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Male satin bowerbirds, *Ptilonorhynchus violaceus*, adjust their display intensity in response to female startling: an experiment with robotic females

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Females of many species preferentially mate with males that produce courtship displays at a high intensity or rate; however, males do not always display at their maximum intensity during courtship. Evidence suggests that this behaviour may be adaptive in satin bowerbirds, because overly intense displays can disrupt courtship by startling females. Females signal the display intensity that they will tolerate from a male; males that respond by adjusting their intensity reduce the likelihood of startling females and increase their courtship success. However, even the most responsive males occasionally startle females. When this occurs, males could avoid further threat to females by decreasing the intensity of their subsequent displays. We used robotic female bowerbirds that mimicked female startling to test the hypothesis that males reduce the intensity of their courtship displays after startling females. Supporting this hypothesis, males displayed at significantly lower intensity after robots were startled in experimental treatments than when they were not startled in control treatments. We found no evidence that the degree of male response to startling was related to male courtship success. In spite of evidence that female bowerbirds prefer the most intensely displaying males as mates, we found that males did not always display at maximum intensity, but rather reduced their intensity in response to female startling during courtship. Our results suggest that males adjust the level of expression of their display traits in response to female behaviours during courtship, and by doing so, males may increase their chances for successful courtship.

The sexually selected display traits of individual males commonly vary over time (Gerhardt 1991; Gerhardt & Huber 2002), but models of sexual selection generally characterize males as having a single trait value (Lande 1981; Kirkpatrick 1982; Grafen 1990; Iwasa et al. 1991). Thus, when variation in male traits is detected in empirical studies, it is often assumed to have little significance in communication, except in making male traits more costly for females to assess (Sullivan 1990; Luttbeg 1996). There is increasing evidence, however, that variation in male traits can be the result of facultative adjustment of displays. Males of many species have been found to adjust their displays according to external factors that affect the costs and benefits of various display behaviours, such as the light environment, the presence of predators or competition from other males (e.g. Endler 1987; Travis & Woodward 1989; Metz & Weatherhead 1992; Zucker 1994; Godin 1995; Candolin 1997; Long & Rosenqvist 1998; Dill & Hedrick 1999; Wong et al. 2004). Less often considered is male adjustment of displays in response to signals and cues given by the female during courtship. Female behaviours, such as posture or the distance the female keeps between herself and the male, may convey information to the male about the effectiveness of his attempts to attract her to mate; males may use this information to maximize their chances for successful courtship (West & King 1988; Balsby & Dabelsteen 2002; Meffert & Regan 2002; Patricelli 2002; Patricelli et al. 2002; Santangelo 2005). Thus, sexual selection may favour both the ability to produce attractive display traits and the ability to adjust those traits effectively in response to female behaviours during courtship.

The facultative adjustment of male displays may function to reduce threat to females during courtship, and thus may be especially important in species where courtship

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displays are aggressive and intense (Borgia & Presgraves 1998; Borgia & Coleman 2001; Patricelli et al. 2002, 2003). Females may use the intensity of male displays as an indicator of genetic or proximate benefits that females gain in mate choice (Andersson 1994); however, these displays may be threatening, especially in the numerous species where courtship displays are similar to agonistic displays (e.g. Borgia 1979; Loffredo & Borgia 1986b; Berglund et al. 1996; Borgia & Presgraves 1998; Mateos & Carranza 1999; Borgia & Coleman 2001; Patricelli et al. 2002, 2003). For example, two studies have shown that female spotted bowerbirds, *Chlamydera maculata*, prefer to mate with males that give highly aggressive courtship displays, and additional male traits have coevolved to reduce the threat of these displays to females (Borgia 1995a; Borgia & Presgraves 1998). Female spotted bowerbirds observe courtship through a see-through wall on the structure built for courtship and mating (the bower); this modified wall reduces the threat of highly aggressive male displays. When the wall between the male and female was experimentally removed, courting males reduced the intensity of their displays (Borgia & Presgraves 1998). This result suggests that threat reduction has influenced the evolution of physical and behavioural displays in spotted bowerbirds, and has favoured the ability of males to adjust their display intensity when the protection provided by the bower is not available.

In satin bowerbirds, males do not display to females through a bower wall but instead reduce threat by modulating the intensity of their displays according to female signals (Patricelli 2002; Patricelli et al. 2002, 2003). Male satin bowerbird courtship displays involve sudden, dramatic movements in which males coordinate feather puffing, wing extensions and running with a loud buzzing vocalization (buzz/wing-flip displays). Evidence supports the hypothesis that female satin bowerbirds prefer the most intensely displaying males as mates (Patricelli 2002; Patricelli et al. 2002; Coleman et al. 2004), but these displays are similar to male–male aggression displays (Borgia & Mueller 1992; Borgia 1995b; Borgia & Presgraves 1998), and females are at risk of forced copulation by courting males and marauding males (Uy et al. 2000). Thus, females are often threatened and may be startled repeatedly by intense buzz/wing-flip displays, jumping rapidly upward or backward immediately following male displays (Patricelli 2002; Patricelli et al. 2003). This startling can disrupt or end courtship and reduce the efficiency of female mate searching (Uy et al. 2001; Patricelli 2002; Patricelli et al. 2002, 2003). Startling behaviour is inversely related to another female behaviour, female crouching, such that males can observe female crouching and gain information about the likelihood that females will be startled (Patricelli 2002; Patricelli et al. 2003). In an experiment with robotic female bowerbirds that mimicked female crouching behaviours, Patricelli et al. (2002) found that males increased their display intensity in response to an increase in female crouching, thus giving their highest-intensity displays when females were least likely to be startled. Males that were more responsive to female crouching signals startled females less often and were thus more successful in courtship. These studies suggest that reduction of threat to females has played an important role in shaping satin bowerbird courtship, favouring male adjustment of displays in response to female signals during courtship.

Even males that are highly responsive to female signals occasionally startle females during courtship (Patricelli et al. 2002, 2003). In this study, we investigated whether male satin bowerbirds would respond to female startling by changing their behavioural displays to mitigate further threat to the female. The startle response occurs in many species, and is thought to function in protection against the threat of injury or attack (Lang 1995; Davis et al. 1997; Varty et al. 1998; Koch 1999; Richardson 2000). In satin bowerbirds, we have often observed that when females are startled from the bower, males will cease movement and vocalization and resume only when the female returns to the bower (G. L. Patricelli & G. Borgia, personal observation). Males may also respond to female startling in less dramatic ways. We experimentally tested the hypothesis that males will reduce their display intensity after they startle females. We tested males from a wild population of satin bowerbirds with robotic females that simulated startling behaviours. By using robots, we were able to manipulate the focal behaviour of the 'signaller' (startling) and control for other signaller behaviours that may influence the receiver's response (Michelsen et al. 1992; Webb 2000; Balsby & Dabelsteen 2002; Patricelli et al. 2002; Narins et al. 2003; Göth & Evans 2004). We predicted that males would display at lower intensity after robots were startled from a crouched to an upright position than during control courtships, where robots remained either upright or crouched. We also examined the consequence of individual variation in male response to startling. We tested the hypothesis that the degree of male response to females startling affects male courtship success, which predicts that males that lower their display intensity in response to robot startling will have higher courtship success.

METHODS

Observation of Natural Courtships

Bowerbirds were captured at feeding sites in Wallaby Creek, New South Wales, Australia (Tooloom National Park; Borgia 1985) from 1995 to 1999, fitted with unique, three-colour plastic leg bands for identification, and categorized into sex and age groups by plumage, morphology and size (Vellenga 1970). From 29 October to 20 December in each year, automatic Hi-8 video cameras that record time and date were used to monitor 29 adjacent bowers covering an area of about 4 km^2. Video cameras were triggered when movement on the bower activated motion sensors, allowing for continuous and simultaneous observations of all behaviours at bowers throughout the mating season (Borgia 1995b). 'Male courtship success' (see below) was measured from videotapes of natural courtships from 1999. For comparisons of male behaviours during courtships with real versus robotic females, we use 'male responsiveness' and 'mean male display intensity' measured from videotapes of natural courtships in 1997

(Patricelli 2002); these data were not available from 1999, but satin bowerbirds are long-lived and male display traits are repeatable across years (Borgia 1993).

Experimental Courtships

Robotic female bowerbirds

To experimentally control female courtship behaviours, we built three robots consisting of remote-control servos mounted on sheet metal frames and enclosed within female satin bowerbird skins (Patricelli et al. 2002). The space constraints of the mount required that we develop custom electronics and firmware to control robot movements. To control servo positions, the experimenter adjusted potentiometers on the hand-held remote controller. These potentiometer adjustments were translated into commands by a microcontroller (Microchip PIC16C44) mounted inside the remote controller, and these commands were sent through a serial interface by wire to a second microcontroller (Microchip PIC12C509) within the robot, which sent commands to the servos. Crouching and startling behaviours were simulated with coupled vertical and forward-tilting body movements, ‘looking around’ was simulated with lateral head and neck rotation, and wing fluffing was simulated with lateral wing movement (Fig. 1). FMA Direct servos S200, S100, S90 and S90 (Rockville, Maryland, U.S.A.) were used to control each of these movements, respectively.

The electronic and mechanical components of each robot were sealed with electrical tape and silicon sealant and then painted brown to repel moisture and reduce conspicuousness of the parts visible from behind the fully crouched robot (Fig. 1b; courting males typically do not approach females from behind unless attempting copulation, which occurs after all of the courtship behaviours scored for this experiment). To support the bowerbird skins, each robot had a body armature and an armature for each wing; armatures were constructed with plastic cross-stitch mesh woven with 22-gauge craft wire. Six female satin bowerbirds were collected for their skins 10 km from Wallaby Creek. This research was conducted within the ABS/ASAB

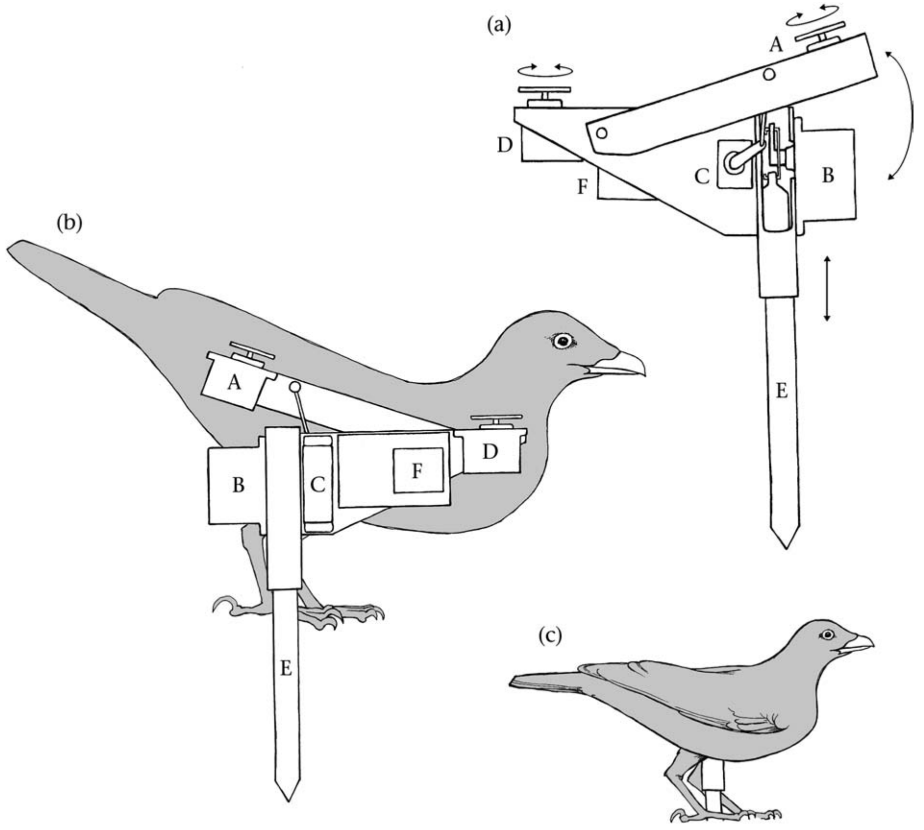

Figure 1. Schematic of a robotic female bowerbird. (a) A side view of the mechanical and electronic components of a partially crouched robot. Robots were capable of four types of movement, each driven by a servo motor (labelled with capital letters). Lateral wing movements were driven by servo A, which was attached to the armature supporting the wings at the posterior (wings were jointed to body armature at the anterior). Vertical body movement was driven by servo B, which lifted the robot upward by pushing down against the top of the sharpened post (E) (this post was pushed into the ground to support the robot). Forward-tilting body movement was driven by servo C, which lifted an arm to which the body armature was attached. Lateral head movement was driven by servo D, to which the head was attached directly. Downward and forward-tilting body movements were coupled to model downward crouching during experimental courtships; the opposite was used to model upward startling. Servo movements were controlled via a circuit board and computer chip inside the robot (F) and another inside the remote controller (see Methods for details). (b) The opposite side view of the robot, showing the relationship of the mechanical and electronic components of the robot to the bowerbird skin and armature. (c) The finished robot in an upright position.

guidelines for ethical treatment of animals. Collection of female bowerbirds was approved by the New South Wales National Parks and Wildlife Service Permit No. A415) and the University of Maryland Animal Care and Use Committee (No. R-97-47A). Birds were captured in cage traps and immediately euthanized with an overdose of ketamine/xylazine. Skins were prepared using sawdust and minimal amounts of borax (hydrated sodium borate) to absorb moisture, and were affixed to the body and wing armatures using flexible craft glue. Each robot was created using the skins of two females, one providing the head and wings and the other covering the body; this was necessary to cover the armature and to prevent gaps between feathers and joints. To create wing-fluffing movement, the anterior of each wing was jointed to the body armature, and the posterior of each wing was attached to a servo motor (servo A in Fig. 1); anterior joints were covered by the scapular and side feathers of the body and were not visible. The head and neck of each robot were supported with wire and cotton and attached directly to the servo controlling head movement (servo D in Fig. 1); the interface between the head and body was covered with feathers from the neck and was not visible. Glass eyes were custom-made to match a photograph of a female bowerbird by the Tohickon Glass Eyes company (Erwinna, Pennsylvania, U.S.A.). To produce legs that bent passively as the robot crouched, the top of each tibiotarsal bone was jointed to the body armature with wire, and the natural tibiotarsal–tarsometatarsal joint (the ‘ankle’) was coated once with melted beeswax to maintain flexibility; the digits were dried in a standing position and thus rested flat on the floor of the bower during experiments (Fig. 1c). Robots could crouch from the upright position (Figs 1b, 2a) downward into the mating position (Figs 1c, 2b); this range of movement was divided into six evenly spaced crouch positions. Wing-fluffing movements were not used in this study.

For experimental courtships, a robot was placed in the bower avenue of the subject male (Fig. 2) by pushing the pointed stake at the base of the robot (Fig. 1b) into the soil under the avenue of the bower. Robot movements were remotely controlled from a blind located at least 6 m from the bower. Power was supplied by a 12-V battery near the blind. Control and power wires running from the back of the robot to the blind were buried under loose leaves. G.P. and an assistant each used one robot to conduct these experiments, and the third robot was used occasionally as a spare; experimenter/robot identity had no significant effect on male display intensity ($P > 0.5$, see below).

Experimental methods

During the 1999 breeding season, we tested with robots 23 of the 29 males whose bowers were monitored with video cameras. For each experiment, we conducted a behavioural observation of 1 h or longer from the blind to allow the male to habituate to the presence of the blind and experimenter. If a natural courtship or copulation occurred during the observation period, we waited an additional 30 min before beginning the experiment. After the observation, the robot was placed in the male’s bower, where the male typically courts females (Vellenga 1970; Donaghey 1981; Borgia 1985). We considered courtship to begin when the male arrived on the bower platform and to end when the male either attempted copulation with the robot or stopped courting and the left the area (38 of 44 experiments ended with attempted copulation). When males attempted copulation, we shooed the male from the robot to avoid damage to the robot’s skin and feathers.

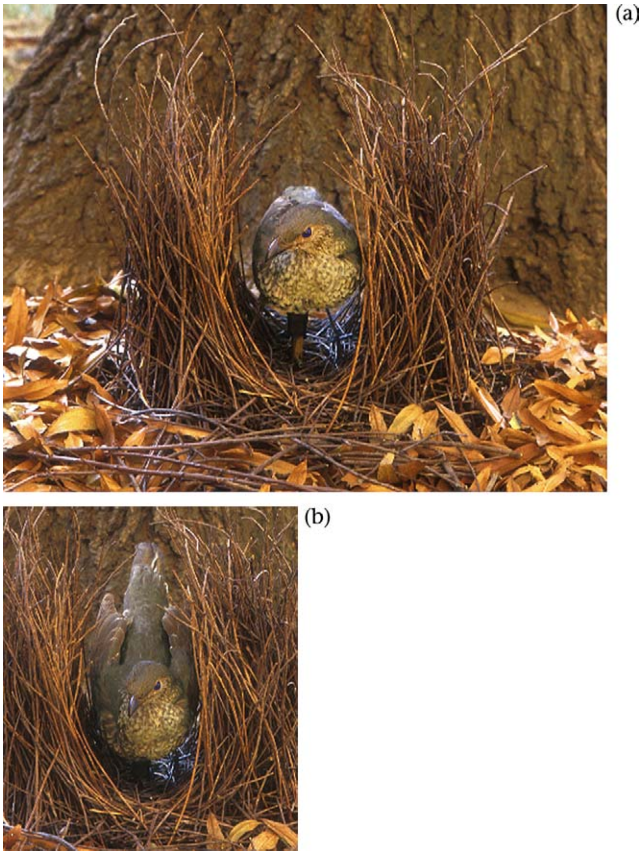

Figure 2. For experimental courtships, robots were placed in the bower of the male being tested (as shown here), and remotely controlled. The robot is photographed here in the upright (a) and fully crouched positions (b). Each male was tested with robots that moved from a partially crouched position to an upright position after males performed a behavioural display (startle treatment), remained partially crouched throughout courtship (crouch treatment), and remained upright throughout courtship (upright treatment).

Each male was tested with a startle treatment and two controls: the crouch and upright treatments. In the startle treatment, the robot began in the upright position, then crouched downward into a partially crouched position (position 3 of 6) at the beginning of courtship; when the male performed his first buzz/wing-flip display, the robot simulated a startle by rapidly moving back into the upright position and then remained there until the end of courtship. By crouching partially, the robot signalled intermediate tolerance for intense male displays, but was not soliciting copulation (Patricelli 2002; Patricelli et al. 2002, 2003). The crouch treatment (the first control) began the same as the startle treatment, but the robot remained crouched (position 3) through the end of courtship. In the upright treatment (the second control), the robot remained in the upright position throughout the courtship. Throughout all treatments, the experimenter rotated the robots' heads in an irregular pattern and at a moderate rate to simulate natural female behaviours ('looking around').

The startle and crouch treatments were conducted between 11 November and 6 December 1999. The order of treatments was randomized between males, and at least 5 days were allowed between sequential treatments on the same male to minimize habituation ($\overline{X}\pm\mathrm{SE}=10.1\pm0.8$ days between treatments). The upright treatment was conducted between 3 and 19 December as a part of another experiment; all males received the upright treatment after the other two treatments. Although an optimal design would have the upright treatment concurrent with the other treatments, our analysis of variance did not show a significant effect of order of treatment on male display intensity, and the date of the experimental courtship was not significant as a covariate in the model (both $P > 0.5$, see below), suggesting that the lack of randomization in treatment order did not affect the results. Experimental courtships were assigned to the two experimenters randomly with respect to treatment and subject (male identity).

Of the 23 males tested with robots, six were not successfully tested and were dropped from the study (four males approached the robot but did not court her, and two males attempted copulation with the robot but did not court her). Of the 51 experiments attempted on the remaining 17 males, seven experiments were unsuccessful and were not included in analyses (two with technical difficulties, one with copulation only, and four with no courtship or copulation). Male behaviour in successful tests of courtship with robots did not differ qualitatively from male behaviour in courtships with natural females (see below; Patricelli 2002). There was no significant difference between the courtship success (measured in natural courtships in 1999) of males that courted robots ($\overline{X}\pm\mathrm{SE}=0.07\pm0.02$, $N = 17$) and males that did not court robots (0.07 ± 0.03, $N = 6$; Student's t test: $t_{21} = 0.08$, $P = 0.94$).

Male Display Intensity

Male courtship displays in the satin bowerbird involve buzz/wing-flip displays, which were given in bouts of 3.6 ± 0.11 displays ($\overline{X}\pm\mathrm{SE}$) in this study, lasting an average of 22 ± 0.5 s per bout (see also Patricelli et al. 2003), followed by vocal mimicry of local species (Loffredo & Borgia 1986a). Females are 2.7 times more likely to be startled during the buzz/wing-flip portion of courtship than in the remainder of courtship, even though buzz/wing-flip displays represent an average of only 17% of the courtship duration (Patricelli et al. 2003); thus, we focused on buzz/wing-flip displays in this study. We were concerned with modulation of male display occurring directly in response to female startling, so we considered only display occurring in the first bout, during which the robot was startled in the startle treatment. Males gave additional bouts of display in 67% of experimental courtships; the second bout of display began a mean ± SE of 8.7 ± 0.04 min after robot startling.

For each buzz/wing-flip display, we quantified three highly variable aspects of display intensity that affect the level of threat to females (Patricelli et al. 2002). The distance run by the male during the display was measured relative to the width of a bower on a scale of 1 to 6 (1: no movement, 6: two average bower widths, or 40 cm). The degree that the male ptiloerected his feathers, making him appear larger, was scored on a scale of 1 to 6 (1: not erected, 6: fully erected). The location of the male on the bower platform was scored on a scale of 1 to 5 (1: furthest from the female, 5: closest to the female; values were normalized to a scale of 1–6). Higher scores indicate more intense displays for all three variables. Males may alter any combination of the distance, ptiloerection and area variables in response to female signals, so scores for the variables were multiplied to calculate the intensity of each buzz/wing-flip display (results were qualitatively the same when intensity was calculated additively). G.P. scored intensity from videotapes of experimental courtship. Nine courtships already scored by G.P. were chosen at random and scored a second time by a volunteer who was unaware of the predictions being tested. Average display intensity index scores for these courtships were completely concordant between G.P. and the volunteer (Kendall's coefficient of concordance: $W = 1.00$, $\chi^2_8 = 16.0$, $N = 2$, $P < 0.042$).

Despite the variability of female behaviours in natural courtships, there was a significant correlation between mean male display intensity during natural courtships measured in 1997 (Patricelli 2002) and mean male display intensity during robot courtships in the present study (Pearson correlation: $r_{10} = 0.64$, $P < 0.024$), and no significant difference in absolute male display intensity between these same natural and robot courtships (paired t test: $t_{12} = 0.71$, $P = 0.55$). These results suggest that male display observed in robot courtships approximates natural male display behaviours.

Male Response

Male response is a measure of the change in male display intensity that occurs in response to female startling. In the startle treatment, robots were startled after the male's first buzz/wing-flip display. Thus for each male, we calculated the 'intensity change' as the difference in intensity between the final buzz/wing-flip display of the bout (after startling) and the first buzz/wing-flip display of the bout (before startling). To control for changes that might occur in male intensity when robot females were not startled, we subtracted the intensity change in the crouch treatment from that in the startle treatment. The resulting value (male response) indicates the degree to which each male changed his intensity after startling the females, controlling for changes that occurred in the male's behaviour when females were not startled (negative value: decrease in intensity in response to startling females; positive value: increase in intensity).

There was a significant correlation between male responsiveness to female crouching in natural courtships measured in 1997 (Patricelli 2002) and male response to robot startling in experimental courtships measured in this study (Pearson correlation: $r_{10} = -0.67$, $P < 0.024$). This result suggests that the response observed in robot courtships approximates natural male responsiveness to signals and cues given by real females.

Male Courtship Success

Male courtship success was estimated from videotapes of natural bower activity in 1999 as the proportion of different females courted by the male that mated with him (Patricelli 2002; Patricelli et al. 2002, 2003). Of females observed to mate on video, 85% were banded and could be individually identified. In 1999, these banded females visited the males in our study an average ± SE of 2.1 ± 0.15 times for courtships not ending in copulation and an average of 1.7 ± 0.25 times for courtships ending in copulation. Thus, to estimate the number of unbanded females courted by each male, we divided his total courtships without copulation with unbanded females by the population mean number of these courtships among banded females (2.1). Similarly, to estimate the number of unbanded females that copulated with each male, we divided his total number of courtships with copulation with unbanded females by the population mean number of these courtships among banded females (1.7). When male courtship success was calculated using the upper or lower 95% confidence limits for the population mean number of courtships and copulations among banded females, results were qualitatively the same. In an unpublished study, copulations observed on video matched genetic paternity, suggesting that mating success is a good estimate of reproductive success in satin bowerbirds (S. M. Reynolds, K. Dryer, J. Bollback, J. A. C. Uy, G. L. Patricelli, T. Robson, G. Borgia & M. J. Braun, unpublished data).

Statistical Analyses

A repeated measures mixed model ANOVA was used for analysis of treatment effects using PROC MIXED in SAS 8.01 (Cary, North Carolina, U.S.A.). Each male was tested with three treatments, so male identity was considered a random block effect. The dependent variable was male display intensity at each sequential buzz/wing-flip during experimental courtships. We began with a model that included the following factors: treatment, the number of the sequential buzz/wing-flip (1–4), treatment by buzz/wing-flip interactions, experimenter/robot identity, order in which treatments were conducted, and the date of courtship as a covariate; the nonsignificant factors (all with $P > 0.5$) were sequentially dropped, leaving only the first three factors in the final model (see results; Table 1). We used the compound symmetry (CS) covariance structure to model the covariance of the repeated measures; we tested eight models, and the CS model showed the best fit using the Akaike and Schwartz' Bayesian information criteria (Littell et al. 1996). Male display intensity was square-root transformed to reduce skew and improve normality; we present reverse-transformed least-square means. Where appropriate, we conducted a priori orthogonal contrasts between means in the ANOVA model. For all a posteriori and/or nonorthogonal contrasts between means, we present *P* values that are corrected for multiple comparisons using the Stepdown Bonferroni method in SAS MULTTEST (Hochberg & Tamhane 1987); corrected *P* values are noted in the text. Least-squares linear regression was used to analyse relationships between variables. Statistical tests are two tailed, unless noted as one tailed in cases where the direction of effect was predicted a priori.

RESULTS

Male Response to Female Startling

We tested the hypothesis that males will reduce the intensity of their displays when their displays startle females, predicting that male display intensity would be lower after robots were startled (the startle treatment) than when robots remained either crouched (crouch treatment) or upright throughout courtship (upright treatment). Using repeated measures analysis of variance, we found a significant main effect of type of experimental treatment on average male display intensity, significant differences in the intensity of the four sequential buzz/wing-flips that constitute a bout of display, and a significant interaction between the experimental treatment and the change in intensity of sequential buzz/wing-flips (Table 1). Comparison of means between treatments shows that mean male display intensity was significantly lower in the startle treatment than in the crouch treatment (ANOVA: $F_{1,41} = 11.69$, one-tailed $P < 0.003$ with Bonferroni correction), but there was no significant difference between the startle and the upright treatments ($F_{1,41} = 1.35$, one-tailed $P = 0.25$ with Bonferroni correction: Fig. 3).

Mean display intensity for each courtship includes buzz/wing-flips that occurred before the robots were startled in the startle treatment, so we next examined changes in male display intensity before and after females were startled between and within each of the experimental treatments. Between the three treatments, we

Table 1. Results from repeated measures ANOVA showing the degrees of freedom (df), *F* statistic and two-tailed probability (*P*) for each factor in the final model

Effect	df	*F*	*P*
Treatment*	2, 41	5.93	0.0054
Buzz/wing-flip†	3, 106	7.95	0.0001
Treatment*buzz/wing-flip‡	6, 106	3.39	0.0042

Dependent variable: male display intensity.

*Differences in mean display intensity between the three experimental treatments (startle, crouch or upright).

†Changes in display over time between the four sequential buzz/wing-flips.

‡Interaction between the two variables.

compared average display intensity in the first, third and fourth sequential buzzes. There were no significant differences between treatments in the intensity of the first buzz/wing-flip display, which occurred before robot startling (startle versus crouch, ANOVA: $F_{1,106} = 0.45$, $P = 0.5$; startle versus upright: $F_{1,106} = 0.13$, $P = 0.72$; Fig. 4). However, the intensity of the third and fourth displays (after startling) were significantly lower in the startle treatment than in the crouch treatment (third display: $F_{1,106} = 9.41$, one-tailed $P < 0.001$; fourth display: $F_{1,106} = 22.02$, one-tailed $P < 0.0001$), and the third and fourth displays were significantly lower in the startle treatment than in the upright treatment (third display: $F_{1,106} = 3.35$, one-tailed $P < 0.035$; fourth display: $F_{1,106} = 3.95$, one-tailed $P < 0.024$; Fig. 4). We also conducted a posteriori comparisons of the means of the first and fourth buzz/wing-flip displays within each treatment. Within the crouch and upright treatments, the intensity of the first buzz/wing-flip was significantly lower than the fourth one (crouch treatment: ANOVA: $F_{1,106} = 31.8$, $P < 0.0001$ with Bonferroni correction; upright treatment: $F_{1,106} = 8.27$, $P < 0.015$ with Bonferroni correction; Fig. 4). Within the startle treatment, in contrast, male display intensity in the first buzz/wing-flip was not significantly higher than in the fourth buzz/wing-flip, which occurs after startling ($F_{1,106} = 0.01$, $P = 0.91$ with Bonferroni correction). Thus males increased their display intensity in sequential buzzes when robots remained crouched or upright, but not when robots were startled.

There was no significant negative relationship between male response to robot startling and male success in natural courtships (regression: $R^2 = 0.04$, $F_{1,14} = 0.06$, one-tailed $P < 0.23$; Fig. 5), which failed to support the hypothesis that more responsive males are more successful in courtship.

DISCUSSION

We tested the hypothesis that males reduce the intensity of their courtship displays when their displays startle females. Supporting this hypothesis, males displayed at lower intensity after robots were startled than when they remained crouched or upright throughout courtship (Fig. 4). Male bowerbirds increase their display intensity in response to increased female crouching (Patricelli 2002; Patricelli et al. 2002); this behaviour alone predicts that male display intensity should be higher in the crouch treatment than in the upright treatment (where robots were not crouched) and higher in the crouch treatment than in the startle treatment (where robots were crouched only until the male's first buzz/wing-flip display). Evidence suggests that female crouching affected male display intensity, because males displayed at their highest intensity in the crouch treatment (Fig. 3). However, our results show that males also responded to female startling during courtship, because males displayed at lower intensity after robots were startled into the upright position than when robots remained upright throughout courtship. This result was not predicted by response to crouching alone.

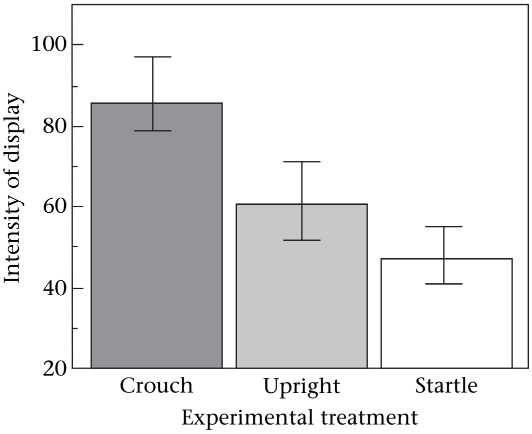

Figure 3. Mean ± SE male display intensity during each treatment (crouch, upright, startle).

Males responded to female startling by displaying at lower intensity than in control courtships when robots were not startled. However, within the startle treatment, males did not display with less intensity after than before robot startling (Fig. 4). If their first display startles a female, why do males continue displaying at that level rather than decreasing their intensity? It is unlikely that males are simply incapable of displaying at lower intensity than the mean before startling females, because the minimum display intensity for a male in the startle treatment was 8.17 (16% of the mean value of 49.16). Perhaps if females are expecting an increase in male intensity in sequential displays, then not increasing their intensity is sufficient for males to mitigate threat to females while still providing an attractive display.

A 'startle' is defined as a rapid response to a sudden intense stimulus (Koch 1999), and the type of rapid movement that occurs during startling varies among species. Female bowerbirds typically move upward and/or backward when startled (Patricelli et al. 2004). Robots moved only upward in this study; further experiments are needed to determine whether males would also respond to rapid backward or downward robot movements. Patricelli et al. (2002) found that males responded to slower downward movements by the robot (crouching) by increasing the intensity of their display. Thus, the decrease in display intensity that we observed in response to upward startling does not appear to be a general response to female movement, but rather a response to rapid upward female movement following male buzz/wing-flip display.

In addition to examining average male response to experimental treatments, we examined whether individual variation in male response to startling affects male success in courtship. We tested the hypothesis that the degree of male response to female startling affects male courtship success. We did not find the predicted relationship between the degree of male response to robot startling and male success in natural courtships (Fig. 5). We did find that male response to robot startling was correlated with responsiveness to female crouching in natural courtships. In Patricelli's (2002) study, responsiveness to crouching was negatively related to the rate at which males startled females with their intense displays and

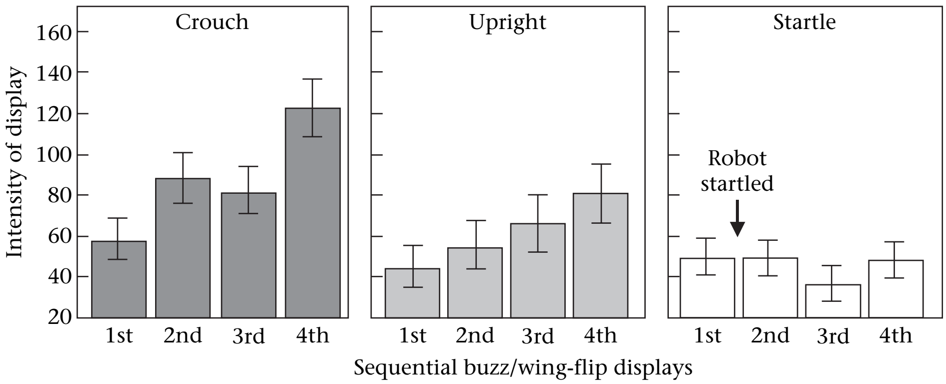

Figure 4. Mean ± SE male display intensity during sequential buzzes within each treatment (crouch, upright, startle).

positively related to male courtship success. The sample size of the present study may have been too small to detect a relation between responsiveness and courtship success, although we found a weak trend in the predicted direction. Alternatively, the degree of male response may be less important than the presence of a response; indeed, 13 of 16 measured males responded to robot startling by displaying at lower intensity than when robots were not startled.

Why Respond to Startling?

Males responded to female startling by displaying with less intensity than when females were not startled. Why might males respond to startling? In experimental and observational studies of this population of satin bowerbirds, the rate at which males startled females with intense displays was negatively related to male courtship success (Patricelli et al. 2002, 2003). This correlation suggests that reducing the threat of intense displays to females is an important component of successful courtship. One way that males do this is to modulate their display intensity in response to female crouching, because crouching signals the likelihood that females will be startled by intense displays (Patricelli et al. 2002). Patricelli et al. (2003) found that male bower decorations may reduce the threat to females during courtship, because there is a negative relation between the number of male bower decorations and the rate at which females are startled by male behavioural displays, even when male responsiveness to female crouching is controlled. However, even males that are responsive to female crouching and have highly decorated bowers startle females occasionally. This may occur because of variation in females' ability to signal their tolerance for intense displays to males by crouching, or because females are easily startled in courtships that occur early in mate searching (Patricelli et al. 2003). Patricelli et al. (2002) found that more intense courtship displays are more likely to startle females (but see Patricelli 2002), so by displaying at a lower intensity after startling a female, males are less likely to threaten the females with subsequent displays.

An alternative hypothesis to explain male response to startling is that the male mistakes female startling as a response to a nearby predator or marauding conspecific male and reduces his intensity to attend to this threat. The primary predators of adult bowerbirds are raptors, and the risk of predation is extremely low at bowers, which are built on the forest floor, protected by logs or shrubs (Borgia 1993; Frith & Frith 2004). In the thousands of hours of satin bowerbird courtship observed and video recorded since 1982, no predation events at the bower have been detected (Borgia 1995a, b; G. Borgia & G. Patricelli, personal observation). Furthermore, the response of males to robotic female startling was qualitatively different from male response to potential predators: bowerbirds of many species 'freeze' upright with sleeked plumage when they observe a potential predator (Frith & Frith 2004), but males in this study continued their noisy displays and dancing postures at a reduced intensity. Alternatively, males may be responding to the threat of marauding conspecific males, who occasionally interrupt courtship and attempt to force copulations with females (Uy et al. 2000, 2001). Again, however, the response to startling that we observed was qualitatively different from the response to marauders, where males typically pause to locate the marauder and then violently attack them if observed (G. Borgia & G. Patricelli, personal observation). Thus, it is unlikely that attentiveness to predators or marauding conspecifics has shaped the complex behaviours reported here.

A second alternative hypothesis for male response to female startling is that male display intensity is an intention signal (Dawkins & Guilford 1994) or a signal

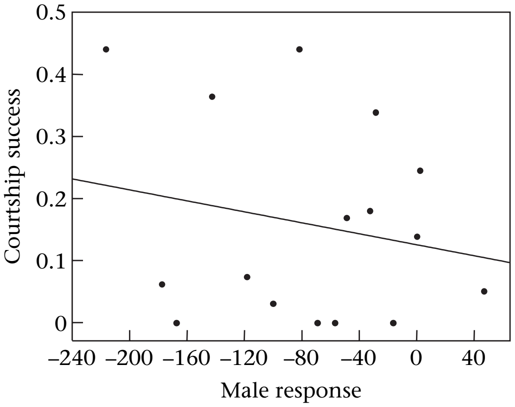

Figure 5. Male response to robot startling and courtship success.

of male motivation to mate (Bradbury & Vehrencamp 1998), and that males thus decrease their intensity when females startle because this indicates a low probability of mating. Intense male displays are unlikely to be an intention signal in bowerbirds, because there is evidence that females instead use the intensity of male display as a mate-choice signal (Borgia & Presgraves 1998; Patricelli 2002; Patricelli et al. 2002; Coleman et al. 2004). Thus, males would be expected to display at a high intensity unless it benefits them to do otherwise (e.g. to reduce threat to females or to conserve energy; see below).

A third alternative hypothesis to explain male response to startling is that males conserve energy by producing lower-intensity behavioural displays when females startle, because startling indicates that females are less likely to be assessing behavioural displays. This hypothesis is suggested by recent evidence in satin bowerbirds that females primarily assess physical traits (bowers and decorations) in early courtships, when startling is more common, and primarily assess high-intensity behavioural displays in later courtships (Patricelli et al. 2003; Coleman et al. 2004). In addition, young females are more likely to be startled by behavioural displays than older females, as well as less likely to assess male behavioural displays while choosing a mate (Coleman et al. 2004). Thus, male response to startling may be favoured by selection to reduce the time and energy costs of producing male behavioural displays when they are unlikely to influence female choice (energy conservation), rather than selection to reduce the threat to females during courtship (threat reduction). However, the energy-conservation hypothesis does not explain (1) the negative relation between the rate at which males startle females and male courtship success (Patricelli et al. 2002, 2003), (2) the positive relation between male display intensity and the rate at which males startle females (Patricelli et al. 2002) or (3) the negative relation between male responsiveness to female crouching and the rate at which males startle females (Patricelli et al. 2002). Together, these relations suggest that male behavioural displays can threaten females, and that male response to female signals reduces this threat and thereby increases male courtship success. In contrast, there is no evidence that reduction of display intensity (response to female startling or crouching) directly affects male courtship success; rather, courtship success is related to startle rate (Patricelli et al. 2002). Although we cannot rule out that energy conservation affects male response to female signals, the evidence presented in this study and in previous observational and experimental work (Patricelli 2002; Patricelli et al. 2002, 2003) is more consistent with the hypothesis that males benefit from this response by reducing their threat to females.

Is Startling a Signal or a Cue?

The startle response is typically considered an involuntary response to threat (e.g. Lang 1995; Davis et al. 1997; Varty et al. 1998; Koch 1999; Richardson 2000) rather than a form of communication. Our finding that males responded to startling by reducing their display intensity raises the question of whether startling in satin bowerbirds has evolved as a signal to convey information to males about the threat felt by females, or whether it has the same function as in other species, with males using startling as a cue, correlated with threat to females for reasons other than the transmission of information (Bradbury & Vehrencamp 1998). To show that startling has been modified into a signal, startles would need to fulfil the following additional criteria: (1) startling must be exaggerated or ritualized to convey information (i.e. movements must be exaggerated beyond those seen in other species or used in different contexts), and (2) senders must benefit, on average, from signalling (Bradbury & Vehrencamp 1998; Lotem et al. 1999). Although startling in satin bowerbirds is not obviously exaggerated beyond what is seen in other species, we cannot address this question quantitatively because data are not available to compare startling in satin bowerbirds with other species. However, a study by Patricelli et al. (2004) provides information about the potential benefit to females of startling. Females that were startled more often were less efficient in mate searching, requiring more courtships to find a mate. This result suggests that startling, and the threat to females that startling reflects, is costly rather than beneficial. However, exaggerated female startling early in courtship may benefit females by encouraging males to reduce their display intensity in subsequent displays. There is insufficient evidence to test this possibility, so it is more parsimonious to assume that satin bowerbird startling has not been exaggerated beyond that in other species, and that males use startling as a cue. Males can benefit by their response to female startling if it reduces threat to females during courtship, so regardless of whether startling has been exaggerated to convey information, it behooves males to pay attention.

Conclusion

Female satin bowerbirds prefer to mate with intensely displaying males, but highly intense displays can threaten females (Patricelli et al. 2002). Thus, sexual selection may favour males with both the intrinsic ability to produce intense courtship displays and the ability to modulate these displays in response to female behaviours. Similar threat-reducing behaviours may be important in males of other species where courtship involves aggressive displays (Borgia 1979; Berglund et al. 1996; Mateos & Carranza 1999; Borgia & Coleman 2001; Santangelo 2005), but male response to female behaviours is certainly not restricted to these species. In cowbirds, juvenile males learn to give more attractive displays by observing cues given by females (King & West 1983; West & King 1988); in whitethroats, *Sylvia communis*, female vocal and jumping behaviour affect the rate of male singing (Balsby & Dabelsteen 2002); and in guppies, *Poecilia reticulata*, males adjust their courtship behaviours in response to changes in female behaviours in the presence of predators (Dill & Hedrick 1999; Evans et al. 2002). Subtle signals and cues given by females may influence male display behaviours in many species where courtship behaviours have not yet been examined in detail. Thus, the variation that is commonly observed in the expression of sexually selected male display traits may often be the result of facultative adjustment of displays in response to female behaviours during courtship. Studies of sexual selection on variable display traits often examine the average of multiple measurements to account for within-male variability. By examining not just the average but also the variability in male traits with respect to female behaviours, we may gain a more complete understanding of how display traits evolve by sexual selection.

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