

**Flower choice and bower decoration in the satin bowerbird  
*Ptilonorhynchus violaceus*: a test of hypotheses for the  
evolution of male display**

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**Abstract.** Flowers are a common decoration used on the bowers of male satin bowerbirds. The characteristics of flowers that promote their use as decorations by males are evaluated. Out of a total of 70 species recorded along transects, inflorescences from 29 species were found on bowers. Seven flower species accounted for 93% of the inflorescences used on bowers. Blue and purple species occurred on bowers at a greater frequency than they occurred in the habitat. White and yellow species appeared on bowers proportionately less often, and orange, pink and red not at all. Male satin bowerbirds used a wider range of colours of flowers than has been previously reported, and preferred blue and purple over yellow and white flowers. Flower choice experiments showed that males may discriminate between flowers only on the basis of colour, and that males favour flowers that appear infrequently on bowers. The results suggest several conclusions about how flowers are used on bowers. (1) Male flower preferences and male ability to collect inflorescences affect how flowers are used on bowers. The common use of flowers shown to be less preferred in choice tests implies that there are constraints on the gathering of more preferred flowers and this causes males to produce suboptimal displays. (2) Male preference for novel flowers suggests that flower choice by males is due to a set of general selection criteria and does not result from preferences for specific flower species. (3) The strong male preference for, and the high rate of use of, rare blue flowers supports the hypothesis that the rarity of colours may influence the evolution of male flower preferences. This strong preference for scarce flowers offers some support for models that suggest that male displays are not arbitrary, but may serve as indicators of male quality as sires.

Bowerbirds (Ptilonorhynchidae) build unique display structures called bowers. Their only apparent function is to facilitate male display to females (Borgia 1985a, b). Each species shows unique preferences for the colourful decorations it uses on and/or about their bowers (Marshall 1954; Cooper & Forshaw 1977). The number of decorations on a bower is an important determinant of male mating success in satin bowerbirds (Borgia 1985a), yet the decorations appear to have no intrinsic value to either sex outside the context of sexual display. Flowers are among the most common types of decorations (Marshall 1954; Gilliard 1969; Cooper & Forshaw 1977).

Numerous recent papers have explored the relationship between sexual competition and display in polygynous species and the ultimate basis for female choice (e.g. Trivers 1972; Zahavi 1975; Davis & O'Donald 1976; Bell 1978; Halliday 1978;

Borgia 1979; Thornhill 1980; Andersson 1982; Hamilton & Zuk 1982; Searcy 1982; Bateson 1983; Borgia et al. 1985; Bradbury 1985). Even so, we still know very little about how male display affects female choice, in large part because of a scarcity of empirical studies.

Here we consider the role of flowers in displays of the satin bowerbird. In contrast to species dependent on morphological characters such as plumage and antlers, bowerbirds choose their physical ornaments. It has long been known that male satin bowerbirds collect yellow and blue flowers for bower decorations (Gould 1865; Nubling 1921; Marshall 1954; Vellenga 1970), and our work has shown that the number of each of these colours of flowers on bowers is significantly correlated with the mating success of males who own those bowers (Borgia 1985a). However, apart from this simple categorization of flower types, there has been no

detailed study of flower preferences of any bowerbird species.

Darwin (1871) suggested that animals possess an aesthetic sense which is associated with the sexual selection process. The decoration of bowers, and especially the use of flowers, is cited as possible evidence for the existence of aesthetic preference (Diamond 1982). Another hypothesis explaining the occurrence of flowers on bowers is that they indicate characteristics of the bower owner that may be related to the male's quality as a sire (Borgia et al. 1985), e.g. the ability to steal rare items from the bowers of other males. It has also been proposed that the display characteristics at bowers are arbitrary results of female choice (Kirkpatrick 1982; Arnold 1983).

Our objective was to determine the function of flowers as bower decorations by studying the characteristics of flowers that affect their selection as decorations by male satin bowerbirds. The relative male preferences for flowers used in sexual display should indicate the importance of different types of flowers in influencing female mating decisions. The presentation of novel flower types was used to determine the characteristics of flowers that are chosen as display objects. The results of these experiments were then used to evaluate hypotheses for the evolution of display.

## METHODS

The study area is at Wallaby Creek, which is 140 km southwest of Brisbane in Beauray State Forest, N.S.W., Australia. The study site is in a valley formed by Wallaby Creek, which constitutes the 2-km eastern border of the rectangular study area that extends 1.5 km into a system of ridges formed by the creek's tributaries. Several distinct forest associations cover the area. *Eucalyptus* is the dominant canopy tree over much of the area. The understory varies and includes grassland, thick thorn scrub, and rainforest species. Rainforest predominates in low areas, along creeks and on the eastern side of higher ridges.

Intensive sampling of bowers and flowers in the surrounding habitat was carried out on a regular basis during the 1984 satin bowerbird mating season. Bowers were checked at regular intervals through the peak of the mating season (1 November–20 December) in 1982 and 1984 to determine which flower species were used on

bowers. Inflorescences were counted, and identified as to species. Flower decorations ranged from single blossoms to the entire inflorescence of plants. We counted all of the blossoms attached to the same stem as a single inflorescence. The size of inflorescences on bowers was relatively constant, and the availability of decorations from any species was measured in terms of these inflorescence units. We assumed that all inflorescence units present on the bowers were placed there by the owner. Other plant materials, including berries and seed pods, were found on bowers, but these are not considered in this report.

The abundance and colour of flowers available to the males were surveyed along transects in 1984. The transects were 1 m in width and extended to the visible limit of the canopy in height and followed the most direct paths between adjacent bowers. These transects passed through all major habitat types and provided a good representation of the plant species that were present. The species of all of the flowers on the transects were identified.

Inflorescences of several species were tested for preference by males by placing them 25 cm from the edge of bower platforms. It was noted twice daily whether inflorescences were moved towards or away from the platform or whether they were not moved. The proportion of all inflorescences used and the time it took for them to appear on bowers were used as measures of a male's preference. Flowers that were used in choice experiments were collected away from bowers, usually off the study area. Flower species used in the tests were chosen based on the known preferences exhibited by males, resistance to withering through the testing period, and availability for choice tests.

The effect of flower colour on decoration preferences was tested in an experiment using dyed *Hibiscus heterophylla* flowers. We chose this species because it was known to be attractive to male satin bowerbirds and because its white colour allowed it to be dyed other colours. All flowers used in the experiment were collected at the same time and either dyed or soaked in water at room temperature for 6 h, then dried overnight. Blue or red food colouring was used to dye flowers. White (natural), red (dyed) and blue (dyed) flowers were placed 25 cm from the edge of the platform at each of 15 bowers. The flowers at each bower were separated by 50 cm and their relative positions were randomized. After their placement at bowers, the movements of these flowers by males were recorded daily

for 3 days. A positive preference was scored for flower types moved closer to the bower (most of these were moved onto the platform), and not moved was scored for flowers not moved or moved away from the platform.

Spearman rank correlations ( $r_s$ ),  $t$ -test ( $t$ ),  $G$ -test ( $G$ ) and chi-squared ( $\chi^2$ ), are used for statistical comparisons. Means are expressed as  $\bar{X} \pm 95\%$  confidence intervals.

## RESULTS

### Flower Use on Bowers

Males showed very similar preferences for flowers in 1982 and 1984. The seven species that are most commonly used by male satin bowerbirds as bower decorations are: *Acacia alata*, *Solanum mauritianum*, *Dianella revoluta*, *Cassinia unicata*, *Solanum densivestitum*, *Geijera parviflora* and *Hibiscus heterophylla* (Table 1). During 2 years these species accounted for 93% of inflorescences on bowers. The relative preference for these seven species remained constant between these 2 years ( $r_s = 0.90$ ,  $P = 0.001$ ).

### Availability in the Habitat and Decoration Use

We found 81 flowering species on surveys of the field site, but only 70 of these species occurred along the transects (Table 1). None of the species missing from transects was common. Of the flower species available in the habitat 34% were used as decorations on bowers.

Two species were greatly over-represented on bowers relative to their occurrence in the habitat. *S. mauritianum* could not be found on the study area, but was collected by almost all bower-holders. These inflorescences are used both before they blossom, with only yellow sepals exposed, and in full blossom with purple and yellow flowers. They appear early in the year when other flowers are not available, and they last for more than a week before they wither. After intensive searching, the closest patch of this large plant (up to 3 m tall) was found 0.5 km north of the study site.

*D. revoluta* also ranks among the most commonly used flowers, and although not common in the habitat, inflorescences on plants could be found. Dried flowers retain their attractiveness and appeared to be extremely attractive to males (see below).

### Colour and Flower Choice

The 70 species found on bowers and along transects were assigned to nine colour classes so that we could evaluate the effect of colour on the flower preference of males. These classes were: purple and yellow, purple, light blue, dark blue, yellow, white, orange, red, and pink (see Table 1).

The number of species and the total number of inflorescences in each class were compared on the basis of their availability in the habitat and their presence on bowers. Inflorescences from 29 species were used as decorations by male satin bowerbirds: 10 white, seven purple, five yellow, three light blue, three dark blue and one purple and yellow. The percentage of total species in each colour class used on bowers was similar to the proportion of each species of that colour class occurring in the habitat, the major exception being that orange, pink and red species did not occur on bowers at all (Fig. 1). The yellow, purple, purple and yellow, and dark blue classes were used through both field seasons; other colours were present on bowers for only part of a season.

The percentage of inflorescences on bowers (1982 and 1984 combined) when classed by colour were: purple and yellow (31%), white (24%), yellow (20%), dark blue (16%), purple (7%), and light blue (1%). Red, pink and orange were not used on the bowers. This is a distinctly different pattern from the distribution of inflorescences in the habitat (Fig. 2), and the distribution of species on bowers.

The results are complicated by *S. mauritianum*, the only species in the purple and yellow colour class that was used; that combination of colours makes it unclear whether the purple, yellow, or the combination of colours contributes to this flower's attractiveness. Because its pattern of use is similar to that of other blue and purple species it has been included with that group.

### Experimental Tests of Flower Preference

#### Choice of flowers presented to males

Flowers were offered to males near their bowers in order to measure absolute preference of males for flowers without regard to availability in the habitat. In one set of experiments, inflorescences of four species were offered separately to males. The preference of males for such species was measured by the rate at which inflorescences were moved onto bowers, and by the percentage of decorations

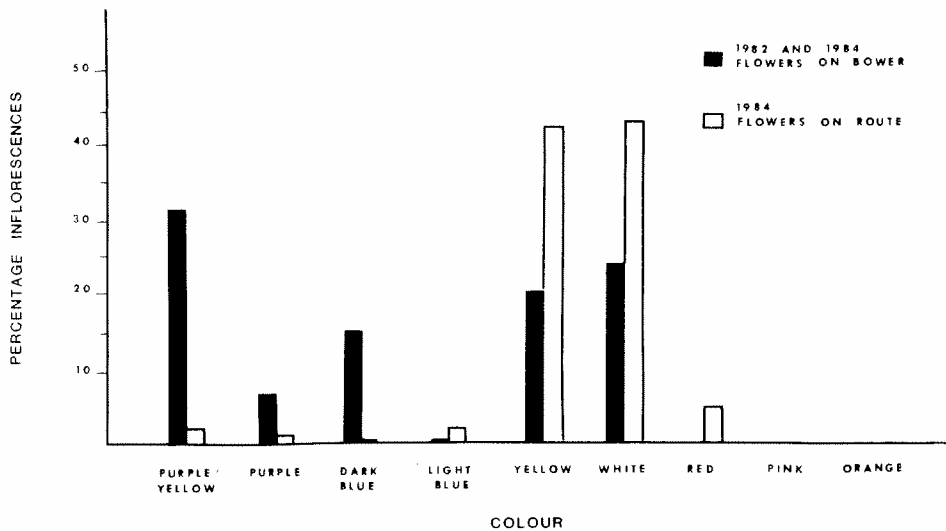


Figure 2. The percentage of inflorescences on bowers (1982 and 1984 combined) compared with the percentage of inflorescences on transects (route) (1984).

offered that were moved onto bowers. Stealing of inflorescences by males at adjacent bowers complicated the above analysis. To minimize this effect, males were excluded from comparisons if flowers were stolen before all of the flowers were moved. The results show (Fig. 3) that for both preference measures, blue *D. revoluta* flowers were the most

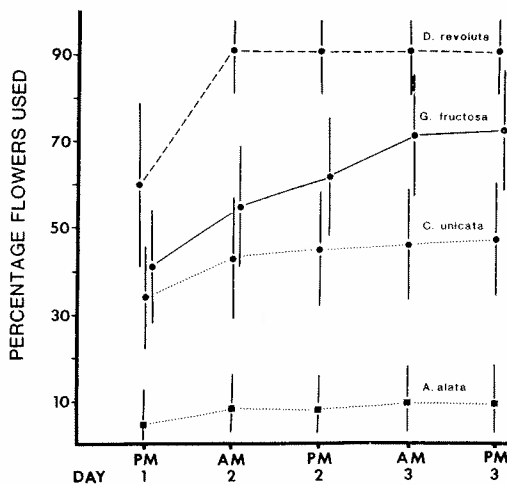


Figure 3. The presentation of inflorescences from single species at bowers. The percentage of flowers of four species moved onto bowers is shown as a function of time since the flowers were presented at the bower. Means are expressed as  $\bar{X} \pm 95\%$  confidence intervals.

preferred of all species used in the tests. *G. fructosa*, which is a rare bower decoration, was significantly more attractive than *A. alata* and *C. unicata*, two species that rank one and four in their frequency of use as bower decorations.

Stealing of experimental flowers provided an independent, and initially unplanned, measure of flower preference. *D. revoluta* was stolen at a much higher relative frequency (from 11 out of 27 bowers) than yellow and white species (nine bouts from 112 bowers;  $\chi^2 = 13.8$ ,  $P < 0.001$ ).

Flower preferences were also tested in direct comparisons in which inflorescences of two or more species were simultaneously offered at male bowers. A four-way comparison of the most common yellow and white species (*G. fructosa*, *A. alata*, *C. unicata* and *Eupatorium adenophorum*) shows that the strongest preference was for *G. fructosa* (Fig. 4).

The offering of *G. fructosa* with *Cassia odorata* showed there was a strong bias in favour of *G. fructosa* (15 out of 18), with almost no use of *C. odorata* (2 out of 18;  $\chi^2 = 19.8$ ,  $P < 0.001$ ).

The presentations of single species of flowers and stealing preferences indicate that *D. revoluta* is the most preferred of all flower species. A shortage of this flower prevented its use in multi-species comparisons. Three preference tests showed that *G. fructosa* was the most favoured of all yellow and white species. In a comparison of the single-species

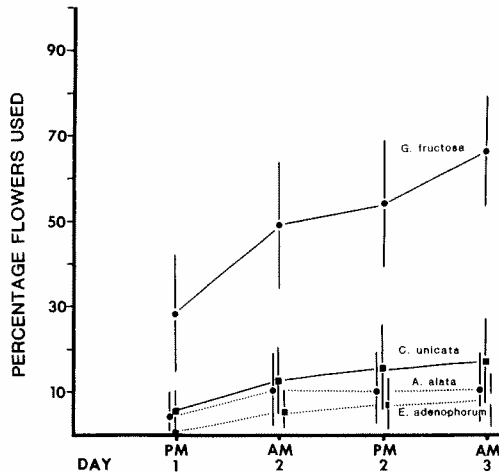


Figure 4. Simultaneous presentation of inflorescences from four species at bowers. The percentage of flowers of four species moved onto bowers used as a function of time since the flowers were presented at the bower. Means are expressed as  $\bar{X} \pm 95\%$  confidence intervals.

(Fig. 3) and the multi-species (Fig. 4) choice tests, *G. fructosa* appears to be even more preferred in multi-species tests. This suggests that the presence of *G. fructosa* reduces the attractiveness of other species. The strong preference for *G. fructosa* is unexpected because it is a creamy-white flower that does not fit the often described yellow preference, and because it is rarely found on bowers. Its scarcity on bowers may be due to a patchy distribution over the study area, and because its inflorescences occur at the top of tall, thin stalks where they are difficult to collect.

#### Flower colour experiment

*H. heterophylla* flowers were dyed and offered to males to test how a change only in the colour of

flowers affects the flower preferences of males. There was a strong preference for white and blue flowers relative to red (Table II). Some decorations disappeared and were most probably stolen; their position was scored from where they were last seen. There were no reversals in which flowers were moved off the bower after being used. Novel blue flowers were accepted as readily as natural white flowers, whereas red flowers were not used. Thus, the colour of the flowers appears to be the critical attribute affecting their use.

## DISCUSSION

We found that the vast majority of flower decorations on bowers are from a small number of species. In some cases, flowers of favoured species are rare, yet large numbers of them are found on bowers. This result implies very strong species-specific preferences for flowers used on bowers. We tested this hypothesis with several observations and experiments meant to determine the characteristics of flowers that cause them to be chosen as decorations.

We compared the colour of flowers used on bowers with those in the habitat in order to determine the importance of colour as a factor affecting the use of flowers on bowers. We found that flower species that were used came from purple, blue, yellow and white species in about the proportions that those colours of inflorescences occurred in the habitat. However, a comparison of the number of inflorescences used relative to their abundance in the habitat showed a different pattern. Purple and yellow, purple, and dark blue inflorescences appear on bowers with greater frequency than expected based on their distribution in the habitat, yellow and white are used, but less than expected, and orange, pink and red are not used. This result suggests that even though yellow and white inflorescences were much more common in the habitat, a strong preference for blue and purple inflorescences caused them to be used to a greater extent than would otherwise be expected. The experiment in which we simultaneously offered different coloured inflorescences to males and our observation of high rates of stealing of *Dianella* demonstrated a strong preference for blue flowers over yellow and white inflorescences. The colour preferences shown here for flowers parallel colour preferences known for the other types of deco-

Table II. Experimental test of preferences of males for dyed *Hibiscus*

Flower position	<i>Hibiscus</i> colour			Total
	Red	Blue	White	
Moved on bower	0	11	10	21
Not moved	15	4	5	24
Total	15	15	15	45

$G = 25.7$ ,  $df = 2$ ,  $P < 0.001$ .

rations. Males collect blue feathers and man-made items, yellow leaves and straw, white and light-brown snail shells and translucent brown cicada exuviae (Marshall 1954; Vellenga 1970; Borgia 1985a). Evidence from other studies of the preferences of males and females for other decorations (Borgia 1985a; Borgia & Gore 1986) indicates that, like flowers, there is a stronger preference for blue than for other colours of decorations.

We also tested the hypothesis that males have species-specific preferences. By offering male satin bowerbirds novel dyed *Hibiscus*, we found that males did not discriminate between white and blue inflorescences and chose not to use red flowers. In this experiment the shape and other characteristics of flowers except colour were the same, and males appeared to discriminate only on the basis of colour. This result suggests that colour is the key factor affecting flower choice, and that other flower characteristics are relatively unimportant in influencing preferences of males. Chiselm's (1934) observation that male bowerbirds often use exotic species, provides additional evidence against the hypothesis that males have evolved species-specific flower preferences.

Results of comparisons of flower choice experiments also showed that some species commonly found on bowers were less preferred than species that rarely appear on bowers. This suggests that flower preferences of males are more general than is indicated by the distribution of flowers on bowers.

The size and location of inflorescences on plants are among the factors that may affect which species of flowers are collected. Bowerbirds are relatively large birds (200–300 g) and may have trouble collecting flowers from shrubs that do not have adequate perches near inflorescences. Among the five species of flowers most used by bowerbirds, four were woody plants (*A. alata*, *S. mauritianum*, *C. unicata* and *H. heterophylla*) that could provide an adequate perch for males collecting blossoms. Flowers of *D. revoluta* seem less accessible for collection by males, unless perhaps males are able to bend to the ground the thin stalks that carry inflorescences.

Local abundance of flowers affects the type of decoration on males' bowers. The patchy distribution of flowers should increase the overall diversity of flowers used. In fact, a comparison of flower decorations on bowers in the two most obviously different habitats, dry *Eucalyptus* forest and rainforest, showed important differences in the flower

species used on bowers. Rainforest bowers have some species in common with *Eucalyptus* forest bowers, e.g. *S. mauritianum*, but they are also the only bowers that had the rainforest species *Calanthe triplicata* and *Geijera parviflora*. A difference also existed when 'eastern' and 'western' bowers were compared. Eastern bowers were near large fields of *Trifolium* and *G. fructosa* and are the only bowers where inflorescences of these species were used. Nonetheless, even with these constraints, the widespread use of a few species creates a high overall similarity of species among bowers.

The ability of flowers to withstand desiccation may also have a significant effect on patterns of flower use. All of the flowers regularly used by satin bowerbirds had relatively thick blossoms that resisted immediate wilting. This is especially true of the flowers of *S. mauritianum* which remained intact on bowers after more than 2 weeks. Bowerbirds may be able to learn the value of flowers as decorations based on their ability to resist wilting and use this information in choosing species to display on their bowers.

Taken together, these results suggest that there is no obvious species-specific preference for flowers. Male choice of inflorescences appears to be based on more general criteria, such as colour. The distribution of species on bowers is in large part influenced by colour, but other factors, such as accessibility, may be important. The flowers we observed on bowers were of a wider range of colours than is commonly described for satin bowerbird preferences (e.g. Morrison-Scott 1937; Marshall 1954).

The aesthetic preference and the matching hypotheses are the most frequent explanations for the use of flowers on bowers (e.g. Marshall 1954; Cooper & Forshaw 1977; Diamond 1982). These hypotheses have limited value because they only describe males' decoration preferences and fail to provide an ultimate explanation of how the existing choice pattern evolved.

The matching hypothesis suggests that bowerbirds may have evolved to match decorations with the male's plumage (Marshall 1954) or eye colour (Morrison-Scott 1937). Adult male satin bowerbirds are a dark iridescent blue-black and have a yellow beak. The colours of the males are similar to their colour preferences both in this and other studies (Morrison-Scott 1937). Even so, the matching hypothesis does not explain all observed colour preferences. Colours of some of the most com-

monly used decorations of satin bowerbirds are not part of the male's plumage, e.g. the bright white of bleached snail shells, the white flowers of *C. unicata* and *H. heterophylla* and the transparent brown of cicada and other insect parts. Hence, the coloration of males cannot be the sole determinant of their colour preferences. Moreover, when the blue-black flight feathers of male satin bowerbirds are offered to males to use as display objects, they reject them (Borgia, unpublished data). Instead, they most prefer the blue feathers of the crimson rosella parrot *Platycercus elegans* (Borgia & Gore 1986).

Male bowerbirds of other species have colour preferences that do not match their plumage. For example, *Chlamydera cerviniventris* has grey plumage and uses large numbers of green berries to decorate its bower (Peckover 1969). Male *Sericulus chrysocephalis* have a black body with a bright gold head and back, and decorate their bowers with blue, green and black fruits on a bed of green leaves inside the bower (Ramsay 1867; Chaffer 1932; Veselovsky 1979; personal observation). *Amblyornis inornatus* males, who are grey-brown and may have evolved from species with a bright yellow/orange crest, use red, yellow, blue, black and white decorations (Gilliard 1969). *A. inornatus* decorations match neither the plumage colour of males nor that of their likely ancestors. Thus, for most bowerbirds there are important differences between the colours used in bower display and that species' plumage.

Darwin's aesthetic preference hypothesis suggests that females have an innate sense of beauty and that this influences their mating preferences. The use of flowers by satin bowerbirds has been cited as an indication of an aesthetic preference (Diamond 1982). There is, however, no evidence to support this claim. The flower colours that satin bowerbirds use do not appear to be different from those of other collected objects, and there is no evidence to indicate a larger effect from flowers than other bower decorations (Borgia 1985a). This does not deny the possibility that choice based on aesthetic criteria, such as a general preference for whole or symmetrically shaped objects, might occur. For instance, satin bowerbirds prefer feathers in good condition and bowers that are symmetrical and in good condition (Borgia 1985a, unpublished data). Even so, for two reasons, the choice of inflorescences of some colours and the rejection of others are unlikely to be explained by an aesthetic preference hypothesis. First, choice

based on aesthetic preference would imply that some colours, or colour combinations, are inherently more aesthetically pleasing than others. We know of no biophysical law that would predict this choice pattern and thereby allow a test for the aesthetic preference hypothesis. Second, bowerbird species differ greatly in the colour of objects they use in display (Marshall 1954), suggesting that there is no obvious colour preference that is aesthetically pleasing to all species. A more parsimonious hypothesis, and one supported by the data reported here, is that the colour of objects is critical in determining their use as decorations on bowers, and that flowers are used because they are among the few available objects of the appropriate colour. What remains to be determined, however, is why bowerbird species evolve preferences for particular colours.

Fisher's runaway model is often cited as the cause for the evolution of many male display characters (e.g. Arnold 1983). Recent versions of this model claim that male characters need not convey information about the relative fitness of males in order to evolve (Lande 1981; Kirkpatrick 1982, 1985). According to these models, flower use and other male display characters are an arbitrary result of sexual selection. The existence of general preferences among satin bowerbirds for blue and yellow and white inflorescences are unrelated to their rarity in the habitat or the distinctiveness of the signals that they offer. Because these models make no explicit predictions about the types of decorations that should be preferred, they are difficult to falsify.

Bowers and their decorations may serve as indicators of a male's quality as a sire (Borgia et al. 1985). Females may favour males who exhibit scarce decorations because the ability to accumulate and hold these decorations indicates a male's good physical condition and high quality as a sire. Borgia & Gore (1986) have shown that the stealing of blue feathers from bowers of other male satin bowerbirds is the major source of this rare decoration, and that a male's success in stealing is correlated with the number of feathers on bowers. In addition, male-male aggressiveness at feeding sites is correlated with a male's success in stealing. Thus, the necessary conditions exist for females to assess the dominance of males based on the number of blue feathers on bowers. Our finding that (1) the most consistently collected flowers (blue and purple) are scarce, (2) there is a much stronger

preference for blue and purple over the more common yellow and white inflorescences, and (3) there is a higher rate of stealing of blue and purple than yellow and white inflorescences, suggests that blue and purple inflorescences serve the same function as blue feathers. If it were found that other species of bowerbirds consistently used (and stole), or did not use (or steal), rare decorations, then we could determine whether decoration preferences are really arbitrary or if they might have been shaped by a preference by females for indicator characters.

Females might obtain high-quality sires by preferentially mating with older males (Halliday 1978; Wilbur et al. 1978; Howard 1979). The ability to accumulate scarce decorations could indicate a male's relative age if past experience enhances his ability to steal decorations from other males. The number of inflorescences on bowers of male satin bowerbirds is correlated with male age (Borgia, unpublished data), so it is possible that the number of flowers on bowers could be used by a female to assess a male's age.

Males may have evolved a preference for certain colours because of the need for unambiguous signals at bower sites. Males who project a distinctive signal to visiting females (see Zahavi 1978; Parker 1983) may gain from providing females with unambiguous cues that indicate the presence of a bower, or aid females in recognizing bowers of males of their own species. Here again, the use of rare decorations alone or in combination with other uncommon objects may provide this distinctiveness to the display court. The combinations purple-blue and yellow-white used by satin bowerbirds are colour combinations not likely to be found away from bowers in the habitat. Other bowerbird species, such as *Chlamydera nuchalis* and *Chlamydera maculatum*, use large numbers of white stones to create a bright background on the platform, and coloured objects are placed over this layer (Marshall 1954; Warham 1957). The production of distinctive signals may also require that displaying males withstand raids by other males, so this and the previous model need not be exclusive.

In summary, the patterns of flower use by satin bowerbirds, and specifically their strong preference for scarce blue and purple flowers, are consistent with models that suggest that females use male displays to detect individual differences between males. Even so, an effective test of these models will require detailed studies of decoration preference in other bowerbird species.

## ACKNOWLEDGMENTS

This work was supported by funds from the American Philosophical Society, Harry Frank Guggenheim Foundation, the University of Maryland and the University Computer Center and the National Science Foundation (BNS 81-13477 and BNS 83-08154). GB was supported by a University of Melbourne Research Fellowship. Thanks for support goes to members of the University of Melbourne Zoology Department, especially M. J. Littlejohn and J. Hook. K. Collis, S. Lukert and E. Thompson were invaluable as assistants. The Jack and Ned Hayes, Mulchay and Bell families provided many forms of assistance and, with the N.S.W. Forestry Commission, allowed access to their property. Richard Donaghey marked birds and provided bower locations at Wallaby Creek. Valuable criticisms of the manuscript were made by A. Houde, C. Loffredo and J. Lauridsen.

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(Received 2 September 1985; revised 30 June 1986; M.S. number: A4606)

