ABSTRACT

Title of Document: THE EFFECT OF SUNLIGHT ON DECORATION PLACEMENT AND MATING SUCCESS IN MALE SATIN BOWERBIRDS

Archer Freni Larned, Master of Science 2012

Directed By: Dr. Gerald Borgia, Professor, Department of Biology

Males of some bird species choose sunlit display sites to enhance their visual signal. Satin bowerbird (*Ptilonorhynchus violaceus*) males place colored decorations on their bower platform as part of their courtship display. Little is known about how illumination affects the attractiveness of decorations. We analyzed photographs to quantify the amount of direct illumination on the bower and the number of blue decorations in sunlight. We found that the proportion of sunlight on the entire bower platform during peak female visitation periods is correlated with male mating success. The North platform, where decorations are concentrated, was proportionately more illuminated than the South platform. Males placed decorations in more sunlit areas on the platform and returned moved blue decorations to their original locations, suggesting that males actively place blue decorations in sunlit areas. This is the first study to demonstrate that greater illumination in off-body displays may be important for attracting females.

THE EFFECT OF SUNLIGHT ON DECORATION PLACEMENT AND MATING SUCCESS IN MALE SATIN BOWERBIRDS

By

Archer Freni Larned

Thesis 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
Master of Science
2012

Advisory Committee:
Professor Gerald Borgia, Chair
Professor Eric Haag
Professor Marjorie Reaka

Dedication

This thesis is dedicated in memory of my sister, Jen, who always believed in me and loved hearing about my work with bowerbirds

Acknowledgements

I would like to thank my advisor, Dr. Gerald Borgia, for his guidance and assistance throughout my thesis research. A special thanks to Jason Keagy and Jean-Francois Savard for their insight and for collecting some of the field data. I would like to thank past and present Borgia lab members for their comments and support during the thesis writing process: Brian Coyle, Stephanie Kriston, Reimi Hicks, and Josh Kiner. Thanks also to my committee members for their time and comments.

Many thanks to all the hard working undergraduate video assistants and the field assistants for their hours spent watching videos and assisting in data collection. Thanks to the Bell, Mulcahy, Veneris and Kennedy families for their hospitality and assistance in Australia. Thanks also to the Biology Department office staff for their logistical help. Last, but not least I wish to thank my friends and family for all their support and guidance during my thesis research at the University of Maryland.

I wish to also extend a huge thanks to my Aunt Gretchen for her support and assistance during this degree process, to which I am eternally grateful.

This work was funded by NSF grants to Dr. Gerald Borgia

Table of Contents

List of Tables

Table Number **Page**

List of Figures

Figure Number **Page**

INTRODUCTION

Visual signals in most organisms require illumination in order to communicate information. The brightly colored plumage of many bird species is an example of a visual signal used during courtship by males in sexually dimorphic species to attract females. In order for this visual signal to function, the receiver needs to be able to distinguish the signal from background noise (Hailman 1977). The sender can increase the likelihood that the signal is perceived by increasing the conspicuousness of the visual signal (Hailman 1977). The ambient light environment is one way in which the conspicuousness of a male's display can be altered (Endler 1993, Thery 2001). Plumage coloration used during displays can be perceived differently depending on the available light (Hailman 1977).

Courtship displays can be temporally or behaviorally altered to ensure that favorable lighting conditions are achieved to highlight visual signals (Endler 1993, McNaught and Owens 2002). In open, sunny areas long distance signaling can be enhanced when viewed against a darker background (Olea 2010). Animals with dark visual signals are more conspicuous and therefore more easily detected by conspecifics when displaying against a sunlit background, instead of dark shadows where the signal cannot be distinguished (Uetz 2007). Another way to increase conspicuousness of a color signal is to create uniformity of color and patterns in the background to contrast with the visual signal (Uy and Endler 2004). Golden-collared manakins remove leaf litter below their display perch so that the ground is uniform in color, which increases the color contrast and thereby conspicuousness of the visual signal (Uy and Endler 2004, see also Endler et al. 2005).

Animals with semi-permanent display areas, such as lekking bird species, can modify their courtship display behavior to increase signal efficacy to take advantage of a particular light environment (Thèry and Vehrencamp 1995, Endler and Thèry 1996, Heindl and Winkler 2003, Uy and Endler 2004). Thèry and Vehrencamp (1995) found that lekking white-throated manakins show preferences for display sites that are sunlit, which enhances the contrast between the white and darker blue plumage. Male manakins received a higher rate of female visits when the sun was the most intense at their display site and the males displayed more frequently in sunny gaps when the sun was visible compared to when it was obscured by clouds (Thèry and Vehrencamp 1995). Heindl and Winkler (2003) also found that other manakin species displayed in sunlight and/or shade to enhance the contrast of their color patches.

Males also orient parts of their body towards the sun during courtship displays to illuminate plumage and increase conspicuousness (Dakin and Montgomerie 2009). Birds with white in their plumage have been found to orient their bodies to face the sun to enhance sunlight reflecting off their plumage for signaling (Penteriani and Delgado 2009, Bortolotti et al 2011). These examples all suggest that males use sunlight to enhance the visual aspects of their plumage displays. Most male bowerbird species use off-body decoration items on their display courts and it has not been determined if illumination of their display is important in attracting females.

Satin bowerbirds are lek-like species that are found along the eastern coast of Australia (Gould 1848, Cooper and Forshaw 1977). The satin bowerbird habitat includes rainforest edges and eucalyptus dominated sclerophyll forest along the eastern coast of Australia, which allows for canopy gaps and sunlight to reach the forest floor. Male satin

bowerbirds have complex, multi-faceted displays consisting of vocalizations, coordinated movements, construction of a bower and collected bower decorations (Gould 1848, Marshall 1954, Vellenga 1970, Borgia 1985). The male builds his bower upon a platform of gathered sticks during the breeding season. The bower itself is a stick structure consisting of two walls with an avenue, where the female stands while she watches the male perform his courtship display (Marshall 1954, Gilliard 1969). Male bowerbirds decorate the bower platform with a layer of yellow straw and/or leaves upon which are placed numerous objects, that are predominantly blue and yellow, including: blue feathers (primarily *Platycercus elegans* and *Platycercus eximius*), white and brown land snail shells, cicada exuviae, blue and yellow flowers, blue, purple, and green berries, dead spiders (*Sparassidae* family), yellow/green lichen and snake skin (Marshall 1954, Gilliard 1969, Vellenga 1970), and appropriately colored man-made objects. The avenue of the bower has a North-South orientation, with nearly all of the decorations on the north side of the bower platform (Chaffer 1931, Marshall 1932, 1954).

The number of blue feathers that a male satin bowerbird uses on his bower platform consistently correlates with mating success (Borgia and Gore 1986, Patricelli et al 2004, Coleman et al. 2004). The decoration types and color preferences have been studied (Morrison-Scott 1937, Borgia 1985, 1987, Borgia 2006, Wojcieszek et al. 2006), but not the placement of the decorations or ambient light illumination of the platform. Marshall (1954) hypothesized that the North-South orientation of the bower is to increase sunlight on the male bowerbirds' display during courtships and to avoid having the female stare directly into the sun during early morning courtships. Males remove leaves from vegetation above and around the bower indicating manipulation of vegetation for

favorable lighting conditions on the bower (Borgia 1986). Doucet and Montgomerie (2003) found that a northern subspecies of the satin bowerbird, which resides in dense, tropical rainforest in more northern latitudes, showed no consistent North- South orientation for 12 bowers, but bower sites were located in the light gaps.

In this study we tested four hypotheses to determine the effect of illumination on mating success and decoration placement. The first hypothesis is that male satin bowerbirds with a greater proportion of the bower platform in sunlight during peak female visitation times have higher mating success. This hypothesis tests the idea that lighting of the bower is important for attracting females. Gould and Gould (1989) stated that bowers in sunlit areas of the forest appeared much more visible. The second hypothesis is that males will have a greater proportion of sunlight on the North bower platform, where the decorations are concentrated, than on the South bower platform during peak female visitation times. Given that the sun shines on the north side of the bower because of the location in the southern hemisphere, this might seem a trivial hypothesis, but it is important to test for several reasons. First, in the early morning, when courtships and copulations peak, the sun is relatively low in the sky and thus the amount of light on different parts of the bower are highly dependent on the level of shading by the surrounding vegetation, so it is not necessarily true that there will be more light on the North bower platform. Second, this hypothesis tests the idea that birds are orienting bowers to capture light where they place decorations to attract females. The third hypothesis is that males place their blue decorations in areas on their bower platform that have the most sunlight during peak female visitation times. We expect to find more blue decorations in sunlight than in shade during peak female visitation times. The fourth

hypothesis is that male satin bowerbirds have preferred locations on their bower platforms for their blue decorations. By experimentally moving decorations we tested this hypothesis. We also tested a possible alternative hypothesis that the sunlight on the bower platform is to illuminate the male's plumage while displaying.

METHODS

Banding and Video Monitoring

This research was conducted at Wallaby Creek, Tooloom National Park, NSW, Australia (28° 28' S, 152° 25' E). Satin bowerbirds of both sexes were banded with a unique color combination made up of three different color bands and one metal band with a unique number supplied by the Australian Bird and Bat Banding Scheme, authority number 946 (G.B.).

Throughout peak breeding season, from 5 November to 20 December 2003, we collected data at 36 bowers and monitored all courtship behavior. Automated infrared sensor camera systems with custom-built omnidirectional microphones were set up on all bowers to record all activity when a bird is present (see Borgia 1995 for more detail). This enables us to accurately assess the male mating success and to identify birds that visit each bower (Reynolds et al. 2007). Camera systems were checked twice daily to ensure proper camera and tape functioning. Bower quality and decoration counts were assessed daily and bower measurements were taken weekly (see Borgia 1985 for more detail). Mating success was found to be a good indicator of reproductive success because females typically mate with a single male in a mating season (Reynolds et al. 2007).

Measuring proportion of sunlight on the bower and mating success

We used overhead photos of 28 bowers taken with digital cameras (Minolta DiMAGE 7, 5.1 megapixel) mounted 2 meters above the bowers in order to image the entire bower platform and some of the surrounding area. This was done from 16 November to 12 December 2003. The cameras were set to automatically take photos every 15 minutes from sunrise to sunset and cameras were only run on days with full sun. The sunrise was at 0549 hours on 16 November and 0546 hours on 12 December and the sunset at 1921 hours and 1941 hours (Australian Eastern Daylight Time). The peak time during the breeding season for all copulations, courtships and female visits is between 08:00 and 09:00. These photos were also used in analysis of the blue decoration location experiment and in comparing sunlight on the North and South bower platform.

To test the first hypothesis, measurement of the area of direct sunlight on the bower platform was analyzed using ImageJ (versions 1.44j- 1.46k, Rasband 1997-2012). The photos were scaled by inserting screws into the bower platform. We then measured the distance between the screws. The total bower platform (including vertical bower structure) was outlined in the photos by locating the edge of the straw and collected sticks that define the edge of the bower platform. Photos were changed to 8-bit grey-scale and all pixels above a predetermined threshold were selected to measure the area of direct sunlight on the bower platform. The threshold value was selected using an algorithm preprogrammed in ImageJ to separate pixels that appeared to be in full sunlight.

Spearman rank correlations were computed in R (version 2.14.2) to test the relationship between the proportion of his bower in sunlight and the number of courtships, copulations or female visits a male receives. The amount of sunlight was

averaged for the 8 photos taken during the 2-hour time period from 08:00 to10:00 (AEDT).

In order to separate visits by females from those of juvenile males only color-banded females where sex was determined by plumage from banding records or from behavior from videotapes were used in assessing the number of females visiting the bower. Female visits refer to a visit to the bower by the female when the male is not present. Courtships refer to female visits when a male courts her and no copulation takes place. Copulations are courtships of a female by a male that end in copulation.

Measuring sunlight on north versus south bower platform

Overhead photos were also used to compare light on the front (North) and back (South) bower platform in order to test the second hypothesis. The front court is defined as the area to the North of the bower walls, where the male places nearly all of the yellow straw and decorations, and this is also where the male displays during courtships. The back platform is the area behind the bower, where less display occurs and provides a control area for the front platform to compare for level of illumination. The area of sunlight was measured as described above for both the front and back platforms.

Blue decoration location experiment

In order to test the hypothesis that males place blue decorations in well-illuminated areas males were offered ten blue plastic squares (2.54cm X 2.54cm) that they could move onto their bower platform. The squares were placed 50cm off the bower platform where they would be visible to the male near his bower. Digital photos were

taken every 15 minutes during this time to determine when and where males placed decorations moved from their original location to the bower platform, and the extent to which these positions were well illuminated.

We counted squares as illuminated by sunlight if 50% or more of the square was in sunlight. The observed number of squares in sunlight was averaged for the 8 photos during a 2-hour period. This was calculated for the morning from 08:00 to 10:00 (AEDT), which is the peak period for female visits, courtships and copulations. Only blue squares on the bower platform were counted, excluding blue squares off the bower platform that the males didn't move or use. The proportion of the North bower platform in sunlight was used to determine the expected proportion of blue squares to be found in sunlight on the bower platform. The observed and expected values were compared using a Wilcoxon signed rank test performed in R (version 2.14.2).

Moving blue decorations experiment

Blue decorations were experimentally moved to alternative positions that were less illuminated on experimental bowers (N=13) to test male response. Control bowers (N=15) had their decorations picked up and returned to the same place so that they were disturbed, but decoration position was not changed. This experiment was conducted in 2009 from 28 November to 14 December. The treatment bowers and their controls were paired based on an averaged number of decorations and bower quality, which were recorded daily over a four-day period prior to the start of the experiment. We randomly assigned one bower of each pair to experimental and control groups. For the treatment bowers, we moved their blue decorations from one side of the front of the bower platform

to the other. The bower platform was bisected using a meter stick that was placed through the bower avenue to serve as the north-south axis, over which decorations were moved laterally to an equal distance on the other side and mapped to the nearest centimeter. Most decorations were on the west side and were moved to the east. 16 bower pairs were originally selected, but 3 were excluded due to a lack of decorations or destruction of the bower.

The decorations on experimental bowers were classified as "returned" if they were moved by the male from where we had moved them to the side of where they were originally located. The bowers were checked twice for decoration movement, initially 4 hours after the decorations were experimentally moved and again after 8 hours. Overhead photos and videos were reviewed to confirm that the bower owner, and not another male, moved the decorations.

Measuring male display area

An alternative hypothesis to the decoration illumination hypothesis is that the bower is oriented and illuminated to highlight male plumage. We tested this hypothesis by measuring the proportion of sunlight in the location where the male displays relative to the entire North bower platform. We identified a rectangular area in front of the bower that approximated the location where males perform the majority of their courtship display. We determined this by viewing overhead recordings of courtships. The proportion of sunlight in this courtship area was assessed and compared to sunlight on other parts of the front platform as previously mentioned using ImageJ. All statistical tests are two-tailed.

RESULTS

Measuring proportion of sunlight on the bower and mating success

A significant correlation was found between the percentage of the bower that is sunlit and the number of copulations between 08:00-10:00 (Spearman rank correlation, two-tailed: r_s=0.4807, P=0.027, N= 21), but not for courtships (r_s=0.334, P=0.12, N=21) or female visits (r_s=0.3597, P= 0.10, N=21**)** (Figure 1). There was no significant correlation between the percentage of the front (North) bower platform that is sunlit and the number of copulations at 08:00-10:00 (r_s=0.221, P=0.33, N=21), courtships (r_s=0.201, P=0.41, N=21), or female visits (r_s=0.16, P=0.28, N=21).

Measuring proportion of sunlight on North versus South bower platform

From 08:00-10:00, there is a significantly higher proportion of direct sunlight on the front (North) bower platform than on the back (South) bower platform (V= 202, P= 0.0016, mean front= 23.8%, mean back= 15.2%, N= 22).

Blue decoration location experiment

More blue squares were found to be illuminated on the bower platform than expected by chance (V=172, P=0.05, n=22) during the period from 08:00-10:00. This supports the hypothesis that birds are seeking well-lit areas of the bower platform to place their decorations.

Moving blue decorations experiment

We tested the hypothesis that males place blue feathers at particular positions on the bowers. Our test was to move decorations in the experimental group across the North-South midline of the North bower platform to a position of equal distance from the midline. The control decorations were picked up by assistants, but not moved. Of the original 13 bowers selected for the experiment treatment, we were able to score 6 bowers. Among the 6 experimental bower owning males that were included, five males moved their blue decoration items close to their original location across the midline and one male didn't return his feathers to their original location across the midline. Six bowers were excluded from the experimental group because: 1) The male did not return to the bower during the experiment (n=2), 2) feathers were stolen before they could be moved (n=2), and 3) juveniles used decorations for display before the male returned (n=2). For the 7 control bowers, five males did not move their blue feathers across the midline and if picked up returned them to the same location, and in the two cases that were excluded the feathers were stolen (P=0.015, Fisher's exact test)(Table II.). This indicates that males tend to prefer to have decorations on particular places on their bower.

Male display area

We found no significant relationship between the area of illumination of the male courtship display area and illumination on the front bower platform (V=166, P=0.21, N=22). This does not support the alternative hypothesis that the area where males display has a significantly higher level of illumination.

DISCUSSION

We investigated male satin bowerbirds' use of sunlight to illuminate their bower and blue decorations on their bower platform. We tested four hypotheses and the results show positive support for all of them. We found that the male satin bowerbirds that have a greater proportion of sunlight on their entire bower court during the period of high female visitation have a higher number of copulations during that time. There is a higher proportion of sunlight on the north bower platform, where the decorations are concentrated, as compared to the south bower platform, supporting the hypothesis that bowers are constructed to illuminate decorations. Males also place their blue decorations in the sunlight more than expected, consistent with the hypothesis that they are using sunlight to illuminate these decorations. Finally, in experiments in which blue decorations are moved to the opposite side of their bower platform, males attending the bower consistently return them to their original position, suggesting that the location of decorations is important to the male.

While there has been evidence of the use of sunlight to enhance plumage display (Théry and Vehrencamp 1995, Endler and Théry 1996, Heindl and Winkler 2003, Dakin and Montgomerie 2009) in other bird species, this is the first demonstration of the use of light to enhance off-body displays in any species. Satin bowerbirds appear to use illumination of display site and display objects as a way to increase the conspicuousness of their off-body display. Several other papers have addressed the conspicuousness of bowers and decorations (Borgia and Gore 1986, Borgia et al. 1987, Endler et al. 2005), but not specifically the degree to which bowers and decorations are in direct sunlight.

To determine if there is a relationship between the proportion of the entire bower court in sunlight and mating success, we measured the area of sunlight on the bower platform. We found a positive correlation between the number of copulations and the proportion of the entire bower court in direct sunlight at periods of high female visitation. The peak time for all female satin bowerbird visits, courtships and copulations at males' bowers correspond to the time when sunlight initially hits the forest floor, several hours after sunrise. This suggests that successful male satin bowerbirds select and/or modify bower sites so that they have increased amounts of sunlight during these peak female visitation times. Females may be more attracted to more illuminated decorations or it may simply make bowers easier to locate (Borgia et al. 1987). Gould and Gould (1989) noted that the yellow straw on which the blue decorations are placed also appears brighter when in sunlight and increases the conspicuousness by augmenting the contrast between the yellow straw and the dark leaf litter surrounding the bower.

We found that there is a significantly greater proportion of the North side of the bower platform in sunlight than the South side during peak female visitation times. Several authors have speculated that satin bowerbirds orient their bowers North to South to enhance illumination of the bower platform where males court females and place the majority of their decorations (Marshall 1954, Vellenga 1970, Borgia 1985, Doucet and Montgomery 2003), but this has not previously been rigorously tested. The results from this study suggest that males build bowers in a location that allows for effective lighting on the North portion of his bower platform during times when the female is most actively sampling males. The satin bowerbirds live in the southern hemisphere, so the North-

South orientation of the bower might also allow the decorated portion of the platform to remain favorably lit throughout the day.

We also found that the blue squares moved onto the bower platform by the male were in sunlight significantly more often than expected by chance. The blue squares were placed off the bower platform, so that the male could place them where he chose on the bower platform. The result that the blue squares are placed in the sun during the morning, when there is the highest frequency of courtships and copulations, suggests that it is important to illuminate decorations to attract females. The number of blue feathers has previously been shown to have significance for male mating success (Borgia 1985, Patricelli et al. 2004, Coleman et al. 2004), but here we suggest that the placement in sunlight is also important for mating success.

When we moved males' own natural blue decorations from one side of the bower platform across a north-south axis line to the opposite side, the males moved them back near their original location. Given that males consistently place decorations in sunlight and return them to their original positions on bowers suggests that there are areas on the bower platform that are well illuminated that males prefer to display their decorations.

An alternative hypothesis is that the bower is oriented and positioned so that the male's plumage, instead of his decorations, is highlighted by sunlight. We found that in the area in front of the bower on the North court, where the male displays from, there was no enhanced illumination relative to the other parts of the male's North platform. Thus the hypothesis that bower orientation is primarily related to illuminating the displaying male's plumage was not supported by our data. Perhaps a more rigorous study of the effect of direct illumination of male plumage may show an effect that we did not detect.

CONCLUSIONS

1) Male satin bowerbirds that have greater illumination of their entire bower platform receive a higher number of copulations.

2) Male satin bowerbirds have more sunlight on the North side of the bower platform as compared to the South side.

3) Male satin bowerbirds have more blue squares in sunlight than expected by chance.

4) Male satin bowerbirds prefer to place decoration at consistent locations on the bower platform. Generally, light appears to have an important role in affecting design and placement of off-body displays in satin bowerbirds.

TABLE CAPTION

Table I. Spearman correlations between the proportion of sunlight on the entire bower platform and mating success variables. Significant for copulations at $\alpha = 0.05$.

Table II. Fisher's exact test matrix showing the number of males that moved their decoration to the opposite side of the bower platform. "Moved" and "not moved" refer to the number of males who moved their decorations during the blue decoration movement experiment. ($P = 0.015$)

TABLES

Table I.

Mating success variables	N=21
Number of copulations	$\mathbf{r_s}$= 0.481 **P**= 0.027
Number of courtships	$\mathbf{r_s}$= 0.334 **P**= 0.122
Number of female visits	$\mathbf{r_s}$= 0.361 **P**= 0.100

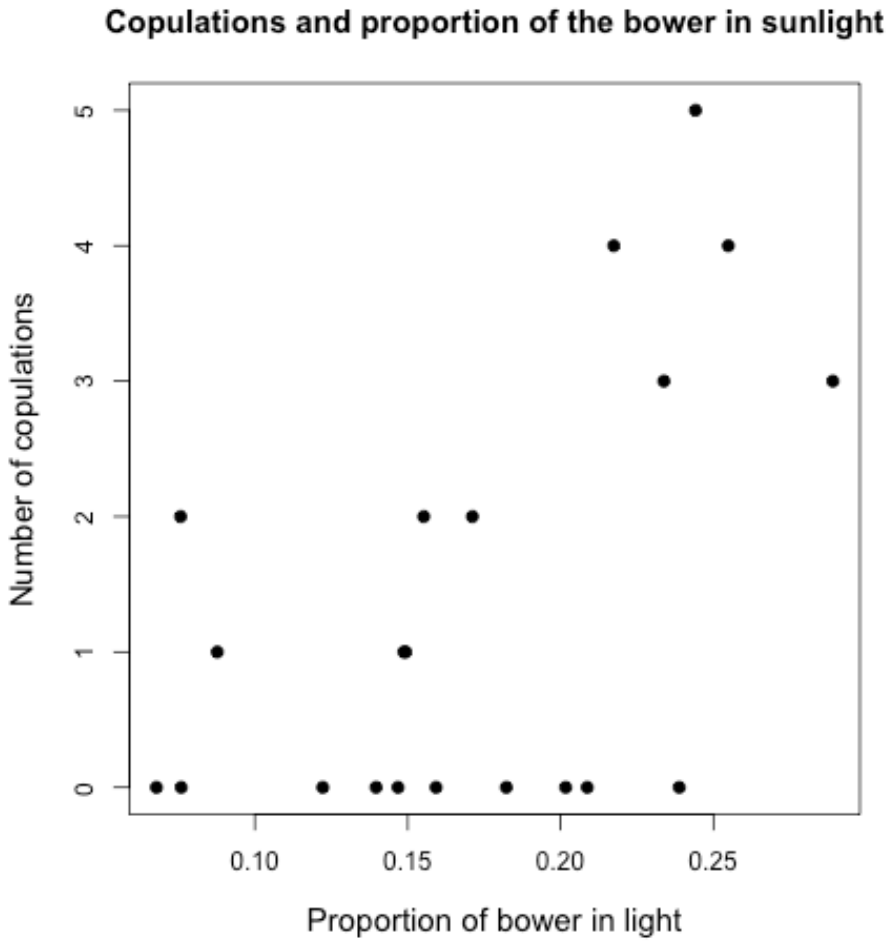
Table II.

	Moved	**Not moved**
Experimental	5	1
Control	0	5

FIGURE CAPTION

FIGURE 1. Relationship between the proportion of the entire bower platform in sunlight and copulations. The proportion of the entire bower platform in sunlight at 08:00-10:00 and copulations during that time (r_s= 0.481, P= 0.027, N= 21; Significant at α=0.05).

Figure 1.


Copulations and proportion of the bower in sunlight
Number of copulations
0
1
2
3
4
5
0.10
0.15
0.20
0.25
Proportion of bower in light

REFERENCES

Borgia, G. 1985. Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behaviour* 33(1): 266-271

Borgia, G., Gore, M.1986. Feather stealing in the satin bowerbird (*Ptilonorhynchus violaceus*): male competition and the quality of display. *Animal Behaviour* 34(3): 727-738

Borgia, G., Kaatz, I.M., Condit, R. 1987. Flower choice and bower decoration in the satin bowerbird *Ptilonorhynchus violaceus*: a test of hypotheses for evolution of male display. *Animal Behaviour* 35(4): 1129-1139

Borgia, G. 1995. Threat reduction as a cause of differences in bower architecture, bower decoration and male display in two closely related bowerbirds *Chlamydera nuchalis* and *C. maculata*. *Emu* 95: 1-12

Borgia, G., Keagy, J. 2006. An inverse relationship between decoration and food colour preferences in satin bowerbirds does not support the sensory drive hypothesis. *Animal Behaviour* 72: 1125-1133

Bortolotti, G.R., Stoffel, M.J., Galvan, I. 2011. Wintering snow owls *Bubo scandiacus* integrate plumage colour, behavior and their environment to maximize efficacy of visual displays. *Ibis* 153: 134-142

Chaffer, N. 1931. The satin birds of National Park, NSW. *Emu* 30: 277-285

Coleman, S.W., Patricelli, G., Borgia, G. 2004. Variable female preferences drive complex male displays. *Nature* 428: 742-745

Cooper, W., Forshaw, J. 1977. The birds-of-paradise and bowerbirds. Collins Press: Sydney

Dakin, R., Montgomerie, R. 2009. Peacocks orient their courtship displays to the sun. *Behavioral Ecology Sociobiology* 63: 825-834

Doucet, S.M., Montgomerie, R. 2003. Bower location and orientation in Satin Bowerbirds: optimising the conspicuousness of male display? Emu 103(2): 105-109
Endler, J.A. 1993. The color of light in forests and its implications. *Ecological Monographs* 63(1): 2-27

Endler, J.A., Thery, M. 1996. Effects of lek placement, display behavior, ambient light, and color patterns in three Neotropical forest-dwelling birds. *The American Naturalist* 148, 3: 421-452

Endler, J.A., Westcott, D.A., Madden, J.R., Robson, T. 2005. Processing illuminates signal evolution animal visual systems and the evolution of color patterns; sensory processing illuminates signal evolution. *Evolution* 59(8): 1795-1818

Gilliard, E.T. 1969. Birds of paradise and bowerbirds. Weidenfeld and Nicholson, London

Gould, J. 1848. The birds of Australia. Vol. 4. J. Murray, London

Gould, J.L., Gould, C.G. Sexual Selection. Scientific American Library, New York. 1989

Hailman, J.P. 1977. 'Optical Signals: Animal communication and light.' Indiana University Press: Bloomington & London

Heindl, M., Winkler, H. 2003. Vertical lek placement of forest-dwelling manakin species (Aves, Pipridae) is associated with vertical gradients of ambient light. *Biological Journal of the Linnaean Society* 80: 647-658

Heindl, M., Winkler, H. 2003. Interacting effects of ambient light and plumage colors patterns in displaying wire-tailed manakins (Aves, Pipridae). *Behavioral Ecology Sociobiology* 53: 153-162

Marshall, A.J. 1954. Bower-birds: their displays and breeding cycles. Clarendon Press, Oxford

Marshall, A.J. 1932. Notes on the Satin Bower-bird. Emu 32(1): 33-38

McNaught, M.K., Owens, I.P.F. 2002. Interspecific variation in plumage colour among birds: species recognition or light environment? *J. Evolutionary Biology* 15: 505-514

Morrison-Scott, T. 1937. Experiments with colour vision in the satin bower-bird (*Ptilonorhynchus violaceus*), with other observations. *Proc. Zoological Society* 107(1): 41-49

Olea, P.P, Casas, F., Redpath, S., Vinuela, J. 2010. Bottoms up: great bustards use the sun to maximise signal efficacy. *Behavioral Ecology and Sociobiology* 64(6): 927-937

Patricelli, G.L., Uy, J.A.C., Borgia, G. 2004. Female signals enhance the efficiency of mate assessment in satin bower-birds (*Ptilonorhynchus violaceus*). *Behavioral Ecology* 15(2): 297-304

Penteriani, V., Delgado, M. del Mar. 2009. The dusk chorus from an owl perspective: eagle owls vocalize when their white throat badge contrasts most. *PLoS ONE* 4(4): e4960

Reynolds, S.M., Dryer, K., Bollback, J., Uy, J.A.C., Patricelli, G.L., Robson, T., Borgia, G., Braun, M.J. 2007. Behavioural paternity predicts genetic paternity in satin bowerbirds (*Ptilonorhynchus violaceus*), a species with non-resource-based mating system. *The Auk* 124: 857-867

Thery, M., Vehrencamp, S.L. 1995. Light patterns for cues for mate choice in the lekking white-throated manakin (*Corapipo gutturalis*). *The Auk* 112, 1: 133-145

Thery, M. 2001. Forest light and its influence on habitat selection. *Plant Ecology* 153: 251-261

Uetz, G.W., Clark, D.L., Roberts, J.A. 2011. Effect of visual background complexity and light level on the detection of visual signals of male *Schizocosa ocreata* wolf spiders by female conspecifics. *Behavioral Ecology and Sociobiology* 65:753-761

Uy, J.A.C., Endler, J.A. 2004. Modification of the visual background increases the conspicuousness of golden-collared manakin displays. *Behavioral Ecology* 15, 6: 1003-1010

Vellenga, R. 1970. Behavior of the male satin bower-bird at the bower. *Austral. Bird Bander* 1: 3-11

Wojcieszek, J.M., Nicholls, J.A., Marshall, N.J., Goldizen, A.W. 2006. Theft of bower decorations among satin bowerbirds (*Ptilonorhynchus violaceus*): why are some decorations more popular than others? *Emu* 106(3): 175-180