

## ABSTRACT

Title of Document: PLUMAGE COLORATION, AEROBIC CAPACITY  
AND THE SPATIAL DYNAMICS OF COURTSHIP IN  
SATIN BOWERBIRDS (*Ptilonorhynchus violaceus*)

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Courtship is the focal activity of mate-choice and is often composed of multiple elements under sexual selection. Bowerbirds are an important model system in sexual selection and I investigated three elements of courtship in satin bowerbirds (*Ptilonorhynchus violaceus*): plumage coloration, aerobic capacity and the spatial dynamics of courtship.

How plumage coloration affects mate-choice has long been discussed in bowerbirds but previous studies haven't found the presumed relationships. Adult males have iridescent, short wavelength saturated blue-black plumage with peak reflectance in the ultraviolet (UV). Here I show that blue, not UV, plumage reflectance is related to mating success. This suggests a mismatch between peak plumage reflectance and female preference and that it's not safe to infer a role of UV in mate-choice simply because of relatively high UV reflectance.

Physiological traits like aerobic capacity are of special interest in sexual selection because they indicate whole-organism performance. Adult male  $\dot{V}_{O_{2\max}}$  predicts male

display quality but not mating success.  $\dot{V}_{O_{2\max}}$  has an effect on male display quality that is not reflected in the relationship between display quality and mating success, suggesting that female choice may be directed at other male qualities. If any general trends are to be expected regarding aerobic capacity and courtship, I believe that simple repetitive courtships may be used as tests of male physiological ability, but that complex courtships involving multiple elements may have evolved to indicate male qualities other than whole-organism performance.

To study the spatial dynamics of courtship, I used vertically mounted cameras above bowers. I found a spatial pattern of male courtship and an association between male movements and the use of the bower as a barrier. This spatial pattern was associated to female startling behavior and males responded to robot startles by moving farther away from females. These findings support the hypothesis that male courtship behavior reduces the threat to females during courtship. Aggressive displays are commonly co-opted for courtship and threat reduction offers a testable hypothesis that can help understand the adaptive significance of the complex and what can otherwise be thought of as arbitrary courtships of many animals.

PLUMAGE COLORATION, AEROBIC CAPACITY AND THE SPATIAL  
DYNAMICS OF COURTSHIP IN SATIN BOWERBIRDS  
*(Ptilonorhynchus violaceus)*

by

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Dissertation submitted to the Faculty of the Graduate School of the  
University of Maryland, College Park, in partial fulfillment  
of the requirements for the degree of  
Doctor of Philosophy  
2011

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## PREFACE

This dissertation contains a single introduction and three chapters. Chapters II and III are presented in manuscript form, with introduction, methods, results and discussion sections, followed by figure captions and figures. Chapter I is presented in the format in which it was published (*Journal of Avian Biology*. 2011. 42: 80-84), with a more detailed discussion and some slight wording changes to increase clarity. A single bibliography section is at the end for references cited throughout the dissertation.

## DEDICATION

A Papa et Maman pour m'avoir encouragé  
de partir à la découverte du monde.

A Mélanie, David, Charles et Olivier pour me  
donner des raisons de revenir souvent.

## ACKNOWLEDGEMENTS

I would like to thank my dissertation advisor, Gerald Borgia, for excellent training in evolutionary biology and behavioral ecology. Fellow students in the lab provided friendship, support and collaboration without which I could have succeeded: Brian Coyle, Sheila Reynolds, Paul Zwiers, Carrie Long, Linda Cendes, Reimi Hicks and Archer Larned. Jason Keagy and I shared multiple field seasons in Australia and we developed a strong friendship and scientific relationship. For helpful suggestions with my dissertation, I thank my doctoral committee.

I would like to thank the many field assistants who made the fieldwork possible and enjoyable: Bard Edgerington, Shona Lawson, Hattie Oswald, Brian Sanchez (2001); Noëlle Beckman, Christen Bossu, Raphaël Demers, Michelle Robinson, Nicole Witteveld (2002); Kyle Elliott, Jamie Garten, Jora Rehm-Lorber, Cara Murphy, Lisa Taylor, Matt Terzi (2003); Gabrielle Gareau, Lori Parker, Lynette Plenderleith, Dave Obenshain, Matt South, Jessica Spence (2004); Bevan Kennedy, Lynette Plenderleith (2005).

I would also like to thank the many undergraduates that helped with video analysis; especially the following students that helped with digitizing videos and tracking using WinBower software: Kathryn Cai, Bobak Manoochehri, Nora McCall and Charlene Wu.

I owe many thanks to Ryan Farrell and Aniruddha Kembhavi of the UM Computer Science Department, whose generosity and interest in my project made the automatic tracking of our videos possible. They developed WinBower, an open-source image tracking software (<http://sourceforge.net/projects/winbower/>) that allowed me to automate the process of locating the male in most of our videos. Without their help, I would have had to either use much more expensive software or spend much more time manually tracking the birds.

I also owe many thanks to Dr. Mark Chappell of the UC Riverside Biology Department, who provided the expertise and experimental setup to measure maximum aerobic capacity in the field and verified my metabolic calculations.

A special thanks to our neighbours in Australia, who made me feel like a part of their family and whose hospitality made Wallaby Creek feel like home: Rose and Glen Kennedy, Rusty and Ann Bell, Victor and Cathy Mulcahy.

The staff of the Biology Department also deserves recognition for their logistical support: Lois Reid, Pamela Brock, KeCia Harper, Cecilia Jordan, Karen Spoerl, Lillian Rollins, Lindsey Johnson, Wan Chan, James Parker, Gerry Donovan and Larry Shetler. My international student paperwork and computer management issues often created extra work for them, yet they always helped me with pleasure.

This work was funded by NSF grants to Gerald Borgia, Ann G. Wylie Dissertation and Master Graduate Teaching fellowships to J-F.S., and Eugenie Clark and UM Biology summer fellowships to J-F.S.

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## INTRODUCTION

Elaborate displays and their evolution have long been of interest to naturalists and evolutionary biologists. Darwin's theory of natural selection (1859) provided a framework to understand how traits such as cryptic coloration could be beneficial in survival, but it was his theory of sexual selection (1871) that provided a mechanism by which gaudy and elaborate plumage coloration or displays could evolve despite the potential cost in increased predation due to these conspicuous traits. Sexual selection can operate either through male-male competition or through female choice by favoring individuals with traits that increase their reproductive fitness, and this usually leads to the elaboration of these sexual traits.

Models of sexual selection via female choice posit that female mate choice can evolve via a number of mechanisms. The largest debate has been between models based on either a Fisherian runaway process (Fisher, 1930; Lande, 1981) or a good genes process (Fisher, 1915; Borgia, 1979). In the runaway process, females prefer males with traits that will be attractive to other females, and a genetic correlation between trait and preference provides a feedback loop for the evolution of more elaborate traits until this mating advantage is balanced by the natural selection cost of the elaborate trait. In good genes models, females prefer males with traits that indicate some underlying genetic quality of the male, such as a better immune system or increased parasite resistance (Hamilton and Zuk, 1982) and this benefit is transmitted to her offspring. The major conceptual difference between these two classes of models is whether or not the female



preference is adaptive beyond simply producing males with similar traits and females with similar preferences. Beyond the dichotomy of these two models, other major models of sexual selection include proximate benefits (Hoelzer, 1989), pre-existing male traits (Borgia, 2006), sensory drive (Endler, 1992) and pre-existing female preferences (Ryan et al., 1990).

Males typically present their display traits to observing females during courtship, and courtship plays a central role in sexual selection through female choice (Andersson, 1994; Höglund and Alatalo, 1995). Traits that females assess during courtship include plumage coloration and courtship vigor. Additionally, recent work has shown that males often alter their courtship behavior in response to females during courtship (Balsby and Dabelsteen, 2002; How et al., 2008; Meffert and Regan, 2002; Santangelo, 2005). This courtship adjustment demonstrated that males should not always display at maximal levels and that the ability to modulate trait expression can itself be a trait favored by sexual selection (Patricelli et al., 2002). Among polygynous species, courtships generally either occur at various locations, at sites where males aggregate (leks), or at displays sites that individual males maintain during the breeding season. Display sites offer the male the opportunity to modify the environment to better present their courtship, and in some species the display site itself can provide the female with information about male quality (Borgia et al., 1985). In many cases, male courtship behavior incorporates elements of the display site and in birds this has led to the evolution of spectacular courtship displays (reviewed in Johnsgard, 1994).

My dissertation research investigates multiple aspects of satin bowerbird (*Ptilonorhynchus violaceus*) courtship display. Adult satin bowerbird males have dimorphic plumage coloration, males produce elaborate vigorous courtship displays presenting their plumage, and these displays are produced at bowers (stick structures built by the male using collected objects) that play an important role in orienting males and females during courtship (Borgia, 1995). Male bowers are widely separated in the forest (~300m) and females visit them individually (Reynolds et al., 2009). Male satin bowerbirds provide nothing but sperm to females, and a few males account for the majority of the matings (Borgia, 1985). Bowerbirds are uniquely suited for detailed studies of courtship because they produce courtships to one female at a time at specific locations allowing for continuous video monitoring of courtship behavior. In the population of satin bowerbirds that I studied, all bower-holding adult males and approximately 80% of females were individually color banded, allowing for precise counts of mating success for males. This observed mating success correlates strongly with reproductive success measured as the genetic paternity of chicks (Reynolds et al., 2007).

In Chapter I, I use color spectrophotometry to quantify male plumage coloration and relate variation in male coloration to male mating success. In satin bowerbirds, adult males have an iridescent short wavelength saturated blue-black plumage with a peak reflectance in the UV (Doucet and Montgomerie, 2003a) and males produce courtship displays that involve rapid extensions of both wings that produce bright flashes likely visible to females standing in the bower. Although how plumage coloration affects mate

choice has long been discussed in bowerbirds (Gilliard, 1956, 1969; Diamond, 1986; Kusmierski et al., 1993, 1997; Endler et al., 2005; Borgia et al., 2007), previous studies of bowerbird plumage have not found a significant relationship between adult male plumage coloration and male mating success (Doucet and Montgomerie, 2003a; Madden et al., 2004). UV coloration has been thought to be of special importance to birds that see farther into these short wavelengths of light than can humans and other mammals. For this reason, satin bowerbird plumage coloration had been only investigated in the UV region (Doucet and Montgomerie, 2003a,b). My results show that blue, but not UV, reflectance is associated with male mating success in satin bowerbirds. This result suggests a mismatch between male plumage display reflectance and female preference for plumage coloration in mate choice. These results suggest that it is not safe to infer a role of UV in mate choice simply because of a relatively high UV reflectance.

In Chapter II, I address another factor that may be important in courtship display: aerobic capacity of displaying males. Physiological traits like aerobic capacity have been of special interest in sexual selection because they indicate whole-organism performance and represent the integrative output of a complex functional system that has large effects on organism function (Irschick et al., 2007; Irschick et al., 2008; Lailvaux and Irschick, 2006a). High whole-organism performance capacity may be a key good genes trait as recent studies have shown that aspects of whole-organism performance can be related to survival (Irschick et al., 2008; Le Galliard et al., 2004; Miles et al., 2001). I investigated how  $\dot{V}_{O_{2max}}$  (the maximal rate of oxygen consumption and a measure of aerobic capacity) might affect male display traits important in female choice in satin bowerbirds.

Adult males have higher  $\dot{V}_{O_{2\max}}$  than juvenile males and females, suggesting that aerobic capacity could play a role in sexual selection.  $\dot{V}_{O_{2\max}}$  predicted the number of blue decorations on a male's bower, the longest courtship he produced as well as the factor scores of males for the first principal component of six display variables, suggesting that it contributes to the overall quality of male display. However,  $\dot{V}_{O_{2\max}}$  did not predict male courtship or reproductive success suggesting that females are not directly assessing male aerobic capacity. Path analysis revealed that  $\dot{V}_{O_{2\max}}$  has an effect on male display quality that is not reflected in the relationship between display quality and mating success. Hence, females do not seem to be selecting mates with increased aerobic capacity indirectly through its effect on male display quality. My results show that high aerobic capacity is required for males to produce high quality displays, but also suggest that female choice may be directed at other male qualities. If any general trends are to be expected with regards to aerobic capacity and courtship display, I hypothesize that simple repetitive courtship displays of high intensity may be used as tests of male physiological ability, but that complex courtship displays involving multiple courtship elements may have evolved to indicate male qualities other than whole-organism performance.

In Chapter III, I used vertically mounted cameras above the bower to study the spatial dynamics of courtship in satin bowerbirds. Courtship is a key trait affecting male mating success and males with the most vigorous courtship displays usually obtain the most matings (Borgia and Presgraves, 1998; Gibson and Bradbury, 1985; Höglund and

Lundberg, 1987). Vigorous courtship displays in polygynous species often include elements co-opted from aggressive displays and these displays can sometimes be threatening to females. Males can benefit from reducing the threat their courtship presents to females and this threat reduction can shape courtship behavior (Borgia and Presgraves, 1998). Therefore, courtship vigor alone may not always be sufficient to maximize male reproductive success and recent evidence has shown that males can alter their behavior in response to females during courtship (Balsby and Dabelsteen, 2002; How et al., 2008; Meffert and Regan, 2002; Santangelo, 2005; Patricelli et al., 2002, 2006). The location where courtship is produced can also play an important role in courtship success. In satin bowerbirds courtship includes aggressive display elements (Collis and Borgia, 1992) and these threatening displays can startle females. I observed natural courtships and used a robotic female bowerbird to look for a spatial male response to female startling behavior. I found a spatial pattern of male courtship behavior and an association between male movements toward the female and the use of a bower wall as a barrier between the male and female. In successful courtships, males courted females from closer in and spent more time directly in front of females without a bower wall than in early unsuccessful courtships. I also found that females startled more often when males were not using a bower wall as a barrier. To control for female behavior I used a previously developed robotic female bowerbird. Males responded to startles of robotic females by moving farther away from females than in control courtships. These findings support the hypothesis that both the male-female courtship distance as well as the male's position relative to the bower walls serve to reduce the threat to females during courtship. Aggressive displays are commonly co-opted for use in courtship display (Borgia, 2006;

Berglund et al., 1996) and the threat reduction hypothesis (Borgia and Presgraves, 1998) offers a testable hypothesis that can help understand the adaptive significance of the often complex and what may be otherwise thought of as arbitrary courtship displays of many animals.

## CHAPTER I

Blue, not UV, plumage color is important in  
satin bowerbird (*Ptilonorhynchus violaceus*) display

### ABSTRACT

Several studies have suggested that peak plumage reflectance in birds matches color preferences used in mate choice. I tested this hypothesis in adult satin bowerbird males that have a short wavelength saturated blue-black plumage with a peak reflectance in the UV. I found that the chroma of the blue (405-480 nm), but not the peak reflecting UV (320-400 nm) portion of the male plumage spectrum was significantly correlated with male mating success. A plot of correlation coefficients between male mating success and plumage saturation showed a well-defined peak in the blue. This result suggests that: 1) blue plumage coloration is more important in mate choice than UV and other colors in affecting male mating success, and 2) that there is a mismatch between the peak reflectance of the plumage of male satin bowerbirds and the range of plumage wavelengths that are correlated with male mating success. Thus it is not safe to infer a role of UV or other colors in mate choice simply because of a peak plumage reflectance of that color.

## INTRODUCTION

Colorful plumage displays are among the most striking examples of sexually selected traits (Darwin, 1871; Andersson, 1994), and these displays are often highly elaborated in polygynous bird species (Oakes, 1992; Johnsgard, 1994). Specific colors are important for mate choice in many polygynous and sexually dimorphic species (e.g. Collias et al., 1979; Stein and Uy, 2006; Siitari et al., 2007). Among the spectral colors, ultraviolet (UV) reflectance and perception is widespread in birds (Eaton and Lanyon, 2003) and much attention has been given to the importance of UV plumage reflectance (e.g. Guilford and Harvey, 1998). UV reflectance has been considered a “special signal” because of its suggested suitability for short-range signaling, generally high contrast with backgrounds and invisibility to some predators (Silberglied, 1977; Bennett and Cuthill, 1994; Hausmann et al., 2003 ), and this has resulted in numerous studies investigating the role of UV in avian mate choice. In many avian species UV plumage coloration does affect male mating success (Andersson and Amundsen, 1997; Andersson et al., 1998; Hunt et al., 1998; Pearn et al., 2001) and this has led to the suggestion that high UV reflectance indicates that it has an important role in mate choice (Hausmann et al., 2003). However, recent studies of species with UV reflecting plumage (Hunt et al., 2001; Ballentine and Hill, 2003; Liu et al., 2007; Siitari et al., 2007) suggest that the proposed relationship between UV reflectance and plumage attractiveness does not hold in all cases.

There has been much discussion of the complex sexual displays of bowerbirds that include plumage, bower, decoration, dancing and vocalization elements (see reviews



by: Marshall, 1954; Gilliard, 1969; Frith and Frith, 2004). Bowerbirds build bowers adjacent to display courts that are decorated with colored objects, and in most species there is sexual plumage dimorphism (Marshall, 1954; Gilliard, 1969; Cooper and Forshaw, 1979; Borgia, 1995b; Frith and Frith 2004). The relationship of most male display elements to mating success has been established in bowerbirds (bower quality: Borgia, 1985; Borgia and Mueller, 1992; Lenz, 1994; Uy and Borgia, 2000; Madden, 2006; number of bower decorations: Borgia, 1985; Borgia and Mueller, 1992; Uy and Borgia, 2000; Madden, 2003; Coleman et al., 2004; quality of vocalizations: Loffredo and Borgia, 1986; Coleman et al., 2007; courtship intensity: Borgia and Presgraves, 1998; Patricelli et al., 2002; Madden, 2006), with the exception of plumage coloration. In satin bowerbirds *Ptilonorhynchus violaceus*, adult males have an iridescent short-wavelength (UV-blue) saturated plumage with peak reflectance in the UV (Doucet and Montgomerie, 2003a), and male courtship display involves rapid extensions of both wings that produce bright flashes likely visible to females standing in the bower. The sexually dimorphic plumage coloration and display of plumage during courtship suggests that it may be an important element of mate choice in satin bowerbirds. Although how plumage coloration affects mate choice has long been discussed in bowerbirds (Gilliard 1956, 1969; Diamond 1986; Kusmierski et al., 1993; Kusmierski et al., 1997; Endler et al., 2005; Borgia et al., 2007), previous studies of bowerbird plumage have not found a significant relationship between adult male plumage coloration and male mating success (Doucet and Montgomerie, 2003a; Madden et al., 2004). Madden et al. (2004) found that male spotted bowerbirds that owned a bower had larger crests than both females and males that did not own a bower, but they did not find a relationship between crest size and male

mating success and did not report any relationships between crest color and male mating success. Doucet and Montgomerie (2003a) found that bower quality and number of bower decorations were significantly correlated with the first principal component (PC1) of a multivariate plumage analysis. This suggested the possibility that plumage reflectance may be important in sexual signalling in satin bowerbirds. However, they used correlated proxies (bower quality and number of bower decorations) for male mating success and their PC1 included a mixture of UV and non-UV specific plumage variables (see methods). Therefore, it is unclear to what extent UV reflectance explains male attractiveness in their analysis and how plumage reflectance of any color is related to male mating success in satin bowerbirds.

Measuring the relationship between plumage color and mating success is complicated by the continuous nature of the plumage reflectance spectrum and determining which parts of this spectrum contribute to male mating success. Siitari et al. (2007) divided the spectrum from 320 to 700 nm into 20 nm segments and plotted the coefficients of the correlations between the average reflectance in each spectral segment and male mating success. They found a peak in correlation coefficients near 420 nm in the black grouse *Tetrao tetrix* and this was near the wavelengths of peak plumage reflectance. This approach offered a novel method to compare the relative strength of the relationship of plumage reflectance to male mating success of different spectral areas. I use a modified version of their approach as a tool to visualize the relationship between male mating success and plumage chroma across the entire avian visible spectrum in satin bowerbirds.

Previous studies of satin bowerbirds have shown a strong preference for blue decorations (Morrison-Scott, 1937; Marshall, 1954; Borgia, 1985b; Borgia et al., 1987; Borgia and Keagy, 2006; Wojcieszek et al., 2006). In a non-experimental study Wojcieszek et al. (2006) showed that frequently stolen decorations were darker blue and had higher UV reflectance than decorations that were not stolen, but a larger experimental study (Borgia, 2008) found that males do not discriminate between UV blocked and control blue decorations, suggesting that UV has no role in decoration preferences. The relevance of UV reflectance in satin bowerbirds has also been suggested for male plumage display (Doucet and Montgomerie, 2003a, b) and here we investigate the relationship between plumage color and male mating success with a particular focus on the UV and blue regions. In this analysis I address three questions: 1) is there a relationship between UV plumage color and male mating success, 2) is there a relationship between blue plumage color and male mating success, and 3) do spectral regions that show highest reflectance correlate significantly with male mating success?

## **METHODS**

### **Study site and general methods**

This study was carried out in 2003 at Tooloom National Park (28° 28'S, 152° 25'E), NSW, Australia (Borgia, 1985a). This site is located in a valley formed by Wallaby Creek and extends 1.5 km into a system of ridges formed by the creek's tributaries. All males used in this study were bower holders in full adult plumage and were previously banded with unique color band combinations (Borgia, 1985a). Males were captured individually using baited traps at feeding sites prior to the start of the mating season for plumage reflectance measurement. Daily counts of decorations at the bowers and assessments of bower quality were averaged over the mating season (November 5th until December 21st) for each male (Borgia, 1985b).

### **Video monitoring**

All courtship and mating behaviors occur at bowers in satin bowerbirds (Borgia, 1985b; Marshall, 1954) and this provides the opportunity to accurately measure male mating success. Field assistants monitored bowers throughout the mating season (early November until late December) using an automated video monitoring system that is triggered by an infrared sensor when birds are present (Borgia, 1995). Cameras at each bower were checked twice daily to ensure that video tapes were changed before they ran out and that battery voltages were sufficient to run the monitoring system, thus ensuring a complete record of courtship and mating behavior at these bowers. The number of

copulations each male achieved during the mating season was scored from these videos and this provides an accurate ranking of male mating success (Reynolds et al., 2007).

### **Color measurements**

I measured plumage reflectance using a S2000 spectrometer and PX-2 pulsed xenon light source (Ocean Optics, Dunedin, Florida, USA). The probe was maintained perpendicular to the feather surface to replicate the measurement geometry used in other reflectance studies of satin bowerbirds (Doucet and Montgomerie, 2003a, b; Doucet et al., 2006). The white-standard used was PTFE tape (Andersson and Prager, 2006; Delhey et al., 2008), layered to produce a uniform white surface whose spectral properties did not change when adding an extra layer. I took 5 spectral measurements from each male: 2 of the auriculars, 2 of the lesser wing coverts and 1 of the rump. The measurements for each individual were averaged across body regions (Doucet and Montgomerie, 2003a) and the resulting spectra were smoothed using a Gaussian kernel prior to statistical analysis (Fig. 1). This spectral smoothing is a low-pass filter that removes high frequency noise in the data. This noise is due in part to the very small distance between points in the spectral sampling ( $\sim 1/3$  nm between data points). This smoothing does not change estimates of spectral saturation (chroma) or total reflectance (brightness) but does provide a better estimate of the location of the reflectance peak (hue) than does the raw spectral data (Montgomerie, 2006).

## Statistical analyses

Since adult male satin bowerbird plumage reflects maximally in the UV portion of the spectrum (Doucet and Montgomerie, 2003a), and because satin bowerbirds prefer blue decorations independent of UV reflectance (Borgia, 2008) I tested for correlations between male mating success and the calculated chroma indices for both the UV wavelengths ( $R_{320-400\text{nm}}/R_{320-700\text{nm}}$ ) as well as for blue wavelengths ( $R_{405-480\text{nm}}/R_{320-700\text{nm}}$ ) of male plumage reflectance (see Siitari et al., 2007).

Furthermore, to test the prediction that there was no relationship between mating success and plumage color in other parts of the spectrum outside the blue and UV spectral ranges I plotted the correlation coefficients of male mating success at 20 nm intervals across the entire avian visible spectrum (see Siitari et al., 2007). Since I wanted to characterize the variation among males in chroma, I standardized the intensity of each male's spectrum by dividing each data point by the total brightness. The resulting correlations are therefore between male mating success and the spectral saturation of male plumage at that wavelength interval. This approach is especially powerful as it allows the visualization of trends in the relationship between plumage reflectance and male mating success across the whole avian visible spectrum. A pattern in the strength of the correlation coefficients of these 20 nm intervals can indicate which part(s) of the spectrum is (are) likely to be important in female mate choice. If no comparisons outside the blue and UV ranges show a strong correlation to male mating success, then other colors are likely not important.

Paralleling previous work by Doucet and Montgomerie (2003a), I calculated the same overall plumage score to allow for comparison between studies. To do this I summarized the male reflectance spectra data using their measures for total brightness (mean  $R_{300-700\text{nm}}$ ), UVV chroma ( $R_{300-420\text{nm}}/R_{300-700\text{nm}}$ ), contrast( $\lambda_{\text{min}} - \lambda_{\text{max}}$ ) and hue ( $\lambda_{\text{max}}$ ). Here I used 300 rather than 320 nm as the lower limit for avian UV vision to replicate their analysis. All results are qualitatively the same using either UV cut-off. The first principal component from these four variables was used to calculate an overall plumage color score (Doucet and Montgomerie, 2003a).

Nonparametric rank correlation tests were used because they are less sensitive to the strongly skewed distribution of matings among males in satin bowerbirds (Borgia, 1985b). All tests of significance are two-tailed.

## RESULTS

I found a significant positive relationship between male mating success and the blue chroma of male plumage in the range between 405 and 480 nm ( $r_s = 0.55$ ,  $p = 0.05$ ,  $n = 13$ ). No relationship was found with UV chroma ( $r_s = 0.20$ ,  $p = 0.52$ ,  $n = 13$ ).

Additionally, when I plotted the correlation coefficients between male mating success and the 20 nm spectral intervals we found a peak in the blue wavelengths and much lower correlation coefficients for wavelength ranges in other parts of the spectrum suggesting that UV and reflectance in other parts of the spectrum are not important in affecting male mating success (Fig. 2).

To compare my data to the previous study of satin bowerbird plumage (Doucet and Montgomerie, 2003a), I calculated the same overall plumage score. This was the first principal component (PC1) of an analysis including total brightness, UVV chroma, contrast and hue (see methods for description of variables). The loadings of PC1 differed between the studies (Table 1). I did not find a significant relationship between this PC1 color score and male mating success ( $r_s = 0.18$ ,  $p = 0.55$ ,  $n = 13$ ), nor did I find a relationship between PC1 and male bower quality ( $r_s = 0.07$ ,  $p = 0.82$ ,  $n = 13$ ). There was, however, a significant relationship between PC1 and number of decorations ( $r_s = 0.63$ ,  $p = 0.02$ ,  $n = 13$ ), and between number of decorations and male mating success ( $r_s = 0.73$ ,  $p = 0.003$ ,  $n = 13$ ).



## DISCUSSION

I found that the blue rather than the UV plumage chroma is correlated with male mating success in satin bowerbirds. Also, the peak in the correlation coefficients between the 20 nm spectral intervals and male mating success is confined to the blue wavelengths suggesting that UV and reflectance of other colors do not affect male mating success.

These results show a mismatch between peak plumage reflectance and the plumage chroma that is associated with male mating success (Fig. 3). The short-wavelength saturated reflectance of male satin bowerbird plumage appears to result from a coherent light scattering feather structure that causes reflectance to be higher at shorter wavelengths (Doucet et al., 2006). This color producing mechanism may cause the most attractive colors not to have the highest reflectance and thereby produce the observed mismatch. Alternatively, the UV reflectance peak of male plumage may have other functions not associated with mating such as reduced detection by predators with UV limited vision (Andersson, 1996; Andersson, 1999).

UV reflectance is predicted to be most important for communication in species that have ‘ultraviolet ornaments’, those with proportionately high UV chroma (Silberglied, 1979; Andersson, 1996; Banks, 2001; Haussman et al., 2003). Similar to satin bowerbirds (Fig. 1), Black grouse (*Tetrao tetrix*) have a low reflectance dark blue breast plumage that reflects most in the UV and has high UV and blue chroma (see Fig. 1 in Siitari et al., 2007). Siitari et al.’s (2007) study of color signals in black grouse failed

to find a relationship between the UV chroma of male plumage and male mating success, but they did find a significant relationship between the blue chroma of male plumage, that shows lower reflectance, and male mating success. Their study and mine suggests that the presence of UV reflection in plumage, even as the most reflective component, does not necessarily indicate that UV is used by females in mate choice, as has been assumed in other studies (Hausmann et al., 2003).

The lack of importance of UV reflectance in male satin bowerbird plumage coloration may be the result of one or more factors that can affect the perception of color. First, the light environment in which plumage is displayed can influence the evolution of color patterns (McNaught and Owens, 2002; Heindl and Winkler, 2003b). Illumination on the forest floor generally contains low amounts of UV light (Endler, 1992; Gomez and Théry, 2004) and this may affect the displays of ground courting species such as satin bowerbirds. Second, the optical properties of natural objects such as feathers are the product of multiple selective forces (Silberglied, 1979), and therefore the reflection of a particular color does not necessarily imply a role for that color in mate choice. Third, the satin bowerbird visual system may not be highly tuned to UV. Satin bowerbirds have blue shifted SWS1 pigments and thus lower sensitivity to UV light than other passerines with a UV shifted SWS1 pigment and in which UV plays an important role in sexual signaling (Zwiers, 2009; Coyle, Hart and Borgia unpublished data). The absence of a positive relationship of UV with mating success suggests that in satin bowerbirds UV is not acting as a special signal and this is consistent with several other recent studies in birds (e.g. Hunt et al., 2001; Siitari et al., 2007; Stevens and Cuthill, 2007).

The importance of blue reflectance is also found in male satin bowerbird decoration preferences (Borgia, 2008). There are several hypotheses that might apply to understanding the convergence in color preference for these display elements. First, decorations and plumage may have evolved to produce a non-conflicting signal. Blue decorations are rare in the environment (Borgia et al., 1987), highly prized and often stolen from neighboring bowers (Borgia and Gore, 1986; Hunter and Dwyer, 1997; Wojcieszek et al., 2006) and males with more of these decorations have higher mating success (Borgia, 1985b). Blue plumage may have evolved to produce a non-conflicting signal consistent with blue bower decorations and differences in the saturation of this blue plumage reflectance might then have been co-opted for use in mate choice. Second, the convergence of color preference in decoration and plumage displays, and in particular the lack of importance of UV, may result from the illumination of forest floor display courts. Satin bowerbirds commonly court and mate when bowers are under variable lighting (Borgia, unpublished data) and with relative UV illumination reduced when bowers are shaded (Endler, 1992, 1993). Females interested in reliable male signals may benefit from using blue if blue provides a more consistent signal than UV under the variable lighting conditions on the forest floor. Third, Gilliard (1956, 1969) proposed that there might have been transference of bright plumage to decoration displays in bowerbirds to reduce predation on males. Results showing that both blue plumage and blue decorations are important to mating success in satin bowerbirds suggest that if satin bowerbirds represent an intermediate stage in the transfer of signal from plumage to bower then this may have led to a convergence of plumage and decoration color.

My finding of an insignificant role of UV plumage reflectance in sexual signaling differs from a previous study of satin bowerbird plumage (Doucet and Montgomerie, 2003a). That study did not show an independent relationship between UV and mating success. In their plumage score (PC1), UVV chroma is the only variable directly assessing variance in UV reflectance and its low loading suggests a comparably low contribution to the PC1 score. Also, they used bower decorations and bower quality as proxies for male mating success and in satin bowerbirds these display traits account for less than half of the variation in male mating success (Borgia, 1985b), so it is quite possible that their proxies for mating success did not accurately estimate values for this variable. In this study I found that only one of the two proxy variables they used showed a significant correlation with mating success. Since I found a direct relationship between blue, but not UV, chroma and a direct measure of male mating success, my results likely provide a more accurate assessment of the relationship between UV plumage color and male attractiveness in satin bowerbirds.

Our differing conclusions could be due to different reflectance patterns in the two satin bowerbird subspecies used in these studies. However, I found that the plumage reflectance spectra are qualitatively the same when museum specimens of these subspecies are compared (J-F Savard unpublished data).

In satin bowerbirds, blue is more important than UV plumage coloration in mate choice even though UV has higher reflectance. The observed mismatch between the peak

reflectance of male plumage and the chroma that is correlated with mating success shows that a peak in plumage reflectance does not necessarily indicate the importance of that color in sexual signaling and that it is not safe to infer a role for UV in mate choice simply because of a relatively high UV reflectance.

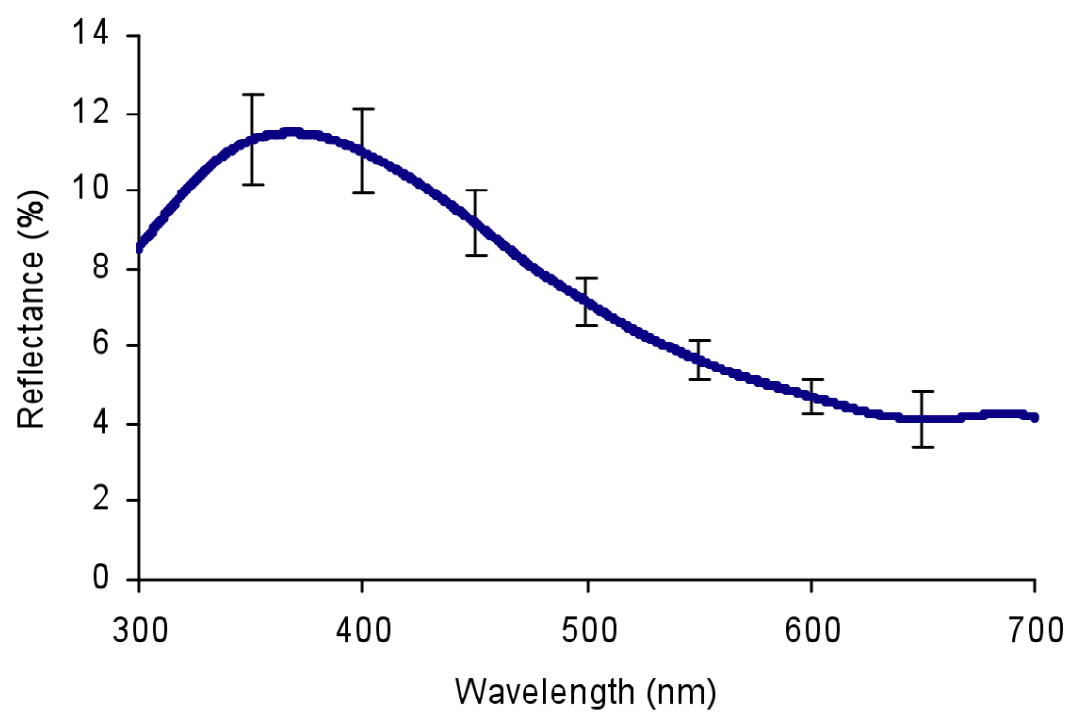
**Table 1:** Comparison of factor loadings of PCs between this study and the first study (Doucet and Montgomerie, 2003a) of satin bowerbird plumage reflectance.

	PC1 loadings	
	this study	Doucet and Montgomerie, 2003a
Total Brightness	0.18	0.70
UVV Chroma	0.97	0.39
Contrast	0.79	0.59
Hue	-0.84	loading not reported

**Figure 1:** Mean reflectance spectra showing 95% CL plotted at 50 nm intervals for bower holding adult males (n=13).

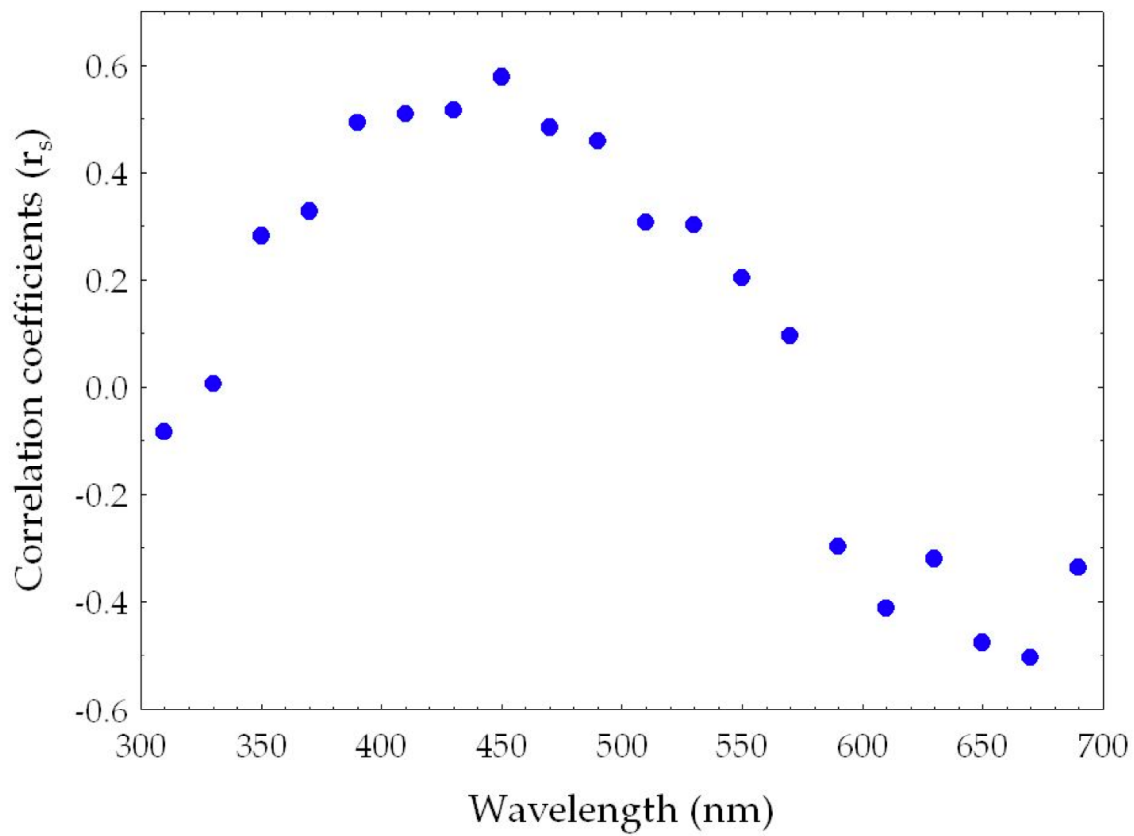
**Figure 2:** Spearman's rank correlation between male mating success and brightness standardized plumage reflectance for 20 nm spectral intervals.

**Figure 3:** Mismatch between peak plumage reflectance and strongest correlations between male mating success and plumage chroma for 20nm spectral intervals.

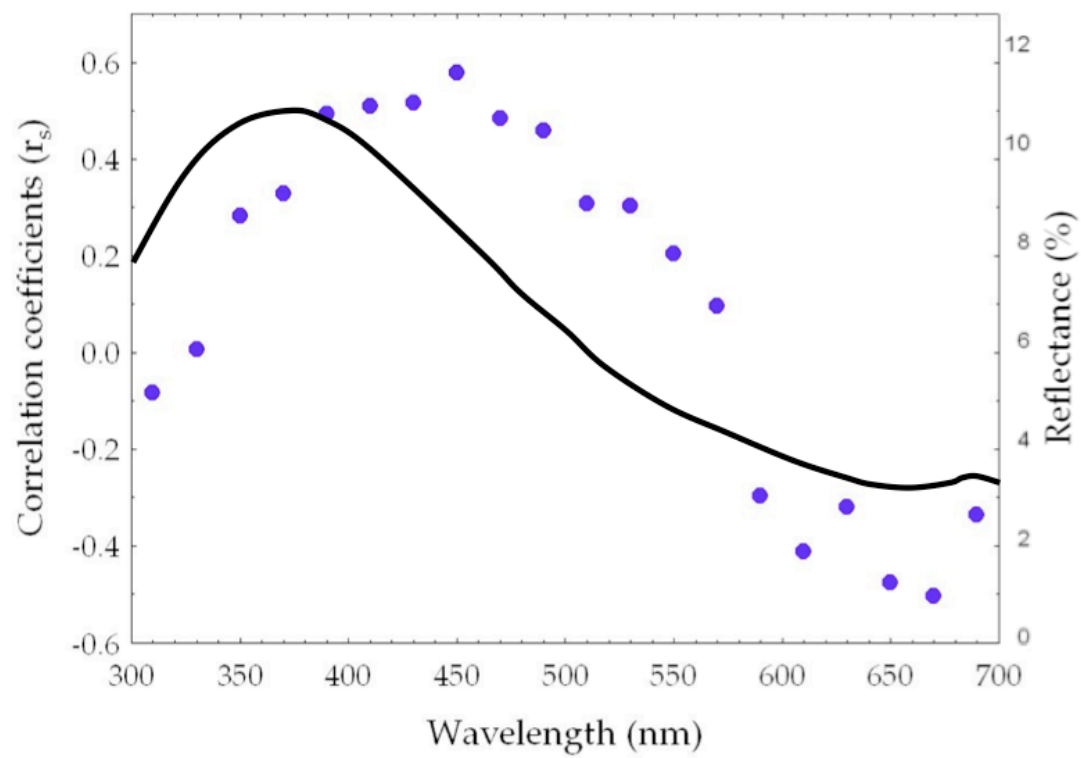


**Figure 1**





**Figure 2**



**Figure 3**

## CHAPTER II

Aerobic capacity predicts the quality of sexual display  
in satin bowerbirds (*Ptilonorhynchus violaceus*)

### ABSTRACT

Studies of sexual selection often focus on individual traits. However performance traits like aerobic capacity have been of special interest because they represent the integrative output of complex functional systems that have large effects on organism function. High whole-organism performance capacity may be a key good genes trait that is expected to be an important component affecting reproductive success. We investigated how  $\dot{V}_{O_{2\max}}$  (the maximal rate of oxygen consumption and a measure of aerobic capacity) might affect male display traits important in female choice in satin bowerbirds, a species with a non-resource based mating system and strong mating skew among males. I found that adult males have higher mass-adjusted  $\dot{V}_{O_{2\max}}$  than juvenile males and females, suggesting that aerobic capacity plays a role in sexual selection. In terms of reproductive behavior,  $\dot{V}_{O_{2\max}}$  predicted the number of blue decorations on a male's bower as well as the longest courtship he produced. Additionally,  $\dot{V}_{O_{2\max}}$  predicted the factor scores of males for the first principal component of six display variables, suggesting that it contributes to the overall quality of male display. However,  $\dot{V}_{O_{2\max}}$  did not predict male courtship or reproductive success suggesting that females are not directly

choosing males based on their aerobic capacity. Path analysis revealed that  $\dot{V}_{O_{2\max}}$  has an effect on male display quality that is not reflected in the relationship between display quality and mating success. Hence, females do not seem to be selecting mates with increased aerobic capacity indirectly through its effect on male display quality. These results show that high aerobic capacity is required for males to produce high quality displays, but also suggest that female choice may be based on other male qualities. If any general trends are to be expected with regards to aerobic capacity and courtship display, I propose that simple repetitive courtship displays of high intensity may be used as tests of male physiological ability and hence genetic quality, but that complex courtship displays involving multiple courtship elements may have evolved to indicate male qualities other than whole-organism performance.

## INTRODUCTION

Physiological traits offer a useful perspective in studies of sexual selection because they often represent the integrative output of a complex functional system (Irschick et al., 2007; Irschick et al., 2008; Lailvaux and Irschick, 2006a). Of particular interest are measures of whole-organism performance, defined as any quantitative measure of how well an organism performs activities that affect an ecologically relevant task (Huey and Stevenson, 1979; Irschick and Garland, 2001). Recent studies have shown that aspects of whole-organism performance affect survival (Hayes and O'Connor, 1999; Irschick et al., 2008; Le Galliard et al., 2004; Miles et al., 2001), suggesting that performance traits used in the context of sexual selection may indicate good genes in males.

High whole-organism performance capacity is thought to be an important component of reproductive success and many aspects of sexual selection are likely to be affected by performance capabilities. For example, endurance can be a key component of sexual selection in mating systems based on male competition (reviewed in Andersson, 1994) and several studies have found relationships between whole-organism performance and male secondary sexual characteristics in these mating systems (e.g. Lailvaux et al., 2005; Vanhooydonck et al., 2005; Whiting et al., 2003). However, the link between female choice and male performance is less clear. Although there is considerable evidence that male ornaments or displays can be energetically expensive (e.g. Hoglund et al., 1992; Prestwich et al., 1989; Vehrencamp et al., 1989), few studies have related variation in whole-organism performance between males to differences in display quality

and reproductive success. In guppies (*Poecilia reticulata*), females prefer male ornaments that are correlated with swimming ability (Kodric-Brown and Nicoletto, 2005; Nicoletto, 1991; Nicoletto, 1993), but in green anoles (*Anolis carolinensis*) females show no preference for high performers (Lailvaux and Irschick, 2006b).

An important measure of whole-organism performance that may reflect overall male quality is aerobic capacity. Aerobic capacity (i.e. the maximal rate of oxygen consumption,  $\dot{V}_{O_{2max}}$ ) is a major determinant of an animals' ability to engage in sustained intense activity and should have implications for fitness components such as the ability to escape predators, forage or compete with other males for access to females (Huey and Dunham, 1987; Chappell and Bachman, 1994, Hayes and O'Connor, 1999; Kvist and Lindström, 2001, Labocha et al., 2004). Since aerobic performance is a highly integrative trait that requires coordinated function of a range of organ systems (e.g., pulmonary, cardiovascular, musculoskeletal, neural), it may be a good indicator of health and vigor, and hence potentially of genetic quality. Given this, it is surprising that there have been very few studies of relationships between aerobic capacity and female mate choice. In red jungle fowl (*Gallus gallus*), successful males (chosen in >50% of paired mate choice trials) had higher  $\dot{V}_{O_{2max}}$  than unsuccessful males (Chappell et al., 1997). Successful males also had higher courtship display rates but the correlation between aerobic capacity and display rate was weak and non-significant. Therefore, although  $\dot{V}_{O_{2max}}$  could predict which males would be chosen in mate trials, it was not clear how (or if) females were assessing differences in male aerobic capacity in the artificial context of these trials. Studies under natural conditions should provide a more realistic indication of the relationship between aerobic capacity, male display, and female response. In natural

populations male movements are not artificially restricted and thus males may be more able to develop high performance levels during display and females are not constrained to choose between only two males. Additionally, differences in aerobic capacity may affect the ability to acquire display sites, sites with advantageous locations, or resources that can influence male display performance and female mate choice.

A long-term study of a natural population of satin bowerbirds (*Ptilonorhynchus violaceus*) provides a unique opportunity to investigate the role of aerobic capacity in mate choice. This species has a non-resource based mating system. Male satin bowerbirds build a stick bower where courtship is performed and they decorate the bower platform with natural and man-made objects. All courtships and copulations occur at bowers. Male courtship behavior includes presentation of decorations and intense running displays that are accompanied by loud buzzing vocalizations, and females prefer males that display at high intensity (Patricelli et al., 2002). Males show a strong preference for blue decorations (Borgia, 1985b; Borgia et al., 1987; Borgia and Keagy, 2006; Marshall, 1954; Morrison-Scott, 1937; Wojcieszek et al., 2006), and the number of blue decorations on the bower platform is important to female choice and is a strong correlate of male mating success (Borgia, 1985b; Coleman et al., 2004).

Making predictions about the relationship between male aerobic capacity and mating success is complicated because there are several conceivable relationships. First, aerobic capacity could be a critical component of male display because effective displays require intense, sustained energetic output. It is also possible that aerobic performance is not important for mating success directly but is instead functionally linked to other traits

that do affect mating success such as endocrine profiles (e.g. high testosterone might elicit high aerobic capacity). In both scenarios, elevated aerobic capacity would predict male mating success. Alternatively, elevated aerobic capacity could be important for all adult males but not affect mating success (for example elevated aerobic capacity might be necessary to hold and defend a display site but not affect female mate choice). Finally, elevated aerobic capacity could be unimportant for adult male display and have no role in determining male mating success. In this study I investigated the relationship between aerobic capacity, sexual display traits and male mating success to understand how aerobic capacity might affect female choice in satin bowerbirds.



## **METHODS**

### **Study site and general methods**

This study was carried out in 2001 at Tooloom National Park (28° 28' S, 152° 25' E), NSW, Australia (Borgia, 1985a). Birds used for aerobic capacity measurements were captured individually prior to the mating season using baited traps at feeding sites prior. If birds had not previously been captured they were fitted with a unique color band combination (Borgia, 1985a). Aerobic capacity was measured within 1 h of capture. Weight, tarsus measurements, and ectoparasite counts were recorded for all captured birds. Satin bowerbird males attain adult plumage in their seventh year (Vellenga, 1980) and monitoring has been uninterrupted at our field site since 1995, which provided me with detailed age information for adult males. Since juvenile bowerbirds cannot be sexed by field characteristics alone, the sex of birds was determined using behavioral data from videos and plumage data from our banding records from 2001-2008. Field assistants with minimal knowledge of the hypotheses being tested made daily counts of decorations at the bowers and assessments of bower quality, which were averaged over the mating season (early November until late December) for each male (Borgia, 1985b).

### **Video monitoring**

All courtship and mating behaviors occur at bowers in satin bowerbirds (Borgia, 1985b; Marshall, 1954) and this provides the opportunity to accurately measure male mating success. Field assistants monitored all bowers in the study area throughout the mating season (early November until late December) using an automated video monitoring system triggered by an infrared sensor when birds are present (Borgia, 1995).

Cameras were checked twice daily to insure a complete record of courtship and mating behavior at these bowers.

### **Reproductive and courtship success**

The number of females each male mated with during the mating season was scored from video records. In 2001, all bower holding males and 72% of females observed to copulate were banded and these females copulated on average 1.98 times. By dividing each male's total number of copulations with unbanded females by this correction factor (1.98) I estimated the number of individual unbanded females involved in copulations with each male. This estimate was then added to the number of banded females a male copulated with to obtain the total number of females each male mated (see Patricelli et al., 2004). Reproductive success measured from our video data provides an accurate measure of female preferences for males and male genetic paternity (Reynolds et al., 2007). Courtship success was measured as the proportion of banded females that a male courted that eventually copulated with him.

### **Courtship duration and display intensity**

Male courtship displays include loud buzzing vocalizations, ptiloerection and vigorous running across the bower platform with wings extended (Borgia, 1986; Frith and Frith, 2004; Loffredo and Borgia, 1986). Previous work has shown that these intense displays are attractive to females (Patricelli et al., 2002) and successful courtships are of longer duration than unsuccessful courtships (unpublished data). I calculated average courtship duration for each male as the mean duration of all the courtships that male produced for females during the mating season. Maximum courtship duration was the

single longest courtship a male produced for a female during the mating season. I also calculated the mean display intensity for each male from all first courtships with each courted female. Using only the first courtship for each male-female dyad helps control for variable female behavior during successive courtships (Coleman et al., 2004; Patricelli et al., 2004) and avoids pseudo-replication. The intensity measure was based on three index variables: 1- the cumulative distance run by the male during his display; 2- the degree of male ptiloerection; and 3- the location of the male on the bower platform (Patricelli et al., 2006; Patricelli et al., 2002).

### **Aerobic capacity measurements**

Oxygen consumption ( $\dot{V}_{O_2}$ ) was measured with open circuit respirometry in an enclosed wheel, as has been used in other studies of avian aerobic performance (Chappell et al., 1999a; Chappell et al., 1996; Pierce et al., 2005; Wiersma et al., 2007). The wheel was constructed of acrylic plastic and was driven by the experimenter. Incurrent air entered through gas-tight axial bearings, and a track of thin carpet provided traction and injury protection. The inside diameter was 52 cm and width was 25.4 cm, yielding a circumference of 1.6 m and an internal volume of 54 l.

Ambient air was supplied under positive pressure with a portable pump, with flow rates adjusted with a needle valve and monitored at about 15 L/min with a Gilmont rotometer. The rotometer was calibrated against a Tylan mass flow controller, and flow rates were adjusted to standard temperature and pressure during  $\dot{V}_{O_2}$  calculations. Excurrent gas from the wheel was subsampled at about 100 ml/min and dried (Drierite), and flowed through the sensor of an oxygen analyzer (Sable Systems FC-1; Henderson,

Nevada, USA). Output from the FC-1 analyzer was sampled every 1.5 sec by a Macintosh computer equipped with a National Instruments analogue-to-digital converter and custom data acquisition software ([www.warthog.ucr.edu](http://www.warthog.ucr.edu)). Multiple readings (60-100) were averaged for each recorded datum. With digital signal averaging, the resolution of the system was 0.0015-0.002% O<sub>2</sub>.

To increase system response time CO<sub>2</sub> was not removed from the excurrent gas subsample and we used the 'Mode 2' equation in LabAnalyst software (Warthog Systems) to compute  $\dot{V}_{O_2}$ . The volume of the wheel was large relative to flow rate, so to compensate for mixing and resolve short-term changes in  $\dot{V}_{O_2}$ , I calculated 'instantaneous'  $\dot{V}_{O_2}$  (Bartholomew et al., 1981) using an effective volume of 56 l. Effective volume was obtained from washout curves resulting from near-instantaneous injections of oxygen-depleted air (Bartholomew et al., 1981). The  $\dot{V}_{O_{2max}}$  was computed as the highest  $\dot{V}_{O_2}$  averaged over continuous 1-min intervals (Chappell et al., 1995; Chappell et al., 1999b; Wiersma et al., 2007). The worst-case cumulative error in  $\dot{V}_{O_2}$  calculations was about  $\pm 4\%$ . Repeatability of the equipment was greater than absolute accuracy, so the maximum cumulative error for comparisons between individuals was about 3%.

Bowerbirds were placed in the wheel and allowed 2-3 min to adjust while baseline O<sub>2</sub> concentration and 'resting'  $\dot{V}_{O_2}$  was measured. During this period the wheel was covered with cloth to reduce stress. The wheel was then started and maintained at a low speed until the bird adjusted to the movement and walked or ran to maintain position. This generally required 15-30 s. Speed was gradually increased while  $\dot{V}_{O_2}$  and behavior

were continuously monitored. Most birds flapped and fluttered (in addition to running) to maintain position. I assumed that  $\dot{V}_{O_{2\max}}$  had been attained when  $\dot{V}_{O_2}$  did not increase with increasing speed, or when birds no longer maintained coordinated locomotion or position in the wheel. Birds showed obvious signs of exhaustion at this point, including heavy panting, drooped wings, or prone posture. However, all recovered quickly and none suffered any injury. Complete measurements lasted 4-8 min (1.5-5 min of actual exercise).

## Statistics

The aerobic capacity of 154 birds (46 adult males, 55 females and 53 juvenile males) was measured prior to the mating season. The repeatability of  $\dot{V}_{O_{2\max}}$  measurements was assessed using data from 49 birds that were captured twice during this period. I used a  $\log_{10}(X)$  transformation for mass and  $\dot{V}_{O_{2\max}}$  data prior to data analysis because metabolism is a power function of mass. To correct for the skew in male reproductive success, I used a  $\log_{10}(X+1)$  transformation. I used ANCOVA to control for mass when testing for differences in aerobic capacity between adult males, females and juvenile males. The residuals of this analysis were used as a mass-controlled  $\dot{V}_{O_{2\max}}$  measure in subsequent analyses. I performed linear regressions to test for relationships between aerobic capacity and both mating success and male display variables (average courtship duration, maximum courtship duration, average courtship intensity, bower quality, number of blue bower decorations and number of non-blue bower decorations). To describe the overall quality of male displays, I calculated the first principal component of the six male display variables measured. Path analysis was performed to determine if there was an indirect effect of  $\dot{V}_{O_{2\max}}$  on mating success mediated through display traits.

Analyses were performed with Statistica 6.0 Software (Statsoft Inc., Tulsa, OK, U.S.A.) and all tests are 2-tailed.

## RESULTS

### Repeatability of $\dot{V}_{O_{2\max}}$

Data on the repeatability of  $\dot{V}_{O_{2\max}}$  was obtained for 49 bowerbirds (28 adult males, 10 females and 11 juvenile males) over intervals of 8-39 days (Mean  $\pm$  SD: 18.3  $\pm$  5.4 days). There was no relationship between run interval and change in  $\dot{V}_{O_{2\max}}$  between runs ( $r=-0.03$ ,  $p=0.835$ ,  $n=49$ ). Repeatability of  $\dot{V}_{O_{2\max}}$  was estimated from the correlation of initial versus final residuals from the regressions of  $\log_{10} \dot{V}_{O_{2\max}}$  on  $\log_{10}$  body mass for the individuals with two  $\dot{V}_{O_{2\max}}$  measurements. Although the mass of these individuals decreased between measurements (Mean change  $\pm$  SD = -7.3  $\pm$  10.5 g,  $t=2.19$ ,  $p=0.03$ ), the measure of aerobic capacity exhibited significant repeatability (Fig. 4;  $r=0.40$ ,  $p=0.004$ ,  $n=49$ ).

### Age and sex effects on aerobic capacity

The mean mass of males (221.6 g) was significantly higher than that of females (202.7 g;  $t=7.40$ ,  $p<0.001$ ), but not of juvenile males (218.8 g;  $t=1.10$ ,  $p=0.27$ ; Table 2). The slopes of the  $\dot{V}_{O_{2\max}}$  versus body mass regressions for adult males, females and juvenile males were not significantly different ( $F_{2, 148}=1.55$ ,  $p=0.22$ ; overall mass exponent = 0.7389). Therefore I used a single-slope ANCOVA model (Fig. 5) to do planned comparisons of mass-controlled  $\dot{V}_{O_{2\max}}$  between adult males and both juvenile males and females. There were significant differences among these sex and age classes ( $F_{2, 150}=4.24$ ,  $p=0.02$ ,  $n=46$  adult males, 55 females and 53 juvenile males). Adult males had the highest  $\dot{V}_{O_{2\max}}$  (46.28 ml O<sub>2</sub>/min) and had significantly higher  $\dot{V}_{O_{2\max}}$  than both females (43.57 ml O<sub>2</sub>/min;  $t=2.16$ ,  $p=0.03$ ) and juvenile males (43.27 ml O<sub>2</sub>/min;  $t=2.77$ ,

$p=0.006$ ; all at the adjusted mass of 213.3 g; Table 2). There was no relationship between the age of adult males (range: 7-22 years) and  $\dot{V}_{O_{2\max}}$  ( $r=-0.010$ ,  $p=0.948$ ,  $n=46$ ) and no simple non-linear relationship was evident in the plotted data.

### **Aerobic capacity and mating success**

I compared aerobic capacity to male reproductive success and display quality for 23 adult bower-holding males that were monitored throughout the mating season. I found no direct relationship between aerobic capacity and measures of male success:  $\dot{V}_{O_{2\max}}$  did not predict male courtship success ( $R^2<0.01$ ,  $F_{1,21}=0.03$ ,  $p=0.867$ ) or male mating success ( $R^2<0.01$ ,  $F_{1,21}=0.01$ ,  $p=0.911$ ).

### **Aerobic capacity and display traits**

$\dot{V}_{O_{2\max}}$  did predict maximum courtship duration and number of blue decorations on a male's bower (Table 3). Both maximum courtship duration and number of blue decorations predicted male courtship and mating success (Table 4). The first principal component of the six display variables explained 46.7% of the total variance (see Table 3 for PC loadings). Males with higher  $\dot{V}_{O_{2\max}}$  had better PC1 factor scores ( $R^2=0.23$ ,  $F_{1,21}=6.43$ ,  $p=0.019$ ), and these factor scores predicted both male courtship success ( $R^2=0.48$ ,  $F_{1,21}=19.59$ ,  $p<0.001$ ) and mating success ( $R^2=0.64$ ,  $F_{1,21}=37.03$ ,  $p<0.001$ ; Table 4).

### **Path Analysis**

I used path analysis to construct a causal model reflecting a hypothesized relationship between  $\dot{V}_{O_{2\max}}$ , display traits and male mating success. I posited the



direction of causality from the knowledge that  $\dot{V}_{O_{2\max}}$  was measured prior to the mating season and could contribute to display quality (rather than vice-versa), and that display traits affect female mate choice. I specified a mediated path model where  $\dot{V}_{O_{2\max}}$  has both a direct effect on mating success and an indirect effect on mating success through its effect on display (Fig. 6). I constructed three such models, using either 1- our PC1 of display variables, 2- blue decorations or 3- maximum courtship duration as the measure of male display. The models are “just-identified” or “saturated” (the set of simultaneous equations to solve equals the number of parameters to estimate) and therefore have no degrees of freedom. This makes the evaluation of model fit trivial and uninteresting. In such models there is a direct path from each variable to each other variable, and the path coefficient between  $\dot{V}_{O_{2\max}}$  and display is the same as the zero-order correlation between the two variables (because there is only one path leading to display). The two path coefficients leading to mating success are equal to the standardized multiple regression coefficients between  $\dot{V}_{O_{2\max}}$ , display and mating success. The path analyses for the three display variables used are qualitatively the same. In all three models the path coefficients [Display  $\rightarrow$  Mating Success] are stronger than the bivariate correlation coefficients and the path [ $\dot{V}_{O_{2\max}}$   $\rightarrow$  Mating Success] are negative. All path coefficients are significant except for one in the model using maximum courtship duration (Fig. 6).

## DISCUSSION

My analyses assume that the measured  $\dot{V}_{O_{2\max}}$  are an accurate assessment of aerobic capacity and are sufficiently consistent for valid comparisons among ages and sexes. The measured values of  $\dot{V}_{O_{2\max}}$  are consistent with the findings of other studies using similar methodologies (Chappell et al., 1999a; Chappell et al., 1996; Pierce et al., 2005; Wiersma et al., 2007). The factorial aerobic scope ( $\dot{V}_{O_{2\max}}$ /basal metabolic rate; BMR) is 15 for an adult satin bowerbird of the mean mass of 213.3 g, based on a  $\dot{V}_{O_{2\max}}$  of 44.36 ml O<sub>2</sub>/min and an estimated BMR of 2.97 ml O<sub>2</sub>/min (McKechnie and Wolf, 2004), and this is also consistent with other studies. I found significant repeatability in  $\dot{V}_{O_{2\max}}$  measurements over substantial intervals ( $18 \pm 5.4$  days), indicating individuals were consistent in aerobic performance and another longitudinal study found repeatability between years and within sex and age classes in satin bowerbirds (Chappell et al. in prep.).

I found that adult males have higher aerobic capacity than juvenile males and females, even when correcting for males' larger body mass (Table 2). This is similar to results from other studies (red jungle fowl; Chappell et al., 1996) and suggests that increased  $\dot{V}_{O_{2\max}}$  may be evolutionarily important to adult males or is functionally linked to traits that are important.

The demands of competition with other males, building and maintaining a display site and courtship behavior may explain the increased aerobic capacity in adult males. Satin bowerbird bower sites are limited by intra-sexual aggression and males must

compete for these limited bower locations (Borgia, 1985a; Reynolds et al., 2009). Once a male acquires a bower site, he must build and defend his bower from marauding neighboring males that can destroy the bower and steal its decorations. Additionally, males spend substantial portions of the day calling from above their bowers to attract females to them. Once a female is attracted to a bower, the male typically courts her and courtship activity involves intense calling and display movements. Top males sometimes court and mate with up to 9 females in a single day (G. Borgia, unpublished data). All of these activities may be energetically demanding and if so males would benefit from an increased maximal aerobic capacity. Also, bower-holding males must spend at least some portion of the day foraging, and it is possible that high aerobic capacity may improve foraging ability and thus minimize the time spent away from the bower.

To test the hypothesis that increased adult male aerobic capacity is important to male display quality and mating success, I first calculated the bivariate relationships between the variables. I found that  $\dot{V}_{O_{2max}}$  predicted the number of blue decorations on a male's bower as well as the longest courtship he produced during the mating season. Additionally,  $\dot{V}_{O_{2max}}$  predicted the factor scores of males for the first principal component of the six display variables, suggesting that aerobic capacity contributes to the overall quality of male display. However,  $\dot{V}_{O_{2max}}$  did not directly predict male courtship or reproductive success. This is puzzling since  $\dot{V}_{O_{2max}}$  predicts 2 of the 6 display variables and overall display quality, and these in turn predict male courtship and reproductive success. The lack of a relationship between aerobic capacity and reproductive success suggests that females are not directly assessing male aerobic capacity.

Bivariate tests do not address the possibility of an indirect relationship between  $\dot{V}_{O_{2\max}}$  and mating success acting through display quality. The path analyses suggest that  $\dot{V}_{O_{2\max}}$  may have a positive indirect effect on mating success through its effect on display quality. However,  $\dot{V}_{O_{2\max}}$  has a negative direct effect on mating success when controlling for display quality. The negative and significant path coefficients from [ $\dot{V}_{O_{2\max}} \rightarrow$  Mating Success], the increased strength of the relationship between the other independent and dependent variables [Display  $\rightarrow$  Mating Success] as compared to the univariate analyses, and the lack of a univariate correlation between  $\dot{V}_{O_{2\max}}$  and mating success suggest that  $\dot{V}_{O_{2\max}}$  is acting as a suppressor variable in the model (Cohen and Cohen, 1975; Maassen and Bakker, 2001). The most common interpretation of a suppressor variable is that it accounts for part of the variance in the independent variable that would otherwise be error variance. When a suppressor variable is included in the model there is less unexplained variance in the remaining independent variable, and its relationship to the dependent variable is strengthened. In the context of this study, this suggests that even though there are relationships between  $\dot{V}_{O_{2\max}}$  and display, and between display and mating success, there is no indirect effect of  $\dot{V}_{O_{2\max}}$  on mating success. Therefore males with higher  $\dot{V}_{O_{2\max}}$  can produce better displays, but females are unlikely to be using  $\dot{V}_{O_{2\max}}$  when choosing a mate.

Alternatively, the negative direct relationship between  $\dot{V}_{O_{2\max}}$  and male mating success in the path analyses may suggest that there is a cost to increased  $\dot{V}_{O_{2\max}}$  that is not being represented in the model. If elevated  $\dot{V}_{O_{2\max}}$  is costly, then the predictions for the relationship of  $\dot{V}_{O_{2\max}}$  to display quality and male mating success change. Under the current paradigm, elevated  $\dot{V}_{O_{2\max}}$  is taken to indicate better genetic quality in males and

it is predicted that females should prefer males with higher  $\dot{V}_{O_{2\max}}$  (e.g. Chappell et al., 1997; Nicoletto, 1993). However, if increased  $\dot{V}_{O_{2\max}}$  comes at a cost, then females may not always benefit from choosing males with high  $\dot{V}_{O_{2\max}}$  and this may explain the negative direct relationship we found in the path analysis. Such a cost could be associated with energy metabolism. For example, males with elevated  $\dot{V}_{O_{2\max}}$  could incur a higher maintenance cost due to an elevated basal or resting metabolic rate, as proposed in the aerobic capacity model for the evolution of endothermy (Bennett and Ruben, 1979). This higher resting or basal metabolic rate could affect energy budgets, food and foraging requirements, and ultimately survival. However, the link between  $\dot{V}_{O_{2\max}}$  and basal metabolic rate is not clear in birds (Chappell et al., 1999a; Hammond et al., 2000; McKechnie and Swanson, 2010; Wiersma et al., 2007).

In satin bowerbirds, blue decorations are a strong predictor of male reproductive success (Borgia, 1985b). My results show that  $\dot{V}_{O_{2\max}}$  predicts the number of blue decorations that a male has on his bower during the breeding season, but also suggest that the portion of the variation in blue decorations that is accounted for by  $\dot{V}_{O_{2\max}}$  may not be the same as that contributing to male mating success. Blue bower decorations are rare in the environment and males compete for them indirectly by removing blue items from the environment, and compete for blue items directly by stealing them from each other (Borgia and Gore, 1986). Increased  $\dot{V}_{O_{2\max}}$  likely allows males to better compete for these valuable decorations. During courtship, blue decorations can facilitate the expression of intense male behavioral displays (Patricelli et al., 2003) and have a more pronounced effect on young females than on older females (Coleman et al., 2004). It is possible that although accumulating blue decorations requires elevated  $\dot{V}_{O_{2\max}}$  levels in

males, other factors are more important in determining the effect of blue decorations on male mating success.

The significant positive relationship between  $\dot{V}_{O_{2\max}}$  and maximal courtship duration as well as the trend between average courtship intensity and  $\dot{V}_{O_{2\max}}$  suggest that some aspects of courtship may be energetically demanding for males. However, even if courtship duration and intensity have the potential to reveal male aerobic capacity, two important aspects of satin bowerbird female mate searching may limit the ability of these courtship variables to consistently reflect overall male physiological vigor. First, female satin bowerbirds mate search individually and visit males one at a time (Uy et al., 2000; Uy et al., 2001). Males display to multiple females per day, and if courtship is energetically demanding then males may not be able to produce intense performances in later courtships. Under those conditions intensity dependent displays could be an unreliable indicator for females because less attractive males that only court a few females would appear more vigorous than exhausted top males that are required to produce many more courtship displays. Second, male satin bowerbird display may not require extremely high aerobic capacity. Although satin bowerbird courtship involves high intensity elements co-opted from aggressive interactions (Borgia and Coleman, 2000) that are attractive to mature females (see Coleman et al., 2004; Patricelli et al., 2002), they tend to be given only in short intermittent bursts. The initial intense phase of wing flipping coordinated with rapid movements across the bower and buzzing is followed by a relatively quiet low intensity phase during which males mimic other species while standing relatively still (Coleman et al., 2007; Loffredo and Borgia, 1986). During this less active period males may have an opportunity to recover before starting a

new phase of intense display. Third, while females generally favor courtship displays with intense elements, if these displays are too intense they can startle females and cause them to abandon courtship (Patricelli et al., 2006). Females signal their comfort during courtship by crouching (Patricelli et al., 2004) and males have evolved to read signals of female comfort and modulate their display intensity in response to these signals (Patricelli et al., 2002). Therefore, the life history of satin bowerbird mate searching suggests that whole-organism performance may not be the primary determinant of male courtship success even though males with higher  $\dot{V}_{O_{2\max}}$  may have the ability to produce longer and possibly more intense courtships.

These results reinforce the view that life history needs to be taken into account when examining the role of whole-organism performance in sexual selection (Byers et al., 2010; Husak and Fox, 2006; Lailvaux and Irschick, 2006a). In satin bowerbirds, elevated  $\dot{V}_{O_{2\max}}$  allows males to accumulate more blue bower decorations and increase the duration of their courtship display, but to be successful males must incorporate these display elements into a complex interactive communication strategy. In true lekking species, where many females visit males at the same time and can observe and compare multiple males displaying in close proximity, courtship display may be better able to reflect male aerobic capacity than in species where females mate search alone. If any general trends are to be expected with regards to aerobic capacity and courtship display, I propose that simple repetitive courtship displays of high intensity, as seen in many lekking species, may be used as tests of male physiological ability, but that complex courtship displays involving multiple courtship elements may have evolved to indicate male qualities other than whole-organism performance.

**Table 2:** Mean body mass, mean aerobic capacity ( $\dot{V}_{O_{2\max}}$ ), and  $\dot{V}_{O_{2\max}}$  adjusted to the common mass of 213.3 g in satin bowerbirds. Results are shown as mean  $\pm$  SD.

	N	Mass (g)	$\dot{V}_{O_{2\max}}$ (ml O <sub>2</sub> /min)	Adjusted $\dot{V}_{O_{2\max}}$
Adult males	46	221.6 $\pm$ 13.3	47.84 $\pm$ 5.43	46.28
Adult females	53	202.7 $\pm$ 13.5	42.24 $\pm$ 5.43	43.57
Juvenile males	55	218.8 $\pm$ 12.6	44.43 $\pm$ 6.06	43.27



**Table 3:** Linear regressions between male display traits and residuals of mass-corrected aerobic capacity ( $\dot{V}_{O_{2\max}}$ ) for bower owning adult males (n=23). Factor loadings are for the first principal component of these six display variables. Asterisks (\*) denote regression coefficients and factor loadings significant at the p=0.05 level.

	Aerobic Capacity ( $\dot{V}_{O_{2\max}}$ )	PC1 Factor Loadings
Average courtship duration	$R^2=0.13$ , $F_{1,21}=3.24$ , $p=0.086$	0.202
Maximum courtship duration	$R^2=0.26$ , $F_{1,21}=7.40$ , $p=0.012$ *	0.532 *
Average courtship intensity	$R^2=0.09$ , $F_{1,21}=2.19$ , $p=0.153$	0.837 *
Bower quality	$R^2=0.04$ , $F_{1,21}=0.84$ , $p=0.369$	0.734 *
Blue bower decorations	$R^2=0.25$ , $F_{1,21}=6.93$ , $p=0.016$ *	0.736 *
Non-blue bower decorations	$R^2=0.08$ , $F_{1,21}=1.93$ , $p=0.179$	0.834 *

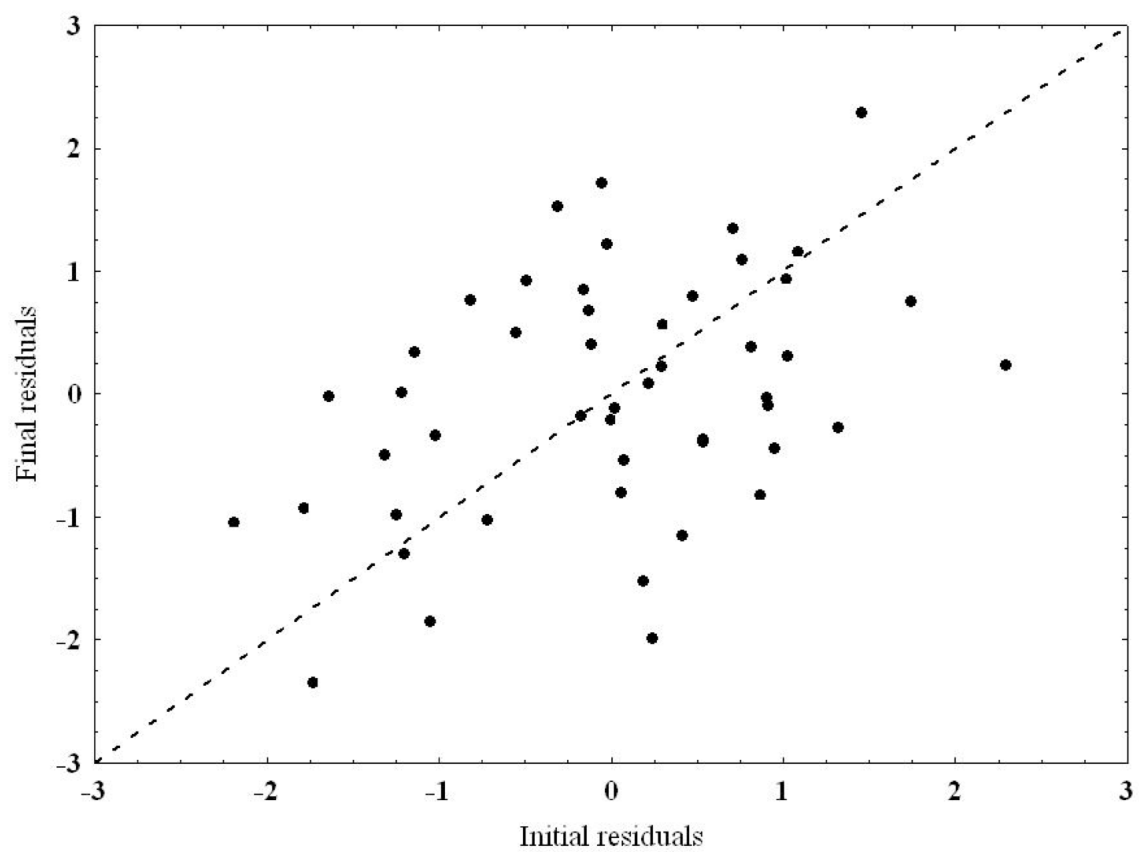
**Table 4:** Linear regressions between male display traits and mating success for bower owning adult males (n=23). Maximum courtship duration and number of blue bower decorations were the only display variables that were related to male aerobic capacity.

	Mating Success	Courtship Success
Maximum courtship duration	$R^2=0.18$ , $F_{1,21}=4.54$ , $p=0.045$	$R^2=0.18$ , $F_{1,21}=4.68$ , $p=0.042$
Blue bower decorations	$R^2=0.41$ , $F_{1,21}=14.84$ , $p=0.001$	$R^2=0.27$ , $F_{1,21}=7.67$ , $p=0.011$
PC1	$R^2=0.64$ , $F_{1,21}=37.03$ , $p<0.001$	$R^2=0.48$ , $F_{1,21}=19.59$ , $p<0.001$

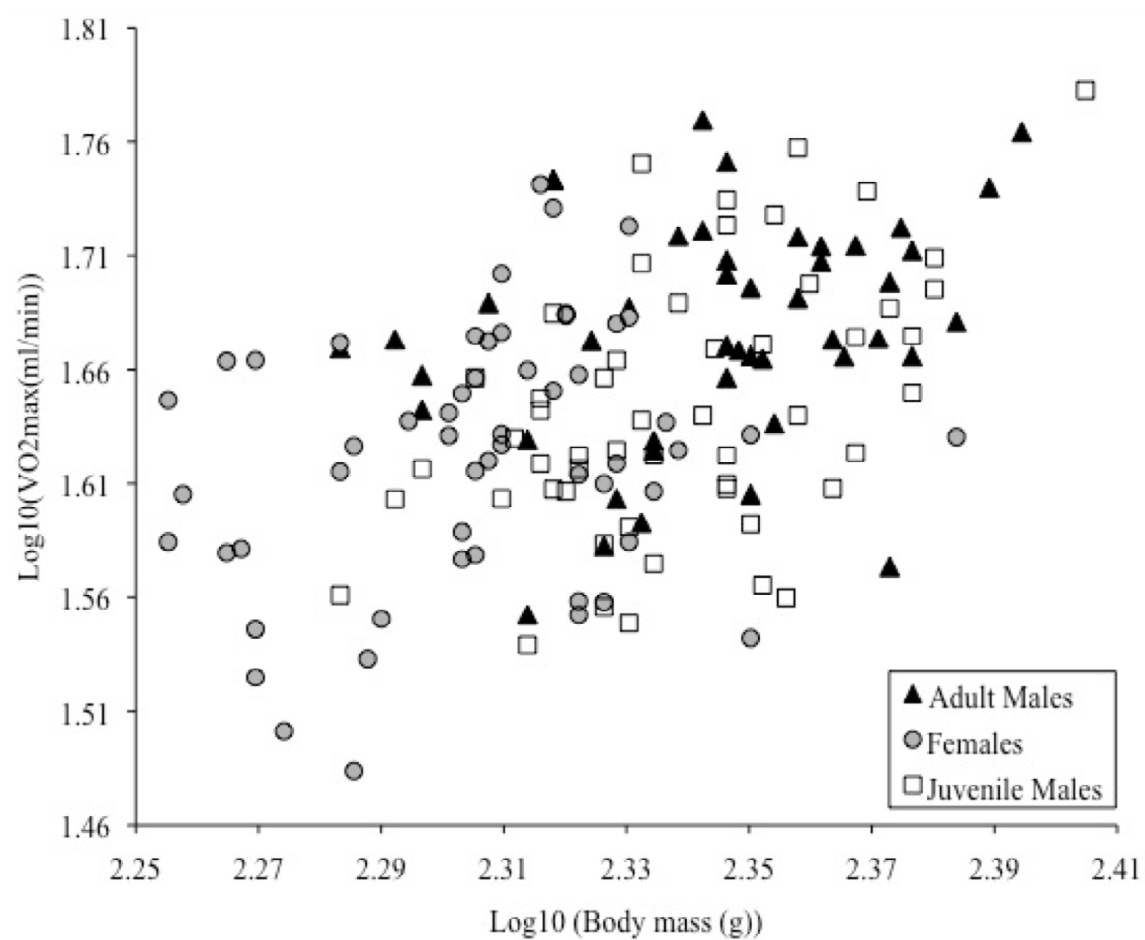
**Figure 4:** Repeatability of aerobic capacity ( $\dot{V}_{O_{2\max}}$ ) was estimated from the correlation of initial versus final residuals from the regressions of  $\log_{10} \dot{V}_{O_{2\max}}$  on  $\log_{10}$  body mass for the individuals with two  $\dot{V}_{O_{2\max}}$  measurements. The stippled line depicts the 1:1 correspondence between initial and final residuals.

**Figure 5:** Aerobic capacity ( $\dot{V}_{O_{2\max}}$ ) as a function of body mass in satin bowerbirds. The homogeneity-of-slopes ANCOVA model interaction term was not significant and thus the simple ANCOVA model was used rather than a separate-slopes model (see text).

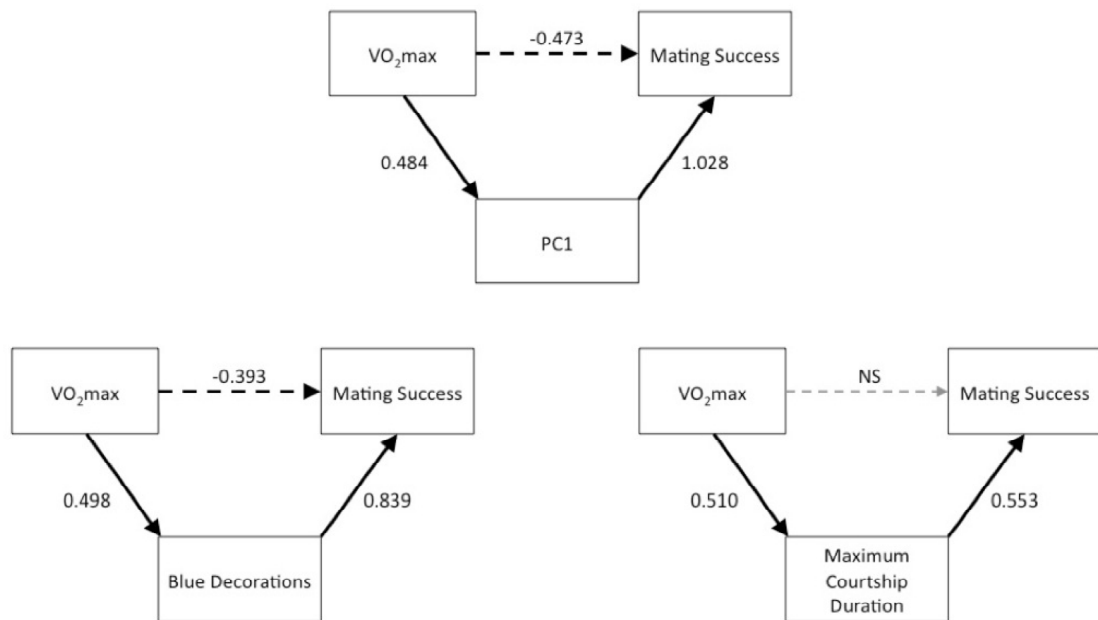
**Figure 6:** Path analysis between residuals of mass-corrected aerobic capacity ( $\dot{V}_{O_{2\max}}$ ), male display traits and mating success. Solid paths indicate positive relationships and dashed lines represent negative relationships. All paths are significant except the one marked “NS”. The three models are qualitatively the same and the path coefficient between PC1 and mating success greater than 1 is possible because it represents a beta weight (standardized multiple regression coefficient).



**Figure 4**



**Figure 5**



**Figure 6**

## CHAPTER III

The spatial dynamics of courtship in  
satin bowerbirds (*Ptilonorhynchus violaceus*)

### ABSTRACT

Courtship is a key trait affecting male mating success and males with the most vigorous courtships usually procure the most matings. Vigorous courtship displays in polygynous species often include elements co-opted from aggressive displays. These displays can sometimes be threatening to females and males may benefit by modifying their display to appear less threatening to females. Therefore, courtship vigor alone may not always be sufficient to maximize male reproductive success. Recent evidence has shown that males can alter their behavior in response to females during courtship. The location where courtship is produced can also play an important role in courtship success. Display sites have evolved independently multiple times in birds and the most elaborate display sites are built by bowerbirds. Investigating the relationship between male courtship behavior and display site is important for understanding how elaborate courtship behaviors evolve. I used vertically mounted cameras above the bower to study the spatial dynamics of courtship in satin bowerbirds. Satin bowerbird courtship includes aggressive display elements and these threatening displays can startle females. I used a robotic female bowerbird to look for a spatial male response to female startling behavior. I

**found a spatial pattern of male courtship behavior and an association between male movements toward the female and the use of a bower wall as a barrier between the male and female. Males courted females from closer in and spent more time directly in front of females without a bower wall barrier in successful courtships than in unsuccessful courtships. I also found that females startle more often when males are not using a bower wall as a barrier. Additionally, males responded to robot startles by moving farther away from females than in control courtships. These findings support the hypothesis that both the male-female courtship distance as well as the male's position relative to the bower serve to reduce the threat to females during courtship. Aggressive displays are commonly co-opted for use in courtship display and the threat reduction hypothesis offers a testable hypothesis that can help understand the adaptive significance of the often complex and what may be otherwise thought of as arbitrary courtship displays of many animals.**



## INTRODUCTION

Males of many taxa use elaborate behavioral displays during courtship to attract mates. These displays are important to pair bond formation and maintenance in monogamous species (Malacarne et al., 1991; Wachtmeister, 2001) and to mating success in polygynous species (Fiske et al., 1998; Höglund and Alatalo, 1995). Females in polygynous species rely heavily on male displays to assess males during mate choice (Bateson, 1983) and the males with the most vigorous courtships usually obtain the most matings (e.g. Borgia and Presgraves, 1998; Gibson and Bradbury, 1985; Höglund and Lundberg, 1987). Many studies suggest that female choice for vigorous courtship displays contributes to the evolution of the elaborated courtship displays found in many polygynous species (reviewed in Andersson, 1994).

Vigorous courtship displays in polygynous species often include elements co-opted from aggressive displays (Borgia, 1979, 2006; Berglund et al., 1996). Dominant males that are successful in fights demonstrate their lifetime success at a number of ecologically relevant tasks such as collecting food and resisting disease. Therefore, aggressive displays that are used by males in confrontations with rivals can also be used by females as indicators of male genetic quality. In species where aggressive displays have a dual function, the context of display presentation is important. For example, females that are threatened by and subordinate to aggressive males at feeding sites may also need to attend to the displays of these males when assessing male quality during courtship. However, even when taken in the proper context, aggressive courtship displays

may still sometimes elicit threat responses by females and males may benefit by reducing the threat their display presents to females (Borgia and Presgraves, 1998).

Therefore, courtship vigor alone may not always be sufficient to maximize male reproductive success. Recent work has shown that males often alter their courtship behavior in response to females during courtship (e.g. whitethroats, *Sylvia communis*: Balsby and Dabelsteen, 2002; fiddler crabs, *Uca perplexa*: How et al., 2008; house flies, *Musca domestica*: Meffert and Regan, 2002; convict cichlids, *Archocentrus nigrofasciatus*: Santangelo, 2005) and in one case even demonstrated the adaptive significance of interactive courtship communication between males and females (satin bowerbirds, *Ptilonorhynchus violaceus*: Patricelli et al., 2002, 2003, 2004, 2006). Female satin bowerbirds prefer intense male courtships that include aggressive elements (Collis and Borgia, 1992), but can also be startled by them and often end courtship without copulating after having been startled. They signal their level of comfort with male display during courtship by crouching, and males benefit from attending to this female signal. Males differ in their ability to respond to female signals of comfort and those that adjust display intensity accordingly startle females less often and have higher mating success than males that do not adjust display intensity (Patricelli et al., 2002). This result demonstrated that displaying at maximal levels is not always advantageous for males and that the ability to modulate trait expression can itself be a trait favored by sexual selection.

In addition to behavioral responses during courtship, the location where courtship occurs can play an important role in courtship success. Courtship often occurs at particular display sites, and males may even modify the site to enhance the quality of their displays. This is most common in birds, and the diversity of avian display sites is remarkable (see Johnsgard, 1994 for a detailed review). In the simplest display sites, males do not alter the environment and simply aggregate at sites that lack unique environmental features (i.e. arenas) (e.g. ruffs, *Philomachus pugnax*: Hogan-Warburg, 1966) or may instead select suitable ground (i.e. stages) (e.g. great argus pheasants, *Argusianus argus*: Davison, 1982) or elevated sites (i.e. display perches) (e.g. bearded bellbirds, *Procnias averano*: Snow, 1970) for their display. Alternatively, males may modify the environment and clear ground courts (e.g. Jackson's widowbird, *Euplectes jacksonii*: van Someren, 1958), create mound courts (e.g. superb lyrebird, *Menura novaehollandiae*: Watson, 1965), create arboreal courts (e.g. greater bird of paradise, *Paradisea apoda*: Dinsmore, 1970) or build bowers (i.e. complex display court structures that use collected materials) for courtship display (bowerbirds, family *Ptilonorhynchidae*: Gilliard, 1969). The variety in form and the repeated independent evolution of avian display sites indicate their important role in the evolution of elaborated avian courtship displays (Borgia et al., 1985; Johnsgard, 1994).

Species that use display sites are well suited for detailed studies of courtship behavior, including the interactions between males and females during courtship, because these sites offer predictable locations where courtship and mating will occur. Among species that use display sites, bowerbirds are ideally suited for such studies because males

maintain specific display sites throughout the mating season and across years, which are separated from each other by >100m. Females visit male display sites alone and assess each male individually rather than in an aggregation as in leks. Male bowerbirds decorate their display courts using natural and often man-made objects and most species build bowers (Borgia, 1995c; Frith and Frith, 2004; Gilliard, 1969; Marshall, 1954). In several species bower quality has been shown to influence male mating success suggesting that the bower serves as a marker of male quality (Borgia, 1985; Borgia and Mueller, 1992; Lenz, 1994; Madden, 2006; Uy and Borgia, 2000), but bowers are also central to male courtship display with the bower structure commonly serving as a physical barrier between the female and the courting male. It has been proposed that one function of the bower is to provide the visiting female protection from forced copulation by the courting males (Borgia, 1995c, 1996) and in one species (spotted bowerbird, *Chlamydera maculata*) bowers also protect females from aggressive courtship (Borgia, 1995a; Borgia and Presgraves, 1998) that includes elements co-opted from aggressive display (Borgia and Coleman, 2000). Thus, in bowerbirds, the elaboration of the display site suggests its importance to male mating success and the bower itself seems to have a functional role in courtship.

An implicit, yet rarely tested assumption made in discussions of courtship display is that male distance to the female and male position in relation to the display court are important. Changes in the distance between the male and female during courtship have long been noted (e.g. Wood-Gush, 1956) in a wide range of animals (e.g. medflies, *Ceratitis capitata*, Briceño and Eberhard, 2002; guppies, *Poecilia reticulata*: Long and

Rosenqvist, 1998; red jungle fowl, *Gallus gallus*: van Kampen and Hogan, 2000), and previous work has shown changes in male behavior in response to female behavior (Balsby and Dabelsteen, 2002; Patricelli et al., 2002, 2006; West and King, 1988) or in response to the manipulated distance of a female (How et al., 2008). The co-option of aggressive displays into the courtship of many species (Berglund et al., 1996; Berglund and Rosenqvist, 2001; Borgia, 1979, 1995c; Borgia and Coleman, 2000; Borgia and Presgraves, 1998; Borgia et al., 1985; Loffredo and Borgia, 1986b; Mateos and Carranza, 1999) and the possibility of forced copulation by the courting male suggest that the distance separating males and females should be important in female choice.

To investigate the spatial dynamics of courtship in satin bowerbirds I recorded male courtship behavior using a dual camera system, with one video camera placed above the bower to allow for the precise quantification of male and female positions on the display court and the other camera placed horizontally to allow for identification of marked individuals. Here I describe the spatial pattern of natural satin bowerbird courtship display and experimentally test the hypothesis that males adjust their distance to females in response to female startling behavior using a robot female bowerbird to control female behavior. I then relate the spatial dynamics of male courtship behavior to the threat reduction hypothesis for the evolution of courtship displays that include aggressive elements.

## **METHODS**

### **Study site and general methods**

This study was carried out in 2004 and 2005 at Wallaby Creek (28. 28' S, 152. 25' E), NSW, Australia (Borgia, 1985a). Behaviors at bowers were monitored throughout the mating season (early November until late December) using an automated video camera system in which cameras were placed in front of each bower. A passive infrared (PIR) detector activated a Hi-8 camcorder via a custom designed control box powered by a 12-volt automotive battery. A signal from the PIR detector to the control box turned the camcorder on and initiated recording for 45 seconds, and this timer was reset every time the PIR detector detected the bird while the camcorder was on. Field assistants checked the camcorders twice daily to change tapes and batteries as necessary. This equipment has proven to be very reliable and allows accurate identification of visitors' leg bands. The number of copulations each male achieved during the mating season was scored from these videos (Borgia, 1995a). Male mating success measured from videos is a highly reliable indicator of genetic paternity (Reynolds et al., 2007). All monitored males were bower holders in full adult plumage that were previously banded with unique color band combinations (Borgia, 1985a). Daily counts of decorations at the bowers and assessment of bower quality were averaged over the entire breeding season for each male (Borgia, 1985b).

### **Dual camera monitoring**

In order to precisely measure male and female positions and movements on the display court during courtship I developed a monitoring system where an additional video

camera that looks down on the bower. Using the same infrared trigger as the horizontally positioned camera I produced synchronized tapes with horizontal and vertical views of behaviors at the bower. The spatial aspects of display have been hard to quantify in the past because of the horizontal position of the video cameras needed to effectively identify individual leg bands do not allow to accurately measure movements relative to the bower. The additional video camera was positioned on a wooden crossbar placed 2.4 m above the bower. This rig was designed to be stable, have a low visual impact on the display site, and allow field assistants to rapidly service the above cameras without disturbing the area around the bower. The vertical camera and crossbar had a small visual profile and appeared to have no effect on male and female behavior. In 2004, 35 bowers were video monitored with the horizontal cameras and a subset of 20 bowers were followed throughout most of the mating season with the additional vertical camera to provide data on the spatial distance measures of courtships under natural conditions. In 2005, the vertical cameras were used for the experimental trials with the robotic female bowerbird at 12 bowers.

### **Male courtship behavior**

The sequence of male satin bowerbird courtship behaviors has been previously described in detail (*P. v. violaceus*: Borgia, 1995b; Loffredo and Borgia, 1986a; *P. v. minor*: Frith and Frith, 2004). Briefly, courtship begins with the female standing between the walls of the bower facing the male that is positioned on the decorated front bower platform. The male then produces a series of mechanical vocalizations that progresses into the typical bout of 4 intense wing-flips (WF) coordinated with buzzing vocalizations

and this is followed by interspecific avian vocal mimicry. Females crouch during courtship to indicate their level of comfort with the male's display. The fully crouched position (low to the ground, tilted forward and fluffing wings) is similar to the copulation solicitation of many passerines and females are more crouched in courtships ending in copulation than in earlier courtships in their mate searching sequence (Patricelli et al., 2004). However, females can also be startled by a male's display, jumping rapidly upward or backward in response to an element of male display. Previous work showed that females are nearly 3 times more likely to be startled during the wing-flip displays than during the rest of courtship, even though these intense displays represent only 17% of courtship duration (Patricelli et al., 2003). Therefore I focused on the spatial relationship between males and females during the intense wing-flip portion of the courtship display in this study. Males typically only produce a single wing-flip bout in unsuccessful courtships and usually produce two wing-flip bouts in courtships ending in copulation.

### **Courtship tracking of male behavior**

Courtship videos taken from above the bower were recorded on Hi-8 camcorders (Samsung SCL-810) at 29.97 frames per second and captured using analog to digital converters (Canopus ADVC 110 and 300) at a resolution of 720x480 pixels. The aspect ratio for the digitized pixels was 0.9 and I calculated separate calibration coefficients for the X and Y directions from video frames including reference meter sticks. There were  $3.2 \pm 0.08$  (mean  $\pm$  SD) pixels/cm in the X direction and  $2.9 \pm 0.09$  pixels/cm in the Y direction. The length of the bowerbird in the video frames was roughly 90 pixels and



male position on the display court (centroid of the bird) was tracked automatically using software developed at the University of Maryland. This image tracking software is open source and available for off-line analysis of videos at (<http://sourceforge.net/projects/winbower/>). Because of varying illumination and the heterogeneous background of the bower platform, the tracking software could not correctly identify the location of the male in all cases. A study describing the tracking software algorithm and evaluating the accuracy of this automatic tracking against human ground-truthing found that the software was able to track the bird within the specified tolerance of 15 pixels in 83% of the frames tracked and for most videos that number goes beyond 90% (Farrell et al., 2008). All tracking results presented here were checked for instances where the automated system failed to record the bird's location correctly within 15 pixels of the actual centroid and manually edited if needed. The tracking coordinates were output to a spreadsheet and male position during courtship was mapped onto Cartesian coordinates such that the origin was at the front of the bower and the ordinate (Y axis) ran down the center of the bower avenue. The position of the female in the bower was determined from a video frame capture and calculated using ImageJ (v. 1.43u, National Institutes of Health, Washington, D.C.). Females did not noticeably change their position during courtship so I used the first video frame of a courtship for measurement of female position in the bower. The distance of the female to the front of the bower was calculated from the front of her head (where her eyes are situated) to the front of the bower to describe the distance from which she was viewing the male's display. For the experiment using the robotic female bowerbird, the position of the robot

within the bower was the same in all trials and was similar to female positioning in natural courtships.

### **Female robot experiment**

To control female communication to males, I used a previously developed mechanical robot covered by female satin bowerbird skins collected near Wallaby Creek (Patricelli et al., 2002, 2004). Males actively courted these robots and mounted them for copulations as if they were live females. Crouching and startling behaviors were simulated with coupled vertical and forward-tilting body movements (see Patricelli et al., 2006 for a full description of the robot). During the experiment, robot movements were remotely controlled from a blind located 10m from the bower and set up the day before the experiment.

For the experimental courtships, the robot was placed in the bower avenue of the male being tested, simulating the female position in the bower during natural courtships. In the control treatment, the robot was placed in an intermediate crouch position throughout the courtship, which in natural courtships indicates intermediate comfort with the male's display (Patricelli et al., 2006). In the manipulation (startle) treatment, the robot was initially placed in the intermediate crouch position and then we mimicked a female startle by moving the robot out of the crouch in a rapid rise after the male's first intense wing-flip display element. All experimental courtships were conducted using the same robot and were performed by the same observer.

Each male was presented both the control and startle robot treatments in a randomized order, at least 7 days apart. Only males that courted and mounted the robot in both treatments were used in the analyses (two males did not court and mount the robot in one of the trials and the vertical camera malfunctioned during one trial of a third male).

### **Statistical analyses**

All statistical analyses were performed in Statistica 6.0 (Statsoft Inc., Tulsa, OK). I used non-parametric tests because of small sample sizes. Unpaired tests were used for comparisons between the wing-flip bouts of early unsuccessful courtships and successful courtship and paired test were used when comparing the first and second wing-flip bouts of successful courtships. A Chi-squared analysis was used to test for an association between type of wing-flip and the use of a bower wall as a barrier during courtship. Paired comparisons between the control and manipulation robot treatments allowed me to test whether individual males modulate their distance to the female in response to female startles. All tests are two-tailed.

## RESULTS

### **Spatial pattern of courtship behavior**

I analyzed the first available (early) unsuccessful courtship between 11 males and females and successful courtships ending in copulation for 10 males. Eight males were sampled in both types of courtship for a total of 13 unique males. These males produced a single wing-flip bout in early unsuccessful courtships and two wing-flip bouts in successful courtships. In all cases, I found that male satin bowerbird courtship movements showed a distinct spatial pattern where males alternate between approaches and movements away from the female while performing the wing-flip portion of their courtship display (Fig. 7). The first and third wing-flips are produced while moving toward the female, while the second and fourth wing-flips are produced while moving away from the female.

Females enter the bower from the back at the beginning of courtship, while males are in front of the bower on the bower platform. At the beginning of courtship females positioned themselves relative to the back of the bower, entering about half their body into the bower. They typically remained in this position throughout the entire courtship and the distance from the female's head to the front entrance of the bower did not differ between early unsuccessful and successful courtships (unsuccessful courtship vs. first bout of successful courtship: Mann-Whitney U test:  $Z=0.56$ ,  $p=0.573$ ,  $n_1=11$ ,  $n_2=10$ ; unsuccessful courtship vs. second bout of successful courtship: Mann-Whitney U test:  $Z=0.99$ ,  $p=0.324$ ,  $n_1=11$ ,  $n_2=10$ ; first vs. second bout of successful courtship: Wilcoxon matched pairs test:  $Z=0.18$ ,  $p=0.859$ ,  $n=10$ ; Fig. 8). Male bower avenues vary in length,

and female distance behind the front of the bower was significantly correlated to bower avenue length ( $r_s=0.717$ ,  $p=0.006$ ,  $n=13$ ; Fig. 9), further supporting the hypothesis that females position themselves relative to the back of the bower.

This female positioning toward the back of the bower creates a specific viewing geometry during courtship (Fig. 10). Male courtship behaviors occurring directly in front of the female are visible to her while male courtship behaviors occurring to the sides of the bower are partially or entirely obstructed by the bower wall. Bower walls are thought to play an important role in threat reduction in bowerbird species with intense displays and this female viewing geometry allows the classification of male behaviors as occurring either with or without a bower wall separating the male and female. I considered a wing-flip to have occurred with a bower wall separating the male and female if the male was not positioned in front of the bower avenue or did not run across the front of the bower avenue during his wing-flip display. The presence of a bower wall as a barrier between the male and the female was not random with respect to male wing-flips with movements toward or away from females, but this association differed between early unsuccessful and successful courtships. In early unsuccessful courtships, the presence of a bower wall as a barrier occurred much more often than expected by chance when males performed wing-flips with movement toward the female ( $\chi^2 = 17.2$ ,  $df=1$ ,  $p<0.001$ ; Table 5). This association between presence of a bower wall as a barrier and wing-flip with movements toward the female was also found in the first wing-flip bout of successful courtships ( $\chi^2 = 5.6$ ,  $df=1$ ,  $p=0.02$ ; Table 5), but not in the second wing-flip bout of successful courtships ( $\chi^2 = 0.29$ ,  $df=1$ ,  $p=0.59$ ; Table 5).

Further differences were found between wing-flip bouts in early unsuccessful courtships and successful courtships. The average distance between the male and the front of the bower during a wing-flip bout was greatest in early unsuccessful courtships and smallest in the last wing-flip bout of successful courtships (unsuccessful courtship vs. first bout of successful courtship: Mann-Whitney U test:  $Z=2.18$ ,  $p=0.029$ ,  $n_1=11$ ,  $n_2=10$ ; unsuccessful courtship vs. second bout of successful courtship: Mann-Whitney U test:  $Z=3.24$ ,  $p=0.001$ ,  $n_1=11$ ,  $n_2=10$ ; first vs. second bout of successful courtship: Wilcoxon matched pairs test:  $Z=2.29$ ,  $p=0.022$ ,  $n=10$ ; Fig. 11). Additionally, the amount of time males spent directly in front of females, with no bower wall separating them was significantly greater in the second wing-flip bout of successful courtships than in either the first wing-flip bout of successful courtships or than in the single wing-flip bout of early unsuccessful courtships (unsuccessful courtship vs. first bout of successful courtship: Mann-Whitney U test:  $Z=2.82$ ,  $p=0.005$ ,  $n_1=11$ ,  $n_2=10$ ; unsuccessful courtship vs. second bout of successful courtship: Mann-Whitney U test:  $Z=3.87$ ,  $p<0.001$ ,  $n_1=11$ ,  $n_2=10$ ; first vs. second bout of successful courtship: Wilcoxon matched pairs test:  $Z=2.49$ ,  $p=0.013$ ,  $n=10$ ; Fig. 12).

For unsuccessful courtships, 6 of the 11 male-female dyads eventually mated together. I found no differences in comparisons between unsuccessful courtship dyads eventually ending in copulation and dyads not mating together, although the power of these tests is very low due to small sample sizes (female distance behind the front of the bower: Mann-Whitney U test:  $Z=0.18$ ,  $p=0.855$ ,  $n_1=6$ ,  $n_2=5$ ; male distance in front of the bower: Mann-Whitney U test:  $Z=0.73$ ,  $p=0.465$ ,  $n_1=6$ ,  $n_2=5$ ; proportion of time male is in

front of bower avenue:  $Z=0.18$ ,  $p=0.855$ ,  $n_1=6$ ,  $n_2=5$ ). Despite this low power, the results are qualitatively the same for comparisons of unsuccessful to successful courtships if only dyads not ending in copulation are used (Table 6).

### **Female startling behavior in natural courtships**

The distinct spatial pattern of male courtship behavior allows us to make predictions about when females should startle in natural courtships. If wing-flip displays are more threatening when produced with a movement toward the female, then wing-flips with movements towards the female should startle females more often than wing-flips when males are moving away from them. On the other hand, if separation by a bower wall is more important in reducing threat to females during courtship, then females should be startled more often when males are moving across the entrance of the bower than when a bower wall barrier is present. To distinguish between these hypotheses, I counted the number of startles during each of the wing-flips in a bout for the first courtship of 107 unique male-female dyads (30 males and 76 females) in 2004. None of these courtships ended in a copulation. I used the first courtship in a male-female dyad to control for female behavior and avoid pseudo-replication (Patricelli et al., 2003). Since wing-flips 1 and 3 involve male movement toward the female with a bower wall separating the male and female, I grouped startles that occurred during these wing-flips. Similarly, I combined the number of startles that occurred during wing-flips 2 and 4, where the male crosses the front entrance of the bower and involves a movement away from the female. I found that startles occur more often in wing-flips 2 and 4, where the male is moving across the front of the bower, than in wing-flips 1 and 3 (Wilcoxon

matched pairs test:  $Z=4.51$ ,  $p<0.001$ ,  $n=107$ ; Table 7). This result is qualitatively the same if each male is only used once (Wilcoxon matched pairs test:  $Z=2.35$ ,  $p=0.019$ ,  $n=30$ ; Table 7) or if each female is only used once (Wilcoxon matched pairs test:  $Z=3.40$ ,  $p<0.001$ ,  $n=76$ ; Table 7).

### **Spatial response of males to robotic female startles**

Males responded naturally to the female robot by courting it and even attempting to copulate with it at the end of the trials. Prior to the robot startle, when both treatments were identical, I found no differences between the control and startle treatments in male distance to the front of the bower at the beginning or end of the first wing-flip of a wing-flip bout. Because I made the a priori prediction that the greatest differences in male behavior between the robot treatments would be immediately after the robot startle, and to be able to include courtships from two males who showed fewer than 4 wing-flips in either the control or the experimental treatment, I restricted my analyses to the comparisons of male behavior immediately after the second wing-flip. I found that males move farther away from the bower following a startle than in control courtships (Wilcoxon matched pairs test:  $Z=2.07$ ,  $p=0.038$ ,  $n=9$ ; Fig. 13). Eight of the nine males showed this spatial response to the female robot startle. Variation in male response to the robot startle (i.e. change of distance between control and startle treatment) did not correlate with male mating success in natural courtships ( $r_s=-0.017$ ,  $n=9$ ,  $p=0.966$ ), number of decorations present on the bower platform ( $r_s=-0.200$ ,  $n=9$ ,  $p=0.606$ ) or male age ( $r_s=0.094$ ,  $n=9$ ,  $p=0.810$ ).



## DISCUSSION

The use of video cameras placed above the bower allowed me to quantify how far into the bower females positioned themselves during courtship. Females enter about halfway into the bower during courtship and the distance from the female to the front of the bower is correlated to bower avenue length, supporting the hypothesis that females position themselves relative to the back of the bower during courtship. There is no difference in female distance to the front of the bower between early unsuccessful and successful courtships, suggesting that female position in the bower is not related to female comfort during courtship or readiness to mate. This female position at the back of the bower influences her viewing geometry during courtship and females only have an unobstructed view of the male when he is directly in front of the bower avenue. When males court outside of this area, a bower wall separates the male and the female.

The view of courtship from above the bower also revealed a spatial pattern of male wing-flip displays showing an alternation of movements toward and away from females. This pattern was not predicted in earlier studies of satin bowerbird courtship behavior (Borgia, 1995b; Patricelli et al., 2002) and is associated with the presence or absence of a bower wall separating the male and female. In early unsuccessful courtships, a bower wall was almost always present between the male and female when the male produced a wing-flip with a movement toward the female.

The function of bowerbird bowers in courtship has long been debated (Diamond, 1982a, b; Gilliard, 1963, 1969; Marshall, 1954; Söderberg, 1929). Since then, Borgia has

offered several adaptive explanations for the origin and elaboration of bowers that are supported by a series of comparative and detailed behavioral analyses. First, the marker hypothesis (Borgia et al., 1985) proposed that bowers advertise male quality to females by showing ownership of defended, decorated display sites and that females could benefit by attending to the quality of the bower. The marker hypothesis is attractive because it is not bowerbird specific and can be applied more generally to other types of display sites, but it makes no prediction about the shape or use of bowers. Second, to address the function of bowers, Borgia proposed (1995c, 1996) that bower building originated as a trait that attracts females to display sites by providing females protection from forced copulations. The courtship behavior of bowerbird species with different bower types is consistent in all cases with the bower functioning as a barrier between the male and female giving the female an opportunity to escape forced copulations if she is not ready to mate. Furthermore, this hypothesis can explain the origin of bowers as even incipient bowers could have provided such a protective function. Third, Borgia proposed the threat reduction hypothesis (Borgia, 1995b; Borgia and Presgraves, 1998) to explain large differences in bower architecture and the aggressive display elements of the avenue building spotted bowerbirds (*Chlamydera maculata*). The threat reduction hypothesis posits that when male display is very intense it can threaten females who are trying to assess male display and that males will adjust their behavior and utilize their bower during courtship to allow females to view display with reduced threat. Taken together, this suite of hypotheses attempt to explain the evolution of bowerbird display sites and offers testable predictions concerning variation in courtship behavior.

The spatio-temporal pattern of courtship behaviors and the differences between early unsuccessful and successful courtships in satin bowerbirds are consistent with the proposed threat reduction role of bowers. In satin bowerbirds, successful courtships differ from early unsuccessful courtships in several respects. First, in the second wing-flip bout of successful courtships, the association between male wing-flips with movements toward the female and the presence of a bower wall as a barrier between the male and female breaks down, and males produce half their wing-flips with movements toward the female without a bower wall present between the male and female. This type of wing-flip should potentially be the most threatening to females because the male is moving toward her without a bower wall separating them. Second, males spend approximately 45% of the time in front of the female without a bower wall separating them in the second wing-flip bout of successful courtships, which is significantly more than the approximately 5% in both early unsuccessful courtships and the first wing-flip bout of successful courtships. Third, the average distance of the male from the front of the bower is significantly smaller in the second bout wing-flip bout of successful courtships than in either early unsuccessful courtships or the first wing-flip bout of successful courtships. These differences in male courtship behavior, with males courting females from a shorter distance and spending more time directly in front of females without a bower wall separating them when females are showing copulation solicitation behaviors suggests that males adjust their behavior to reduce the threat to females when females are not soliciting copulations.

Females can startle when they are threatened by male wing-flip displays, and the occurrence of female startles in relation to the spatial pattern of male wing-flips as well as the male response to female startles can be informative in terms of understanding threat reduction. In early courtships, females are often startled by male display (Patricelli et al., 2006) and I found that in early unsuccessful courtships females startle more often when males are crossing in front of the bower avenue during wing-flips 2 and 4 than during wing-flips 1 and 3 when the male wing-flip is associated with a bower wall barrier. This result suggests that females are more threatened by male displays when a bower wall is not present as a barrier between the male and female. In addition to the presence of a bower wall as a barrier, the distance between the male and female is also important to threat reduction. My experiment with a robotic female bowerbird showed an independent spatial effect of male response to simulated female startles. I found that males moved farther away from females in wing-flip 2 following a startle than in the control treatment. This effect was small but consistent across males, suggesting that males have the ability to fine-tune their courtship display. The degree of male response to simulated female startles was not related to either male mating success, number of bower decorations present on the bower platform or male age, and a previous study on startling in this species also failed to find a relationship between degree of male response to startling and male quality (Patricelli et al., 2006) so it is possible that it is the presence of a response that is more important than the magnitude of this response. Taken together, these results from natural courtships and experimental courtships using a robotic female suggest that both the position of the male relative to the bower and the distance between

the male and female are important spatial components of threat reduction of courtship display in satin bowerbirds.

These results quantitatively support earlier suggestions that males spatially modulate intense display elements in bowerbirds (Borgia and Presgraves, 1998). The observed spatial pattern of satin bowerbird courtship is fairly simple, yet it was not described until I used cameras positioned above the bower. Furthermore, differences in this pattern between successful and unsuccessful courtships would be difficult to interpret without the threat reduction hypothesis. Spatial positioning and distance modulation of courtship display has rarely been investigated and may be especially important in species where males produce vigorous displays that contain elements of aggressive interactions. Given the importance of the co-option of aggressive displays in the evolution of elaborated display traits in bowerbirds (Borgia and Coleman, 2000) and more generally among many taxa (Berglund et al., 1996; Borgia, 2006), it is likely that courtship behaviors that mitigate the threat to females are more common than presently recognized. The threat reduction hypothesis is an important theoretical framework when studying the evolution of elaborate display sites and courtship displays because it offers a testable model to investigate the adaptive significance of the often complex (Prum, 1990; Scholes, 2008), and what may otherwise be thought of as arbitrary (Lande, 1981; Mead and Arnold, 2004), courtship displays of many animals.

**Table 5:** Number of wing-flips with movement toward female and presence of a bower wall as a barrier for wing-flips in early unsuccessful courtships, the first and second wing-flip bouts of successful courtships.

Early unsuccessful courtship WF bout	Wing-flip toward female	Wing-flip away from female
Bower wall between male and female	20	0
No bower wall separation	1	23

Successful courtship, 1 <sup>st</sup> WF bout	Wing-flip toward female	Wing-flip away from female
Bower wall between male and female	14	0
No bower wall separation	4	22

Successful courtship, 2 <sup>nd</sup> WF bout	Wing-flip toward female	Wing-flip away from female
Bower wall between male and female	8	0
No bower wall separation	6	20

**Table 6:** Eventual dyad outcome for male-female dyads in unsuccessful courtships does not affect results of comparisons of unsuccessful courtships to courtships ending in copulation.

<b>Female distance behind the front of the bower</b>	Comparison of the WF bout of unsuccessful courtships to the first WF bout of successful courtships	Comparison of the WF bout of unsuccessful courtships to the second WF bout of successful courtships
11 male-female dyads	M-W U: $Z=0.56$ , $p=0.573$ , $n_1=11$ , $n_2=10$	M-W U: $Z=0.99$ , $p=0.324$ , $n_1=11$ , $n_2=10$
5 dyads not eventually ending in copulation	M-W U: $Z=0.61$ , $p=0.540$ , $n_1=5$ , $n_2=10$	M-W U: $Z=0.86$ , $p=0.391$ , $n_1=5$ , $n_2=10$
6 dyads eventually ending in copulation	M-W U: $Z=0.33$ , $p=0.745$ , $n_1=6$ , $n_2=10$	M-W U: $Z=0.76$ , $p=0.448$ , $n_1=6$ , $n_2=10$

**Table 6 (continued):** Eventual dyad outcome for male-female dyads in unsuccessful courtships does not affect results of comparisons of unsuccessful courtships to courtships ending in copulation.

<b>Male distance in front of the bower</b>	Comparison of the WF bout of unsuccessful courtships to the first WF bout of successful courtships	Comparison of the WF bout of unsuccessful courtships to the second WF bout of successful courtships
11 male-female dyads	M-W U: $Z=2.18$ , $p=0.029$ , $n_1=11$ , $n_2=10$	M-W U: $Z=3.24$ , $p=0.001$ , $n_1=11$ , $n_2=10$
5 dyads not eventually ending in copulation	M-W U: $Z=1.59$ , $p=0.111$ , $n_1=5$ , $n_2=10$	M-W U: $Z=2.45$ , $p=0.014$ , $n_1=5$ , $n_2=10$
6 dyads eventually ending in copulation	M-W U: $Z=1.95$ , $p=0.051$ , $n_1=6$ , $n_2=10$	M-W U: $Z=2.82$ , $p=0.005$ , $n_1=6$ , $n_2=10$



**Table 6 (continued):** Eventual dyad outcome for male-female dyads in unsuccessful courtships does not affect results of comparisons of unsuccessful courtships to courtships ending in copulation.

<b>Proportion of time male is in front of bower avenue</b>	Comparison of the WF bout of unsuccessful courtships to the first WF bout of successful courtships	Comparison of the WF bout of unsuccessful courtships to the second WF bout of successful courtships
11 male-female dyads	M-W U: $Z=2.82$ , $p=0.005$ , $n_1=11$ , $n_2=10$	M-W U: $Z=3.87$ , $p<0.001$ , $n_1=11$ , $n_2=10$
5 dyads not eventually ending in copulation	M-W U: $Z=2.57$ , $p=0.010$ , $n_1=5$ , $n_2=10$	M-W U: $Z=3.06$ , $p=0.002$ , $n_1=5$ , $n_2=10$
6 dyads eventually ending in copulation	M-W U: $Z=2.06$ , $p=0.039$ , $n_1=6$ , $n_2=10$	M-W U: $Z=3.25$ , $p=0.001$ , $n_1=6$ , $n_2=10$

**Table 7:** Number of startles during each of the wing-flips in a bout of intense display elements for the first courtship of 107 unique male-female dyads (30 males and 76 females) in 2004. Wing-flips 1 and 3 typically involve male movement toward the female with a bower wall separating the male and female. During wing-flips 2 and 4 the male crosses the front entrance of the bower and moves away from the female.

Wing-Flip	WF1	WF2	WF3	WF4
# of startles	35	64	34	55

n=107 unique male-female dyads

Wing-Flip	WF1	WF2	WF3	WF4
# of startles	13	19	10	19

n=30 unique male dyads

Wing-Flip	WF1	WF2	WF3	WF4
# of startles	20	42	24	34

n=76 unique female dyads

**Figure 7:** Courtship maps for the intense wing-flip display elements for the male-female dyad OMR-HLW. A) an early unsuccessful courtship wing-flip bout, B) the first wing-flip bout of a courtship ending in copulation, and C) the second wing-flip bout of a courtship ending in copulation. The tracking follows the “center of gravity” of the male (centroid of minimum ellipse totally encompassing male). Coordinates are in cm. The notation WF1 indicates the point where the male started his wing-flips and the numbers 2, 3 and 4 indicate the starting position for the other wing-flips in the bout. In all cases the female was standing near the rear entrance of the bower and the bower walls are outlined by the rectangles in the map.

**Figure 8:** Female distance behind the front of the bower (cm). This distance was calculated from her head to the front of the bower to describe the distance from which she was viewing the male’s display. “CN” is the wing-flip bout of early unsuccessful courtship, “CC-1” is the first wing-flip bout of successful courtships, and “CC-2” is the second wing-flip bout of successful courtships.

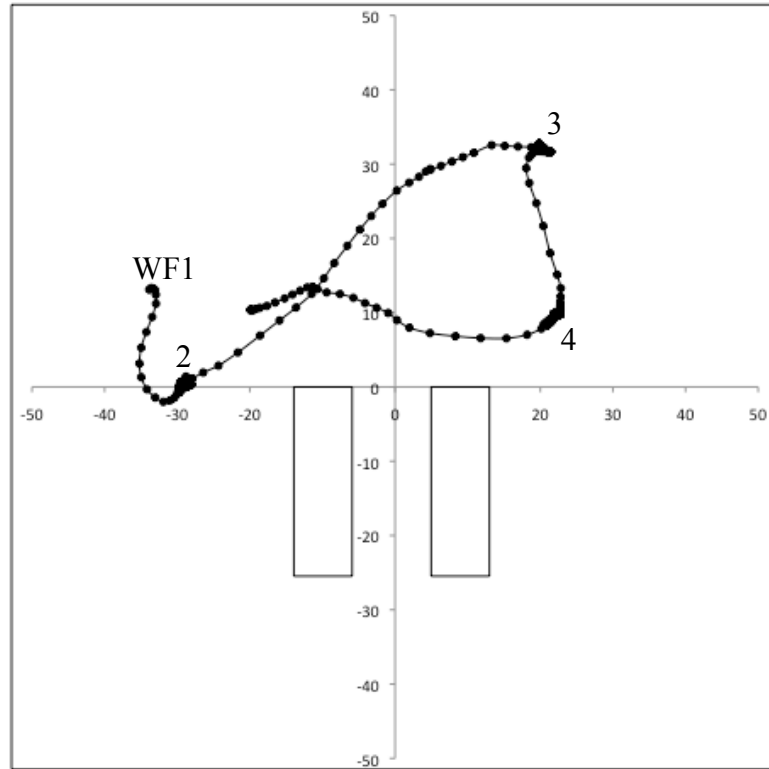
**Figure 9:** Plot of bower avenue length against female distance behind the front of the bower. Each unique male (n=13) is represented once and data were averaged for males with more than one wing-flip bout measured. Results are qualitatively the same if data are not combined.

**Figure 10:** Female viewing geometry during courtship. Grey area represents area directly in front of the bower avenue where no bower wall is between the male and female. A wing-flip was considered to have occurred with a bower wall separating the male and female if the male was not positioned in front of the bower avenue or did not run across the front of the bower avenue during his wing-flip display.

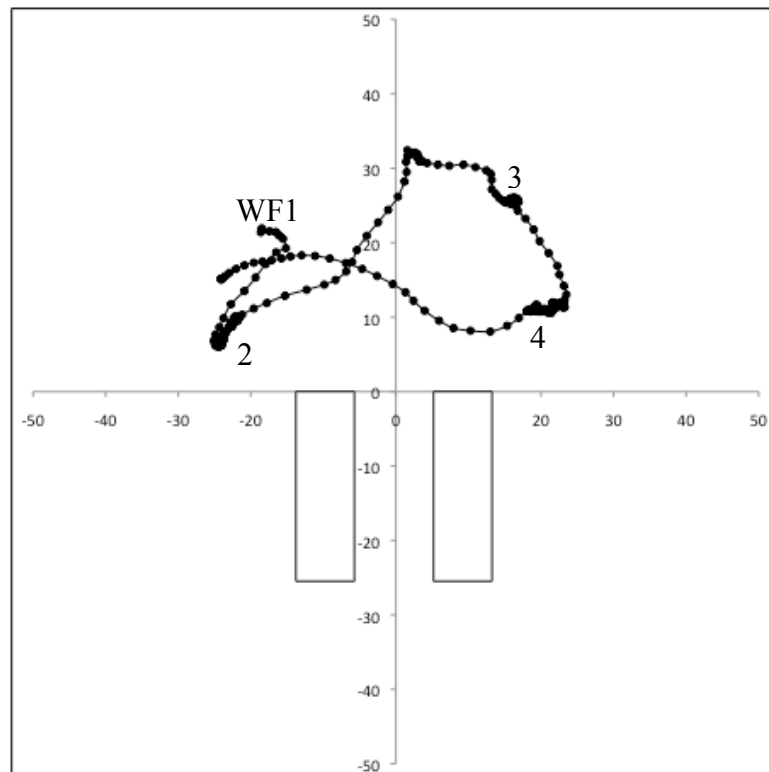
**Figure 11:** Average male distance (cm) in front of the bower during a wing-flip bout. “CN” is the wing-flip bout of early unsuccessful courtship, “CC-1” is the first wing-flip bout of successful courtships, and “CC-2” is the second wing-flip bout of successful courtships.

**Figure 12:** Proportion of time that male spent directly in front of female, with no bower wall separating them, during a wing-flip bout. “CN” is the wing-flip bout of early unsuccessful courtship, “CC-1” is the first wing-flip bout of successful courtships, and “CC-2” is the second wing-flip bout of successful courtships.

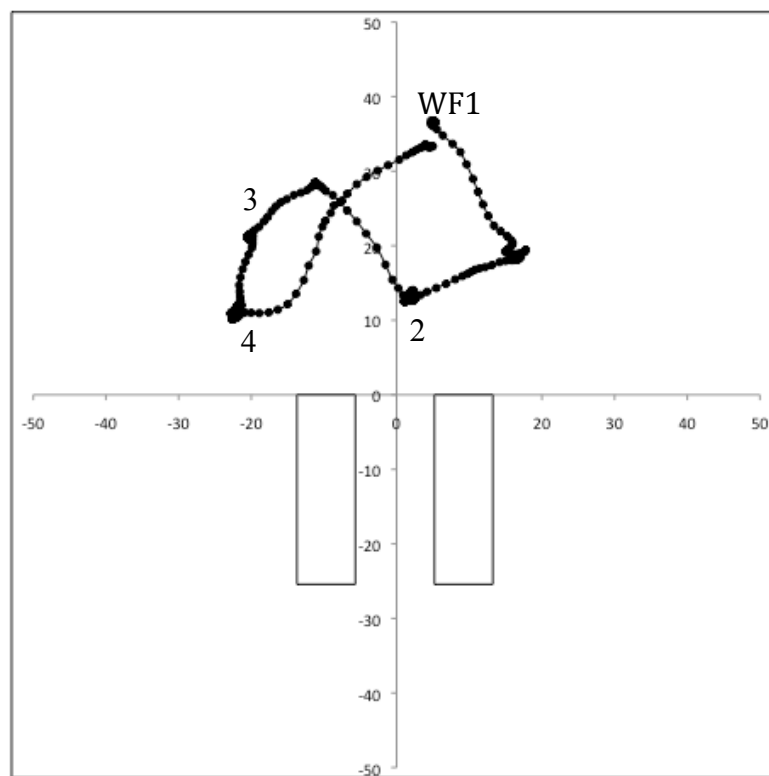
**Figure 13:** Male spatial response to simulated startles by a robotic female. Male distance (cm) in front of the bower at the end of wing-flip 2 in startle and control robot trials. All but one male moved farther away from the robotic female following a startle.



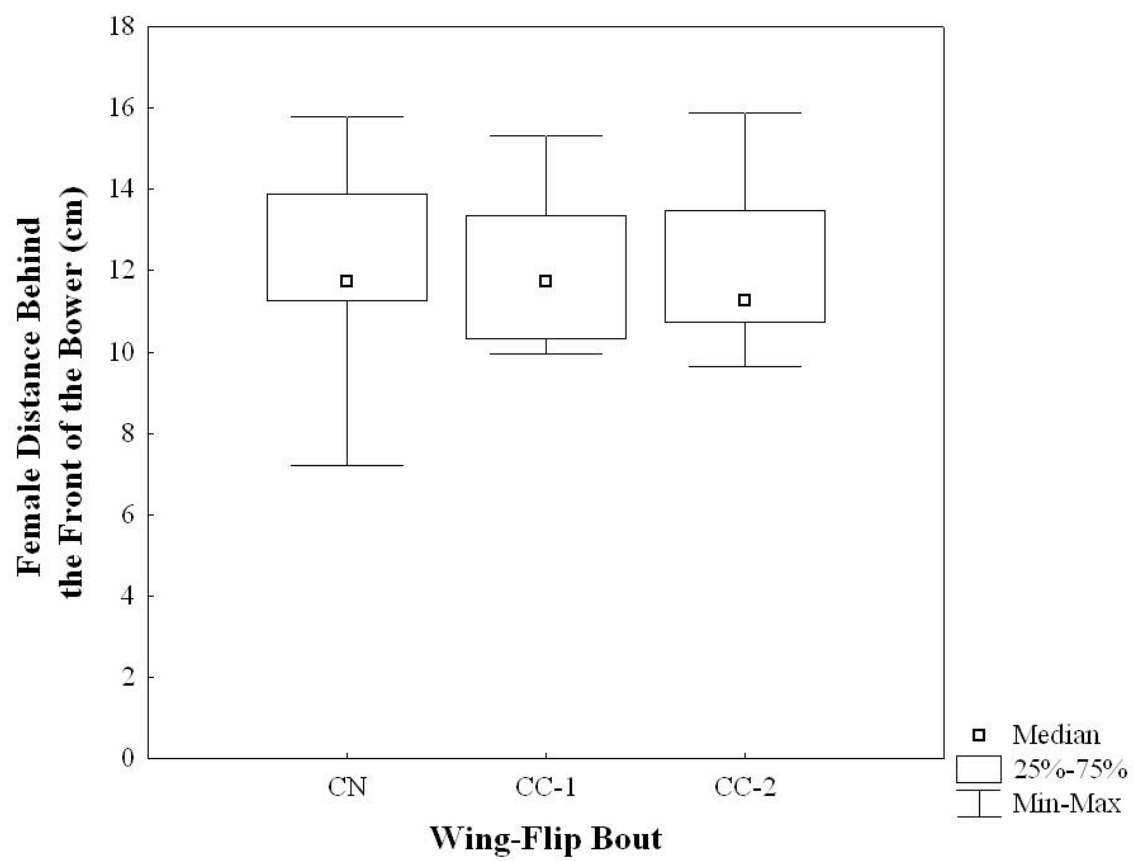
**Figure 7A**



**Figure 7B**

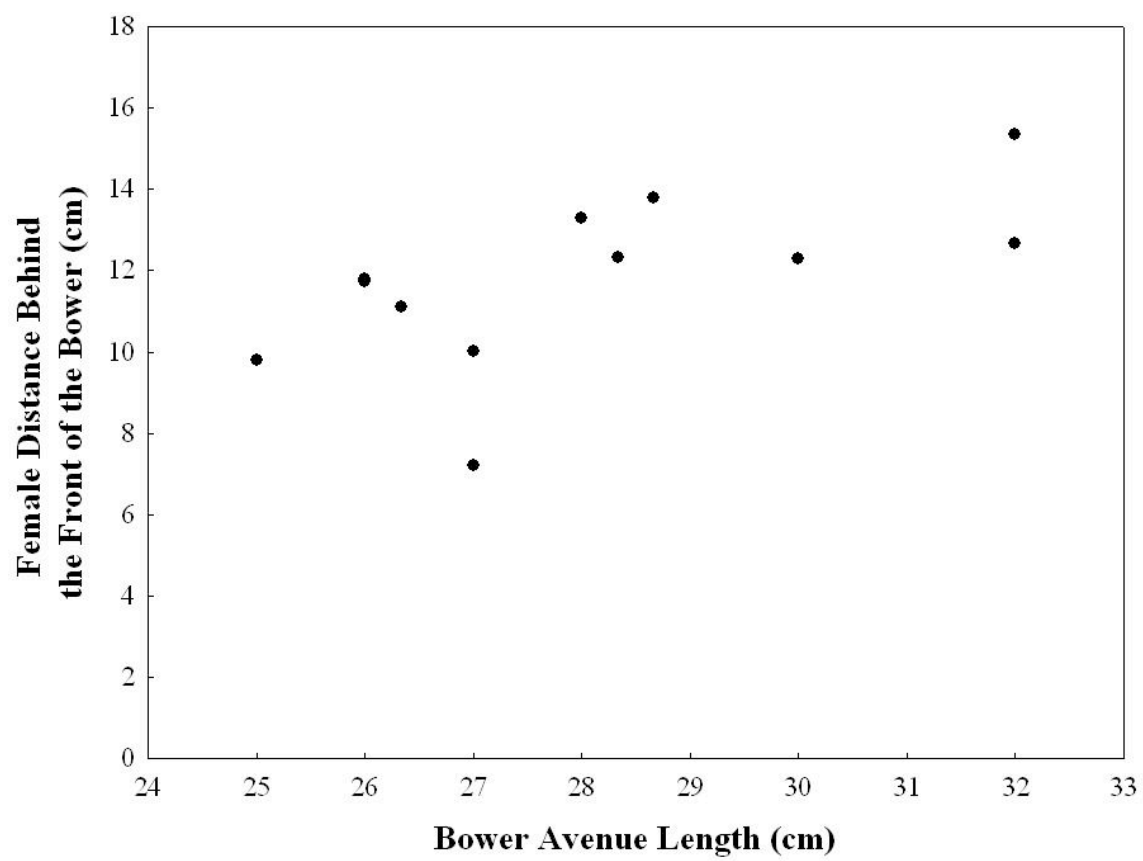


**Figure 7C**

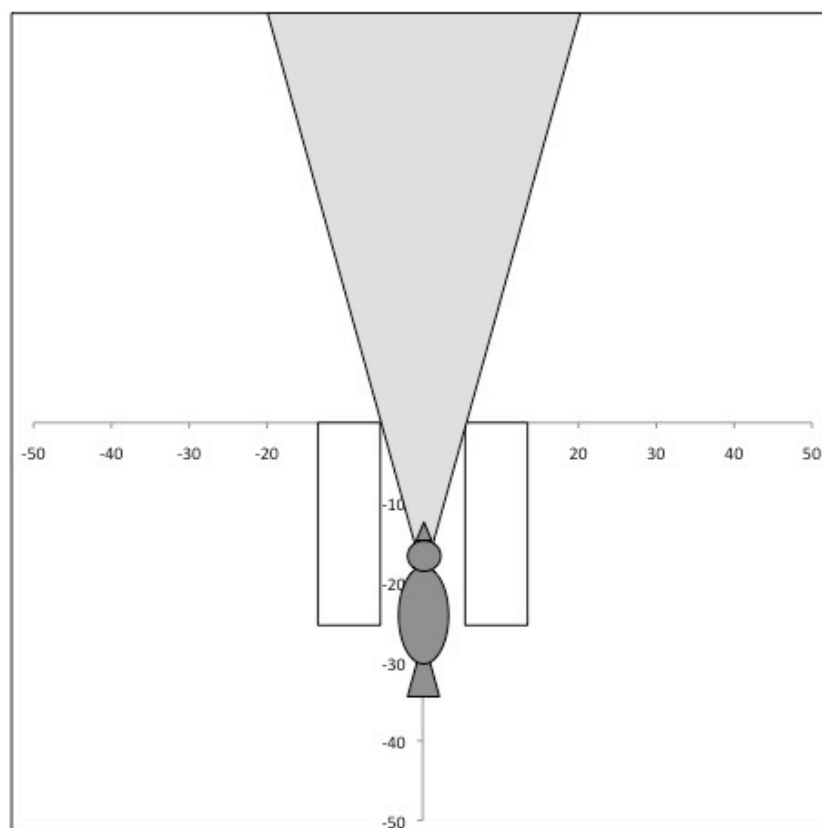


**Figure 8**

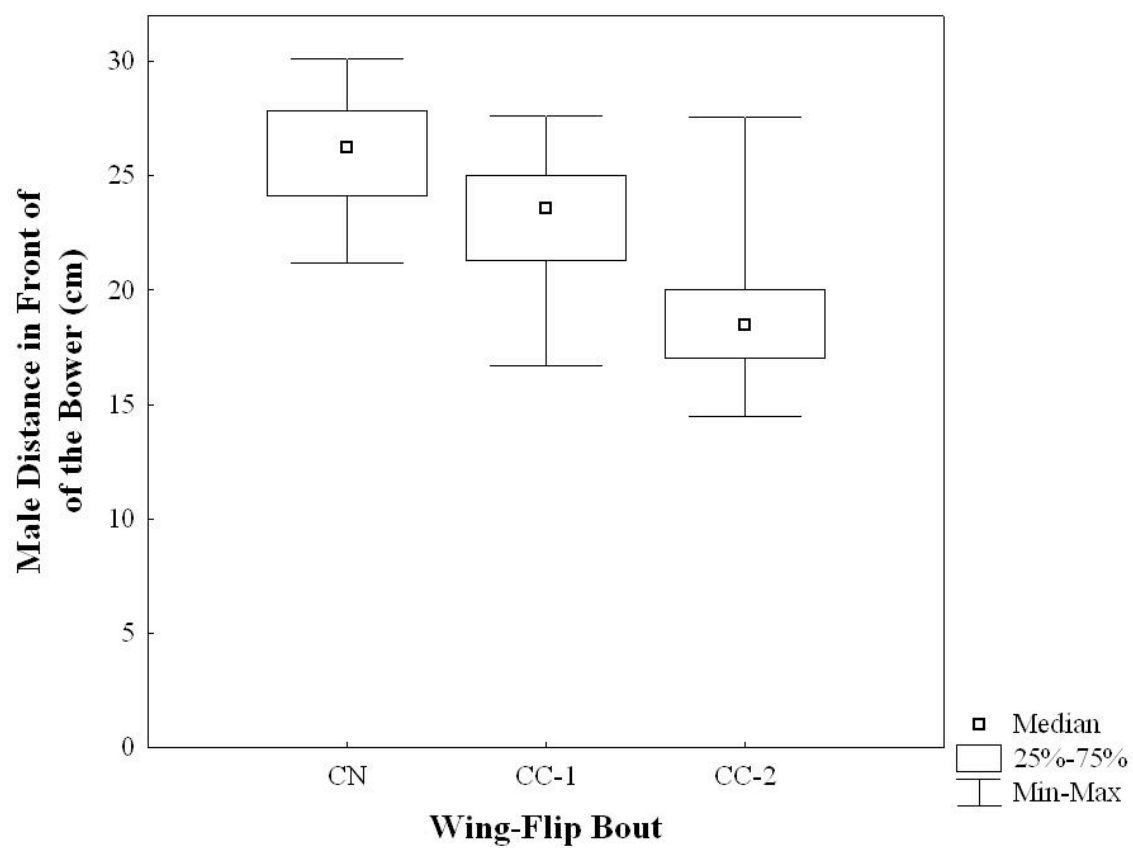




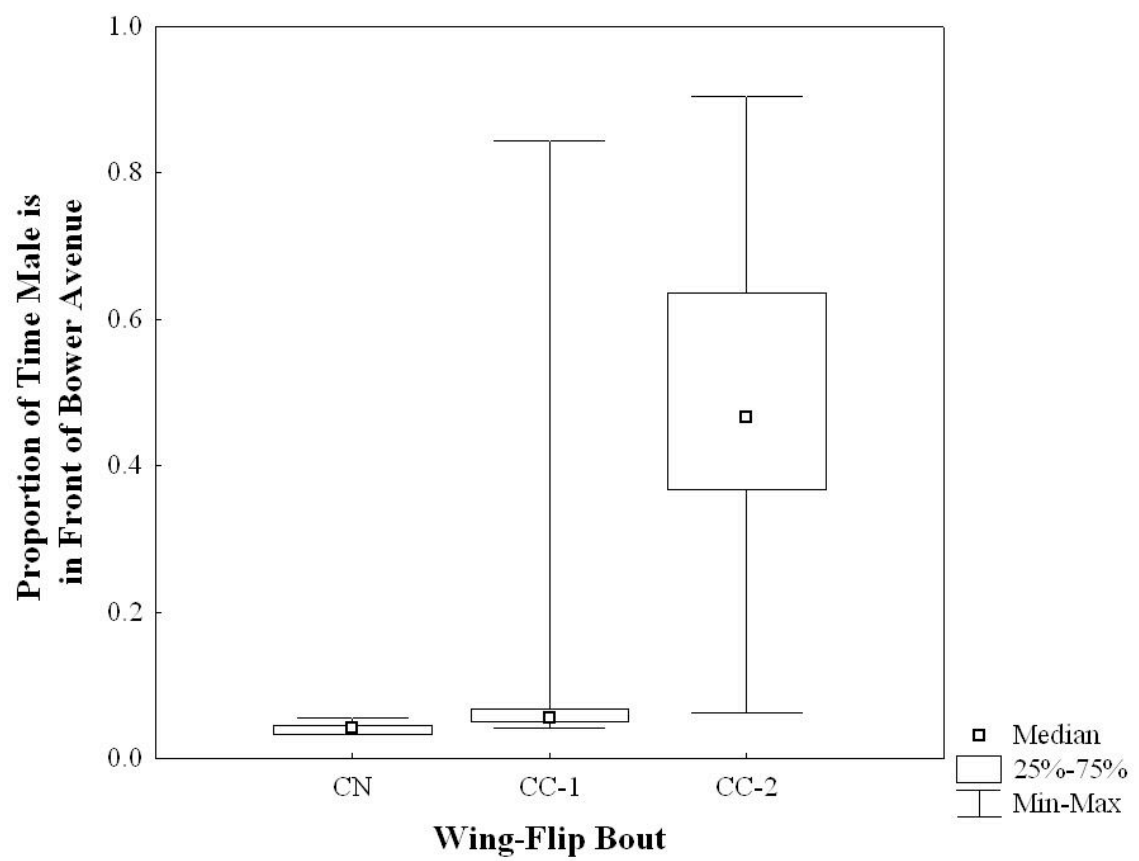
**Figure 9**



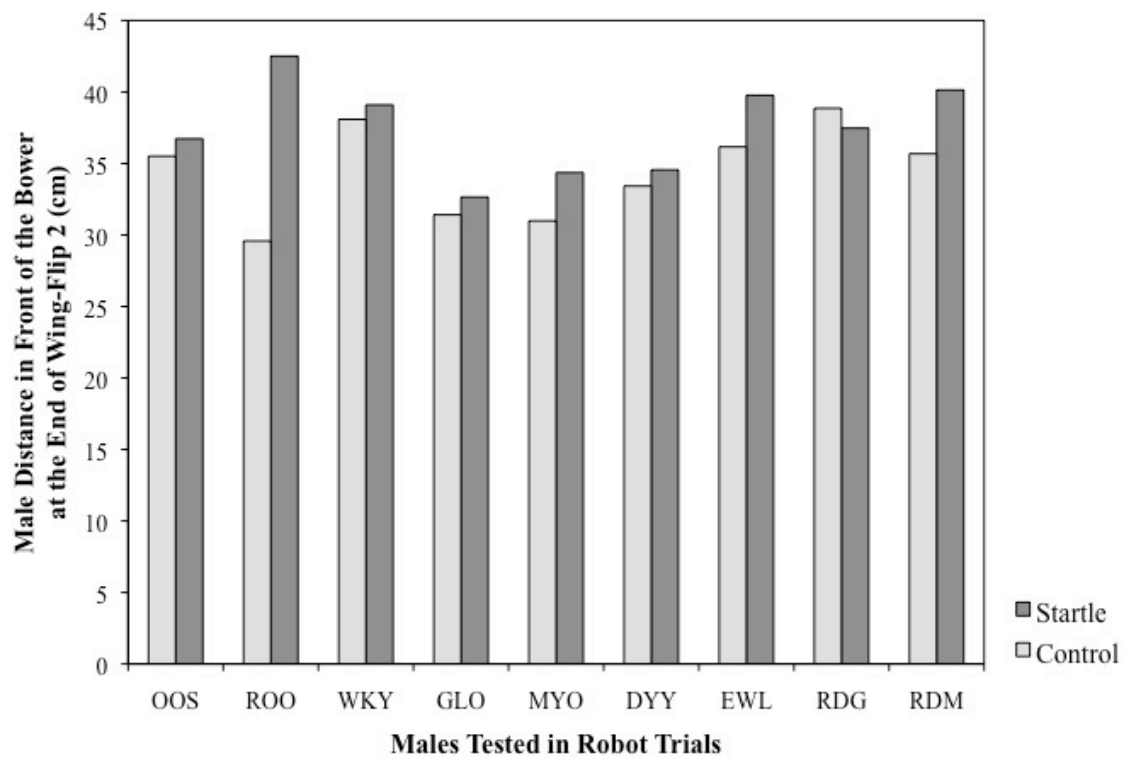
**Figure 10**



**Figure 11**



**Figure 12**



**Figure 13**

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