

# Multiple male traits interact: attractive bower decorations facilitate attractive behavioural displays in satin bowerbirds

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Sexually selected male courtship displays often involve multiple behavioural and physical traits, but little is known about the function of different traits in mate choice. Here, we examine female courtship behaviours to learn how male traits interact to influence female mating decisions. In satin bowerbirds (*Ptilonorhynchus violaceus*), successful males give highly aggressive, intense behavioural displays without startling females. Males do this by modulating their displays in response to female crouching, which signals the display intensity that females will tolerate without being startled. Females typically visit multiple males for multiple courtships before choosing a mate, and females show differing tolerance for intense displays during their first courtship with each male. We test three hypotheses that may explain this: (i) familiarity with the courting male; (ii) the order of the courtship in mate-searching; and (iii) the attractiveness of the courting male. We found that females are more tolerant of intense displays during first courtships with attractive males; this increased female tolerance may allow attractive males to give higher intensity courtship displays that further enhance their attractiveness. We then examined why this is so, finding evidence that females are less likely to be startled by males with better physical displays (bower decorations), and this reduced startling then contributes to male courtship success. This role of physical displays in facilitating behavioural displays suggests a novel mechanism by which multiple physical and behavioural traits may influence female choice.

**Keywords:** female signals; courtship; sexual selection; multiple traits; behavioural traits; satin bowerbirds

## 1. INTRODUCTION

Males of many species have multiple sexual display traits (Andersson 1994). There has been a great deal of interest in how multiple male display traits evolve and how they are maintained (e.g. Møller & Pomiankowski 1993; Johnstone 1996). To understand the evolution of multiple traits, it is critical to understand how each trait influences female choice (e.g. Borgia 1995a; Gibson 1996; Rowe 1999; Kodric-Brown & Nicoletto 2001). One way that we might do this is by examining female behaviours during courtship. During courtships with potential mates, signals and cues given by the female may reflect her state: for example, her 'interest' in the courting male or her 'comfort' with his displays. We analyse female courtship behaviours and show that multiple male traits may interact to influence female choice, with some traits affecting female behaviours and thereby facilitating the expression of other traits.

The sexual display of the male satin bowerbird (*Ptilonorhynchus violaceus*) involves multiple physical display traits, as well as behavioural displays that males adjust in response to female signals during courtship (Patricelli 2002; Patricelli *et al.* 2002). The behavioural displays given by male satin bowerbirds are aggressive and intense,

and females prefer the most intensely displaying males as mates (Patricelli *et al.* 2002). These displays may serve as indicators of genetic or proximate benefits (Andersson 1994), but they can also threaten females, because they involve sudden movements and are similar to male–male aggression displays (Borgia & Presgraves 1998), and because females are at risk of forced copulation by courting males (Borgia 1995b). Thus females are often startled repeatedly by intense displays, jumping upward and sometimes leaving the bower, which can disrupt or end courtship (Uy *et al.* 2001; Patricelli 2002; Patricelli *et al.* 2002, 2003). During courtship, females gradually crouch by lowering and tilting forward towards the mating position, a fully crouched position with wings fluffed. Females crouch to varying degrees in most courtships, even in courtships that occur a week or more before mating and with males that are not later chosen as mates (Patricelli *et al.* 2003). As female crouching increases, the likelihood that females will be startled by intense male display decreases; this suggests that crouching signals the degree of display intensity that a female will tolerate without being threatened (Patricelli 2002; Patricelli *et al.* 2003). In an experiment with robotic female bowerbirds that mimic female crouching behaviours, Patricelli *et al.* (2002) found that males increase their display intensity in response to an increase in female crouching. Males that are more responsive to crouching startle females less often and are thus more successful in courtship. These studies have shown that female crouching is critical in determining the intensity with which a male can display, and that a male's display intensity and the rate at which he startles females are critical in affecting his courtship success. Here, we

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consider the factors affecting female crouching and startle behaviours.

While searching for a mate, the average female satin bowerbird engages in six courtships over 15 days; first visiting multiple males for courtship, then returning for further courtships with a subset of males, and finally copulating with a single male (Uy *et al.* 2001). Patricelli *et al.* (2003) observed that female crouching increases and female startle decreases during subsequent courtships with attractive males. But these changes during mate searching do not entirely explain the observed variation in female behaviours, because there is also variation in female behaviours among the first courtships that she initiates with each of her potential mates.

In this study, we examine female behaviours during her first courtship with each potential mate. We test three alternative hypotheses to explain female tolerance of intense displays in first courtships: the familiarity hypothesis, the courtship-order hypothesis and the attractiveness hypothesis. The familiarity hypothesis posits that females are more tolerant of intense displays from males with whom females have previous experience, regardless of the attractiveness of the male. Satin bowerbirds are long-lived, and females generally visit previous mates for courtship in subsequent years. If previous mates are attractive, females generally re-mate with these males (faithful females) and if previous mates are less attractive, females reject them (unfaithful females (Uy *et al.* 2000)). If familiarity alone affects female behaviour, this predicts that faithful and unfaithful females will not differ in their tolerance for intense displays in courtships with previous mates (even though these males differ in attractiveness). The courtship-order hypothesis posits that female tolerance for intense displays increases in subsequent courtships as females search for mates, predicting a positive relationship between female tolerance for intense displays and courtship order. This may occur, for example, if female behaviours are affected by habituation to male displays or by physiological changes as females approach mating. The attractiveness hypothesis posits that female courtship behaviours are affected by the attractiveness of the courting male, predicting a positive relationship between female tolerance for intense displays and male attractiveness. This may occur, for example, if the risk or potential cost of forced copulation is reduced during courtships with attractive males.

Our results support the hypothesis that females will tolerate more intense displays from their first courtship with an attractive male, using male mating success as a measure of male attractiveness. This result leads to another question: why are female behaviours related to male attractiveness? We examined two possible causes for the relationship between startle and male attractiveness: first, that male sexual displays reduce the likelihood that females will be startled, and second, that males that startle females more often are less successful in courting females. Both the quality of the male's bower and the number of decorations placed around his bower are related to male mating success (Borgia 1985; Patricelli 2002). We examine the influence of these bower traits on female startle and crouching behaviours, and we examine the effect of bower traits and the rate at which males startle females on male success in mating. We find evidence both that male

bower decorations reduce female startle, and that reduced female startle in turn makes males more successful in attracting females to mate.

## 2. METHODS

### (a) *Video recording and analysis*

This study was conducted in 1997 at our field site in Wallaby Creek, NSW, Australia (see Borgia 1985). From 1995–1997, over 1200 bowerbirds were captured and fitted with unique, three-colour plastic leg bands for identification. From 9 November to 20 December 1997, automatically-triggered Hi-8 video cameras that record time and date were used to monitor 29 adjacent bowers covering an area of *ca.* 4 km<sup>2</sup>, allowing for continuous and simultaneous observations of all behaviours at bowers throughout the mating season (see Borgia 1995b).

All of the 1274 courtships captured on video in 1997 were scored for duration, outcome (copulation or no copulation) and band identification of individual birds. Out of these courtships, we scored 134 which are the first between male–female dyads. G.L.P. and four assistants scored behaviours from videos; assistants were unaware of the predictions being tested. A subset of courtships scored by G.L.P. were randomly chosen and scored again by all assistants to measure concordance of each variable; the average of all scorers was used in analyses. Courtship behaviour data were scored for 54 females; 33 of these females were observed to mate in 1996 and 1997, thus we were able to determine if females re-mate with the same male for two consecutive years (faithful females,  $n = 19$ ) or whether they choose new mates (unfaithful females,  $n = 14$ ; Uy *et al.* 2001).

### (b) *Female startle and crouching behaviours*

The startle response has been used in many species to measure response to auditory and visual threats (Lang 1995; Koch 1999). In this study, startles were scored when a courted female that was inside the bower moved rapidly upward or backward immediately after a male 'buzz/wing-flip' display (Patricelli *et al.* 2002, 2003). Startled female bowerbirds often hop out of the bower away from the male. We calculated the 'startle rate' for each courtship as the proportion of male buzz/wing-flip displays that startled females. Startle rate scores for each courtship were highly concordant among observers ( $W = 0.91$ ,  $\chi^2 = 14.5$ , d.f. = 4,  $n = 4$ ,  $p < 0.006$ ). For each female, we calculated mean startle rate during first courtships with males chosen as mates, and mean startle rate with males not chosen as mates (rejected males). For each female classified as either 'faithful' or 'unfaithful', we calculated mean startle rate during first courtships with previous mates (from 1996), and mean startle rate with all other males visited for courtship. To examine the factors affecting each male's tendency to threaten females, we calculated the 'rate of startle females' as the mean startle rate of females during first courtships with the focal male (Patricelli *et al.* 2002).

Female crouching is the gradual movement downward from the upright position to the mating position. To quantify female crouching, we used a crouch index that reflects both crouch rate and position (Patricelli 2002; Patricelli *et al.* 2003). We divided the natural range of female motion into six positions that could be reliably scored, and we measured the time spent in each position while the female was inside the bower. We then multiplied the proportion of the total courtship duration that females spent in each position by a value from 1 to 6, with the upright position as 1 and the fully crouched position as 6. These values were then added, so that non-crouching females scored the minimum

crouch index of 1 and females that spent the entire courtship in the mating position scored the maximum crouch index of 6. Crouch index scores were highly concordant among observers ( $W=0.96$ ,  $\chi^2=15.4$ , d.f. = 4,  $n=4$ ,  $p<0.004$ ). For each female, we calculated mean crouch index with mate(s), mean crouch index with rejected males, mean crouch index with 1996 mates and mean crouch index with other males. For each male, we calculated 'mean of female crouching' as the crouch index score of females during their first courtship with the focal male. In analyses of female behaviour, sample sizes are larger in tests involving crouch index than in tests involving startle rate, as female startling was not observable in some courtships where crouching was observable.

### (c) Male mating success and bower traits

We used male mating success as a measure of the male's attractiveness to females. Males do not provide parental care or associate with females after mating, thus males are not choosy about their mates and variance in male mating success is extremely high (Borgia 1985). Females arrive at bowers individually, thus female mate-choice copying is unlikely to affect male mating success (G. L. Patricelli, J. A. C. Uy and G. Borgia, unpublished observations). We estimated each male's mating success from videotapes of natural bower activity as the number of females that mated with the male. Out of females observed to copulate on video, 72% were banded and could be individually identified. We estimated the number of unbanded females involved in copulations with each male by dividing each male's total number of copulations with unbanded females, by the average number of copulations ( $1.8 \pm 0.11$ ) that banded females had with males in our population in 1997 (Patricelli 2002; Patricelli *et al.* 2002, 2003). When mating success is calculated using the upper or lower 95% confidence limits for the average number of copulations among banded females, results are not qualitatively different. In correlations between female behaviours and the mating success of males she visited for courtship (figure 1), we excluded the focal female from calculations of male mating success to avoid circularity (Uy *et al.* 2000).

Each week during the mating season, field assistants with minimal knowledge of male mating success estimated male bower quality as a category from excellent (4) to poor (1); we used average bower quality for each male in these analyses. Bowers that were ranked the highest were symmetrical, had fine straight sticks that were densely packed and had thick walls; poor bowers were asymmetrical, had branching sticks of uneven thickness that were loosely packed and had thin walls (Borgia 1985). Weekly counts were made of yellow leaves, yellow and blue flower blossoms, blue feathers and snail shells present on the bower platform. Multiple decorations are correlated with mating success in males (Borgia 1985), thus we used the average of total bower decorations in these analyses (untransformed mean among males =  $25 \pm 3.9$ ; min = 6.0; max = 111.3).

### (d) Statistical analyses

A Kendall's coefficient of concordance ( $W$ ) was used to measure concordance among observers during video analysis. For females with at least three first courtships with potential mates, we calculated a Kendall's correlation coefficient ( $r_k$ ) between female startling and crouching behaviours in each courtship, and the order of the courtship in the female's mate-search sequence or the mating success of the courting male (mean =  $3.73 \pm 0.21$  courtships each for 12 females for startling data; mean =  $3.73 \pm 0.21$  courtships each for 16 females for crouching

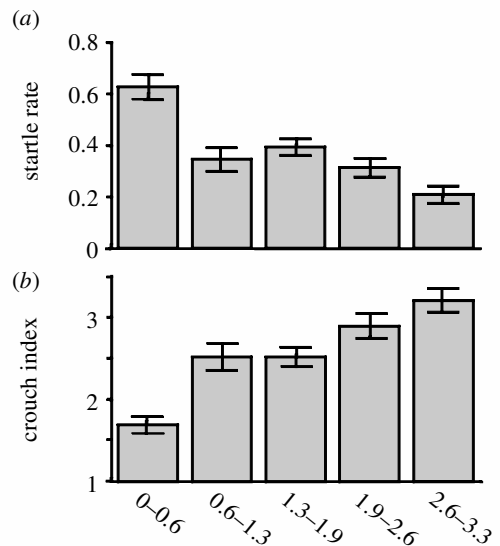


Figure 1. Female behaviours vary with male attractiveness. (a) On average we found a negative relationship between the female's startle rate and the mating success of the courting male, which is used as a measure of male attractiveness, and (b) a positive relationship between the female's crouch index and the mating success of the courting male. These graphs illustrate these relationships by showing mean startle rate and crouch index values among females for intervals of male mating success.

data). We tested whether the mean of  $r_k$  values among females was significantly different from zero with a  $t$ -test (Sokal & Rohlf 1995). We used a  $2 \times 2$  factorial repeated-measures design to examine the behaviours of faithful versus unfaithful females in courtships with their 1996 mates versus other males, using contrasts for three comparisons of interest (PROC MIXED, SAS 8.02); separate variance estimates were used for mean crouching, because variances were heterogeneous among groups; d.f. were calculated using the  $ddfm=kenwardandrog$  option in SAS. We used least-squares linear regressions; standardized regression coefficients ( $b_x$ ) are reported for each independent variable in multiple regressions. Male mating success was  $\log_e(Y+1)$  transformed and bower decorations were  $\log_e$  transformed to improve normality and homoscedasticity; presented means are back-transformed (Sokal & Rohlf 1995). All tests are two-tailed; means are  $\pm$  s.e.m.

## 3. RESULTS

### (a) Tests of the familiarity, courtship order and attractiveness hypotheses

We tested three hypotheses to explain the observed variation in female behaviours during a female's first courtship with each potential mate: the courtship-order hypothesis, the attractiveness hypothesis and the familiarity hypothesis. We did not find support for predictions of the courtship-order hypothesis: there was no significant negative relationship between startle rate and the order of the courtship in the female's mate search sequence (mean  $r_k = 0.04 \pm 0.16$ ;  $t = 0.26$ , d.f. = 11,  $p = 0.8$ ), and no significant positive relationship between crouch index and the order of the courtship in the female's mate search sequence (mean  $r_k = 0.18 \pm 0.12$ ;  $t = 1.45$ , d.f. = 15,  $p = 0.17$ ). In these same courtships, however, we found

support for predictions of the attractiveness hypothesis. We found a significant negative relationship between startle rate and the mating success of the courting male (mean  $r_k = -0.42 \pm 0.13$ ;  $t = 3.29$ , d.f. = 11,  $p < 0.007$ ; figure 1a), and a significant positive relationship between female crouch index and the mating success of the courting male (mean  $r_k = 0.46 \pm 0.12$ ;  $t = 3.77$ , d.f. = 15,  $p < 0.002$ ; figure 1b), even when faithful females were excluded (startle rate mean  $r_k = -0.36 \pm 0.15$ ;  $t = 2.49$ , d.f. = 9,  $p < 0.03$ ; crouch index mean  $r_k = 0.42 \pm 0.15$ ;  $t = 2.69$ , d.f. = 11,  $p < 0.02$ ).

To test the familiarity and attractiveness hypotheses, we compared the behaviours of faithful and unfaithful females in courtships to males with whom females mated the previous year (1996 mates), and with other males. The familiarity hypothesis predicts that faithful and unfaithful females should not differ in crouching and startling behaviours during courtships with 1996 mates, as they are familiar with these previous mates. The attractiveness hypothesis predicts that faithful females should crouch more and startle less than unfaithful females, as their 1996 mates are more attractive (mean attractiveness of 1996 mates in 1997, unfaithful females = 6.94, faithful females = 12.77,  $n = 33$  females,  $t = 2.64$ , d.f. = 31,  $p < 0.013$ ; see also Uy *et al.* 2000). Supporting the attractiveness hypothesis, we found that faithful females startle less and crouch more with their 1996 mates than unfaithful females (figure 2). In addition, faithful females startle less and crouch more with their 1996 mates than with other sampled males, whereas unfaithful females crouched less with their 1996 mates than with other sampled males, and did not differ in startling behaviour (figure 2). Thus familiarity with previous mates alone does not significantly increase female tolerance for intense displays; previous mates must also be attractive to increase female tolerance.

Further supporting the hypothesis that male attractiveness influences female behaviours, we found a highly significant difference between female startling in first courtships with males that are chosen as mates versus males that are rejected (figure 3a) and a highly significant difference between female crouching in first courtships with males that are chosen as mates versus rejected males (figure 3b). Similarly, when faithful females were excluded, we found that females startle marginally less and crouch more with mates than with rejected males (mean startle rate, with mates =  $0.29 \pm 0.09$ , with rejected males =  $0.54 \pm 0.07$ , paired  $t = 2.0$ , d.f. = 18,  $p = 0.066$ ; mean crouch index, with mates =  $2.66 \pm 0.25$ , with rejected males =  $1.63 \pm 0.13$ , paired  $t = 3.4$ , d.f. = 20,  $p < 0.002$ ).

#### (b) Why are female behaviours related to male attractiveness?

We examined two possible causes for the observed relationship between startling and male attractiveness. First, we examined whether males that have more attractive bower displays (more decorations and higher-quality bowers) startle females less often in first courtships. We found that the average rate at which males startle females with their intense displays in first courtships is negatively related to the number of decorations they have on their bower platform (figure 4a) and negatively related to the

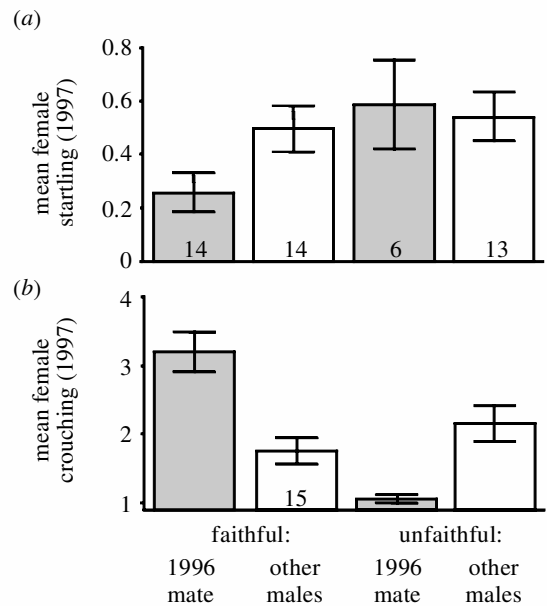


Figure 2. Female behaviours with attractive versus familiar males. A comparison of the behaviours of faithful and unfaithful females in courtships with males with whom females mated the previous year (1996 mates), and with other males visited for courtship (other males). (a) Faithful females startle less with their 1996 mates than unfaithful females ( $n = 20$  females,  $t = 2.20$ , d.f. = 43,  $p < 0.033$ ). Furthermore, faithful females startle less with their 1996 mates than with other males ( $n = 14$  females,  $t = 2.17$ , d.f. = 29,  $p < 0.039$ ), whereas unfaithful females did not differ in startling behaviour with 1996 mates and other males ( $n = 13$  females,  $t = 0.30$ , d.f. = 34,  $p = 0.77$ ). The number of observations in each category is noted in each bar; numbers are the same for crouching, unless noted. This is a repeated-measures analysis (see § 2), so the number of observations in each comparison is not equal to the number of females. (b) Faithful females crouch more with their 1996 mates than unfaithful females do ( $n = 20$  females,  $t = 6.36$ , d.f. = 14,  $p < 0.001$ ). Faithful females crouch more with 1996 mates than with other males ( $n = 15$  females,  $t = 4.03$ , d.f. = 18,  $p < 0.001$ ), whereas unfaithful females crouched less with their 1996 mates than with other males ( $n = 13$  females,  $t = 4.06$ , d.f. = 13,  $p < 0.001$ ).

quality of their bower ( $r^2 = 0.23$ ,  $F_{1,27} = 8.25$ ,  $p < 0.008$ ). Decorations and bower quality are correlated (Borgia 1985; Patricelli 2002), and when we examined these traits together, we found that number of decorations was significantly related to the rate of startling females but bower quality was not ( $b_{\text{decorations}} = -0.50$ ,  $p < 0.01$ ;  $b_{\text{bower quality}} = -0.19$ ,  $p = 0.31$ ;  $r_2 = 0.40$ ,  $F_{2,26} = 8.70$ ,  $p < 0.001$ ). These results suggest that male bower decorations have a larger effect on the likelihood that females will be startled by male display.

Second, we examined whether males that startle females more often with their courtship displays are less successful in mating. We found a significant negative relationship between the average rate at which males startle females with their courtship displays in first courtships and male mating success (figure 4b). Because decorations are also related to startle rate (see above), we examined startling and decorations together to determine whether both are independently related to mating success. We found that startle rate is significantly related to male mating success

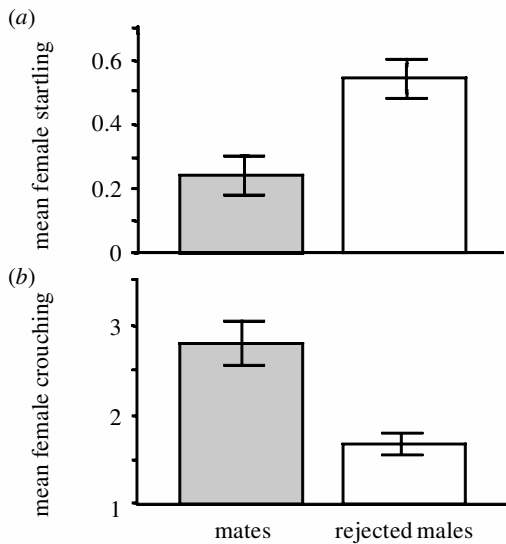


Figure 3. Female behaviours with mates versus rejected males. We found a highly significant difference between: (a) female startling in first courtships with males that are chosen as mates versus males that are rejected (mean startle rate, with mates =  $0.24 \pm 0.06$ , with rejected males =  $0.54 \pm 0.06$ , paired  $t = 2.9$ , d.f. = 25,  $p < 0.007$ ); and (b) female crouching in first courtships with males that are chosen as mates versus males that are rejected (mean crouch index, with mates =  $2.78 \pm 0.23$ , with rejected males =  $1.67 \pm 0.11$ , paired  $t = 4.3$ , d.f. = 27,  $p < 0.001$ ).

but male decoration number is not ( $b_{\text{startling}} = -0.46$ ,  $p < 0.03$ ;  $b_{\text{decorations}} = 0.21$ ,  $p = 0.3$ ;  $r_2 = 0.37$ ,  $F_{2,26} = 7.50$ ,  $p < 0.003$ ). This supports the hypothesis that the rate at which a male startles females influences his mating success.

In addition, we examined female crouching behaviours. We found a marginal relationship between the mean of female crouching during first courtships with each male and male mating success ( $r_2 = 0.13$ ,  $F_{1,27} = 3.9$ ,  $p = 0.059$ ). We did not find a significant relationship between female crouching and male bower decorations ( $r_2 = 0.03$ ,  $F_{1,27} = 0.03$ ,  $p = 0.87$ ) or bower quality ( $r_2 = 0.04$ ,  $F_{1,27} = 1.13$ ,  $p = 0.3$ ). Unlike female startling behaviours, both crouching and decorations are independently related to male mating success when considered together ( $b_{\text{crouching}} = 0.34$ ,  $p < 0.041$ ;  $b_{\text{decorations}} = 0.48$ ,  $p < 0.007$ ;  $r_2 = 0.35$ ,  $F_{2,26} = 7.09$ ,  $p < 0.003$ ); thus decorations do not influence male success in mating by affecting female crouching.

#### 4. DISCUSSION

##### (a) Female behaviours and male attractiveness

Although it has long been known that male attractiveness affects female mating decisions (reviewed in Andersson 1994), little is known about the interaction between male attractiveness and female behaviours during courtship. Our results indicate that a female's tolerance for intense courtship display during her first courtship with each potential mate is strongly related to the attractiveness of the courting male (figure 1), but not the order of courtship in mate searching. In addition, we found that females crouch more and startle less with males that are more attractive, regardless of whether females previously mated with those males (figure 2), suggesting that male attractive-

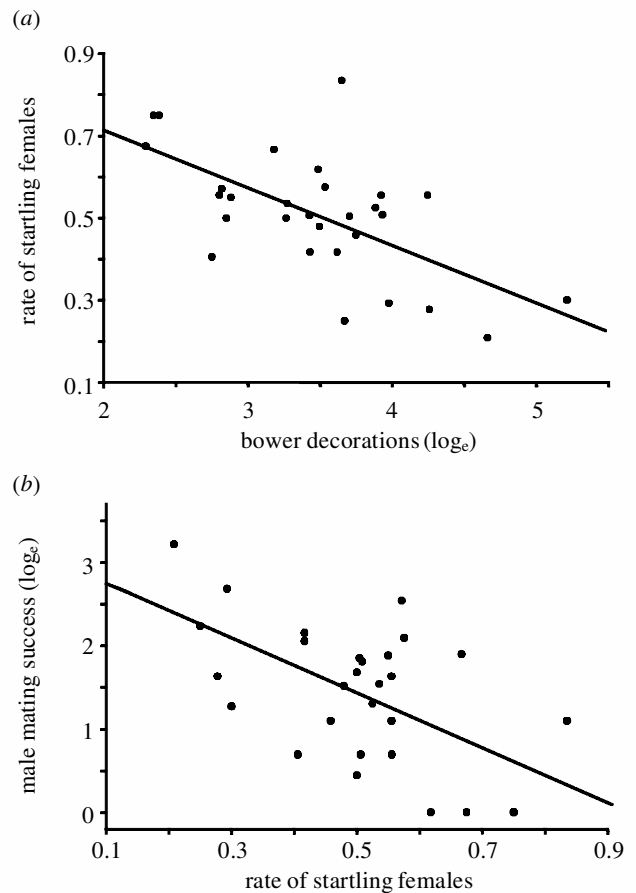


Figure 4. Female startling and male attractiveness. (a) We found a highly significant negative relationship between the average rate at which the focal male startles females with his intense displays in first courtships and the number of decorations he has on his bower platform ( $r_2 = 0.38$ ,  $F_{1,27} = 16.28$ ,  $p < 0.001$ ). (b) We found a highly significant negative relationship between the average rate at which the focal male startles females with his intense displays in first courtships and male mating success ( $r_2 = 0.34$ ,  $F_{1,27} = 13.88$ ,  $p < 0.001$ ).

ness is more important than familiarity in affecting female behaviours. Further supporting the relationship between male attractiveness and female behaviours, we found differences in female crouching and startling behaviours during first courtships with males that are chosen as mates versus less attractive males that are rejected (figure 3), even when faithful females are excluded. In summary, our results suggest that female behaviours in first courtships do not change as females approach mating, or with the familiarity of the male alone; rather, female behaviours are related to the attractiveness of the courting male.

Previous studies have found that male satin bowerbirds give more intense displays when females increase their crouching and that more intensely displaying males are more successful in mating (even when crouching is statistically or experimentally controlled (Patricelli 2002; Patricelli *et al.* 2002)). Thus increased female tolerance during first courtships with more attractive males may give these males an advantage: they can give higher intensity courtship displays from their first courtship with a female without threatening her, and thus further enhance their chances for mating.

**(b) Why are female behaviours related to male attractiveness?**

Male satin bowerbirds have complex and multifaceted courtship displays. Previous studies have found relationships between physical traits (the quality of the bower and the number of decorations) and behavioural traits (the intensity of male courtship displays, responsiveness to female signals and the quality of male vocal mimicry) and male success in mating (Borgia 1985; Loffredo & Borgia 1986; Borgia 1993; Patricelli 2002; Patricelli *et al.* 2002). However, we do not yet know how each of these traits influences female choice. We present evidence that the relationship between female behaviours and male attractiveness is due in part to a decreased tendency to be startled during courtships with males that have attractive display traits, and in part to a reduction in mating success by males that startle females with their behavioural displays.

Supporting the hypothesis that females are more tolerant of intense displays with males that have more attractive physical display traits, we found that the rate at which a male startles females is negatively related to the number of decorations on his bower (figure 4). This is not because males with more decorations are also better at responding to female signals by modulating their displays (Patricelli *et al.* 2002), as both responsiveness and decorations are independently related to the rate at which males startle females (Patricelli 2002). This suggests that having more decorations on a male's bower by itself reduces the threat of intense displays to females. Results from an experimental manipulation of bower decorations are forthcoming and will allow us to directly test causal relationships among these variables (S. W. Coleman and G. Borgia, unpublished data).

Supporting the hypothesis that males that startle females more often are less successful in attracting females to mate, we found a negative relationship between the rate at which males startle females during courtship and male mating success. This result is not surprising, given the negative relationship between startling and mating success that we found among courtships of individual females (see figure 1), and the relationship between startling in first courtships and courtship success reported by Patricelli *et al.* (2002). When we considered startle rate and bower decorations together, we found that startle rate was significantly related to male mating success, but decorations were not. This suggests that males who startle females less often are more successful in attracting females to mate; and that bower decorations are related to male mating success in part because they reduce the likelihood that females will be startled by male behavioural displays.

Although we found that females crouch more during their first courtships with males who have higher mating success, we did not find that bower decorations and bower quality affect female crouching. Thus females crouch more for attractive males, but it is not yet clear what male traits elicit increased crouching. Other aspects of male sexual displays that were not considered here may influence crouching, such as male vocal mimicry (Loffredo & Borgia 1986).

**(c) Why are females less threatened by attractive males?**

Females are more tolerant of high-intensity displays from attractive males; but why might this be so? Despite

evidence that females prefer highly intense courtship displays from males, these displays can also be threatening to females, who are at risk of forced copulation (Borgia 1995*b*; Borgia & Presgraves 1998). In courtships with attractive males, the aggressive and sudden movements of intense male courtship displays may be less threatening to females, if the risk or potential cost of forced copulation by the courting males is reduced (Patricelli *et al.* 2002, 2003). Female assessment of physical displays, such as bower decorations and bower quality, may be important in this initial assessment of male attractiveness. Alternatively, males may decorate their bowers to exploit the startle-inhibiting effect of decorations on females (e.g. Ryan 1990): the startle response in rats and humans can be inhibited by 'pleasant' visual stimuli (e.g. Lang 1995; Koch 1999), and decorations may have a similar effect on female bowerbirds, which may not be adaptive for females. This seems unlikely, however, because bower decorations are correlated with other sexually selected display traits (Borgia 1993; Patricelli 2002), which would not be predicted by sensory exploitation alone but would be expected if decorations are used in initial assessments of male attractiveness.

We found that female satin bowerbirds crouch more and startle less during their first courtships with attractive males, and we provide evidence that male bower decorations contribute to this decrease in female startling. These results suggest that physical display traits facilitate the expression of behavioural displays by decreasing female tendency to be threatened in early courtships. This is a novel mechanism by which multiple male traits may interact to affect female choice. Multiple male display traits are generally assumed to function independently (Møller & Pomiankowski 1993; Johnstone 1996; but see Hasson 1989; Rowe 1999; Kodric-Brown & Nicoletto 2001); these results suggest that by considering interactions among traits, we may gain new insight into the evolution and maintenance of multiple male display traits.

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