

ABSTRACT

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DISPLAY PREDICTS FEMALE
UNCERTAINTY IN MATE CHOICE

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Information on how females use male display elements can be critical in understanding mate choice. Females often passively sample male displays, therefore female use of an element can be difficult to quantify. In satin bowerbirds, female tasting associated with male paint offers an opportunity to study how females actively assess of male display. In a preliminary study, I found that tasting was less common by females during courtships ending in copulation. This suggested that females with a greater proportion of tastes are less certain in their mate choice. I tested this hypothesis in several ways, and each indicated that a greater proportion of tasting was associated with measures suggesting mate choice uncertainty: visiting more times and more males, mating with multiple males, and switching among males. This active sampling behavior allows for examination of female assessment of a single component of male display and to predict certain female characteristics.

ACTIVE FEMALE SAMPLING OF MALE DISPLAY PREDICTS FEMALE
UNCERTAINTY IN MATE CHOICE

By

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Dedication

To my loving and always supportive parents.

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Chapter 1: Introduction

Mate selection is a complicated process, and while the results are relatively easy to score, understanding how females react to different male display elements as courtship progresses can be more difficult to measure. In species where males and females court each other, courtship behaviors by each member of the pair can reveal changes in their readiness to mate (e.g. Santangelo, 2005). In species where males actively court females and females observe male displays more passively, as is common in lekking species, it can be hard to directly quantify female reaction to male display. Quantifiable female behaviors during male assessment can provide insight into the female 'mental state' relative to mate choice which can affect subsequent behavior during her mate search. These behaviors that reveal information about the mental state of females can be exceedingly valuable in understanding the function of different elements of male display in mate choice, how females assess these elements, and how differences among females influence their mate choice. For example, mate choice is known to be affected by differences among females based on their size (Morris et al., 2006), age (Kodric-Brown & Nicoletto, 2001; Coleman et al., 2004), condition (Suk & Choe, 2008), and experience (Collins, 1995; Uy et al., 2000; Kodric-Brown & Nicoletto, 2001; Hebets, 2003). These differences in female choice may reflect variation in the pattern of female decision making and may affect how different male display elements are utilized by females.

A few studies show behaviors that reveal females' mental state in species in which males have the primary role in display. Female whitethroats' jumps and calls during male courtship can affect the attention of males, number of songs, and

copulation attempts (Balsby & Dabelsteen, 2002). Female cowbirds communicate to males singing attractive songs by producing wing strokes, which stimulate males to sing more of these songs, which subsequently trigger female copulatory postures (West & King, 1988). These female behaviors appear to function as signals to males about his display and also reveal her mental state in regard to her readiness to mate. Researchers can use these rare, yet valuable, signals to better understand the important aspects of male display and how females respond (West & King, 1988; Gros-Louis et al., 2003; King et al., 2003).

Previous work with satin bowerbirds (*Ptilonorhynchus violaceus*) has showed the value of quantifying variable female behavior during courtship that reveals a female's mental state (Patricelli et al., 2002; Patricelli et al., 2004). Satin bowerbirds males have displays involving multiple elements that include the bower, bower decorations, and coordinated visual and vocal displays, which are assessed by females in multiple visits to bowers (Borgia, 1985b; Uy et al., 2000). Males court females standing in the bower with active dancing and vocal displays (Loffredo & Borgia, 1986; Coleman et al., 2007). Females visiting bowers typically start in a standing position and then gradually lower into a crouch indicating a female's comfort with the male and his display and also her readiness to copulate (Patricelli et al., 2002). Females differ in their display preferences with older females preferring intense active male courtship displays, while young females attend more to blue decorations (Coleman et al., 2004). Young females appear to be threatened by intense courtships which often cause them to startle out of a crouch position and sometimes leave the bower (Coleman et al., 2004; Patricelli et al., 2004). The studies on crouching have

allowed consideration of how female behavior in the bower can signal their reaction to males and readiness to mate. Even with this information, however, it can be difficult to determine to what degree and when in the mate selection process females are focusing on a particular aspect of male display because crouching occurs not only in response to multiple elements of the male display, but it also occurs relatively late in the mate searching process (Patricelli et al., 2004).

The paint applied to bowers by male satin bowerbirds is a trait likely used by females in mate assessment, yet female sampling of paint has not been studied. Male satin bowerbirds frequently chew dried hoop pine (*Araucaria cunninghamii*) needles and apply the resulting brown paste to their bower walls. Bravery et al. (2006) found that males painted 24% of the total amount of time spent at their bower, and painting rate has been shown to be correlated with mating success when female visitation rates are controlled (Robson et al., 2005). During visits to bowers, females nip at the bower walls and can be visibly seen to swallow, appearing to taste the paint (Robson et al., 2005; Bravery et al., 2006). Such tasting occurred at 39% of all courtship visits (Bravery et al., 2006). Bravery et al. (2006) and Robson et al. (2005) suggest that paint may be a chemical signal used in mate assessment, and more specifically, Reynolds et al. (2009) suggest a role in kinship recognition.

Studying female use of paint in bowerbirds offers a potentially important and novel window on female assessment of males. While crouching acts as a signal indicating female comfort and a female's mental state during searching (Patricelli et al., 2004), it is not a direct response to a female's assessment of a single component of male display. Tasting, on the other hand, provides information about when females

assess a component, and how that may affect her decision during her mate search. I can examine how tasting relates to male assessment by measuring if and when she tastes on visits to males' bowers, assess if female differences relate to tasting behavior, and if differences among females can provide insight to a female's mental state during her search.

Previous work has shown variation in mate searching among female satin bowerbirds (Uy et al., 2001a). Uy et al. (2001a) described how, after multiple visits to males, most females (75%) choose a single male for a mate. While faithful females return to the same mate from the previous year, which reduces searching (Uy et al., 2000), other females mate with multiple males within a breeding season (Uy et al., 2001a). Uy et al. (2001a) found that multiply mating females visited more males, had more courtship visits, and copulated more times than those that mated with one male. I hypothesize that females with different mating classes, such as mating with multiple males or returning to the previous year's mate, may utilize paint differently.

We can use female tasting as a model for active female assessment of males in order to better understand how female differences might affect mate searching. During preliminary analyses of tasting behavior, I examined female tasting across various visit types at bowers. I found that across all females, the proportion of visits with tastes was lowest during courtships ending in copulation (Cendes, pers. obs.). This suggested that paint is used more by females early in the mate selection process, leading to the hypothesis that females who are less certain in their mate choice may have a greater proportion of tastes as they gather information about males. Thus, I predicted that females exhibiting behaviors that suggest uncertainty or indecision in

relation to their mate choice, such as more visitations or more switching among males during her sequence of visits, will have a greater proportion of tastes.

In this paper, I examine this hypothesis through multiple analyses. First, I examine the number of visits and number of males visited across all females, predicting that females that visit more will have a greater proportion of tastes. Similarly, I predict that non-tasting females should visit less. Second, I assign females to one of three of mating classes which may reflect increasing uncertainty in mate choice: females faithful to last year's mate, females that mated with a male they did not mate with the previous year, and females who mated with multiple males. I predict that females whose behavior suggests uncertainty would taste more. Third, I study the relationship between tasting and switching among visited bowers, assuming that switching indicates uncertainty. I predict uncertain females (i.e. multiply mating females) should have a greater proportion of switches than other females, and also that a greater proportion of switching should be positively related to the proportion of visits with tastes. In addition, I examine the relationship between age and tasting. Older females, having more mate searching experience, may be expected to be more certain in their mate choice than younger females, so I test the hypothesis that older females tasted less. Female uncertainty in mate choice is difficult to measure directly, thus I test multiple variables that are likely to be associated with uncertainty (e.g. proportion of switching visits between males). If these variables are associated with tasting, it would suggest that tasting may be used to resolve uncertainty in mate choice.

Chapter 2: Methods

Behavioral monitoring

This study was conducted at Wallaby Creek, NSW, Australia (28°28'S, 152°30'E). Male and female satin bowerbirds were uniquely banded before the mating season (Borgia, 1985a). This bowerbird population has been banded from 1980-1987 and then continuously since 1995. From the banding records, I am able to determine the minimum age for each female in 2004. Bowers were monitored with Hi-8 video cameras controlled by an infrared sensor which recorded all breeding season behaviors (Borgia, 1995). Data was collected at 37 bowers in 2003 and 34 bowers in 2004. This included all known bowers found by intensive searching through the study site. Female mate searching was reconstructed from date and time stamps on the video tapes with 2004 as the focal year.

Female visits at bowers were separated into three types: 'non-courtship' (NC) during visits when no bower owner was present (n=208), 'courtship' (C) (n=495), or 'copulation' (CC) when a courtship ended with mating (n=212). Female tastes during any of these visits were scored as 'yes' or 'no' for the visit.

Female mating classes

In order to examine how female mate class influences tasting behavior, three exclusive classes were defined. Faithful (F) females are those that mated with the same male in 2003 and 2004 (n=12) (see Uy et al., 2001a). Novel mate (N) females mated with a male in 2004 who was not their mate in 2003 (n=40). Multiple mate (M) females mated with more than one male in 2004 (n=13). Females that did not fit into

any of these classes, such as females who did not search in 2003 (n=21) including one-year old females (n=4), were excluded from these analyses.

In accordance with previously published work (Uy et al., 2001a), M females visited significantly more males than either F ($U_{mw} = 20.5$, $p=0.0009$) or N females ($U = 117.5$, $p=0.0016$) across their mate search, and appeared significantly more times at bowers (F:M $U_{mw} = 46.0$, $p=0.04$; N:M $U_{mw} = 116.0$, $p=0.0015$). To control for these differences between female groups, the proportion of visits with tastes was always used during analyses (see *Statistical Analyses*). There was no significant age difference between F and M ($U_{mw}= 66.0$, $p= 0.51$). N females were significantly younger than M females ($U_{mw}= 146.0$, $p=0.02$), and there was a trend for them to be younger than F females as well ($U_{mw}= 153.0$, $p= 0.06$).

Statistical Analyses

Data were analyzed using Statistica 6.0 (Statsoft Inc., Tulsa, OK). In order to investigate how tasting behavior varied across female visit types, I calculated the proportion of each visit type where tasting occurred to total visits for each female in 2004. This controlled for the different number of visits per female. Proportion of bower switches was calculated as the number of times a female switched between bowers in her mate searching sequence divided by the total number of males visited, to control for the differing number of males visited by each female. Data were checked for normality and homogeneity of variances, but these parametric test assumptions were violated. The data were rank transformed and the appropriate nonparametric test was used. The Mann-Whitney U test (U_{mw}) was used to determine

differences between independent groups and Spearman's rank correlation (r_s) was used for correlations.

We predicted *a priori* that the proportion of visits with tastes would be positively related to behaviors suggesting less certainty in the female choice of a mate, such as number of visits, number of males visited, and the proportion of switches among bowers visited, because these females invest more in mate searching among males. Statistical tests of this directional hypothesis are one-tailed to provide the most appropriate balance of type I and type II error (Quinn & Keough, 2002). All other tests are two-tailed.

Chapter 3: Results

We examined the relationship between tasting and females that visited more males and visited more times, suggesting a level of uncertainty in mate choice.

Supporting my hypothesis, I found a significant positive relationship between the proportion of visits with tastes and total number of visits at bowers ($r_s = 0.177$, $p = 0.052$, $n = 86$) and the number of males visited ($r_s = 0.242$, $p = 0.013$, $n = 86$).

There were 18 females that did not taste during their mate search. These females did not differ from tasting females ($n = 68$) by age ($U_{mw} = 510.5$, $p = 0.28$). Non-tasting females visited significantly fewer males ($U_{mw} = 318.5$, $p = 0.002$) and appeared fewer times at bowers ($U_{mw} = 163.5$, $p < 0.001$) than those females who tasted at least once during their mate search. Non-tasting females were not significantly less likely to mate than tasting females ($U_{mw} = 486.0$, $p = 0.16$). Since the non-tasting females searched less, this result supports my hypothesis that tasting is related to more bower visitation during mate searching.

In order to examine how tasting relates to mating class, those females that did not search in 2003 were excluded for the analyses (see *Methods*). Tasting females were evenly distributed among the three female classes: 83% of F females ($n = 12$), 83% of N females ($n = 40$), and 100% of M females ($n = 13$) tasted at least once during their mate search ($\chi^2 = 2.25$, $df = 2$, $p = 0.32$). F, N and M females did not differ significantly in the proportion of males they tasted (mean \pm SD; F: 0.64 ± 0.40 , N: 0.55 ± 0.37 , M: 0.73 ± 0.26) or in the probability of tasting the paint of the male they eventually copulated with at least once during the mate search (F: 0.66 ± 0.49 , N: 0.55 ± 0.50 , M: 0.78 ± 0.24).

We examined how the overall proportion of visits with tastes related to females with different mating classes (Fig. 1a). I found no significant difference between the proportion of visits with tastes between F and N females ($U_{mw}= 189.0$, $p= 0.27$). They both had significantly smaller proportion of visits with tastes than M females (F:M $U_{mw}= 19.5$, $p= 0.001$; M:N $U_{mw}= 129.5$, $p= 0.007$). Overall, M females had a greater proportion of visits with tastes during their mate search than either F or N females.

We decomposed the proportion of visits with tastes for each female mating class into the amount of tasting per visit type (Fig. 1b). There was only one significant difference between behavior types within a female mating class: F females had significantly smaller proportion of copulations with tastes than non-courtships with tastes ($U_{mw}= 40.0$, $p= 0.04$). There were, however, significant differences among the female classes. While F and N females did not differ significantly in the proportion of tasting across any visit type (NC, $U_{mw}= 205.5$, $p= 0.45$; C, $U_{mw}= 191.0$, $p= 0.29$; CC, $U_{mw}= 206.0$, $p= 0.46$), they both differed from M females significantly during courtships and courtships ending with copulation. F and N females had a smaller proportion of courtships and copulations with tastes than M females (F:M C, $U_{mw}= 18.5$, $p= 0.001$; CC, $U_{mw}= 23.0$, $p= 0.003$) (M:N, C, $U_{mw}= 115.5$, $p= 0.003$; CC, $U_{mw}= 160.5$, $p= 0.040$).

Examining the relationship between tasting and bower switching, I found that, combining the female mating classes, the proportion of visits with tastes across a female's mate search was significantly correlated with the proportion of bower switches, controlling for the number of males visited by each female ($r_s= 0.208$, $p=$

0.049, n=65). In addition, following my prediction, I found that M females had a greater proportion of male switches, controlling for the number of males visited, than either F or N females (F:M $U_{mw} = 11.5$, $p=0.0002$; N:M $U_{mw} = 91.5$, $p=0.0002$). Specifically, during visits around switches, I found that M females had a greater proportion of switches with tastes occurring in the visit before and after a switch to total switches compared to either F (*before*: $U_{mw} = 11.0$, $p= 0.00013$; *after*: $U_{mw} = 3.0$, $p< 0.0001$) or N females (*before*: $U_{mw} =89.0$, $p= 0.0002$; *after*: $U_{mw} =115.5$, $p= 0.0015$). Therefore, M females were tasting proportionally more around a switch than when F or N females switch.

When I related tasting behavior and age, I found no significant correlation between age and the proportion of all visits with tastes ($r_s= -0.153$, $p= 0.16$, $n= 86$). There was a trend for 20+ year-old females to taste less than other females ($U_{mw}= 44.5$, $p= 0.06$), although with the small sample size of very old females ($n=3$), this may not be meaningful.

Chapter 4: Discussion

Our results indicated that paint was used during mate choice and supported the hypothesis that females attended to paint more frequently when they were most involved in comparing males while uncertain in mate choice. I supported this hypothesis with three different lines of evidence. First, I showed that the proportion of visits by females with tasting is positively correlated with the number of males visited and number of visits across all females. Also, non-tasting females visited fewer males and appeared at bowers less, again suggesting a positive relationship between visitation and tasting. Second, when females were placed into mating classes, M females had a greater proportion of visits with tastes, especially during courtships and courtships ending with copulation. Third, I found the proportion of visits with tastes to be related to the proportion of switches among males by females as they search. M females in particular were found not only switch more than other females, but they also had a greater proportion of switching than F or N females. This supported my hypothesis that M females are more uncertain about their mate choice; they not only mate with more than one male, but they visited more times, visited more males, and had a greater proportion of switching when controlling for number of visited males than either F or N females.

Although other studies of bowerbirds have shown that females of different ages attend to decorations and courtship displays differently (Coleman et al., 2004), I did not find an effect of age in female tasting behavior. This is consistent with my finding that age was not related to my estimators of certainty, as F and M females did not differ in age (see *Methods*). Uy et al. (2001b) found that information females

gather from previous searches may not apply from year-to-year; when top mates die, females dramatically expand their mate searching. Therefore, age and experience may not correlate with behaviors that suggest uncertainty in mate choice.

An alternative hypothesis is that my putative indicators of uncertainty do not indicate uncertainty, but occur because females arbitrarily vary in activity level and females with a higher level of activity taste, visit and mate more. While one cannot easily rule out this possibility, it is not consistent with Uy et al.'s (2001a) findings that female mate searching is well explained by an adaptive model in which females use multiple searching bouts to find suitable mates.

It appears that females who are uncertain in their choice had a greater proportion of visits with tastes, because more visitations, more frequent switching, and mating with multiple males were related to more tasting. Given the complexity of bowerbird display, and the many male traits that appear to be involved in mate choice, it is interesting that paint sampling behavior is, by itself, a reasonable measure of female uncertainty. This suggests that the information gained from sampling paint is particularly critical in mate choice and samples in repeated visits are important to females when comparing males. Currently, the likely functions of paint and the kinds of information females gain from this behavior are being investigated. This should allow for better understanding of why this sampling appears to be important across pre-copulation visits to bowers. Even though this story is incomplete, the ability to predict female certainty in mating decisions from tasting behavior suggests that this is a very useful tool for understanding courtship, and in particular, the female's mental state with regard to mating.

It has been suggested that satin bowerbird paint may have a chemical role in mate assessment or allow for kinship recognition through Major Histocompatibility Complex (MHC)- based phenotype matching (Robson et al., 2005; Bravery et al., 2006; Reynolds et al., 2009). Until recently, avian chemical communication has not been well studied, even though it has been shown to occur in a number of social circumstances (review: Hagelin & Jones, 2007) including mating situations (Bonadonna & Nevitt, 2004; Jones et al., 2004). Although my study does not directly address the potential chemical function of paint, knowing the exact nature of paint, while desirable, is not a requirement to study the pattern of female use this trait, just as previous studies have not required a demonstration of the how females ultimately use other display elements such as bower decorations (Borgia et al., 1987; Coleman et al., 2004) or courtship displays (Patricelli et al., 2004) in their mate choice.

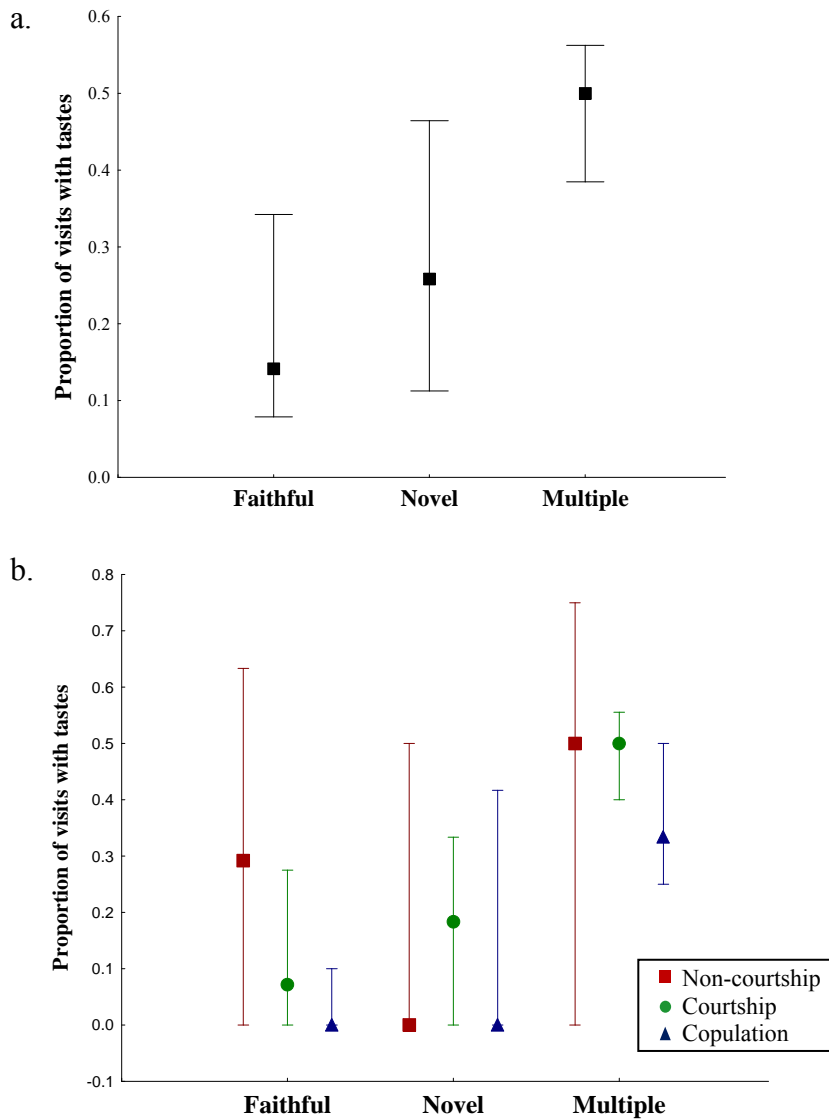
Previous studies have shown female crouching is also a signal of the mental state of females during their mate search. Females who are certain and have chosen a mate crouch more during courtship displays and are less likely to be startled by the male's display, while females who feel threatened startle more frequently (Patricelli et al., 2002; Patricelli et al., 2004). While crouching behavior does allow better understanding of how the female is responding to the male's display, it is a reaction both to her status during her mate search and to her perceived threat from the male. Tasting behavior allows examination of female uncertainty during mate searching without the effect of female response to male threat. Additionally, paint sampling may provide information about female mental state earlier in the mate search process.

In future studies, crouching behavior will be examined as it relates to tasting behavior of females.

By examining a quantifiable female behavior during mate assessment, I was able to dissect the mate assessment process in relation to a single component of male display. I can use this behavior as a predictor of some female characteristics during mate searching, for example, her mate class or her likelihood to switch males. It is possible that satin bowerbird males have evolved to observe tasting to inform him about a female as well. Tasting could inform him about a female's chances of switching to or mating with another male, and he could modify his display in response. This could provide another striking example of signaling between males and females during mate assessment and choice. In conclusion, my study has shown that paint is used by females during mate assessment and that females who appear uncertain are more likely to attend to this cue when they visit and switch among bowers.

Appendix

Figure 1. Proportion of visits with tastes across female mating classes. a.) Median proportion of visits with tastes across faithful, novel mate and multiple mate females, showing upper and lower quartiles. b.) Median proportion of each visit type with tastes across female classes showing upper and lower quartiles.



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