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

GERALD BORGIA*, INGRID M. KAATZ† & RICHARD CONDIT‡

*Department of Zoology, University of Maryland, College Park, MD 20742, U.S.A.
†Department of Biology, Cornell University, Ithaca, NY 14853, U.S.A.
‡Department of Biology, Thimann Laboratories, University of California, Santa Cruz, CA 95064, U.S.A.

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 that this affects 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 Beura 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 shrub, 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 used 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 if the bower type moved closer to the bower, and if these were moved onto the platform or moved was scored for flowers not moved away from the platform.

Spearman rank correlations (r_s), t-tests (t6) and chi-squared (x2) are used for comparisons. Means are expressed as ±1 standard error confidence intervals.

RESULTS

**Flower Use on Bowers**

Males showed very similar preferential flower use in 1982 and 1984. The seven species most commonly used by male satin bower decorations are: *Acacia alata*, *D. mauritiam*, *Dianella revoluta*, *Cassia*, *Solium densifolium*, *Geijera parviflora* and *Hibiscus heterophylla* (Table 1). During all months these species accounted for 93% of inflorescences on bowers. The relative preference for the most preferred species remained constant between the years (r = 0.90, P = 0.001).

**Availability in the Habitat and Decoration on Bowers**

We found 81 flowering species on survey in the study field site, but only 70 of these species remained along the transects (Table 1). None of the species were missing from transects was common. Of the species available in the habitat 83% were seen on bowers.

Two species were greatly over-represented on bowers relative to their occurrence in the habitat. *D. mauritiam* could not be found on the study site, but was collected by almost all bowers. *H. heterophylla* are used both by bower decoration, with only yellow sepal exposed, sunflower bald with purple and yellow flowers are appear early in the year when other flowers were available, and they last for more than a week before they wither. After intensive searching, a 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 were not found. Dried flowers retain their attractive appearance and appeared to be extremely attractive to males (below).
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 (x^2), are used for statistical comparisons. Means are expressed as x ± 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 unica, Solanum densiflorum, 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...
Table I. Plant species flowering on the study site during the satin bowerbird mating season shown with their colour and distribution in the habitat and on bowers

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Colour*</th>
<th>On routes</th>
<th>1982</th>
<th>1984</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Abutilon oxycarpum</em></td>
<td>O</td>
<td>13</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Acacia alata</em></td>
<td>Y</td>
<td>21500</td>
<td>928</td>
<td>325</td>
</tr>
<tr>
<td><em>Acmena smithii</em></td>
<td>W</td>
<td>7180</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Anethelma biflorum</em></td>
<td>W</td>
<td>60</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Angophora subrelatina</em></td>
<td>W</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Aphanopetalum resinosum</em></td>
<td>W</td>
<td>7</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td><em>Araujia hortorum</em></td>
<td>W</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Anisoptera curassaria</em></td>
<td>R</td>
<td>26</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Brachycome multifida</em></td>
<td>P/Y</td>
<td>16</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Brunoniella australis</em></td>
<td>B</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Caladenia carnea</em></td>
<td>P</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Calanthe triplicata</em></td>
<td>W</td>
<td>5</td>
<td>21</td>
<td>0</td>
</tr>
<tr>
<td><em>Cassia planticola</em></td>
<td>Y</td>
<td>645</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Cassinia unica</em></td>
<td>W</td>
<td>3399</td>
<td>623</td>
<td>172</td>
</tr>
<tr>
<td><em>Ceratium sulphureum</em></td>
<td>P</td>
<td>28</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td><em>Cissus hypoglauca</em></td>
<td>Y</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Citriobatus pauciflorus</em></td>
<td>W</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Clematis aristata</em></td>
<td>W</td>
<td>10</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td><em>Commelina cyanea</em></td>
<td>Y</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Cordylina stricta</em></td>
<td>P</td>
<td>31</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Crotalaria linifolia</em></td>
<td>Y</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Dendrobium falcatus</em></td>
<td>W</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Dianella cerulea</em></td>
<td>LB</td>
<td>22</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td><em>Dianella revoluta</em></td>
<td>DB</td>
<td>346</td>
<td>697</td>
<td>297</td>
</tr>
<tr>
<td><em>Dipsadium punctatum</em></td>
<td>R</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Diospyros australis</em></td>
<td>W</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Diseris aurea</em></td>
<td>Y</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Drymophila moorei</em></td>
<td>W</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Ehretia acuminata</em></td>
<td>W</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Epilobium billardieri</em></td>
<td>P</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Eucalyptus punctata</em></td>
<td>Y</td>
<td>18048</td>
<td>0</td>
<td>50</td>
</tr>
<tr>
<td><em>Eupatorium adenophorum</em></td>
<td>W</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Geranium molle</em></td>
<td>LB</td>
<td>2844</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Geijera parviflora</em></td>
<td>W</td>
<td>0</td>
<td>247</td>
<td>5</td>
</tr>
<tr>
<td><em>Glycine clandestina</em></td>
<td>P</td>
<td>147</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td><em>Gomphocarpus fructosa</em></td>
<td>W</td>
<td>511</td>
<td>1</td>
<td>35</td>
</tr>
<tr>
<td><em>Grevillea robusta</em></td>
<td>R</td>
<td>13056</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Hardenbergia violacea</em></td>
<td>P</td>
<td>25</td>
<td>77</td>
<td>76</td>
</tr>
<tr>
<td><em>Hedranta hylomorphophytopetala</em></td>
<td>P k</td>
<td>276</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Hibiscus heterophylla</em></td>
<td>W</td>
<td>45</td>
<td>282</td>
<td>80</td>
</tr>
<tr>
<td><em>Hybanthus sp.</em></td>
<td>O</td>
<td>16</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Hymenosporum flavum</em></td>
<td>Y</td>
<td>0</td>
<td>0</td>
<td>31</td>
</tr>
<tr>
<td><em>Hypericum japonicum</em></td>
<td>O</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Lantana camara</em></td>
<td>P/Y</td>
<td>4134</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Leptosia sp.</em></td>
<td>LB</td>
<td>752</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Maytenus silvestris</em></td>
<td>W</td>
<td>1541</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Melia azedarach</em></td>
<td>W</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Milleria megasperma</em></td>
<td>P</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Notelaea linearis</em></td>
<td>Y</td>
<td>595</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Oxalis corniculata</em></td>
<td>Y</td>
<td>1130</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Parakebe sp.</em></td>
<td>P</td>
<td>140</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Passiflora alba</em></td>
<td>W</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Plectranthus greveolens</em></td>
<td>LB</td>
<td>56</td>
<td>4</td>
<td>76</td>
</tr>
<tr>
<td><em>Pittosporum revolutum</em></td>
<td>Y</td>
<td>0</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td><em>Pseudanthemum variabile</em></td>
<td>W</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure I. The percentage of specific transects (route) (1984).
Table I. cont.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Colour*</th>
<th>On routes</th>
<th>1982</th>
<th>1984</th>
</tr>
</thead>
<tbody>
<tr>
<td>Psychotria daphnoides</td>
<td>W</td>
<td>1414</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ranunculus lappaceus</td>
<td>Y</td>
<td>22976</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rubus parvifolius</td>
<td>Pk</td>
<td>59</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rubus rosifolius</td>
<td>W</td>
<td>11</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>Solanum mauritianum</td>
<td>P/Y</td>
<td>0</td>
<td>887</td>
<td>1198</td>
</tr>
<tr>
<td>Solanum densiflorum</td>
<td>P</td>
<td>1004</td>
<td>274</td>
<td>36</td>
</tr>
<tr>
<td>Spiranthus sinensis</td>
<td>P</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Swainsona galegiformia</td>
<td>LB</td>
<td>160</td>
<td>23</td>
<td>2</td>
</tr>
<tr>
<td>Taraxacum sp.</td>
<td>Y</td>
<td>197</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Thysanotus tuberosus</td>
<td>Y</td>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trifolium repens</td>
<td>W</td>
<td>83170</td>
<td>29</td>
<td>60</td>
</tr>
<tr>
<td>Velleia paradoxa</td>
<td>Y</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Verbascum virgatum</td>
<td>Y</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Verbena bonariensis</td>
<td>LB</td>
<td>730</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>Verbena rigida</td>
<td>P</td>
<td>1684</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Veronica cinerea</td>
<td>P</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Vigna vexillata</td>
<td>P</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Viminaria juncea</td>
<td>Y</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Viola betonicifolia</td>
<td>W</td>
<td>2</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>Viola hederacea</td>
<td>P</td>
<td>58</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>Wahlenbergia stricta</td>
<td>DB</td>
<td>17</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Youngia japonica</td>
<td>Y</td>
<td>30030</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Zelneria cunninghami</td>
<td>W</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

* O = orange; Y = yellow; W = white; R = red; P/Y = purple and yellow; B = blue; P = purple; LB = light blue; DB = dark blue; Pk = pink.

Figure 1. The percentage of species on bowers (1982 and 1984 combined) compared with the percentage of species 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 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 2](image1.png)

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

![Figure 3](image2.png)

**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.

![Figure 4](image3.png)

**Figure 4.** Simultaneous presentation of four species at bowers. The percentage of four species moved onto bower used as a function since the flowers were presented at the bower expressed as \( \bar{x} \pm 95\% \) confidence intervals (Fig. 3) and the multi-species (Fig. 4).

_G. fructosa_ appears to be even more attractive to species. The strong preference for _G. fructosa_ reduces the attractiveness of species. The strong preference for _G. fructosa_ is expected because it is a creamy-white flower which does not fit the often described yellow and white and because it is rarely found on bower inflorescences. The scarcity on bower may be due to the distribution of the study area, and which inflorescences occur at the top of tall bower where they are difficult to collect.

**Flower colour experiment**

_H. heterophylla_ flowers were dyed a different colour and males moved onto bower at males to see how a change in the

| Table II. Experimental test of preference for males for dyed Hibiscus |
|-------------------------|---------------|---------------|
| **Hibiscus colour**     | **Red**       | **Blue**      |
| Flower position         | Moved on bower| Not moved     |
|                        | 0             | 15            |
|                        | 11            | 4             |
|                        | 10            | 5             |
| Total                  | 15            | 15            |

\( G = 25.7, df = 2, P < 0.001. \)
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* flowers

<table>
<thead>
<tr>
<th>Hibiscus colour</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flower position</td>
</tr>
<tr>
<td>Moved on bower</td>
</tr>
<tr>
<td>Not moved</td>
</tr>
<tr>
<td>Total</td>
</tr>
</tbody>
</table>

\[G = 25.7, df = 2, P < 0.001.\]
lations. 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. Chisim’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 bower 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 bower.

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’ bower. The patchy distribution of flowers should increase the overall diversity of flowers used. In fact, a comparison of flower decorations on bower in the two most obviously different habitats, dry *Eucalyptus* forest and rainforest, showed important differences in the flower species used on bower. Rainforest bowerbirds have some species in common with *Eucalyptus* forest bowerbirds, e.g. *S. mauritianum*, but they are also the only bower that had the rainforest species *Calanthe trilicata* and *Geijera parviflora*. A difference also existed when ‘eastern’ and ‘western’ bowerbirds were compared. Eastern bowerbirds were near large fields of *Trifolium* and *G. fructosa* and are the only bower birds 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 bower.

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 bower for 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 bower.

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 bower 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 bower (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 commonly used decorations of satin I part of the male’s plumage, e.g. 1 bleached snail shells, the white flc and *H. heterophylla* and the trout cicada and other insect parts. Her of males cannot be the sole det colour preferences. Moreover, wt flight feathers of male satin bow to males to use as display objects (Borgia, unpublished data). Ins prefer the blue feathers of the parrot *Platycercus elegans* (Borgi.

Male bowerbirds of other se preferences that do not match the example, *Chlamydera cervinvent* mage and uses large numbers of decorate its bower (Peckover 1969; *chrysocephalus* have a black body w head and back, and decorate th blue, green and black fruits on a be inside the bower (Ramsay 1867; Veselovsky 1979; personal observa *nis inornatus* males, who are grey-l have evolved from species with a orange crest, use red, yellow, blue, 1 decorations (Giilliard 1969). *A. h* rations match neither the plumage nor that of their likely ancestors. bowerbirds there are important between the colours used in bower and species’ plumage.

Darwin’s aesthetic preference hy suggests that females have an innate se and that this influences their matin The use of flowers by satin bowerbird cited as an indication of an aesthe (Diamond 1982). There is, however, t support this claim. The flower color birds use do not appear to be of o other collected objects, and evidence to indicate a larger effect th other bower decorations (Borgia 1985a) does not deny the possibility that tastes or aesthetic criteria, such as a general pl whole or symmetrically shaped of occur. For instance, satin bower fea in good condition and bow symmetrical and in good condition (E published data). Even so, for two se choice of inflorescences of some colt rejection of others are unlikely to be an aesthetic preference hypothesis.
forest bowers have
Eucalyptus forest
not they are also the
rainforest species parsiflora. A differ-
tern’ and ‘western’
7n bowers were near
fuctiosa and are the
1ces of these species in
with these con-
a few species creates
1ces among bowers.

Instead desiccation flcet on patterns of
gularly used by satin
nick blossoms that
is especially true of
n which remained
an 2 weeks. Bower-
vale of flowers as
lily to resist wilting
choosing species to
suggest that there is
ference for flowers.
appears to be based
ich as colour. The
ers is in large part
iter factors, such as
nt. The flowers we
a wider range of
described for satin
orison-Scott 1937;
and the matching
ent explanations for
\qg Marshall 1954;
mond 1982). These
because they only
ferences and fail to
of how the existing
1 suggests that bow-
ch decorations with
1954) or eye colour
male satin bower-
-black and have
males are similar to
in this and other
Even so, the match-
all observed colour 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. unciata
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 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 bowers of other species have colour
preferences that do not match their plumage. For
example, Chlamydera cerviniventris has grey plum-
age and uses large numbers of green berries to
decorate its bower (Peckover 1969). Male Sericulus
chryscephalum 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 de-
corations 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 sug-
gests 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 bowler 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 bowers 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 inher-
ently 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 parsim-
onous 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 bowers 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.

Bowes 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 accumu-
late 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 deco-
ratation, 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 pur-
ple) 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 bower of male satin bowerbirds is correlated with male age (Borgia, unpublished data), so it is possible that the number of flowers on bower 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 bower 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 bower 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.

REFERENCES
Chaffer, N. 1932. The regent bird. Emu, 32, 8–11.


(Received 2 September 1985; revised 30 June 1986; MS. number: A6666)