

Experimental blocking of UV reflectance does not influence use of off-body display elements by satin bowerbirds

Gerald Borgia

Department of Biology and Behavior, Ecology, Evolution and Systematics Program, University of Maryland, College Park, MD 20742, USA

UV reflectance of plumage display is important in mate choice of many avian species, but its role in off-body display has received little consideration. Male satin bowerbirds (*Ptilonorhynchus violaceus*) collect objects for use as bower decorations. Here, I test the hypothesis that UV and non-UV colors are important in choice of satin bowerbird bower decorations (colored squares and blue parrot feathers) in an experiment using UV blocking agents at the bowers of 31 males. I found a highly significant preference for blue decorations but no evidence of a preference for UV-reflecting decorations. UV-blocked blue objects were used to the same extent as identical unblocked decorations, and UV-reflecting decorations that were not blue were not attractive. The evolution of off-body decoration displays may have contributed to a reduced role for UV-reflecting decoration displays in satin bowerbirds in 3 ways: 1) use of UV-reflecting display objects that are not made by the bird does not directly signal their owners' condition as would the birds own plumage, 2) because of the relatively low level of ambient UV light available to illuminate decorations displayed on a court the forest floor, UV may be less effective than other wavelengths for these displays, and 3) decorations that are both blue and UV reflective may be too rare under natural conditions to be effective signals of male quality. Off-body displays may provide very different kinds of information from plumage displays, and these differences may have contributed to the evolution of complex multicomponent displays. *Key words:* bowerbird, sexual display, UV reflectance. [*Behav Ecol*]

The color of male display traits is a key feature in mate choice in a large number of species (e.g., Houde 1997). Recently, UV reflectance of plumage has been implicated in mate choice in many avian species (e.g., Bennett et al. 1996, 1997; Andersson and Amundsen 1997; Andersson et al. 1998; Hunt et al. 1998, 1999; Johnsen et al. 1998; Pearn et al. 2001; Arnold et al. 2002; Hausmann et al. 2003; Korsten et al. 2006), but in other species its importance is less apparent (e.g., Hunt et al. 2001). In satin bowerbirds, an important component of male display involves bower decorations that are collected from the habitat by males (often stolen from other bowers, see Borgia and Gore 1986) and displayed on the bower platform where males display to females. Male bowerbirds use both natural objects (e.g., blue crimson rosella, *Platycercus elegans*, feathers; blue flowers and fruit; yellow leaves; yellow flowers; brown cicadae exuviae; and bleached white snail shells and bones) and man-made objects (e.g., blue plastic) as bower decorations (Marshall 1954; Borgia 1985; Borgia et al. 1987; Wojcieszek et al. 2006) and these decorations reflect UV to varying extents (all colors unless designated as UV are colors in the human visible range). There have been many studies of non-UV decoration color preferences by experimental manipulation of decorations on bowers (Morrison-Scott 1937; Marshall 1954; Chaffer 1984; Diamond 1986; Borgia et al. 1987; Borgia 1993; Borgia and Keagy 2006; Coleman and Borgia 2004; Endler and Day 2006; Uy and Borgia 2000) suggesting that males of different species have particular decoration color preferences.

In a recent survey of 108 species, Hausman et al. (2002; see also Eaton and Lanyon 2003) found that UV reflectance

in plumage was commonly associated with traits used in male display, and they concluded that use in display has favored the evolution of these display elements. They review several hypotheses that may explain why UV is commonly incorporated into male courtship displays: 1) UV displays may be more effectively directed at nearby intended receivers while remaining obscure to distant eavesdroppers because of particle scattering over long distances (Lythgoe 1979; Andersson 1996). 2) Displaying in the UV spectral range may not be seen by potential predators, thus lowering risks to displaying males (Jacobs 1993; Silbergeld 1977; Guilford and Harvey 1998). 3) UV reflectance of male plumage may be a condition-dependent indicator of male quality because structural colors are unusually good indicators of feather age or feather quality (Prum et al. 1994; Fitzpatrick 1998; Andersson 1999; Keyser and Hill 1999, 2000; Prum 1999; Doucet 2002). 4) UV signals may be favored because they contrast strongly with background foliage that absorbs UV wavelengths of light (Andersson et al. 1998). 5) UV signals may act as "amplifiers" of behavior that allows recipients of display to better assess differences in the dynamic aspects of male courtship display. 6) UV signals may have evolved via "sensory exploitation" to utilize a possible preexisting avian preference for UV signals that may result from their relatively high sensitivity to UV wavelengths of light (Burkhardt and Maier 1989).

Bower decoration displays differ from male plumage displays in several important respects that make a test of preferences for UV reflectance of bower decorations of special interest. Bowerbird decoration display is disassociated from the plumage of the displaying male and, consequently, several of the above arguments may not apply to the choice of bower decorations. For instance, bright bower decoration displays may incur a lowered predation risk to displaying males than similarly bright plumage displays in other species (see Gilliard 1969). Thus, males displaying decorations may be less likely to benefit from a "private channel" or lowered long-distance detectability that

Address correspondence to: Gerald Borgia. E-mail: Borgia@umd.edu.

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reduces the visibility of bright males to predators. Also, because the fine structure of decorations such as parrot feathers used as decorations is not produced nor maintained (e.g., preened) by the male displaying them, they may be less effective indicators of male quality than personal plumage traits (Shawkey et al. 2007). Bower decorations are displayed primarily on the ground on mats of dead yellow leaves, which, unlike UV-absorbing living plant leaves, are unlikely to produce high brightness contrast with UV-reflecting display elements, although there may be greater color contrast (Andersson et al. 1998). Males use a subset of decorations in beak displays that may serve as amplifiers that enhance differences in male motion. Thus, among the above hypotheses, only amplification of dynamic displays and a preexisting preference for UV-reflecting decorations caused by sensory exploitation might explain a preference for UV-reflecting decorations. A sensory drive hypothesis that the high visibility of UV makes decorations more noticeable and advertises them more effectively is also possible.

In the only investigation of UV in bowerbird plumage display, Doucet and Montgomerie (2003), studying the northern subspecies of satin bowerbird (*Ptilonorhynchus violaceus minor*), explored the association between UV reflectance and traits used in mate choice. They found a correlation between their estimates of bower quality and bower decoration with a complex variable that included overall plumage brightness, contrast (they measure as the difference between the maximum and minimum reflectance across the 300- to 700-nm range), and UV-Violet chroma of male plumage. UV chroma was the third most important variable in their principal components measure and did not, by itself, correlate with either of the 2 dependent variables. Also, they found a correlation between UV brightness and blood parasite load. However, because there was less than 10% peak UV reflectance, which is below what is typically found for UV reflecting display traits (e.g., Hausmann et al. 2003; Hofmann et al. 2006) and because none of these variables was related to female choice, we do not know if UV plumage reflectance is used in satin bowerbird mate choice.

Bower decorations provide an alternative opportunity to assess the role of UV reflectance in satin bowerbird mate choice. Advantages of studying bower decoration are 1) the number of blue decorations is known to affect male attractiveness (Borgia 1985; Patricelli et al. 2003; Coleman and Borgia 2004), 2) male decoration color preferences are easily measured at the bower, 3) the reflectance spectra of objects that may be used as decorations can be experimentally manipulated by using UV blocking agents (Andersson and Amundsen 1987), and 4) decorations commonly used by satin bowerbirds reflect UV, so it is possible that UV reflectance affects satin bowerbird decoration preferences. Two recent studies found a high level of UV reflectance by some blue decorations used by satin bowerbirds (Mullen 2006; Wojcieszek et al. 2006), but it is unclear if these decorations were selected because of their UV reflectance or because they were blue and the observed UV reflectance is a side effect resulting from relatively broad short wavelength reflectance of these objects.

I conducted 2 experiments to test the general hypothesis that UV reflectance is important in male satin bowerbird decoration choice. This involved offering UV reflecting colored poster board squares and crimson rosella feathers in which paired decorations were treated with either UV block or a similar control UV-transparent coating painted on objects offered as bower decorations. For both experiments, I predicted that UV-blocked objects should be less preferred than otherwise identical potential decorations with a UV-transparent coating if there is a preference for UV-reflecting decorations. I also predicted for the first experiment that if UV reflectance was

important, then decorations with high UV chroma (% reflectance in the UV range) should be preferred and that those with the highest absolute UV reflectance should be favored over those with less UV reflectance.

METHODS

This decoration preference study was conducted on a natural population of satin bowerbirds in September and October in 1998, at Wallaby Creek, New South Wales, Australia (28°28' S, 152°26' E). Decorations were offered at bowers owned by a single mature male. All males were individually banded (see Borgia 1985), and our observations showed that the males moving colored objects in these 2 experiments were the bower owners.

Colored square experiment

I used 2 colored squares (2.5 × 2.5 cm) with the same color on both sides cut from 11 different colors of poster board. These squares were assigned to 2 treatment groups for a total of 22 colored squares offered to each male. The colors of squares used were violet (118,66,148), royal blue (65,76,142), turquoise (79,200,219), sky blue (188,216,228), light green (176,214,95), yellow (252,246,134), orange (247,204,40), brown (163, 127, 113), silver (152,168,201), ivory (251,247,220), and off white (248,246,233) (numbers after each color are the RGB color code from colors in sunlight that is the best match with the Munsell color chart at: www.triplecode.com/munsell/, reflectance data provided on request). I limited this experiment to 22 squares so that males would not be overwhelmed by the presentation of decorations and thus possibly make erroneous choices that did not represent the bird's true preferences. Because of this limit on the number of colors, I used information from past color preference trials and UV reflectance in guiding our choice for the limited set of colors to be used (e.g., Borgia et al. 1987). I biased the sample with colors that reflected short visible wavelengths because the peak reflectance curve for these colors extended into the UV and because satin bowerbirds are known to like blue. I used squares of several other colors from across the spectrum (but excluded red because of a known dislike for this color [e.g., Borgia et al. 1987]) to compare their usage against violet/blue squares. Additionally, I included 3 colors (sky blue, ivory, and silver) that were chosen because of their high UV reflectance with the expectation that if UV were critical in decoration choice, then UV-unblocked (UV+) but not UV-blocked (UV-) squares would be preferred for these colors. On natural bowers, satin bowerbirds use white sun-bleached snail shells that have a high broadband UV reflectance that was similar to that seen in reflectance measures of the ivory and silver squares.

All spectral measurements were made relative to a white "Spectralon" cube using an Ocean Optics S2000-UV-VIS with illumination provided by a PX-2-pulsed xenon light source attached to a notebook PC running OOIBase32 software (Ocean Optics Inc., Dunedin, FL). A split fiber optic cable that provided illumination and received the reflected spectra was held 45° relative to the surface of the object being measured with an Ocean Optics probe holder.

One member of each pair of identical colored squares was treated with UV block and an identical control was coated with a non-UV blocking agent on both sides. These squares were then placed near the margin of the bower platform, and I recorded which squares the bower owners moved toward the bower onto the bower platform and where they were placed. Numbers coding square color and treatment were each written on a corner of the square with a permanent marking pen to allow for accurate recording of results. Squares from each

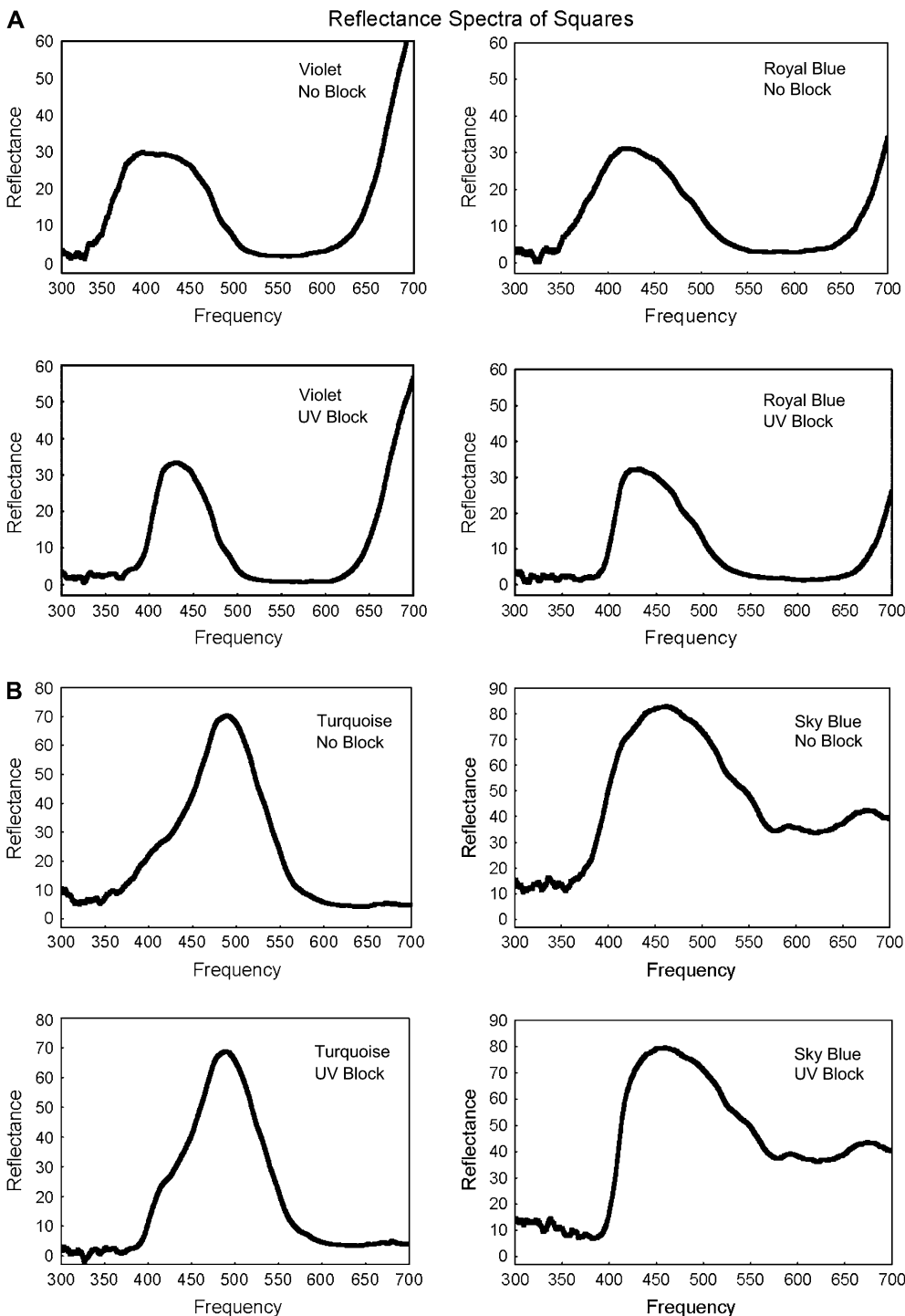


Figure 1
Reflectance spectra for UV- and UV+ experimental squares of the most used 4 colors. (A) Violet and royal blue. (B) Turquoise and sky blue.

treatment were kept in separate bags to insure that UV blocking agent would not be transferred between sets. I used an equal by weight mixture of the UV blocking agents Parsol 1789 (avobenzone) (4-tert, buty-4'-methoxy-dibenzoylmethane) that blocks radiation in the near UV range (320–400 nm) and Parsol MCX (octyl methoxycinnamate) that blocks far UV (290–320 nm) provided by Hoffmann-LaRoche Inc. (see Andersson and Amundsen 1987). The control squares received a transparent, odorless petroleum jelly-based non-UV blocking cream (see Bize et al. 2006) of similar consistency as the Parsol mixture applied directly to the squares. The spectra of each square was

measured and those in the UV block treatment showed a sharp drop off in reflectance at 400 nm and below, whereas the control squares did not show a loss of reflectance. There was an 86% average reduction of UV reflectance for UV-blocked objects, but reflectance was not significantly changed in the non-UV part of the spectrum (Figure 1a,b). This level of UV blocking is equal or greater than other studies in which a chemical UV block was used (e.g., Andersson and Amundsen 1997; Alonso-Alvarez et al. 2004; Robertson and Monteiro 2005).

For the test of male decoration preferences, pairs of the 11 decoration colors were arranged in an arc 40–50 cm from

the bower entrance, beyond the edge of the bower platform on bowers of 31 males. The position of different colored pairs was randomized on this arc with the exception that experimental and control decorations were displayed next to each other to minimize position effects on decisions by birds to use UV reflective and nonreflective decorations. The position of each treatment in each colored pair was also randomized. The position of squares was recorded prior to the experiment and at the end of the experiment approximately 6 h later. This length for the experiment allowed most males to show preferences for decorations and limited the number of decorations that would be stolen by nearby males in a longer experiment that would complicate the interpretation of results. As in previous "harvesting" experiments (e.g., Diamond 1986; Borgia et al. 1987; Uy and Borgia 2000), squares moved closer to the bower were considered to be attractive, whereas those not moved, or moved away, were scored as not attractive. By mapping decoration position on the bower, I was able to assess the location of their placement relative to the bower and to test the hypothesis that UV reflectance affects decoration position on the bower platform. In 2 cases, squares were stolen and found on another bower and in both cases the UV+ and UV- dark blue square were taken.

Feather experiment

A second, more limited experiment involved placing 3 UV-blocked (UV-) and 3 control (UV+) blue crimson rosella flight feathers at the margin of the male's bower platform and assessing use of these decorations by 6 different males. These feathers are the most preferred natural decorations used by male satin bowerbirds, as measured by high rates of decoration stealing (Borgia and Gore 1986; Wojcieszek et al. 2006). Parts are dark gray, light blue, and dark blue (Figure 6) with the latter seemingly accounting for their attractiveness. Although male satin bowerbirds commonly use man-made objects such as colored paper and plastic when available on their bowers, I thought it useful to test male attraction to natural objects with high UV reflectance that are commonly used on bowers. Feathers were matched for quality (size and condition) and then, as above, one of each pair was coated with UV block. For feathers, the Parsol mixture was combined with a small amount of UV-transparent duck grease, and this grease was used alone for the controls (see Andersson and Amundsen 1997). Feathers were arrayed so that there was an alternating pattern of UV- and UV+ feathers at the edge of the bower platform 45–55 cm from the bower entrance. The preferences of males were recorded as above after feathers were made available for one 6-h observation period at each bower. No feathers were stolen during this experiment.

Statistical analysis

I used a chi-square test to assess overall differences in color use. To further define color preferences, I tested for differences (t -test) between the number of blue and other (not blue) decorations used because earlier experiments have shown a strong preference for blue. In these experiments, more saturated violet/blue colors were preferred so the same comparisons were made excluding the relatively unsaturated sky blue. A paired t -test (t_{paired}) was used to test for different preferences between UV+ and UV- squares. A Mann-Whitney U test was used for comparisons of placement of squares differing in UV treatment. Regression (R) and Spearman rank correlations (r_s) were used for comparing variables measuring association between UV reflectance and other traits. All results are reported for 2-tailed tests to allow for outcomes in either direction unless otherwise noted. Means are expressed as $\bar{X} \pm \text{SD}$.

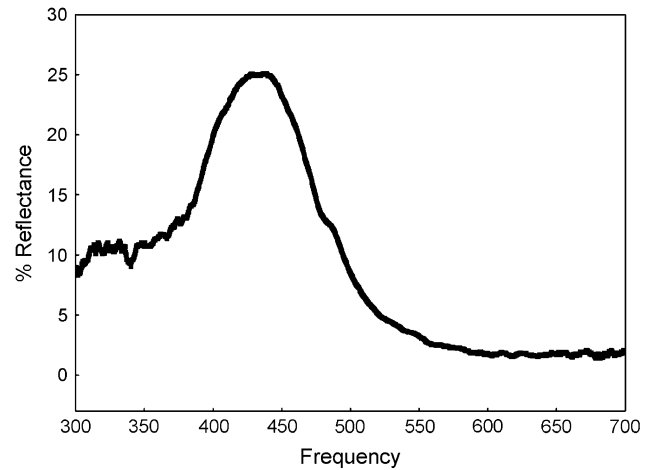


Figure 2
Unblocked reflectance spectra from dark blue area of crimson rosella feather.

RESULTS

The decoration square choice experiment showed a strong effect of color ($\chi^2 = 200.9$, degrees of freedom [df] = 10, $P < 0.000001$). Earlier experiments have shown a preference for blue, and I found a preference for the 4 violet/blue squares over other colors ($\bar{X}_{\text{blue}} = 27.75 \pm 17.4$, $\bar{X}_{\text{not blue}} = 3.29 \pm 1.6$; $t = 3.85$, $df = 9$, $P = 0.004$). Previous experiments typically showed a preference for more saturated violet/blues, so I compared usage with sky blue excluded, and there was an even stronger preference for the 3 more saturated violet/blue colors ($\bar{X}_{\text{blue}} = 35.0 \pm 11.8$, $\bar{X}_{\text{not blue}} = 2.89 \pm 1.6$; $t = 7.59$, $df = 8$, $P = 0.00006$). There was a marginally significant preference for UV- over UV+ colored squares ($\bar{X}_{\text{UV+}} = 5.45 \pm 7.8$, $\bar{X}_{\text{UV-}} = 6.72 \pm 8.0$; $t_{\text{paired}} = 2.06$, $N = 11$, $P = 0.07$). The number of UV- and UV+ squares of each color used was highly correlated ($r_s = 0.70$, $t = 2.91$, $P = 0.017$, Figure 3). I found no relation of the number of UV+ colored squares used with percent UV reflectance ($r_s = 0.18$, $N = 10$, $P = 0.63$) and average UV reflectance ($r_s = -0.069$, $t = -0.196$, $P = .85$). The UV+ square colors with the 5 highest UV reflectances were chosen only 14 times out of a total of 60 UV+ squares taken (23.3%) from all 11 colors, suggesting that UV reflectance was not highly

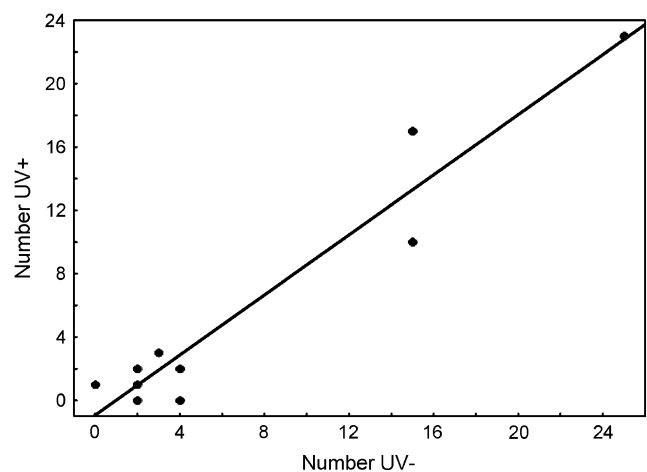


Figure 3
Correlation of the number of UV- and UV+ squares used of each color ($r_s = -0.70$, $t = 2.91$, $P < 0.017$).

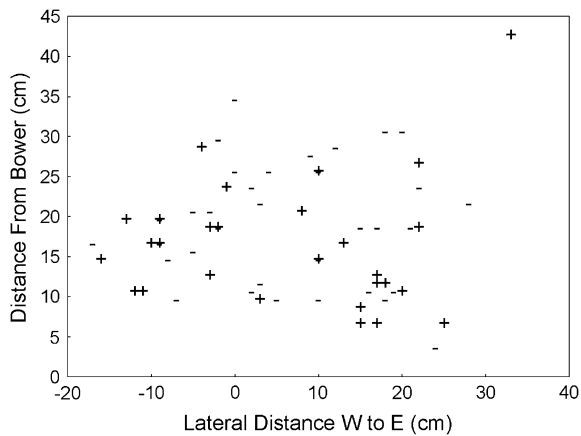


Figure 4
A composite map of placement of all moved UV- (–) and UV+ (+) squares of all colors shown in lateral distance from the middle of the bower entrance (x axis) and distance parallel to the bower walls from the front entrance (y axis).

attractive to males gathering decorations. There was no difference in the lateral (right to left relative to the bower entrance) placement of UV- and UV+ decorations on the bower ($\bar{X}_{UV-} = 6.31 \pm 11.23$, $\bar{X}_{UV+} = 6.13 \pm 13.91$; $t_{(63)} = 0.06$, $P = 0.95$) nor for distance from the bower (parallel to the bower avenue) ($\bar{X}_{UV-} = 17.6 \pm 7.68$, $\bar{X}_{UV+} = 14.9 \pm 7.56$; $t_{(63)} = 1.43$, $P = 0.15$; Figure 4).

Reflectance spectra of 2 of the violet and royal blue squares show a second “red” peak near 700 nm. Strong preferences were shown in other experiments for blue decorations with or without the second red peak (Borgia and Keagy 2006; Borgia G, personal observation), suggesting that male satin bowerbirds do not attend to the red peak in selecting decorations. This hypothesis was supported in a comparison of regression models plotting peak wavelength against number of squares used. A model that limited peak wave length to 600 nm and lower and excluded red peaks provided a better prediction of square use ($R^2 = .34$, $df = 1,9$, $F = 4.66$, $P = .03$ [1-tailed]; Figure 5) in relation to other models that considered peaks at higher wavelengths (e.g., 700 nm; $R^2 = .002$, $df = 1,9$, $F = .015$, $P = .90$).

For the feather experiment, 59.4% of the feathers offered to males were used by the 6 males in the experiment.

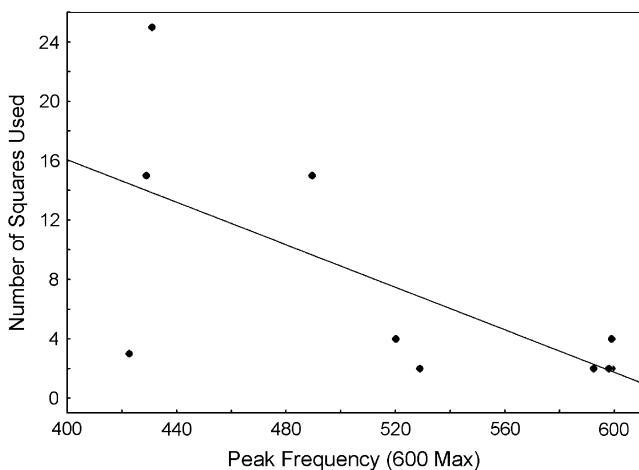


Figure 5
Number of squares used by color versus the peak frequency of that color under 600 nm.

These included use of nearly equal numbers of UV- (9) and UV+ (10) feathers, and the mean number of feathers used by males was not different ($\bar{X}_{UV+} = 1.67 \pm 1.03$, $\bar{X}_{UV-} = 1.5 \pm 1.05$; $t_{\text{paired}} = .23$, $P = .82$). The UV+ and UV- feathers that were moved did not differ in their distance from the bower ($\bar{X}_{UV+} = 18.0 \pm 9.04$, $\bar{X}_{UV-} = 17.1 \pm 8.08$; $U = 40.5$, $Z = -0.72$, $P = .47$). The near-equal response by males to UV+ and UV- feathers was consistent with results of the colored square experiment.

DISCUSSION

The results presented here indicate no significant effect of UV reflectance on decoration choice. In the choice test of UV+ and UV- squares, there was a close to significant preference for UV- squares. In other comparisons, neither average UV reflectance (UV brightness) nor % UV reflectance (UV chroma) was related to the number of squares used, and there was a strong correlation between the number of UV- and UV+ squares taken of the same color, suggesting absence of a clear preference for UV+ reflecting squares. The feather choice experiment also suggested a lack of discrimination between UV+ and UV- for these natural decorations. Taken together, these results suggest that male satin bowerbirds in our study population do not use UV in the choice of decorations.

I found very strong preferences for blue/violet squares (ca. 400–495 nm peak frequencies), as has been shown in previous studies. This result shows that even though males do not discriminate based on UV, they do have strong preferences for particular colors (violet/blue). Two of the violet/blue colors males commonly chose had a second peak in the far red extending to 800 nm (Figure 1), but it appears that male satin bowerbirds do not attend to this red peak. There was also some limited use of other colors (Table 1).

The use of decorations that reflect UV by male satin bowerbirds appears to be a side effect of their strong preference for violet/blue decorations that had wide reflectance curves that extend into the UV (e.g., Figures 1a,b and 2). None of the highly used UV+ squares or feathers had a reflectance peak in the UV (e.g., Figures 1a,b and 2) as might be expected if their use was driven by UV reflectance. For these objects, there was a reflectance peak in the violet/blue range with the tail of this curve reaching into the UV. The control light green-colored squares had a peak in the UV, but they were among the least used colors. Generally, apart from violet/blue squares, those with the highest UV reflectance tended not

Table 1
Use of UV+ and UV- decorations

Decoration color	Number of squares used		%UV+ used	%UV- used	Color rank
	UV+	UV-			
Violet	10	15	0.32	0.48	3
Royal blue	23	25	0.74	0.80	1
Turquoise	17	15	0.55	0.48	2
Sky blue	2	4	0.06	0.12	4
Aqua	0	2	0	0.06	10
Light green	1	2	0.03	0.06	8
Yellow	1	2	0.03	0.06	8
Orange	1	0	0.03	0	11
Silver	3	3	0.06	0.10	4
Ivory	0	4	0	0.13	6
Off white	2	2	0.06	0.06	6
Total	60	74			

to be selected for use on bowers. The overall high correlation in use of UV+ and UV- squares of the same color (Figure 3) suggests that even though UV reflectance has not been favored, there has been no selection against the use of UV reflective decorations; thus male satin bowerbirds appear indifferent to UV reflectance in choosing decorations.

These results contrast with Mullen's (2006) study of the northern subspecies of satin bowerbird in which he suggests a preference for untreated UV+ blue crimson rosella feathers over those with UV-block sunscreen. However, this conclusion is based on a sample of males tested, which was too small (2) to statistically support his conclusion, and because the feathers used in his control treatment did not receive a UV-transparent coating, these feathers may have been preferred because they were uncoated rather than because they were UV reflective. Also, it is possible that the northern but not the southern subspecies of satin bowerbirds uses UV in decoration choice.

Wojcieszek et al. (2006) considered UV reflectance in relation to stealing of blue decorations on bowers in 2 analyses. First, they compared reflectance patterns of 21 frequently stolen with 24 never stolen blue decorations. Both classes of decoration had low mean UV reflectance, and the never stolen decorations showed a significantly higher UV reflectance in the 370- to 400-nm range. They also found that the most frequently stolen decorations, 4 bottle tops and 4 Crimson rosella feathers, had higher UV reflectance than the mean for 37 other blue decorations on the bower. Based on this second comparison, they suggested a preference for UV-reflecting decorations. But, in their study, feathers were stolen only slightly more than expected and ranked sixth among the 9 decoration types that are stolen more than expected, and to the extent that these are the only 2 decoration types showing high UV reflectance, they indicate no clear stealing preference for UV reflecting decorations. Further, the effects of UV and blue on stealing are confounded, and because other attributes that likely affect decoration stealing were not properly controlled for (e.g., mass, size, proportion of blue on the object, other colors on the object, etc.), their claim that UV affects preferences for stolen decorations is not convincingly supported.

The absence of evidence for a strong preference for UV-reflecting decorations in satin bowerbirds in this study differs from the important role for UV reflectance in plumage characters used in mate choice by many birds (e.g., Bennett et al. 1996, 1997; Amundsen et al. 1997; Andersson and Amundsen 1997; Andersson et al. 1998). This raises the question of why does UV reflectance of bower decorations appear to be unimportant in contrast to studies of UV reflecting plumage traits? There may be several reasons. First, because bower decorations are not made by the male, any role for UV reflectance as a direct indicator of health or physiological condition of the bower holder's quality is limited and this may contribute to the absence of a role for UV reflectance in the choice of these decorations. Second, a previous study has shown that blue natural objects are rare in the habitat (Borgia et al. 1987) and male satin bowerbirds compete intensively for blue decorations (Borgia and Gore 1986; Wojcieszek et al. 2006). This supports the hypothesis that male competition for rare decorations may make these decorations a good indicator of male quality (Borgia 1985; Borgia and Gore 1986; Borgia et al. 1987; Hunter and Dwyer 1997). According to this hypothesis, in order for blue decorations to signal quality, blue objects must be sufficiently rare so that all males do not have easy access to them but also sufficiently common so that males can signal their quality. Wojcieszek et al. (2006) found that most blue decorations used by satin bowerbirds in southern Queensland had low UV reflectance. This suggests that satin bowerbird decoration preference may not have evolved to require UV reflectance because natural objects that reflect

both blue and UV are too rare to be useful in indicating male quality. A third possibility is that because ambient UV light is reduced in the forest under story (Endler 1993; Gomez and Théry 2004), satin bowerbirds may not benefit from requiring UV reflectance from decorations used for display on their ground court. In the case of crimson rosella feathers, UV reflectance probably evolved as plumage signals in the UV-rich light of the forest canopy and open fields. When these same feathers are used for displays on the bowerbird court, the diminished ambient UV light produces a lower intensity UV signal that is less valuable to displaying males and may cause them to ignore UV reflectance when selecting decorations. Low ambient UV light on male courts would limit the opportunity for sensory drive or sensory exploitation for UV reflective decorations and could also limit the role of UV reflectance in enhancing the ability of females to detect motion in male display.

The ability of many avian species to see UV (see Ödeen & Håstad 2003) and use UV in male plumage display and mate selection (e.g., Bennett et al. 1996, 1997; Andersson and Amundsen 1997; Andersson et al. 1998; see also, Hausmann et al. 2003) raises the possibility that UV was used in the plumage displays of bowerbird ancestors. Currently, it is unknown if the limited UV reflectance of satin bowerbird plumage functions as an indicator trait in mate choice. It is possible that limited UV reflectance of plumage or the high UV reflectiveness of male eyes (Marshall J, personal communication) serves this function or that UV reflectance has taken on a more limited role in mate selection as bowerbirds have become more dependent on decorations. As bowerbirds evolved to use forest ground courts where there is less ambient UV to illuminate male plumage and their decorations, and decorations displays provide less information about male quality from UV reflectance (see above), there may have been an overall lessening of the importance of UV in mate choice. The indifference to UV reflectance found in the decoration choice experiments reported here and the failure of male satin bowerbirds to evolve highly UV reflective plumage are also consistent with the possibility that satin bowerbirds do not see UV. Studies of the bowerbird vision system and the role of UV reflectance of plumage in mate choice should lead to a better understanding of the role of UV in satin bowerbird display.

The results reported here suggest that the occurrence UV reflectance of display traits may not always indicate an important role for UV in the attractiveness of these traits. These results suggest that special care should be used in assessing displays that have a reflectance peak in the violet/blue part of the spectrum because UV reflectance may be a side effect of these displays. Also, for off-body displays, UV reflectance may be less effective in indicating important aspects of a male's physiological condition than plumage displays and may have a reduced role in courtship signaling. Importantly, off-body displays may provide very different kinds of information from plumage displays, and these differences probably contribute to the evolution of complex multicomponent sexual displays.

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