors 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 inside bower walls. Some females that visit the bower during the mating season sample this paint by nipping at and swallowing it, suggesting that paint may be a signal that is utilized in mate choice. A few studies have investigated the potential significance of painting to mate choice. Cendes (2009) examined how female tasting of bower paint was related to factors that reflect her certainty of mate choice. Results from Cendes (2009) showed that females sample paint more often early in the mate searching process and that females who appeared uncertain of their mate choice (e.g., females that visited many males) tended to sample paint later in the mate searching process as well. Robson et al. (2005) quantified several male display traits and behaviors in order to determine which display traits best predicted mating success. They found that male painting rate significantly predicted mating success. However, in order to facilitate data collection, only high quality males who received several visitors were utilized in Robson et al.'s study, so it is unclear whether this effect is present when considering bower-holding males of poorer quality as well. Furthermore, for the subset of males that was considered in Robson et al.'s study, mating success was only measured for a fraction of the mating season. A more detailed account of bower painting is provided by Bravery et al. (2006), who found that males painted 24% of the total time spent at their bower and that tasting of bower paint occurred at 39% of courtships. A bower-washing experiment was also performed in Bravery et al.'s study to determine if males responded to a single instance of removal of bower paint. They found no effect of this manipulation on male behavior, though male behavior was only assessed during two hours following the paint removal. It is possible that the response was not detected over this short time period. Also, because paint removal was only performed once, one could not determine how this manipulation of bower paint affected mate-searching females. Additionally, Bravery et al. (2006) found that males whose bowers were supplemented with freshly painted sticks showed no change in male painting or stick removal behavior.

In this study, I examined two main hypotheses for the function of bower paint using several approaches that allow for a more detailed and comprehensive examination of this trait. First, the ‘paint quantity hypothesis’ suggests that females utilize bower paint in mate choice decisions by assessing the quantity of bower paint. 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. Consequently, this hypothesis predicts that females share a preference for males that have the greatest quantity of bower paint resulting in a correlation between paint quantity and male mating success. Similarly, the paint quantity hypothesis predicts that amount of paint correlates with other display traits known to be important in mate choice and with male quality. Additionally, this hypothesis predicts that in response to a reduction in paint quantity, males should increase painting effort in order to replace the lost paint. Finally, we would expect females to also respond to reduction in paint quantity by choosing not to receive courtships or copulations from males whose paint has been removed or reduced in quantity.

Second, the ‘paint quality hypothesis’ suggests that females assess male quality as indicated by bower paint by evaluating the paint’s composition. The fact that searching females sample paint by nibbling and swallowing it suggests that they may be able to evaluate its composition. Females may gain a variety of types of information from assessing the composition of paint, so I present two forms of this hypothesis. One form, the ‘best quality hypothesis’, suggests that the composition of paint may indicate male genetic quality. The ability for chemical composition, for example, to indicate aspects of male quality such as physical condition, genetic heterozygosity and sperm fertility has been demonstrated in several taxa (e.g. Martin et al., 2007; Charpentier et al., 2008; Giaquinto et al., 2010; Ruther et al., 2009). The best quality hypothesis suggests that variation in paint composition reflects variation in male quality. According to this hypothesis, females should assess paint composition in order to find males with the best genetic quality. This hypothesis predicts that males whose bowers contain paint from an individual of lower quality should attempt to paint over or remove sticks with foreign paint while this would not be expected for males whose bowers contain paint from higher quality individuals.

The ‘individual-specific quality hypothesis’, suggests that the composition of paint is an individual signature that provides females with information about the suitability of that male’s unique genetic profile if he is chosen as a mate. This information might benefit the female by allowing her to match or avoid similar relatedness or MHC profiles. In this case, a female may not share preferences with other females for a particular male but instead should use a male’s individual signature to find a genetically compatible mate (e.g. Charpentier et al., 2010; Aeschlimann et al., 2003; Setchell et al., 2011; Conrad et al., 2010; reviewed in: Setchell and Huchard, 2010). According to the individual-specific quality hypothesis, males should show a predictable pattern of response to the presence of another individual’s paint regardless of the quality of that other individual. For instance, if it’s important to advertise truthfully, males should respond by attempting to paint over sticks containing paint from another individual, by painting first on sticks containing another male's paint or by removing sticks with foreign paint. This type of response would suggest that the presence of another individual's paint is detrimental to the male perhaps by deterring compatible females from mating with him. In contrast, a male may respond to foreign paint by painting more or painting first on sticks that do not contain another individual's paint (i.e., the male may avoid painting over the foreign paint). This type of response would suggest that the presence of another individual's paint is somehow beneficial to males perhaps by attracting incompatible females who would have otherwise not preferred that particular male's paint. In either case, assuming that males can recognize paint from another individual, the absence of a response to foreign paint would suggest that paint does not act as an individual-specific signal.

I examined the 'paint quantity hypothesis' using four approaches that test predictions made by this hypothesis. First, I investigated whether paint quantity is related to male mating success using a complete record of mating success for all bower-owning, adult males in the population. Second, I examined if paint quantity is related to other display traits that predict mating success. Third, I performed a paint removal experiment to determine how males and females respond to a reduction in quantity of bower paint. For all bowers, paint removal was performed daily for 37 days during the peak mating season thus allowing us to determine how female mate-searching decisions were affected by paint reduction. Fourth, I tested whether paint quantity correlates with male physical condition, one aspect of male quality.

Additionally, I addressed the paint quality hypothesis by assessing how males respond to the experimental addition of another individual's paint to their bower. This is the first study to use an experimental approach to examine how bower paint may affect females and the first to address the importance of paint in the context of hypotheses for the function of bower paint.

METHODS

Bird Banding and Behavioral 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 color bands and a numbered metal band (Borgia, 1985*b*). 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 and Collis, 1989). I calculated an index of body condition using $mass/(mean\ tarsus\ length)^3$ and calculated tarsus asymmetry as *(left tarsus length-right tarsus length)/mean tarsus length*, such that a value of 0 signifies no asymmetry. Behavioral monitoring of all bower sites was performed throughout the entirety of the mating season for 29 adult bowers in 2008 and 30 adult bowers in 2009. Automatic video monitoring systems triggered by infrared detectors (Borgia 1995*b*) recorded all behaviors that occurred at bowers between October 31 and December 20 in 2008 (approx. 2176 hours) and between October 25 and December

19 in 2009 (approx. 3832 hours). The camera setups were checked at least twice daily in order to assure that all behaviors were captured. Counts of decorations and assessment of bower quality made during each bower visit were used to calculate season averages (Borgia, 1985*b*). This setup allows for a comprehensive record of male mating success, a measure that provides an accurate estimate of male reproductive success in our system (Reynolds et al., 2007).

Paint Length Measurements

In 2009, each adult male was randomly assigned one of four sample locations: east wall toward the north end, east wall toward the south end, west wall toward the north end or west wall toward the south end. For each bower, I assessed the quantity of bower paint by taking two measurements. First I measured the mean length (cm) of paint on 10 sticks from the assigned sample location. Second, I scored the thickness of paint in the sample location from 1-3 in half point intervals. These two measures of paint quantity were significantly correlated with each other (r_s= 0.452, N=29, P= 0.007), so I chose to use only length of paint as my measurement to reflect overall quantity of paint at bowers. To investigate whether length of paint correlates with other bower display traits, I created 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). I performed principal component analysis on these four variables and used the first principal component, PC1 as an index for overall bower and decoration display quality (Table 1).

Paint Removal Experiment

A paint removal experiment was performed from Nov. 9 to Dec 15, 2008 to determine how both males and females responded to the removal of bower paint. Using measurements of bower quality and number of blue blossom decorations (two indicators of mating success), adult bower-owning males were paired in order to maximize similarity in these display traits (Borgia, 1985*b*). Within each dyad, one male (washed male) was randomly selected to receive the paint removal treatment, where paint was removed by spraying sticks with 500ml of water and gently brushing away visible paint for approximately five minutes. Following the protocol used in Bravery et al. 2006, I measured the amount of paint on bower walls before and after the wash treatment to confirm that paint was indeed removed. I found that bower washing removed on average 99.98 % of visible paint on bower walls. The other male (control male) in the dyad received the control treatment in which sticks on the outside bower walls, that are not painted, were washed in a similar fashion, ensuring that the paint on inside bower walls was left undisturbed. Because males paint more frequently in the morning (Bravery et al., 2006; R. Hicks, *personal observations*), paint removal and control treatments were performed between 6 AM and 10 AM AEDT for most days (due to technical problems or poor weather conditions, 14 of the 1,036 treatments performed occurred between 10 AM AEDT and 1PM AEDT instead).

I used this experiment to test the paint quantity hypothesis, predicting that males and females should be affected by repeated reduction in bower paint quantity. Because juvenile males and females have similar plumage, I was unable to determine the sex of all individuals who received courtships. Consequently, I addressed the question of whether or not females respond to removal of bower paint by analyzing how female-plumaged birds were affected by paint removal. This classification excludes birds that had female plumage but demonstrated behaviors during any part of the mating season that distinguished them as juvenile males.

To examine the response of females to paint removal, I first categorized females based on the type of visit they made to each male (i.e., females that only visited a male once for a first courtship (first courtship), females that visited a male for more than one courtship (return courtship) and females that copulated with a male (copulation). Next, I 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'd predict 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, I compared painting rate of control and washed males over two days during the paint removal experiment.

Paint Transplant Experiment

A paint transplant experiment conducted between Nov. 11 and Dec. 12, 2009 was used to assess how males respond to transplants of another male's paint into his bower. Adult males experienced a transplant of painted sticks performed between 6 AM and 10 AM AEDT. First, male bowers were paired based on proximity to one another in order to minimize paint degradation during transfer. Within each pair, one bower was assigned as the donor while the other was assigned as the recipient.

Recipient bowers were then randomly designated a treatment location on either the east or west bower walls.

In paint transplants, ten 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 ten 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 these transplants, I measured the length of paint in control and treatment locations to confirm that there was no difference in the length of paint on donated sticks in the treatment location vs. sticks in the control location (Wilcoxon Matched Pairs test: $Z=0.395$, $N=23$, $P=0.693$).

To determine male response to paint transplants, I analyzed how males behaved during the first painting bout following the transplant. In particular, I noted whether males manipulated or removed transferred sticks containing paint from another individual. I also noted whether males placed their first paint stroke on the wall containing the transferred paint to determine if males preferentially placed their first paint stroke in the treatment location. Finally, I compared number of paint strokes applied on sticks in the treatment location to 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 behavior. In order to test this assumption, we measured the size of east and west walls and the proportion of east and west walls covered in paint following the protocol used 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 Matched Pairs test: Z=0.723, N=26, P=0.469), in the amount of paint on east and west walls (Wilcoxon Matched Pairs test: Z=1.373, N=26, P=0.170) or in the number of paint strokes applied to east and west walls (Wilcoxon Matched Pairs test: 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 (Copyright 2000-2010--Daniel T. Blumstein, Janice C. Daniel, and Christopher S. Evans), and all data were analyzed using Statistica 6.0 (Statsoft Inc. Tulsa, OK, U.S.A). Tests are two-tailed unless predictions were made *a priori*.

RESULTS

Relationship of Paint Length with Mating Success and Bower Display

Because length of paint on sampled sticks was correlated with several other bower display traits important to mate choice (Table II), I calculated PC1 as a summary variable for these other display traits and as an index for overall bower and decoration display quality. I found that PC1 was highly correlated with length of bower paint (r_S= 0.574, N=29, P=0.000) (Figure 1). However, I did not find a significant correlation between length of paint and mating success (r_S=0.228, N=29, P=0.117).

Female Response to Paint Removal

I tested whether females were affected by the repeated reduction in paint quantity. I found that there was a significant association between type of male visited (i.e. control or washed male) and type of visit by female (i.e. first courtship, return courtship or copulation), with fewer females returning for second courtships with washed males compared to control males (χ^2=8.89, df=1, P=0.003) and fewer females copulating with washed males than control males (χ^2=7.10, df=1, P=0.008) (Figure 2).

Male Response to Paint Removal

I also tested if males adjusted their painting effort in response to paint removal. I found there was no difference in painting rate between control males and washed males (Wilcoxon Matched Pairs test: Z=0.175, N=14, P=0.431).

Relationship of Paint Length with Male Condition

I tested if the length of paint was related to male physical condition, one aspect of male quality. The 'paint quantity hypothesis' would predict that paint length is correlated with measures of past and/or current male condition, but our results show no correlation between paint length and condition index, tarsus asymmetry or number of parasites (condition index: r_S=-0.102, N=12, P=0.377; tarsus asymmetry: r_S=-0.217, N=12, P=0.250; parasites: r_S=-0.294, N=10, P=0.177).

Male Response to Paint Transplant

I tested whether males responded to paint from another individual by determining how they reacted when donated paint was transferred to one of their bower walls. In the 23 paint transplants performed, 12 males received paint transplants from males of lower quality (i.e. lower PC1 scores). Within these 12 males, there was no difference in the amount that males painted on the treatment wall vs. the control wall (Wilcoxon Matched Pairs test: Z=0.622, N=12, P=0.267). Similarly, for all 23 males who received paint transplants, there was no difference in the amount that males painted on the wall where paint was transferred vs. the control wall (Wilcoxon Matched Pairs test: Z= -0.213, N=23, P=0.416). Also, males did not place their first paint stroke on the wall with transferred sticks more often than expected by chance (χ^2=0.044, df=1, P=0.835). Furthermore, none of the 23 males who received paint transplants removed or even repositioned transferred sticks.

DISCUSSION

I investigated the function and importance of bower paint using both experimental approaches and natural observations. Results of this study were not consistent with my predictions of the paint quality hypothesis. Instead, my results confirmed two of the predictions made by the paint quantity hypothesis. First, compared to control males, fewer females returned for second courtships and copulations with males whose paint was removed. Second, paint length was highly correlated with overall bower display quality.

The finding that washed males had fewer females return for second courtships and copulations is consistent with the ‘paint quantity hypothesis’ and also provides the first experimental evidence that female behavior is influenced by bower paint. This result demonstrates that quantity of bower paint is important since males that experienced daily reduction of bower paint quantity had fewer returning visitors and fewer mates. This result suggests that 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. It is likely that paint removal reduces the number of females returning for second courtships with washed males, which in turn results in a reduction in the number of females copulating with washed males.

Because I found that females responded to the reduction in paint quantity, I expected to see a response by males as well. My results do not indicate that males adjust their painting effort in response to paint removal since there was no difference in painting rate between control and washed males. It is possible that males may already be painting at their maximal rate and therefore were unable to respond to paint removal by increasing the rate at which they painted.

Paint length, my measure of total amount of paint applied to sticks, was significantly correlated with overall bower and decoration display quality (i.e., PC1), confirming a prediction made by the paint quantity hypothesis. This result suggests that the length of bower paint and the traits encompassed in PC1 (i.e. quality of bower construction, bower stick density, number of blue feathers and number of snail shells) may overlap in the information they provide to searching females.

Although I found a significant relationship between paint length and other display traits important in mate choice, I did not detect a correlation between paint length and mating success. The correlation between paint length and mating success was close to significant though, suggesting that females' assessment of paint length may have some influence on their mate choice decisions. Also, because I found that males whose paint was removed had fewer females return for copulations, it suggests that amount of paint does influence mating success. Given this result, the absence of a significant correlation between paint length and mating success is likely due, not to the unimportance of paint to mating success, but to the inability to detect an effect in this analysis.

In order to test another prediction of the paint quantity hypothesis, I examined the relationship between paint length and male physical condition, predicting a positive correlation between these factors. I did not find a correlation between paint length and any of my indicators of male physical condition. It is important to note that it's possible I did not detect the predicted correlation because of the limited sample size for these analyses (N=10 and N=12).

Finally, I found that males did not respond to transplants of painted sticks from other individuals. Males did not treat their own painted sticks differently from transferred, painted sticks, a result which is inconsistent with my prediction for the individual-specific quality hypothesis. Furthermore, males who received paint transplants from individuals of poorer quality did not attempt to cover up foreign paint, which is inconsistent with my prediction for the best quality hypothesis. This lack of response suggests that paint may not be an individual-specific signal.

Alternatively, the absence of a male response could result if males do not detect the foreign paint. This might occur for several reasons, including males not sampling their own paint or a low probability of finding the few sticks containing foreign paint. Although the tests I performed did not support the paint quality hypothesis, I cannot rule out the possibility that females sample paint in order 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. Further investigation including chemical analysis of bower paint may provide insights into the plausibility of the paint quality hypothesis.

SYNTHESIS

Several lines of evidence suggest an important role for bower paint in female mate choice. I found that females preferentially return to and copulate with males from control bowers, in which paint was not removed, demonstrating that females use paint in the mate searching process. The effect of paint removal on number of females returning for second courtships (and consequently number of females returning for copulations) may result from females using paint during first courtships to decide which males to return to for second courtships. Subsequently, during return courtships, females may use other display traits in their final mating decisions. 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 have been shown to correlate highly with mating success (Borgia, 1985*b*). Although these bower and decoration traits are related to mating success, they may not be reliable indicators early in the mating season, as they are often degraded due to higher stealing and destruction rates during this time (See Borgia, 1985*a*; Borgia and Gore, 1986, R. Hicks, personal observations). 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), it is likely that paint may play a particularly important role early in the season.

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 not be reliable or informative at this time. Subsequently, 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, as has been demonstrated in spotted bowerbirds and other taxa (e.g. Borgia, 1995*a*; Gibson, 1996; Shine and Mason, 2001; Leonard and Hedrick, 2010). Given this possibility, paint may have an important but indirect effect on mating success. This indirect relationship between paint and mating success would explain my result that paint length was highly correlated with PC1 while the relationship between paint length and mating success was close to but not significant.

In conclusion, using several approaches and a comprehensive record of mate searching behavior and mating success, I tested several predictions of the paint quantity hypothesis and the paint quality hypothesis. My results are inconsistent with the paint quality hypothesis but do support the paint quantity hypothesis by confirming two of its predictions. I also provide the first experimental evidence that female search patterns are influenced by bower paint. This result establishes that paint is involved in the mate choice process since paint removal affected mate-searching females' return visitation to male bowers.

TABLE CAPTIONS

Table I. Factor loadings for PC1. Factor loadings for the first principal component from a principal component analysis. $PC1_{overall\ bower\ display}$ explains 66.4% of the total variance.

Table II. Spearman correlations between paint length and four other display traits. All correlations are significant at α=0.05 (N=29).

TABLES

Table I.

VARIABLE	*LOADING*
Bower Density	0.880
Quality of Bower Construction	0.830
Number of Blue Feathers	0.830
Number of Snails	0.710

Table II.

DISPLAY TRAIT	
Stick Density	r_s= 0.466
	p=0.006
Quality of Bower Construction	r_s= 0.393
	p=0.018
Feathers	r_s=0.620
	p=0.000
Snails	r_s=.419
	p=.012

FIGURE CAPTIONS

Figure 1. **Relationship between length of bower paint and overall bower and decoration display quality as indicated by PC1** [higher PC1 score=better bower and decoration display quality](r_S= 0.574, N=29, P=0.000).

Figure 2. Association between type of female visit and type of male visited (i.e. control or washed) during paint removal experiment.

(a) There was a significant association between type of female visit and type of male visited with fewer females returning for multiple courtships with washed males than control males (χ^2=8.89, df=1, P=0.003). (b) There was a significant association between type of female visit and type of male visited with fewer females copulating with washed males than control males (χ^2=7.20, df=1, P=0.008)

FIGURES

Figure 1.

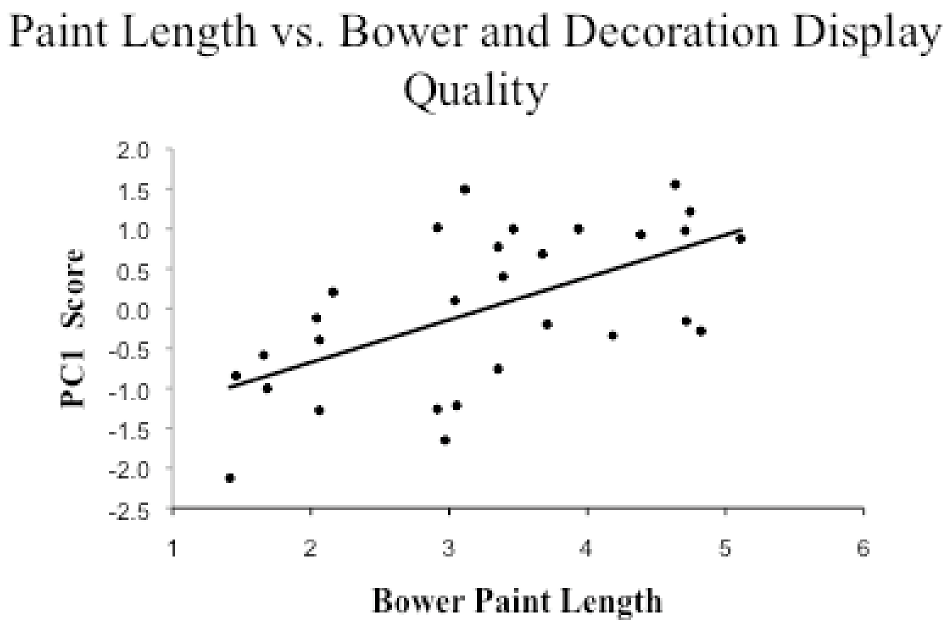
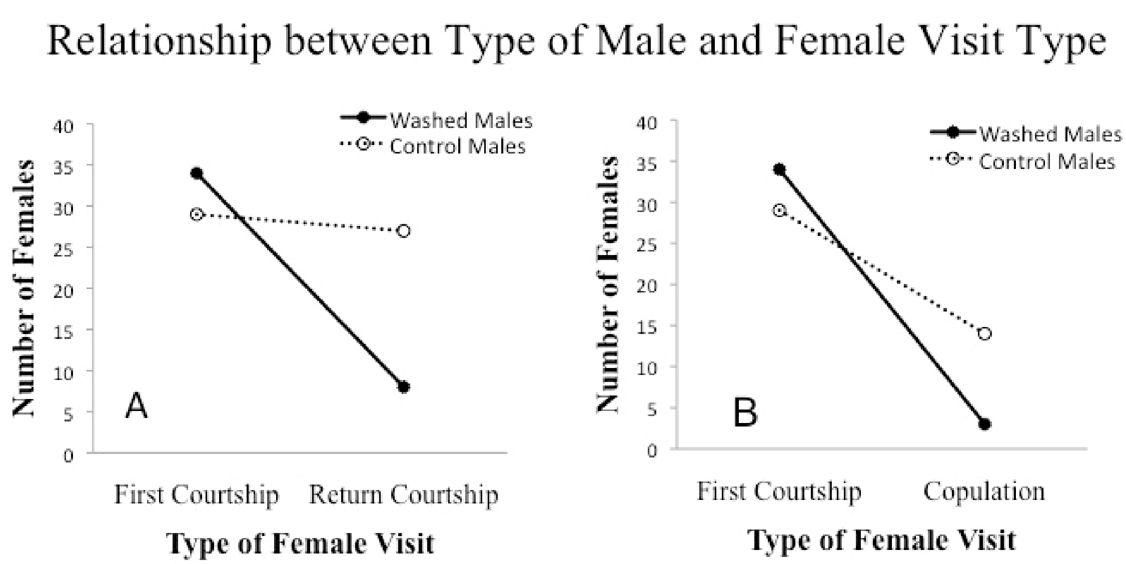


Figure 2.



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