Experiments with robotic females show that successful males modulate courtship both spatially and temporally in response to signals of female discomfort in the satin bowerbird *(Ptilonorhynchus violaceus)*

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Introduction

Discussions of the evolution of elaborate display traits often put forward simple models of sexual selection that characterize male display as arbitrary[1]. These models commonly pay little attention to the dynamics of courtship which may be necessary to fully appreciate the operation of sexual selection. Recent studies of bowerbirds[2-5] showed an important role for male modulation of intense display elements during courtship. Males must balance the benefits of attractive, intense displays against the threat these intense displays also present to females. Studies in the satin bowerbird (*Ptilonorhynchus violaceus*) show that males react to signals of female discomfort by lowering the intensity of their display[3-5]. That work qualitatively scored distance males moved after robotic females showed startle behavior as part of a measure of display intensity, but did not show that distance moved by the male, by itself, was significantly affected by female startles. That work was limited because it used videos that showed only a ground level view of the display court. Here we investigate in greater detail patterns of male movement on bowers in response to female signals. Robotic females were placed at male bowers and males courted them. These courtships were monitored by two cameras, one in a frontal position on the bower and the other directly above the bower. We developed a computer program to track and map male movements on videos. We were able to measure the detailed spatial and temporal dynamics of satin bowerbird courtship in relation to male characters including reproductive success. We hypothesized that male distance from the female during courtship and the duration of intense display elements are important factors that males can control to mitigate the threat to females during courtship[2,6-7].

Predictions

- Males will respond to female signals and move farther away when females show signs of discomfort with the male's courtship.
- Males will respond to female startles by shortening the duration of their loud, intense wing-flip displays.

Methods

- We recorded courtship behaviors using two cameras. One placed horizontally relative to the bower to monitor behaviour on the front court of the bower. The second camera was placed 2.4m above the bower monitoring it from above and synchronized with the horizontal camera. This allowed us to precisely quantify male position and movements at the bower during courtships.
- We used a robotic female bowerbird[5] to successfully monitor experimental courtships at 9 bowers (13 overall) to test how males react spatially and temporally to female startle behavior (the robot rapidly rising from a half-crouch to a standing position) that indicates discomfort with the male display.
- Comparisons between the experimental (startle) and control (half-crouch) robot treatments allowed us to test whether males modulate distance in response to female startles.
- Courtship videos were digitized and male position (center of the bird) was tracked automatically using WinBower software developed at the University of Maryland. The tracking results were then checked manually.
- Male position during courtship was mapped onto Cartesian coordinates such that the origin was at the front of the bower and the ordinate ran down the center of the bower avenue (see image at right).
- All calculated distances were calibrated from video frames that included reference metre sticks.
- Behavior codes were added to the tracking output file for the analyses.
- Statistical analyses were run using Statistica 6.0

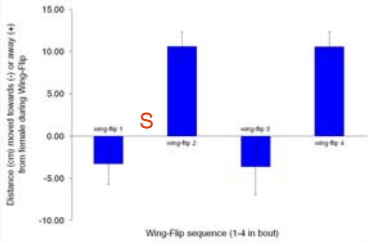

Fig. 1: Males show a distinct spatial pattern of wing-flip (WF) movements during courtship. In experimental courtships, the robot was startled following the 1st wing-flip (S).

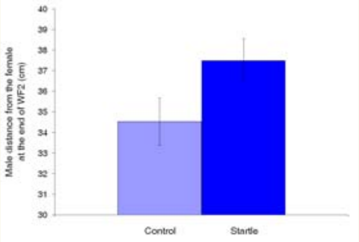

Fig. 2: Males respond to robot startles by moving farther away from robot during 2nd wing-flip

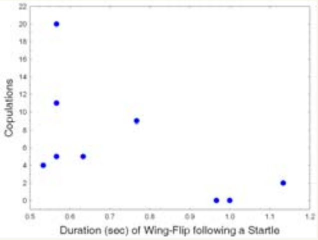

Fig. 3: Male mating success is inversely related to the duration of the WF following a startle.

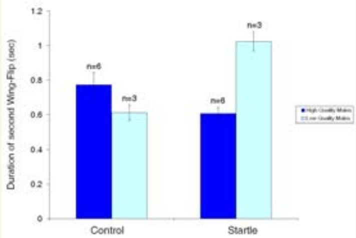

Fig. 4: High quality males produce a wing-flip of shorter duration following a startle.

Video camera mounted above a bower in the field

Map of male position during the intense wing-flip display (bower outline in red)

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Results

- Wing-flip displays during male courtship show a distinct and consistent spatio-temporal pattern (Fig. 1) in which the male alternates approaches and movements away from the female during a series of wing-flip movements.
- In experiments with robotic females, startle and control courtships did not differ in the male's distance from the female at the beginning of the first wing-flip (WF1) (Wilcoxon Matched Pairs Test, Z= 0.0592, n=9, P=0.953) or at the end of WF1 (Wilcoxon Matched Pairs Test, Z=0.4146, n=9, P=0.678), indicating that males behaved similarly in both treatments prior to the manipulation.
- After the robot showed startle behaviour, males reacted by moving farther away from the robotic female in experimental courtships during WF2 than in control courtships (Wilcoxon Matched Pairs Test, Z=2.0732, n=9, P=0.038; Fig 2), showing that males respond spatially to female signals of discomfort.
- After robot startles, the duration of WF2 was inversely related to male mating success (r_s=-0.59, n=9, P=0.046, 1-tailed; Fig. 3), and no such relationship was found in WF2 in control treatments (r_s=0.43, n=9, P=0.25). This shorter duration WF2 after a startle by successful males suggests that they are better able to adjust their display than less successful males.
- To further test the hypothesis that successful males respond temporally to robot startles we compared the difference in WF2 duration between control and experimental courtships. Although there was no overall significant difference with all males combined (Wilcoxon Matched Pairs Test, Z=0.070, n=9, P= 0.94), when males with a high number of copulations (≥4, n=6) were analyzed separately we found that they produced a WF of shorter duration following a startle than in control treatments (Wilcoxon Matched Pairs Test, Z=2.022, n=6, P= 0.043; Fig. 4), showing a temporal response to robot startles limited to high quality males.

Conclusion

This study has shown an important independent effect of male spatial position and wing-flip duration in relation to female signals during courtship. These results quantitatively support earlier suggestions that males modulate intense display elements by moving away from females and show an additional kind of modulation by shortening wing-flip duration. Successful males may make other adjustments but because of the limited sample size of our study these could not be demonstrated. Even so, these subtle responses by males to female startle behavior suggests a high level of tuning of male display and that it is important to pay close attention to the details of display in order to fully understand sexual selection.

Literature Cited

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