Female signals enhance the efficiency of mate assessment in satin bowerbirds (*Ptilonorhynchus violaceus*)

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Recent evidence suggests that males adjust their sexually selected display traits in response to female behaviors during courtships. Little is known, however, about whether females signal to influence male displays and whether females benefit from this interaction. Male courtship displays in the satin bowerbird (*Ptilonorhynchus violaceus*) are highly intense and aggressive. Females may use these displays as indicators of mating benefits, but these displays often startle females and disrupt courtship. Previous studies have shown that successful males decrease female startling by adjusting their display intensity according to female crouching behaviors, suggesting that crouching behaviors function as signals. Here we address whether female crouching is a signal by using observations of natural courtship behaviors. In addition, we examine why females differ in signaling and whether females benefit from signaling. First, we find that female crouching is related to the likelihood that females will be startled by male displays, suggesting that crouching signals the degree of display intensity that females will tolerate from a male without being startled. Second, we find that female tolerance for intense display increases during successive courtships as females assess potential mates, and that female tolerance may also be affected by age and condition. Third, we find evidence that females that reduce startling by signaling their intensity tolerance are more efficient in mate searching. These results suggest that females signal to influence how males display their sexually selected traits, and by doing so, females may increase their benefits in mate choice. *Key words:* courtship, female signals, interactive signaling, *Ptilonorhynchus violaceus*, responsiveness, satin bowerbirds, sexual selection. *[Behav Ecol 15:297–304 (2004)]*

Courtship in many species involves elaborate reciprocal displays given by both the male and the female. These displays may act as signals—traits shaped by selection to elicit a specific response from a receiver. Female signals are known to play numerous roles in facilitating courtship (Cox and Le Boeuf, 1977; Halkin, 1997; Langmore et al., 1996; Markow and Hanson, 1981; Pagel, 1994; Rowland, 2000; Welbergen et al., 1991; West and King, 1988; Wiley and Poston, 1996). However, little is known about whether females signal to affect how males display their sexually selected traits within each courtship (Balsby and Dabelsteen, 2002; Patricelli et al., 2002).

Why might females signal to influence male courtship displays? Recent evidence suggests that males of many species adjust their displays according to external factors that affect the costs and benefits of different display behaviors, such as the light environment or the presence of predators (Candolin, 1997; Dill and Hedrick, 1999; Endler, 1987; Godin, 1995; Long and Rosenqvist, 1998). These and other factors may also affect females that are observing male courtship behaviors; for example, male courtship displays that attract predators may also endanger courted females (Dill and Hedrick, 1999; Gong and Gibson, 1996; Hedrick and Dill, 1993; Magurran and Seghers, 1994). As the costs and benefits of observing male display behaviors change, females may benefit by signaling to influence male displays. Indeed, male guppies change their courtship behaviors in the presence of predators (Endler, 1987; Godin, 1995; Houde, 1997), and recent evidence

suggests that males may be responding in part to changes in female behaviors (Dill and Hedrick, 1999; Evans et al., 2002; Magurran and Nowak, 1991). In satin bowerbirds, males increase their courtship success by adjusting their displays according to female behaviors during courtship (Patricelli et al., 2002). But it is not yet clear whether these female behaviors are signals, what factors affect female behaviors, and whether females benefit by influencing male displays.

Here we examine the possible role of female signals during courtship in the satin bowerbird (*Ptilonorhynchus violaceus*). Male satin bowerbirds are not choosy about their mates, and variance in male mating success is extremely high (Borgia, 1985; Borgia, 1993). Satin bowerbird courtship involves behavioral displays by males, which may be both beneficial and costly for females, and may favor female signaling. Male behavioral displays are similar to male–male aggression displays (Borgia, 1995b; Borgia and Mueller, 1992; Borgia and Presgraves, 1998) and involve coordination of feather puffing, rapid wing-extensions, and running with a loud buzzing vocalization (buzz/wing-flip displays). Females may benefit by using the intensity of these displays as an indicator of genetic or proximate benefits (Andersson, 1994; Berglund et al., 1996; Borgia and Presgraves, 1998). In spotted and satin bowerbirds, females prefer more intensely displaying males as mates (Borgia and Presgraves, 1998; Patricelli, 2002; Patricelli et al., 2002). Thus, to assess male displays and choose the most attractive male, females are predicted to tolerate maximum-intensity displays from males during courtship. Contrary to this prediction, however, high-intensity male courtship displays often threaten females and may startle them repeatedly, disrupting or ending courtship (Patricelli et al., 2002; Uy et al., 2001a). Females may have reason to be wary of aggressive behaviors, because they are at risk of attack and forced copulation by courting males (Borgia, 1995b). This threat may be costly if females are unable to efficiently assess potential mates. The conflicting effects of behavioral displays—threatening females

in some courtships and attracting them to mate in other courtships—may favor females that signal their intensity tolerance to courting males. By doing so, females may be able to assess male display and avoid being unnecessarily threatened by displays more intense than they are willing to tolerate.

In this study, we use observations of natural courtship behavior to address three questions about female signaling in satin bowerbird courtship. First, do females signal their tolerance for intense displays to courting males? Second, what causes variation in female tolerance for intense displays? Third, do females benefit by signaling to responsive males?

First, we examine whether females signal their tolerance for intense displays to courting males. During courtships, females often crouch by lowering and tilting forward toward the mating position, a fully crouched position with wings fluffed. The mating position is used by females in many species to solicit copulation. In bowerbirds, the gradual approach to the mating position is referred to as crouching (Patricelli et al., 2002). Female crouching behavior is extremely exaggerated: both the degree and rate of crouching are highly variable among courtships, and crouching is used outside of the context of copulation/solicitation, occurring in courtships a week or more before copulation and with males that are not later chosen as mates. In an experiment with robotic female bowerbirds that mimic the crouching behavior of real females, Patricelli et al. (2002) found that males respond to graded increases in female crouching by increasing the intensity of their displays correspondingly. Furthermore, males that are more responsive—increasing their intensity only as females increase their crouching—startle females less often during courtship. The extreme exaggeration of female crouching behaviors, and the finding that males respond to female crouching and thereby reduce female startling, suggest that crouching is a signal indicating the degree of display intensity that females will tolerate from males without being threatened. This hypothesis predicts an inverse relationship between female crouching and the likelihood that females will be startled by male displays. Here we test this prediction by examining the relationship between female crouching and female startling in natural courtships.

Second, we examine the causes of variation in female tolerance for intense displays. During mate choice, a typical female 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 one male (Uy et al., 2000, 2001a). Examining the first courtships between a female and each potential mate, Patricelli et al. (2003) found that female tolerance for intense displays is positively related to the attractiveness of the courting male. Thus, male attractiveness influences female behaviors in first courtships, but we do not yet know what happens in later courtships. Here we follow individual females during sequential courtships as they assess potential mates, and we test the hypothesis that female tolerance for intense displays increases in successive courtships. This may occur if females sequentially assess multiple male traits during mate choice, primarily examining other male traits in early courtships and examining high-intensity behavioral displays in later courtships (Borgia, 1995a; Gibson, 1996; Patricelli et al., 2003; Sullivan, 1994), or if females habituate to the threat of male displays with repeated courtships. Alternatively, support for the null hypothesis would suggest that female tolerance for intense displays does not change in successive courtships. This may occur if a female's initial assessment of each male's attractiveness determines her tolerance for intense displays in subsequent courtships with him; females may continue to elicit the same level of display intensity from males in repeated courtships, for example, to increase the accuracy

of their assessment (see Luttbeg, 1996; Sullivan, 1990, 1994). To further examine causes of variation in female tolerance for intense displays, we examine whether female tolerance is affected by female body condition and age.

Third, we examine whether females benefit by signaling to responsive males. Previous studies have shown that males who respond to female signals by modulating their display intensity startle females less often (Patricelli, 2002; Patricelli et al., 2002). This suggests that communication with males may reduce the rate at which females are startled. Startling often disrupts or ends courtship, which may reduce female efficiency in assessing males and require additional courtship visits. Startled females may also lose the opportunity to mate with more intensely displaying, preferred males. Thus, females may benefit by signaling to responsive males, as this may reduce the likelihood of being startled during courtship. We test two hypotheses about the benefits of signaling. We test the hypothesis that females that are startled less often are more successful in mate choice, predicting a negative relationship between the rate of being startled and the attractiveness of the male chosen as a mate. In addition, we test the hypothesis that females that are startled less often are more efficient in mate assessment, predicting a positive relationship between the rate of startling and the number of courtships needed to find a mate.

We find that females signal their tolerance for intense displays to males by crouching, and that females crouch to elicit increasingly intense displays during sequential courtships as they assess potential mates. Further, we find that females that are startled less often are more efficient in mate-assessment, suggesting that female signals—as well as male response—may be favored by sexual selection.

METHODS

Observation of natural courtships

This study was conducted in 1997 at our field site in Wallaby Creek, New South Wales, Australia (Tooloom National Park, see Borgia, 1985). From 1982–1988 and from 1995–1997, bowerbirds were captured at feeding sites before the mating season and fitted with unique, three-color plastic leg bands for identification. Male satin bowerbirds build specialized structures called bowers that are used for courtship and mating and that allow for the continuous video monitoring of natural breeding behaviors (Borgia, 1985, 1995b; Gilliard, 1969; Uy et al., 2000, 2001a,b; Vellenga, 1970). During the mating season of 1997, from 9 November to 20 December, automatic Hi-8 video cameras that record time and date were used to monitor 29 adjacent bowers covering an area of ~4 km². Video cameras were triggered when movement on the bower activated motion sensors, allowing for continuous and simultaneous observations of all behaviors at bowers throughout the mating season (Borgia, 1995b).

Analysis of courtship behaviors from videos

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. Detailed mate sampling patterns of 62 females were reconstructed by using this time- and date-stamped video footage (Uy et al., 2000, 2001a,b). Thirty-two females monitored in 1997 were observed to mate in 1996, and thus, we were able to determine if females remate with the same male for two consecutive years (faithful females) or choose new mates (Uy et al., 2000, 2001b). Out of the available 1997 courtships, we chose 283 courtships for detailed analysis. Courtships were chosen

randomly with respect to male and female courtship behaviors to be analyzed, using the following criteria. Courtships were chosen to be representative of the range of courtship durations and outcomes experienced by each bower-holding male. We included courtships that were the first between male/female dyads, for measurement of mean female startling and mean female crouching (see below). Further, we included courtships that represented complete mate-search sequences for individual females. G.P. and four assistants scored behaviors from videos; assistants were unaware of the predictions being tested in this study. A subset of courtships scored by G.P. were randomly chosen and scored a second time by all assistants to measure concordance of each variable; the average of all scorers was used in analyses. All of these courtships were used in calculating crouching and startling variables, unless otherwise noted.

Startle rate

Startling has been used to measure response to auditory, visual, and tactile threats in insects, birds, and mammals (Davis et al., 1997; Lang, 1995; Richardson, 2000; Varty et al., 1998). We scored a startle when the courted female moved rapidly upward or backward immediately after a male behavior (Patricelli et al., 2002). Startled female bowerbirds often hop out of the bower away from the male. We scored all startles occurring throughout the courtship, noting which male behavior preceded the startle. Because we were primarily concerned with the effects of high-intensity male behavioral displays on females, we calculated the startle rate for each courtship as the proportion of buzz/wing-flip displays that startled females. The buzz/wing-flip displays occur during the most vigorous portion of courtship, and the intensity of these displays is related to male courtship success (Patricelli et al., 2002). Startle rate scores for each courtship were highly concordant among observers ($W = 0.91$, $\chi^2 = 14.5$, df $= 4$, $n = 4$, $p < .006$). For each female, we also calculated mean number of startles during the rest of courtship (everything but buzz/wing-flip displays) for paired comparison of the rate of startling during intense displays and during other aspects of courtship. To examine the effects of startling on mate-searching efficiency, we calculated mean female startling as the mean rate at which the focal female was startled by courting males; to control for the tendency of females to be startled less in repeated visits to a male, only courtships that were the first between a male and female pair were included.

Female crouch index

Female crouching is the gradual movement downward from the upright position to the mating position. We used a crouch index that reflects variation in both crouch rate and position among courtships. We divided the natural range of female motion into six positions that could be reliably scored, and measured the time spent in each position. We then multiplied the proportion of the total courtship duration that females spent in each position by a value from one to six, with the upright position as one and the fully crouched position as six. These values were then summed, so that noncrouching females scored the minimum crouch index of one and females that spent the entire courtship in the mating position scored the maximum crouch index of six. Crouch index scores were highly concordant among observers ($W = 0.96$, $\chi^2 = 15.4$, df $= 4$, $n = 4$, $p < .004$). To examine the effects of crouching on mate-searching efficiency, we calculated the mean female crouching as the mean crouch index score among courtships of the focal female; to control for the tendency of females to crouch more in repeated visits to

a male, only courtships that were the first between a male and female pair were included.

Female age and condition

Birds were weighed and measured during capture for color-banding. Sex was determined by using plumage, morphology, and size (Vellenga, 1970) and confirmed with behavioral observations from video when available (62 of 71 females were observed to copulate). Detailed age data were not available for all birds because no birds were banded from 1988–1994; however, we were able to classify birds as young (less than 10 years) or old (10 years or greater), based on initial capture date and plumage traits. Birds banded in 1987 or before were classified as old, and birds banded in 1995 or after were classified as young. Female condition was estimated by taking the residuals of a regression of individual mass ($\log_e$) on tarsus length (Packard and Boardman, 1987). There was no significant relationship between date of capture (starting from the first day a female was caught) and female mass (Uy et al., 2001a), suggesting that female weight does not change considerably as the mating season approaches.

Male mating success

We used male mating success as a measure of the male's attractiveness to females. Females arrive at bowers individually, so female mate choice copying is unlikely to affect male mating success (Patricelli GL, Uy JAC, and Borgia G, unpublished observations). Each male's mating success was estimated from videotapes of natural bower activity as the number of females that mated with the male. 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 that banded females had with males in our population in 1997 (1.8 ± 0.11 copulations). When male mating success is calculated by using the upper or lower 95% confidence limits for the average number of copulations among banded females, results are not qualitatively different. For each female, we calculated the mean mating success of the males visited for courtships; we used this measure in analyses of mate-searching efficiency using multiple regression. For each female, we also calculated the mean mating success of the male(s) chosen as mates; we used this as a measure of the female's success in mate-searching.

Female mate-search efficiency

We used the number of courtships in a female's mate-search sequence as a measure of her efficiency in finding a mate, with shorter sequences implying greater efficiency. For this analysis, we included only courtships that did not end in copulation, to eliminate variation introduced by differences in number of copulations among females. Results were not qualitatively different when courtships ending in copulation were included in this analysis.

Analysis of female behaviors while mate-searching

For each female with at least three courtships available for analysis, we calculated a Kendall's correlation coefficient (r_k) between crouch index and the order of the courtship in the female's mate-search sequence, between startle rate and the order of the courtship in the female's mate-search sequence, and between crouch index and startle rate. To avoid
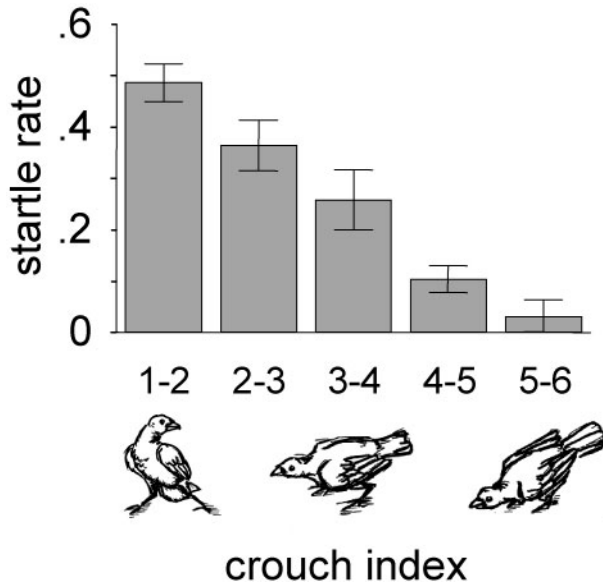
Figure 1
Female crouching during courtship is negatively related to the likelihood that females will be startled by male behavioral displays. This graph illustrates this relationship by showing mean startle rate among females ± SE for each interval of the female crouch index.

pseudoreplication, we calculated the mean r_k among females for statistical analyses (see below). We calculated these correlation coefficients by using three subsets of courtships. First, we examined all courtships available between each female and her potential mates (mean = 5.4 ± 0.4 courtships per female, 176 total). Second, we examined courtships between individual male-female dyads (mean = 4.08 ± 0.2 courtships per dyad, 98 courtships total). Third, we examined courtships between a female and all of her potential mates that did not end in copulation (mean = 4.48 ± 0.4 courtships per female, 108 courtships total). Courtships occurring after the female's final copulation were not considered to be a part of the mate-search sequence.

Statistical analyses

A Kendall's coefficient of concordance (W) was used to measure concordance among observers during video analysis. Wilcoxon matched-pair test (Z) was used for paired comparisons of female startling caused by buzz/wing-flips displays versus other displays, because these data could not be transformed to meet the assumptions of normality for parametric tests. Kendall's correlations (r_k) were used to examine how individual female behaviors changed among courtships as females searched for mates (see above); mean r_k values among females were compared to zero with a t test (Sokal and Rohlf, 1995). Least-square linear regression was used to analyze relationships among variables, standardized regression coefficients (b_x) are reported for each independent variable in multiple regressions. The number of courtships in a female's mate search sequence (used for analysis of mate-search efficiency) was $\sqrt{(Y + 0.5)}$ transformed, and male mating success was $\log_e (Y + 1)$ transformed to meet the assumptions of normality and homoscedasticity for parametric tests (Sokal and Rohlf, 1995). All statistical tests are two-tailed. All means are presented mean ± SE, unless otherwise noted.

RESULTS

Satin bowerbird courtship

A typical satin bowerbird courtship begins with the female in the bower, and the male vocalizes and hops in front of the bower with a decoration in his beak. After an average of 40 s (SD = 70), the male begins buzz/wing-flip displays, in which he coordinates a loud buzzing vocalization, feather puffing, a run in front of the bower, and rapid extension of both wings. An average buzz/wing-flip bout lasts 21 s (SD = 11) and includes 3.4 buzz/wing-flips (SD = 0.9), followed by mimicry of several local species (Loffredo and Borgia, 1986a). Males typically repeat these courtship elements if females remain in the bower for prolonged courtship, as is increasingly common toward the end of the female's mate-search sequence (Uy et al., 2001a). The average courtship involves 4.4 buzz/wing-flips (SD = 2.4). Females are more likely to be startled during the buzz/wing-flip portion of courtship (number of startles per female during buzz/wing-flip displays = 1.6 ± 0.14) than in the remainder of courtship (number of startles per female during the remainder of courtship = 0.6 ± 0.15; n = 69, Z = 5.77, p < .001), even though buzz/wing-flip displays represent an average of only 17 ± 0.8% of the courtship duration. Previous studies suggest that males minimize the threat to females during courtship by modulating the intensity of the buzz/wing-flip portion of their courtship displays (Patricelli, 2002; Patricelli et al., 2002). Thus, we focus on female startling during the buzz/wing-flip portion of male displays in this study.

Does female crouching signal female tolerance for male display?

We tested the hypothesis that female crouching signals the degree of display intensity that females will tolerate from males without being threatened, predicting an inverse relationship between female crouching and the likelihood that females will be startled by male behavioral displays. We found support for this hypothesis: female crouch index was negatively related to female startle rate in courtships between each female and all of her potential mates (mean r_k = −.45 ± 0.07, t = 6.61, df = 32, p < .001) (Figure 1).

What causes variation in female behaviors?

We tested the hypothesis that female tolerance increases in successive courtships. This predicts a positive relationship between female crouching (and a negative relationship between female startling) and the order of the courtship in the female's mate-search sequence. To test this hypotheses, we first examined sequential courtships between each female and all of her potential mates. Female tolerance for male behavioral displays increased during sequential courtships: female crouching was positively related to the order of the courtship in the female's mate-search sequence (mean r_k = .38 ± 0.05, t = 6.94, df = 38, p < .001) (Figure 2a), and female startling was negatively related to the order of the courtship in the female's mate-search sequence (mean r_k = −.35±0.08, t = 4.37, df = 32, p < .001) (Figure 2b). Similarly, we examined a subset of these courtships to determine whether female behaviors change during sequential courtships with individual males. Female crouching increased (mean r_k = .34 ± 0.08, t = 4.17, df = 23, p < .001) (Figure 2c) and female startling decreased (mean r_k = −.25 ± 0.11, t = 2.30, df = 20, p < .032) (Figure 2d) during sequential courtships with an individual male. These results support the hypothesis that females tolerate increasingly intense displays in successive courtships.
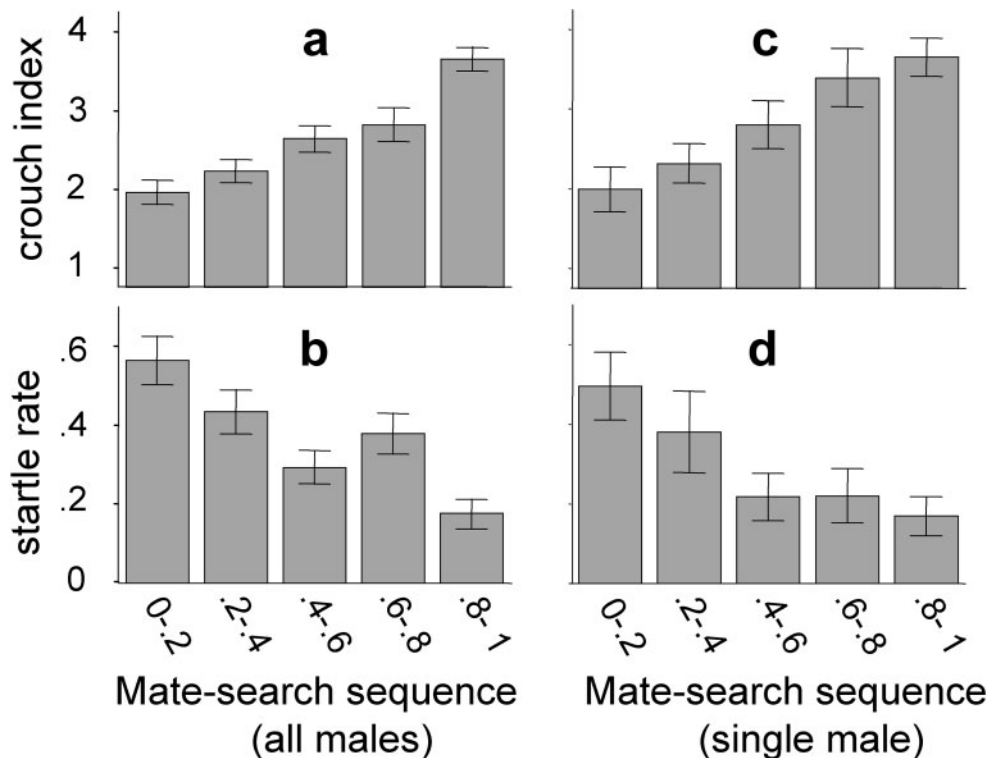
Figure 2
The rate at which females are startled by intense male displays significantly decreases, and female crouching significantly increases, during sequential courtships as females assess potential mates. This graph illustrates female behavioral changes by showing mean female startling ± SE and mean female crouching ± SE for each interval in the female's mate-search sequence (the number of each courtship in a female's mate-choice sequence was divided by the total number in the sequence, to control for variation in sequence length). (a and b) Female behaviors in courtships between each female and all of her potential mates. (c and d) Female behaviors during sequential courtships with individual males.

Courtships occurring toward the end of the female's mate-search sequence may end in copulation and thus involve maximum crouching by females to solicit copulation. To determine whether the observed increase in female tolerance for intense displays during sequential courtships is caused by copulation solicitation only, we examined only courtships that did not end in copulation. Crouch index increased during sequential courtships not ending in copulation (mean $r_k = .28 \pm 0.08$, $t = 3.42$, df = 22, $p < .002$); startle rate decreased during sequential courtships not ending in copulation (mean $r_k = -.23 \pm 0.10$, $t = 2.41$, df = 18, $p < .027$); and crouch index was correlated with startle rate in these courtships (mean $r_k = -.50 \pm 0.09$, $t = 5.72$, df = 18, $p < .001$). This result supports the hypothesis that females gradually signal their increasing tolerance for high-intensity displays during successive courtships not only in final courtships ending in copulation.

We also investigated whether female behaviors vary with female condition and age class. To do so, we examined mean female startle rate and crouch index in first courtships with each potential mate. Female condition was unrelated to mean female crouching ($r^2 = .05$, $F_{1,46} = 2.34$, $p < .133$), whereas females in poorer condition tended to be startled more often by male displays, although not significantly ($r^2 = .06$, $F_{1,46} = 3.13$, $p < .084$). There was also a nonsignificant tendency for young females to be startled more often than were old females (mean young female startling = 0.49 ± 0.04; mean old female startling = 0.30 ± 0.08; $t = 1.86$, df = 53, $p < .068$), and a nonsignificant tendency for young females to crouch less than did old females (mean young female crouching = 2.12 ± 0.14; mean old female crouching = 2.72 ± 0.21; $t = 1.93$, df = 54, $p < .059$).

Do females benefit from signaling?

We tested two hypotheses about benefits that females gain by reducing the likelihood that they will be startled by overly

intense male displays: (1) females that are startled less often are more successful in mate choice, and (2) females that are startled less often are more efficient in mate assessment. The hypothesis that reduced startling increases mate-searching success predicts a negative relationship between the rate at which females are startled during courtship and the attractiveness (mating success) of the male(s) chosen as a mate. We did not find support for this hypothesis: there was no significant relationship between mean female startling and the mean mating success of the chosen mates ($r^2 = .01$, $F_{1,57} = 0.67$, $p < .41$).

The hypothesis that reduced startling increases female mate-searching efficiency predicts a positive relationship between the rate at which females are startled during courtship and the number of courtships in the female's mate-search sequence. Supporting this hypothesis, mean female startling was positively related to the number of courtships in a females' mate-search sequence ($r^2 = .13$, $F_{1,57} = 8.49$, $p < .005$) (Figure 3). Because female tolerance for intense displays is influenced by the attractiveness of the courting male (Patricelli et al., 2003) and because male attractiveness may also influence female mate-searching, we examined the relationship between female startling and efficiency while controlling for male attractiveness and female crouching. Mean female startling was positively related to the number of courtships, even when we controlled for mean female crouching and the average mating success of the males sampled by each female ($b_{mean\ startling} = 0.27$, $p < 0.04$; $b_{mean\ crouching} = -0.25$, $p < .06$; $b_{mating\ success} = -0.04$, $p < 0.78$; $r^2 = 0.19$, $F_{3,55} = 4.3$, $p < .008$). Further, we examined the relationship between startling and mate-searching efficiency when controlling for female-specific factors that might influence female startling and female mate-searching behaviors: female crouching, female body condition, female age, and faithfulness to previous mates (Uy et al., 2000). Mean female startling was positively related to the number of courtships, even when we excluded faithful females and
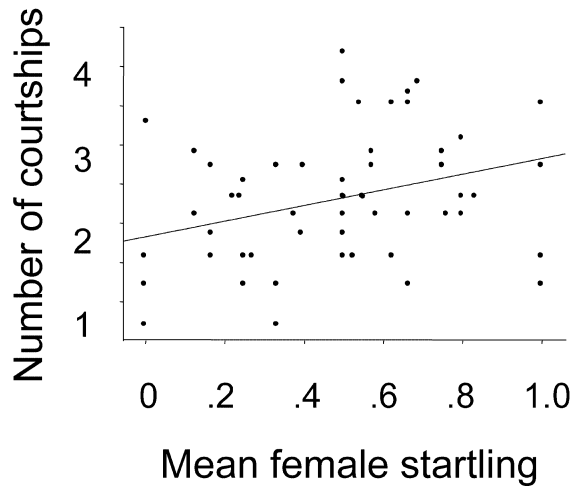
Figure 3
Females that are startled more often are less efficient in finding a mate: there is a significant positive relationship between the average rate at which females were startled by intense displays and the number of courtships in the female mate-search sequence ($r^2 = .13$, $F_{1,57} = 8.49$, $p < .005$).

controlled for female condition, female age class, and mean female crouching ($b_{\text{mean startling}} = 0.42$, $p < .022$; $b_{\text{mean crouching}} = 0.001$, $p < .99$; $b_{\text{condition.}} = -0.27$, $p < .13$; $b_{\text{age}} = 0.05$, $p < .76$; $r^2 = .30$, $F_{4,28} = 2.95$, $p < .038$). The relationship between female startling and number of courtships was not owing to a higher number of males sampled (i.e., more first courtships) by females with longer mate-search sequences, because we used the mean rate of startling in first courtships, not the overall rate of startling.

DISCUSSION

Does female crouching signal female tolerance for male display?

In satin bowerbirds, females prefer the most intensely displaying males as mates, but these displays can also be threatening and thus startle females (Patricelli et al., 2002). We found a highly significant relationship between female crouching and the likelihood that females will be startled by male displays (Figure 1). This suggests that crouching conveys information to the courting male about female tolerance for intense behavioral displays (i.e., the likelihood that the female will be startled). In addition, there is evidence that males respond to female behaviors; Patricelli et al. (2002) controlled female crouching by using robotic female bowerbirds and found a positive relationship between male display intensity and female crouching (Patricelli, 2002). Thus, by adjusting their crouching behaviors during courtship, females may influence male behavioral displays and thereby reduce the likelihood of being startled by displays more intense than they are willing to tolerate. Further, we found evidence that females benefit from this reduced startling by increasing the efficiency of their mate-searching, suggesting that crouching behavior may be favored by selection (discussed below). Taken together, these results support the hypothesis that crouching is a signal—a trait shaped by natural selection to elicit a response from a receiver—and that females use crouching to signal their tolerance for male display intensity.

What causes variation in female tolerance?

We examined the crouching and startling behaviors of individual females during successive courtships as they search for mates. We found support for the hypothesis that females tolerate higher intensity behavioral displays during sequential courtships as they search for mates (Figure 2), even when we exclude courtships which end in copulation.

This gradual increase in female tolerance for male display may be caused either by the order of the courtship in mate-searching (e.g., if females habituate to the threat of male behavioral displays or if female behaviors change with increasing readiness to mate) or by the fact that females become more tolerant of intense behavioral displays as they assess males to be attractive. Examining only the first courtships that a female has with each potential mate, Patricelli et al. (2003) found no relationship between female tolerance and the order of the courtship in the female's mate-search sequence. In these same first courtships, however, there was a strong, positive relationship between female tolerance for male behavioral displays and the courting male's attractiveness. These results suggest that female tolerance does not necessarily change with the timing of courtship, but that male attractiveness can affect female tolerance for intense displays.

If females assess male attractiveness in their first courtship (Patricelli et al., 2003), why do females return for multiple courtships and gradually increase their tolerance for intense behavioral displays? Previous studies suggest that female satin bowerbirds prefer more intensely displaying males as mates, and that each male's display intensity can be highly variable among courtships (Patricelli, 2002; Patricelli et al., 2002). Models predict that variable male display traits may require assessment by females during repeated courtships to gain more accurate information about male attractiveness (Luttbeg, 1996; Sullivan, 1990, 1994). Our results suggest that female satin bowerbirds are unlikely to gain more accurate information about male display intensity in repeated courtships, because females generally do not tolerate high-intensity displays in early courtships. The gradual increase in female tolerance for male displays suggests that females assess different male traits sequentially during mate choice (Borgia, 1995a; Gibson, 1996; Patricelli, 2002; Sullivan, 1994; Uy et al., 2001a). Male satin bowerbirds have multifaceted sexual displays, and male display intensity, responsiveness to female signals, bower decorations, bower quality, and vocal mimicry are all related to male success in courting females (Borgia, 1985; Loffredo and Borgia, 1986a; Patricelli, 2002; Patricelli et al., 2002). By crouching less and eliciting low-intensity behavioral displays in early courtships, females may avoid being startled while they primarily assess other male display traits. During later courtships with attractive males, the risk and potential cost of forced copulation may be reduced. Thus, females may assess high-intensity displays primarily in later courtships to discriminate among more attractive males. This sequential assessment of male display traits may allow females to increase their mate-searching efficiency.

In addition to variation within individual females, we examined variation among females of different body condition and age class. Female body condition and age were not significantly related to female tolerance for intense displays, but there was a tendency for young females to startle more and crouch less than did old females. More detailed age data are needed to address age-related changes in female behavior, because our age classes were too broad (less than 10 years and 10 years or greater) to examine behaviors over the first few years of mating. It seems likely that females learn to signal more effectively as they age or that females are less easily threatened due to habituation and/or positive conditioning

with age (Davis et al., 1997; Koch, 1999). There is also evidence that age-related changes in brain function may reduce the tendency to startle (Varty et al., 1998). Because startling affects female choice in bowerbirds (Patricelli et al., 2002, 2003), age-related changes in mate choice are possible.

Do females benefit from signaling?

Patricelli et al. (2002) found that males who respond to female signals by modulating their display intensity startle females less often. This suggests that communication with males reduces the rate at which females are startled. We tested the hypothesis that this reduction in startling benefits females by increasing their efficiency in mate assessment, such that fewer courtships are needed before finding a mate. Females that are startled less often had fewer courtships in their mate-search sequences (Figure 3). The relationship between startle rate and courtship efficiency is significant even when we control for female crouching and other factors that may affect startling and the number of courtships in a female's mate-search sequence—faithfulness to mates from the previous year, female condition, female age, and the attractiveness of courting males. Startling may be related to mate-searching efficiency because startled females often hop in and out of the bower; this can disrupt courtship, when males pause their intense displays until females return to the bower, or end courtship, when females leave the area (Patricelli, 2002; Uy et al., 2001a). Thus, startling may interfere with the female's ability to assess male behavioral displays and other traits (e.g., vocal mimicry, bower quality and decorations), causing females to make additional courtship visits. We did not find support for the hypothesis that startling affects the female's mate-searching success, suggesting that startling does not affect a female's ability to find an attractive mate, although they require more courtships to find them.

Theory suggests that efficient mate assessment is critical to maximize the benefits of mate choice (Janetos, 1980; Luttbeg, 1996; Real, 1990; Sullivan, 1994), and there is growing empirical evidence that female mate-searching behaviors are shaped by selection to maximize efficiency (Rintämaki et al., 1995; Trail and Adams, 1989; Uy et al., 2000). The costs of decreased efficiency may include direct costs, such as energetic expenditure, and indirect costs, such as delayed clutch initiation or forced copulations from low-quality males (Reynolds and Gross, 1990). Uy et al. (2000) found a positive association between increased mate searching and the occurrence of costly and violent force-copulation attempts by marauding juvenile and adult males. Thus, signaling females may be more efficient in mate assessment and may have greater benefits in mate choice.

Although signaling to males may reduce the rate of startling (Patricelli et al., 2002), females are often startled during courtship and thus pay a cost of decreased efficiency—if efficiency is critical, why does startling persist? Variation in male responsiveness to female signaling is related to the rate at which males startle females (Patricelli et al., 2002), suggesting that females are likely to see displays more intense than desired as they visit males differing in responsiveness. Furthermore, females may have reason to remain wary during courtship because they are at risk of attack and forced copulation by courting males and marauding males (Borgia, 1995b), which may explain why the startle response persists. Trends in our data suggest that female-specific factors such as age and body condition may also contribute to differences among females in tendency to be startled.

Conclusions

Interactive signaling during courtship—with female signals and male response—may benefit both sexes. By responding to female signals and modulating their display intensity, males may reduce the threat of their behavioral displays and increase their success in courtship (Patricelli, 2002; Patricelli et al., 2002). By signaling their intensity tolerance to courting males, females may reduce startling and increase their mate-searching efficiency. This type of communication may be important in the many other species in which courtship involves aggressive male displays (Berglund et al., 1996; Borgia, 1979; Borgia and Coleman, 2001; Loffredo and Borgia, 1986b; Mateos and Carranza, 1999). More generally, factors such as variation in environmental conditions or female preference may alter the costs and benefits of male courtship display for females (see Endler, 1987; Jennions and Petrie, 1997), causing variation in female tolerance for male display. In these cases, females may communicate their tolerance to responsive males by signaling—even if those signals are subtle and nonvocal such as female crouching or the distance that the female keeps between herself and the male. Thus, sexual selection in many species may favor interactive signaling, with males and females influencing each other's behavior to maximize their own chances for successful courtship.

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