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Theft of bower decorations among male Satin Bowerbirds (*Ptilonorhynchus violaceus*): why are some decorations more popular than others?

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Abstract. Male Satin Bowerbirds (*Ptilonorhynchus violaceus*) build stick structures known as bowers that serve as the focus for courtships and matings. Males decorate their bowers with numerous coloured decorations and are known to steal these decorations from one another. We investigated the stealing of bower decorations among males at the Bunya Mountains in Queensland, Australia. We aimed to (1) determine which classes of decorations were targets for theft in the studied population, and (2) examine whether the frequency at which individual decorations were stolen related to their intrinsic properties. To address our first aim, all decorations on the bowers of 21 adult males were labelled and their movements tracked throughout one mating season. To address our second aim, decorations stolen at least three times during the season were collected and their morphological and reflectance properties compared to those of decorations that were not stolen. In terms of the classes of decorations, tail feathers of Crimson Rosella (*Platycercus elegans*) were stolen more than any other class of decoration, but blue plastic bottletops were the most popular decorations relative to their availability on bowers. Frequently stolen individual decorations were similar to non-stolen items in their weights and surface areas, but were darker blue in colour than the decorations never stolen. Both bottletops and feathers reflected higher levels of ultraviolet (UV) light than did all other classes of bower decorations tested, thus suggesting that males may be using UV reflectance in sexual signalling. The darker blue, stolen decorations may increase contrast between the decoration collection and the platform, while the UV-reflecting subset of most frequently stolen decorations (bottletops and feathers) may increase contrast within the decoration collection. This in turn may increase the attractiveness of the display to females.

Introduction

Satin Bowerbirds (*Ptilonorhynchus violaceus*) are found in rainforests and various types of eucalypt forests along the eastern coast of Australia (Frith and Frith 2004). Satin Bowerbirds are polygynous and males do not take part in parental care (Vellenga 1970; Frith and Frith 2004). During the mating season, male Satin Bowerbirds build stick structures known as bowers. These are comprised of a platform base and two parallel vertical walls forming a central avenue (Frith and Frith 2004). Males adorn their bowers with various natural and man-made decorations and perform elaborate courtship displays on their bower platforms (Coleman *et al*. 2004; Frith and Frith 2004). Mating success is skewed among males, with only a few individuals obtaining most annual matings (Borgia 1985). Many aspects of the males' displays are correlated with mating success, including the type and number of bower decorations and the quality of the bower (Borgia 1985; Coleman *et al*. 2004). Interactions among male Satin Bowerbirds are common, as males steal bower decorations from one another and destroy bowers of rival males (Borgia and Gore 1986). Our study focused on theft of decorations among males, and specifically on which decorations were most popular during bouts of stealing and why.

Bowerbirds display species-specific preferences for certain colours of bower decorations (Morrison-Scott 1937; Borgia *et al*. 1987; Diamond 1988; Frith and Frith 2004). For example, male Satin Bowerbirds prefer to use blue and yellow objects (Morrison-Scott 1937), male Spotted Bowerbirds (*Chlamydera maculata*) and Great Bowerbirds (*Chlamydera nuchalis*) prefer green items, male Regent

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Bowerbirds (*Sericulus chrysocephalus*) prefer blue items (Madden and Tanner 2003) while the colour preferences of male Vogelkop Bowerbirds (*Amblyornis inornatus*) vary between populations (Diamond 1988). Many hypotheses have been put forward to explain these broad colour preferences. The 'matching hypothesis' suggested that males prefer items that are similar in colour to their plumage and iris colour (Morrison-Scott 1937; Borgia *et al*. 1987). This hypothesis is plausible for Satin Bowerbirds as the satin blue plumage of males matches their preference for blue decorations. There are, however, many species of bowerbirds that are devoid of blue plumage, but do collect and often prefer blue decorations, including the Vogelkop, Adelbert (*Sericulus bakeri*) and Flame (*Sericulus aureus*) Bowerbirds (Frith and Frith 2004). A recent cross-species comparison rejected the matching hypothesis as bower decorations were not shown to be elaborations of a male's plumage (Endler *et al*. 2005). On the contrary, males seemed to be choosing decorations of novel and rarely encountered colours, perhaps to offer females a more effective signal (Endler *et al*. 2005). Despite research that has investigated preferred colours of decorations in bowerbirds, comparatively little work has been done to examine whether there are preferences within the broad colour categories.

Theft preferences of male Satin Bowerbirds offer a novel way of investigating colour preferences within a bowerbird species. Borgia and Gore (1986) found that the blue tail feathers (rectrices) of Crimson Rosellas (*Platycercus elegans*) were the items most commonly targeted by thieving males, and feather possession was one of the best predictors of mating success in this species (Borgia 1985). Unfortunately, in their study only the movement of feathers was monitored, and thus it is not known whether any other classes of decorations were targeted for theft. We aimed to clarify exactly which classes of decorations males target when stealing from rivals. We tested three hypotheses for why specific individual decorations may be stolen more than others. First, specific bower decorations may be preferred because they are lighter in weight, reducing the cost of carrying them back to the bower and making the simultaneous theft of multiple items easier. Second, preferred decorations could have larger surface areas, thus providing a greater signal to females or rival males or both. Third, some decorations may display distinct reflectance properties, potentially providing more contrast to the underlying bower platform and other bower decorations (Endler *et al*. 2005), making them easier for females or rival males to see.

Our aims were: (1) to determine which classes of decorations were targets for theft in the studied population, and (2) to examine whether the frequency at which individual decorations were stolen related to their intrinsic properties. We tested whether frequently stolen decorations differed from those that were never stolen in terms of their weight, surface areas or reflectance properties.

Methods

Study site

This study was conducted at the Bunya Mountains (26°51′54″S, 151°35′15″E), 160 km north-west of Brisbane, Australia. The movement of decorations among the bowers of 21 adult male Satin Bowerbirds was monitored. These bowers were situated in a 1-km^2 block, and neighbouring bowers were an average of 106.35 ± 15.38 m apart. This study was approved by the Queensland Parks and Wildlife Service (scientific purposes permit: WISP02093904) and the University of Queensland Animal Experimentation Ethics Committee (reference: ZOO/ENT/355/04/UQ).

Marking of decorations and monitoring of theft

We categorised all of the non-perishable decorations on bower platforms into the following groups: feathers (all tail feathers of the Crimson Rosella), plastic bottletops, plastic bottle rings, plastic straws, pens and pen lids, packing tape, other tape (e.g. flagging and electrical tape), pegs with springs, pegs without springs, small plastic milk containers (UHT containers), ribbons, wire, miscellaneous soft plastic (e.g. chocolate wrappers), miscellaneous hard plastic (e.g. containers or parts of containers) and bones (small bird and possum skulls, and vertebrae from various animals). With the exception of bones, all the above categories of decorations included only blue items (thus the majority of non-perishable decorations collected by Satin Bowerbirds were blue). All of these non-perishable items were individually labelled with a small number using permanent black markers. Short, individually labelled pieces of white string (<4 cm in length) were tied to perishable items, such as tufts of grass and flowers. New perishable decorations appeared on bowers most days and disappeared from the pool of marked objects within a few days of attachment of the string. None of the perishable items were stolen in the first 3 weeks of monitoring and, since they appeared to be only temporary decorations, the marking of them ceased thereafter. The marks made on non-perishable decorations were small (<1 cm in diameter) and no more conspicuous than pre-existing marks on the items, so were unlikely to have affected the attractiveness of these decorations. While string tied to the perishable decorations could have influenced their attractiveness, the pieces of string used were small and of similar colour to most of these decorations, so again were unlikely to have influenced the behaviour of the birds or their perception of the attractiveness of these decorations. Decorations embedded deep in the platform matrix were not labelled to prevent disruption to platforms (in accordance with Hunter and Dwyer 1997).

The initial labelling of decorations took place over 2 days, and tracking the movement of decorations began on the third day. The movement of bower decorations was monitored between 11 September and 1 December 2004. We only examined movement of decorations across consecutive days, and there were 44 such pairs of days in the time period. Bowers were visited by us at the same time, and in the same sequence, on each of these days. Visits to bowers were brief (no longer than 10 min) to minimise disturbance to the birds. During bower inspections, the identities of the decorations present were recorded and any new (that is unmarked) decorations were labelled as described above. Theft was defined as the presence of a labelled item (or items) at one bower that had been recorded as present on another male's bower the previous day. This could have underestimated the total amount of theft for two reasons. First, we assumed that new unmarked decorations had been found in the surrounding environment by males and not stolen from unstudied males or from studied males with decorations yet to be labelled. Second, we could have missed multiple bouts of theft that occurred within the 24-h period, particularly if unrecorded victims of theft stole back their decorations.

Which classes of decorations were targets of theft in the studied population?

At the end of the study we determined how frequently each class of decorations was stolen and compared this to the availability of each class of decorations on the studied bowers. The null hypothesis was that males would steal decorations in proportion to their availability on bowers over the season.

Did the intrinsic properties of individual decorations relate to the frequency at which they were stolen?

At the end of the study, 21 individual decorations that had been stolen at least three times were collected so that their physical properties could be examined. These decorations included four feathers, four bottletops, one straw, three milk bottle rings, three pegs without springs, one piece of packing tape, two pieces of blue tape, three pieces of soft plastic and three pieces of hard plastic. For comparison, 24 decorations that were not stolen once during the study were randomly selected and collected. These decorations included three pieces of packing tape, three straws, one milk bottle ring, two pegs without springs, three pieces of blue tape, four pieces of soft plastic, five pieces of hard plastic, two lengths of wire and one pen (all decorations collected were blue in colour).

Determining the intrinsic properties of the most stolen bower decorations

All collected objects were weighed and their surface areas calculated after tracing their dimensions onto 1 × 1 mm graph paper. The reflectance spectrum of each object was determined using a fibre optic spectrometer (model S2000; Ocean Optics Inc., Fort Pierce, FL) and the OOI Base program (Ocean Optics Inc.). A single fibre optic cable provided light to each of the decorations and the light reflected back was directed to the spectrometer. The fibre optic cable was shielded by a metal covering to exclude ambient light. The system was calibrated using no light (pure black felt) and white light (a white 'Spectralon' laboratory sphere). An integration time of 3 ms was specified and the mean spectrum from ten integrations was used as the true spectrum for each object. The spectra of decorations frequently stolen and decorations never stolen were then compared. In addition, the spectra of both bottletops and feathers (previously included in the 'frequently stolen' category) were compared to the mean spectrum of all of the other decorations, as bottletops and feathers were the most frequently stolen objects (see Results). Spectra are reported here in intervals of 5 nm.

Results

Which classes of decorations were targets of theft in the studied population?

Feathers were stolen more than any of the other labelled classes of decorations (Fig. 1), but were also the most abundant class of decoration on bowers. However, objects were not stolen in proportion to their abundance on bowers, with feathers, bottletops, straws, miscellaneous soft plastic and bottle rings all stolen more than was expected (Pearson's χ^2 test: $\chi^2 = 23.6397$, d.f. = 14, $P < 0.05$; Fig. 1). In particular, bottletops were stolen twice as many times as expected. In fact, there were no labelled bottletops or feathers that were not stolen during the study. In contrast, other hard plastic items and bones were stolen far less than expected.

Did the intrinsic properties of individual decorations relate to the frequency at which they were stolen?

The 21 frequently stolen decorations and the 24 decorations never stolen were of comparable weights (*t*-test: $t = 0.53$, d.f. = 43.99, $P = 0.59$) and surface areas (*t*-test: $t = 1.51$, d.f. = 32.34; $P = 0.14$). The sizes of the decorations collected ranged from 1.2 cm^2 to 38.5 cm^2. The weights of the collected items ranged from 0.5 g to 5.75 g. The most frequently stolen items were darker blue in colour than items that were not stolen (Fig. 2). Included among the most stolen bower decorations were four feathers and four bottletops (these bottletops were identical to the human eye). These feathers and bottletops reflected more ultraviolet (UV) light than did the 37 other decorations tested (Figs 3 and 4).

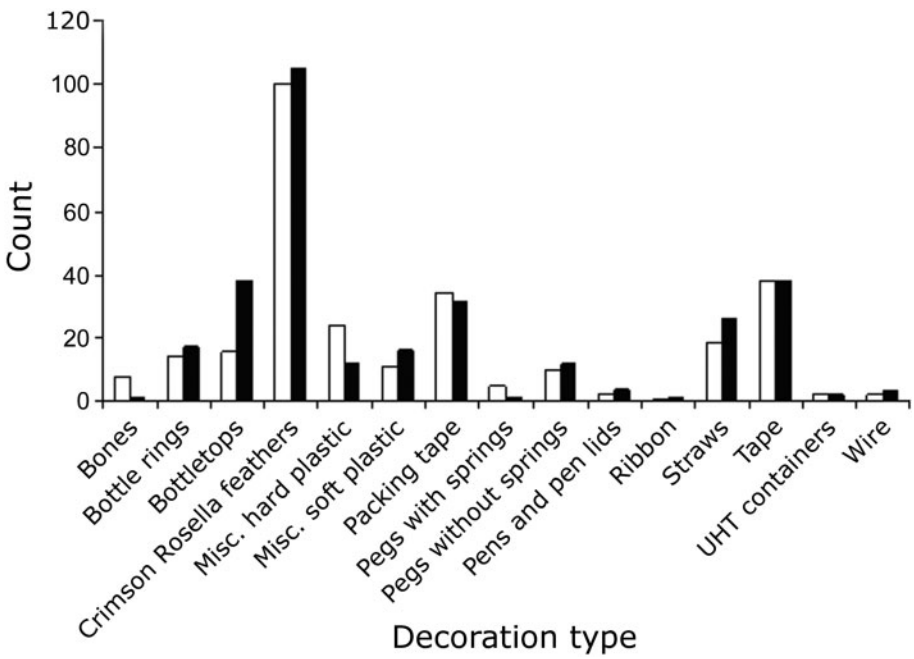

Fig. 1. Comparison of numbers of expected and observed thefts involving non-perishable Satin Bowerbird bower-decoration classes. Open columns are expected counts assuming objects were stolen in proportion to their abundance; solid columns are observed counts. With the exception of bones, all classes of decorations represented in this figure were blue.

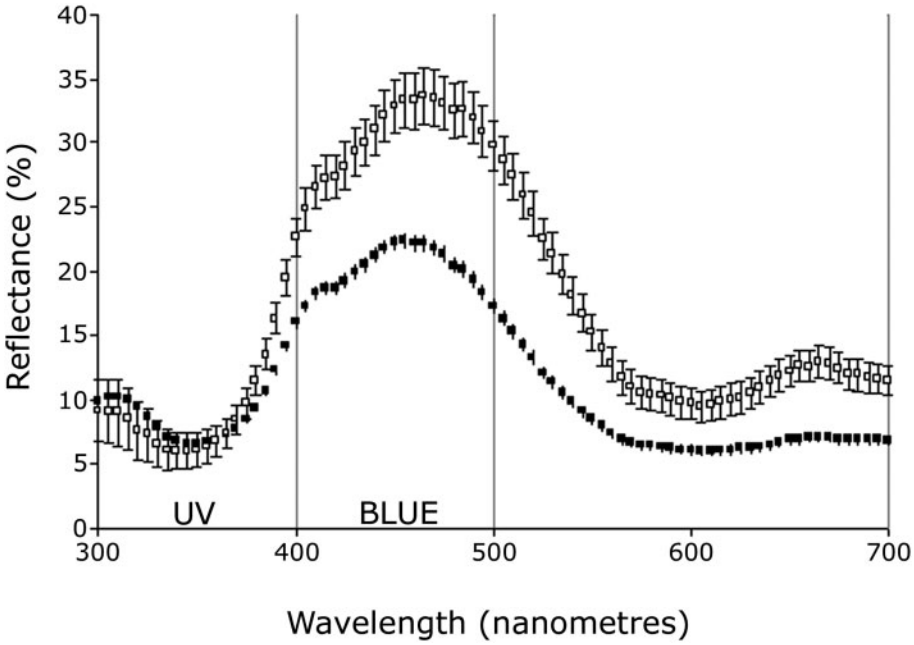

Fig. 2. Mean spectra (± s.e.) of the 21 frequently stolen decorations (solid points) and 24 decorations never stolen (open points). Spectra are plotted at 5-nm intervals. The UV and blue light regions of the spectrum are highlighted.

Discussion

This study indicates that some, but not all, decorations were targets for theft among male Satin Bowerbirds in the Bunya Mountains population. Feathers were stolen more than any other class of decoration, as has been found previously (Borgia 1985; Borgia and Gore 1986), but relative to their availability, bottletops were stolen most frequently. Possession of feathers has been shown to correlate with mating success in another Satin Bowerbird population (Borgia 1985). Our study suggests that some man-made objects, such as bottletops, may be just as important in this system as the natural objects previously focused on (see Borgia 1985; Borgia and Gore 1986). Further work is required to ascertain whether bottletops or other artificial decorations are popular in other Satin Bowerbird populations, and whether the popularity demonstrated by males in the Bunya Mountains extends to patterns of mate choice by females.

The 21 most frequently stolen individual decorations reflected blue light of lower intensity than did the 24 decorations never stolen. However, these decorations did not weigh less, nor were their surface areas significantly different to those of the decorations never stolen. This finding suggests

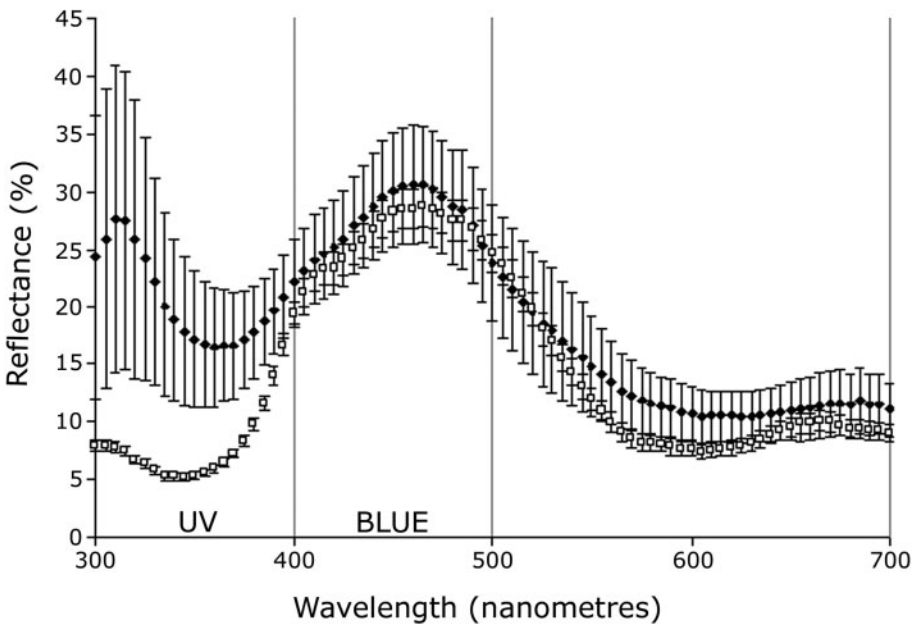

Fig. 3. Mean spectra (± s.e.) of the four feathers (solid points) and of the 37 other bower decorations, excluding bottletops (open points). Spectra are plotted at 5-nm intervals. The UV and blue light regions of the spectrum are highlighted.

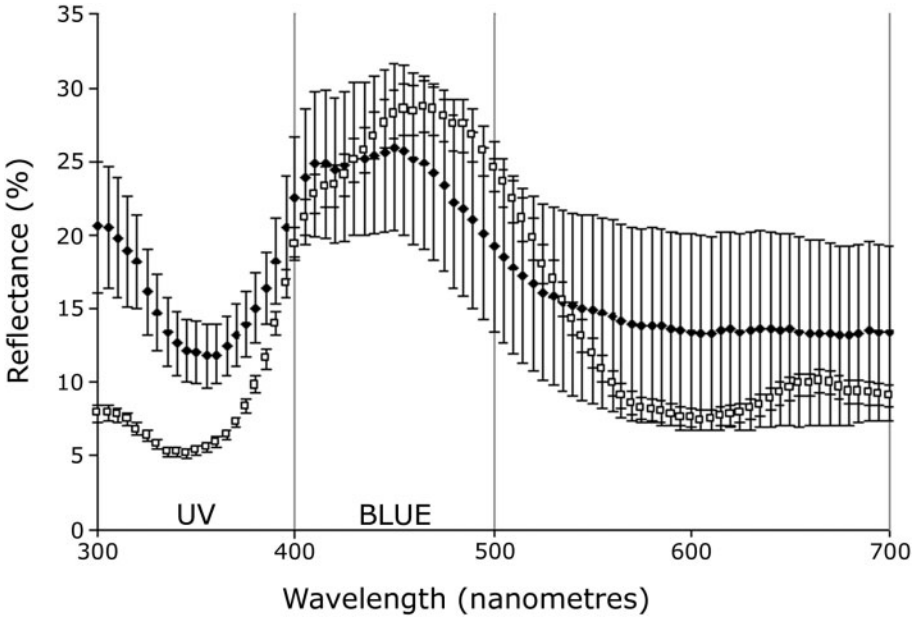

Fig. 4. Mean spectra (± s.e.) of the four bottletops (solid points) and of the 37 other bower decorations, excluding feathers (open points). Spectra are plotted at 5-nm intervals. The UV and blue light regions of the spectrum are highlighted.

that males preferred certain decorations because of their light reflectance properties and not for reasons pertaining to costs involved in carrying them. A cross-species study on the light characteristics of bowers suggested that decorations that are darker blue provide greater contrast to the brighter yellow and brown platform sticks upon which they are displayed (Endler *et al*. 2005). In fact, male Bowerbirds may even actively avoid decorations that are similar in colour to the items found in the environment surrounding bowers (Endler *et al*. 2005). Research on Golden-collared Manakins (*Manacus vitellinus*) has shown that the contrast between a male's display and the visual background is important in increasing the conspicuousness of their displays (Uy and Endler 2004). These Manakins clear 'courts', upon which they display to females. This is not unlike the behaviour of bowerbirds, given that males construct bowers upon platforms that then serve as the focal point of displays. The greater contrast that darker blue bower decorations potentially provide may be important in alerting rival males and attracting and impressing female Satin Bowerbirds.

The most popular decorations – bottletops and feathers – were shown to display higher levels of UV reflectance than other decorations. The perception of colour is dependent on the visual system of the perceiving animal (Bennett *et al*. 1994). Birds, in particular, have well developed visual systems (Goldsmith 1994; Vorobyev and Osorio 1998) and most of the diurnal birds that have been tested can see UV light (Bennett and Cuthill 1994; Hart 2001). In fact, some birds may pay more attention to UV light than to light elsewhere in the spectrum (Burkhardt and Maier 1989; Bennett and Cuthill 1994; Hausmann *et al*. 2003). Ultraviolet sensitivity may be important in orientation, foraging or signaling, or in a combination of these (Bennett and Cuthill 1994; Hausmann *et al*. 2003). The results presented here suggest that the UV reflectance of certain bower decorations may function in social signalling among Satin Bowerbirds. Some sections of an adult male Satin Bowerbird's blue plumage are known to reflect UV light (Doucet and Montgomerie 2003; Endler *et al*. 2005) and research has shown that parasite loads are negatively correlated with male plumage brightness (Borgia and Collis 1990; Doucet and Montgomerie 2003). It is therefore possible that female Satin Bowerbirds assess the UV reflectance from both a male's plumage and his decorations. While stolen decorations in general had different reflective properties to decorations that were not stolen (Fig. 1), and hence probably contrasted more strongly with the bower platform, the high levels of UV reflectance of the very popular and most frequently stolen decorations means they also contrasted with both the non-stolen and less frequently stolen decorations (Figs 3 and 4). Possession of feathers and bottletops may provide a display of even greater contrast that is more attractive to females, thus explaining their popularity among males.

Decorations giving a high degree of contrast with the underlying bower platform could certainly aid in the long-range attraction of females (Endler *et al*. 2005). Given that such decorations are also those most often stolen, they may even serve as 'honest signals' of a male's fitness and competitive ability. Honest signals have been observed in many species and are thought to have evolved to allow males to assess rivals accurately and respond to 'cheats' (Rohwer 1975; Johnstone 1995; Berglund 1996). Females could also use these honest signals as reliable indicators of male quality (Johnstone 1995; Berglund 1996). Research on Spotted Bowerbirds has shown that certain bower decorations do act as honest signals as they attract females, but at the same time

provoke theft from rival males (Madden 2002). Crimson Rosella tail feathers, blue plastic bottletops and decorations that are dark blue in colour may play a similar role in Satin Bowerbirds. Given that these decorations are assessed by females and play a role in competition among males, they may be honest signals.

Ours is the first study to show that in Satin Bowerbirds frequently stolen bower decorations are dark blue in colour and that the most sought after decorations, bottletops and feathers, reflect higher amounts of UV light than do other bower decorations. However, in this study there were only two classes of decorations that reflected UV light, so the relationship between high UV reflectance and decoration popularity requires further testing. Future work could experiment by planting items of known high UV reflectance levels on bowers to see whether this instigates thefts, or even heightens female sampling of males and male mating success. It is also not known how sensitive Satin Bowerbirds' visual systems are to the UV realm of the light spectrum. Recent molecular research into colour vision of birds suggests that perception of UV light differs among species (Ödeen and Hastad 2003; Endler and Mielke 2005). Further research into how bowerbirds perceive UV light is therefore required in order to validate the conclusions made here.

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