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An inverse relationship between decoration and food colour preferences in satin bowerbirds does not support the sensory drive hypothesis

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Male bowerbirds collect and decorate their bowers with coloured objects that influence female choice. A recent version of the sensory drive hypothesis claims that female food colour preferences have driven the evolution of female preferences for the colour of male display traits. This hypothesis predicts a positive correlation between male display and food colour preferences. A positive correlation between food and decoration preferences could also arise because of sensory biases built into bowerbirds or the environment. Here we test hypotheses that (1) male and female satin bowerbirds show well-defined food colour preferences, (2) these preferences correlate with independently assessed preferences for bower decorations, and, in a cross-species comparison, (3) food items were used as the first bower decorations. We found that male and female satin bowerbirds, *Ptilonorhynchus violaceus*, preferentially use long wavelength and were colours as food items. Male decoration preferences were biased towards colours of short wavelength and were negatively correlated with food colour preferences. Our reconstruction of ancestral character states is most consistent with the hypothesis that the original bower decorations were inedible objects and were thus unlikely to have been dual-use traits that also functioned as food items. Our results do not support the hypothesis that food colour preferences have driven the evolution of bower decoration colour preferences nor that sensory drive has caused similar food and decoration preferences, but instead suggest that different factors have shaped female preferences for male display and food colour preferences in bowerbirds.

There are divergent views as to how female preferences for elaborated male display traits evolve. One class of sexual selection models, including good genes models, argues that female mating preferences evolved because of the benefits that females gain from choosing high-quality mates. Numerous studies have shown female preferences for male traits that indicate good genes benefits (e.g. Hill 1991; Kempenaers et al. 1992; Petrie 1994; Hasselquist et al. 1996; Hoikkala et al. 1998; Welch et al. 1998). Alternatively, preexisting receiver (or sensory) bias models (see Endler & Basolo 1998; Basolo 2002) suggest that already existing but previously unexpressed female preferences can become important in mate selection (e.g. Basolo 1990; Ryan 1990; Ryan & Rand 1990; Proctor 1991; Sakaluk 2000). These remain controversial because preexisting receiver biases are suggested to occur as side effects of selection for other traits, and consequently may often be maladaptive (see Ryan & Rand 1990). As such, it may be difficult to maintain such traits in competition with benefit-producing female preferences shaped by selection (see Sherman & Reeve 1999; Reeve & Sherman 2001; Borgia 2006). Several studies offer alternative interpretations for classic examples of preexisting receiver bias models (Meyer et al. 1994; Shaw 1995; Rosenthal & Evans 1998; Gabor 1999).

Rodd et al. (2002) proposed a version of the preexisting receiver bias hypothesis (which we label the food colour drive (FCD) hypothesis) in which preexisting female food colour preferences are secondarily used as female colour preferences for male display traits. Specifically, Rodd et al. argued that, in guppies, a female preference for eating orange calabash fruit, an important food source in some Trinidadian populations, causes females to prefer orange-spotted males in mate choice. This differs from the hypothesis that carotenoid-based orange spots on male guppies evolved as indicators of male genetic quality

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(e.g. Kodric-Brown 1989; Sargent et al. 1989), which is supported by positive correlations of orange coloration with condition (Nicoletto 1991, 1993) and courtship intensity (Nicoletto 1993) and negative correlations with parasite infection (Houde & Torio 1994).

Recently, Madden & Tanner (2003) have suggested that bowerbird decoration colour preferences are derived from food colour preferences. To test this hypothesis they offered peeled grapes dyed five different colours to males and females of several bowerbird species in Australian zoos. They scored grapes taken by females as indicators of food preferences and colours of grapes taken by males as indicators of male decoration preferences. They found a significant positive correlation in the colours of grapes selected by male and female regent bowerbirds, *Sericulus chrysocephalis*, and a nearly significant positive correlation in satin bowerbirds, *Ptilonorhynchus violaceus*, and concluded that this was positive support for the FCD hypothesis. However, because grapes taken by male bowerbirds could have been used as food, and because placement of the grapes on the bower was not a requirement for scoring them as decorations, it was unclear whether the male preferences measured were for decorations, food or a combination of both. Significantly, their results showed an intermediate preference for red objects as bower decorations by satin bowerbirds when previous work has shown that red is consistently not used but is actively removed as a bower decoration (Morrison-Scott 1937; Marshall 1954; Chaffer 1984; Borgia et al. 1987). Also, recent studies suggest little difference in food preference between satin and regent bowerbirds (Donaghey 1996; Lenz 1999) even though the colours of decorations that they use on bowers are different (Lenz 1999). These issues indicate that a more definitive test of the FCD hypothesis is necessary.

Alternatives to nonadaptive hypotheses have been proposed that may explain decoration colour use in bowerbirds. For example, male and female satin bowerbirds show a preference for blue decorations (Borgia 1985, 1995a; Borgia et al. 1987; Coleman et al. 2004), which are scarce (Borgia et al. 1987) and which males compete for (Borgia & Gore 1986) and use in displays (Borgia 1985; Patricelli et al. 2003) because they indicate male quality. Several other hypotheses have also been offered to explain colour preferences (e.g. preferences evolve to match male plumage: Morrison-Scott 1937; to enhance female recognition of bower sites: Borgia et al. 1987; or to contrast with the male and/or other decorations, causing increased visibility: Borgia et al. 1987).

Here we conducted two tests of the FCD hypothesis. First, we independently measured food and decoration colour preferences in satin bowerbirds to determine whether these preferences are similar, as predicted by the FCD hypotheses (see Madden & Tanner 2003), or whether they are different. This provided an opportunity to test and evaluate different sexual selection hypotheses in a species in which the influence of coloured display traits on female mate choice is well established. We offered an array of six different coloured food items and observed which colours were picked first by males and females to indicate food colour preferences. We independently measured male decoration colour preferences by offering an array of inedible Plexiglas squares with colours similar to those of the food items offered. We then tested for a correlation between decoration and food colour preferences. The test for the predicted positive correlation is also useful for evaluating two other hypotheses. Instead of food colour preferences driving decoration colour preferences, the reverse could be true. Since success in mate choice is critical for individual fitness, this seems a plausible alternative and could explain a correlation between food and decoration colour preferences. It is also possible that decoration and food colour preferences may be similar because of sensory drive (in the more limited sense of Endler 1992 rather than the more encompassing version of Endler & Basolo 1998), whereby neural circuitry and/or the environment might drive convergence in preferences for food and decoration colour. For example, in fish, water colour and turbidity (Endler & Houde 1995; Boughman 2001) and the sensory system (McDonald & Hawryshyn 1995) appear to have far-reaching effects on the evolution of male display that could also lead to the convergence of colour preferences for food and display.

Second, we made cross-species comparisons of decoration use by bowerbirds to test the hypothesis that food colour preferences shape decoration colour preferences. For example, food colour preferences might have affected the evolution of decoration colour preferences if food items were initially dual-use traits that were also used as bower decorations. We reconstructed ancestral character states to test the hypothesis that food items were initially used as bower decorations. This hypothesis would be supported if there was evidence that the predominant decorations on bowers of the ancestral bowerbird were edible. This test is valuable because the use of coloured decorations preceded the evolution of extant species and evidence of a relationship between food and decoration preferences at the time bower decoration evolved (see Kusmierski et al. 1997) would support the FCD hypothesis.

METHODS

Food Colour Choice Experiment

We conducted food colour preference studies on a natural population of satin bowerbirds in September and October in 2003 and 2004, at Wallaby Creek, New South Wales, Australia (28°28′ S, 152°26′ E). Our ability to attract birds that we had individually colour banded (see Borgia 1985) to traps with food at Wallaby Creek allowed us to test satin bowerbird food colour preferences in a natural population. We assessed the birds' food colour preferences by offering them six colours (red, yellow, orange, green, blue, violet; reflectance spectra are available on request) of Kellogg's Froot Loops cereal. Individual loops were cut into five equal parts to facilitate feeding by birds. We used the cereal because it provided a readily available supply of consistently coloured food objects of appropriate colours that were readily eaten by satin bowerbirds. In preliminary experiments, we placed the cereal in a linear array and the birds disproportionately fed on the ends of the array. To eliminate this effect, we placed six piles of cereal (each containing five pieces of the same colour) arrayed around the perimeter of a disk (30-cm diameter) that was easily observed from hides. The position of coloured cereal piles was randomized on the disk to remove possible effects of associations between colours and position. When birds arrived at the disk, observers recorded the order of colours eaten. In almost all cases, birds ate all five pieces of a single colour before moving on to the next colour, so the reported colour sequences represented transitions between colours eaten. Trials were scored only when one bird consumed food from the array. Individual birds ate on average 73.4% of the 30 pieces of cereal offered in a trial. The array was replenished before a new trial was scored. In blind trials, human observers found no differences in taste among the different colours of cereal and were unable to predict the colour of cereal based on its taste ($\chi^2_5 = 0.67$, $P = 0.98$). The first choices of naïve birds were not different from their later choices (see below), suggesting no effect of taste on the colour of cereal selected.

We analysed the results of these food colour preference trials in three ways. The first two measures were concerned with establishing the extent to which there were consistent food colour preferences. First, for 'average first food colour preferences', we recorded the first colour chosen by each bird in each trial for that bird, and then assigned each bird a colour preference based on the most common colour chosen among these trials. In the case of ties, the same colour preference rank was distributed among the tied colours, with each colour weighted inversely to the number of colours in the tie when the overall colour preference rank was calculated. We used this information to compute a rank for each colour across all birds (e.g. the colour chosen first most often had the highest rank). Second, we calculated the 'mean food colour preference' scores for each food colour by ranking the order of consumption of food items in each trial on a scale from 1 to 6, where 6 was the first colour eaten, 5 was the second colour eaten, and so on, to the last colour. An average score for each colour was computed for each bird. We then averaged these individual bird scores across all birds in a particular class (age or sex) to obtain our final ranking for that class. We also computed a third food colour preference measure, 'initial first food colour preference', based on each bird's first colour choice in its initial visit to our testing site. This last measure used only the limited information of a single trial, but it was useful for indicating preferences of naïve birds that had not previously tasted the cereal. A correlation between this last measure and our other two measures of food colour preference would suggest that colour preferences of naïve and experienced birds did not differ, and thus, were not due to differences in taste between the different coloured pieces of cereal. Food colour preferences were measured for both males and females. We observed more males because males were more aggressive and often chased females from areas where food was offered.

Decoration Colour Choice

We tested bower decoration colour preferences in satin bowerbirds by using six different coloured plastic (Plexiglas) squares (2.5 cm). Red, orange, yellow, green, blue and violet coloured squares were randomized on an array centred 15 cm from the middle of the bower entrance near the centre of the bower platform. We chose decoration colours so that we would approximate colours of the cereal pieces. Birds consistently reacted to the presence of squares, moving some closer and others further from the bower. We recorded the order in which plastic squares were picked up and the distance they were moved relative to the bower entrance for 19 adult male bower owners. Decorations that birds placed nearest the bower entrance were given the highest preference score and those moved the furthest away were given the lowest score.

Reflectance values were taken for bower decorations and cereal using an Ocean Optics S2000 spectrometer with a Xenon strobe light source using standard techniques. Three measurements were taken for each decoration type and the mean value was used as our measure of reflectance. We calculated the area under the reflectance curve from 400 to 700 nm as a measure of overall reflectance. Satin bowerbirds do not discriminate between blue decorations that have and have not had UV reflectance blocked experimentally (G. Borgia, personal observation), suggesting that UV reflectance is not critical in satin bowerbird decoration choice. For that reason we did not measure reflectance values in the UV range. We used chi-square tests and Spearman rank correlations for statistical comparisons. All tests were two tailed unless otherwise noted.

Cross-species Comparisons of Decoration Use

We compared decoration use for 14 bowerbird species (including Arfak and Fak Fak populations of Vogelkop bowerbirds, which are considered separate species: see Uy & Borgia 2000) using information collected from studies between 1981 and 2003 in Australia and New Guinea (Borgia 1985, 1995b, personal observations; Lenz 1994; Frith et al. 1996; Uy & Borgia 2000). For each species, we scored the use of potentially edible items (fruit and flowers) and man-made objects on male bowers. The data included results of tests of decoration preference in which an array of multicoloured man-made objects was placed near a male's bower and an observer recorded where each object was moved onto the bower (see Uy & Borgia 2000). Use of an array of different coloured inedible man-made objects excluded the possibility that inedible objects would have been used but appropriate coloured objects were not available. Species differed in the types of man-made objects they used (e.g. paper, ceramic tile, plastic beads), so individuals were tested with a wide array of like-coloured objects made of different material (Borgia 1993, personal observations; Uy & Borgia 2000). To reconstruct ancestral character states, we mapped the species scores onto a molecular (mt-DNA) bowerbird phylogeny (Kusmierski et al. 1997) using the ANCML computer program (Schluter et al. 1997). The first reconstruction produced a predicted percentage of edible decorations on bowers of ancestral bowerbirds based on the percentages of edible decorations used in extant species. We also reconstructed the tendency for ancestral bowerbirds to accept inedible but appropriately coloured man-made objects. Extant species received a score of one if they used man-made objects and zero if they did not. While these reconstructions have potential flaws (Cunningham et al. 1998; Losos 1999), they provide an unbiased (at least with regard to the hypotheses we were testing) means of inferring character states at the time bower decoration use evolved, and are thus useful in addressing the question of whether initial decorations were dual-use traits functioning both as food and as sexual display traits.

RESULTS

An Experimental Test of Food Colour Preferences in Satin Bowerbirds

We assessed food colour preferences in each of 35 birds (27 males and 8 females). In 2003 there were 15 males and 4 females tested, and in 2004 there were 21 males and 5 females tested. All colours of cereal were consumed by both sexes but there was unequal consumption by colour (chi-square test: $\chi^2_5 = 12.67$, $P < 0.\ 027$). A similar analysis based on all first choices in each trial (all trials included) showed a highly significant difference in colour use ($\chi^2_5 = 62.5$, $P < 0.0001$), with red, orange and yellow cereal eaten the most. There was a significant correlation between males and females for average first food colour preference (Spearman rank correlation: $r_S = 0.83$, $N = 6$, $t = 2.96$, $P = 0.04$), and mean food colour preference scores showed a marginally significant correlation ($r_S = 0.77$, $N = 6$, $t = 2.43$, $P = 0.07$).

The nearly significant positive association suggested no difference between the sexes in food colour preferences, so we combined the data for the individual sexes for all subsequent analyses. Average first food colour preference was correlated between adult and juvenile males ($r_S = 0.77$, $N = 6$, $t = 2.42$, $P = 0.037$, one tailed), suggesting that colour preferences do not differ as males age. Wavelength and initial first food colour preferences were also correlated ($r_S = 0.88$, $t = 3.82$, $P = 0.019$), suggesting that bowerbirds favoured coloured food items with longer wavelengths.

Bower decoration colour preference ranks were negatively correlated with both average first food colour preference ranks ($r_S = -0.94$, $N = 6$, $t = 5.66$ $P = 0.005$; Fig. 1) and mean food colour preference ranks ($r_S = -0.94$, $N = 6$, $t = 5.66$, $P = 0.005$; Fig. 2). This is opposite to the relationship predicted by the FCD hypothesis, and suggests that different kinds of preferences are used for choice of bower decorations and food. Natural bower decoration colour-use rankings (Table 1) also showed nonsignificant negative associations with average first food colour preference ($r_S = -0.75$, $t = 2.29$, $P = 0.084$) and mean food colour preference ($r_S = -0.64$, $t = 1.65$, $P = 0.17$), a result not consistent with the positive relationship predicted by the FCD hypothesis.

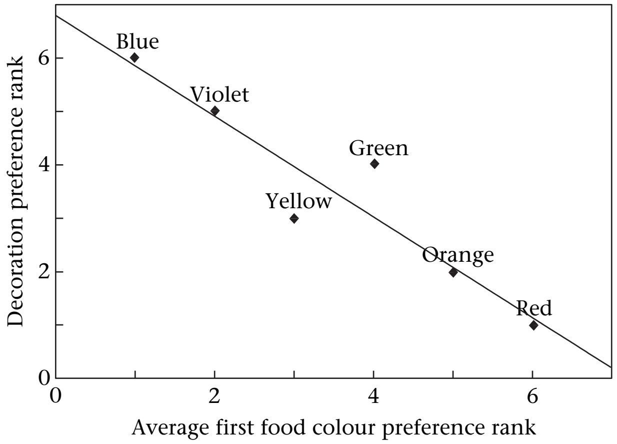

Figure 1. Relation between decoration colour preference and average first food colour preference in satin bowerbirds.

Initial first food colour preferences were also marginally correlated with mean food colour preference scores ($r_S = 0.79$, $N = 6$, $t = 2.62$, $P = 0.059$) and highly negatively correlated with male decoration preferences ($r_S = -0.94$, $N = 6$, $t = 5.659$, $P = 0.005$). These results suggest that food colour preferences that existed before the birds had ever tasted the cereal were retained in further trials, and that these initial food preferences were also not positively correlated with decoration preferences. This result is consistent with the suggestion that the birds used only colour and not another correlated character such as taste in their food choice decisions.

Were Food Items Historically Used as Decorations?

If female food preferences drive male decoration preferences, then appropriately coloured food items may have been used as bower decorations by ancestral male bowerbirds. With a few exceptions among bowerbird species (Vogelkop, Arfak population, *Amblyornis inornatus* A, and fawn-breasted bowerbirds, *Chlamydera cerviniventris*; Fig. 3a), the great majority of decorations used on bowers are not flowers or fruits, and even in species where these

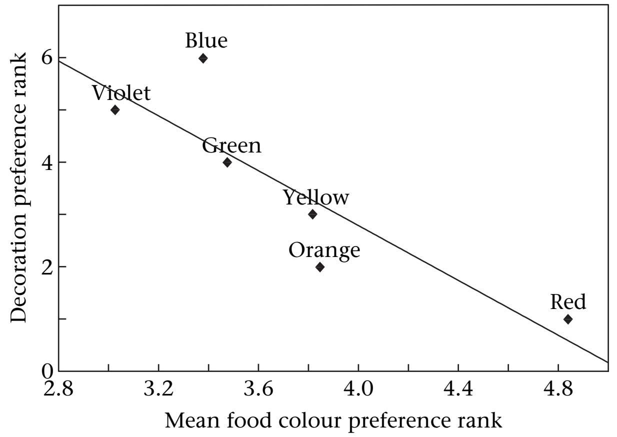

Figure 2. Relation between decoration colour preference and mean food colour preference in satin bowerbirds.

Table 1. Number of decorations by colour on 44 adult bowers at Wallaby Creek, New South Wales in 1982

Decoration colour	Mean number per bower
Yellow	37.3
White	11.7
Violet	10.0
Brown	9.1
Blue	7.5
Green	0.07
Orange	0
Red	0

are used, these objects are not typically eaten by males or females. Across the bowerbirds, 86% of bower decorations are not edible. Bowerbirds are known for collecting inedible objects (e.g. plastic, glass, metal and ceramic; Marshall 1954), and our survey of the bowerbird family (Fig. 3b) showed that inedible man-made objects are used when offered in 11 of 14 species. The mean ± SE percentage of potentially edible items on the bowers of ancestors was 18.1 ± 24.1%, indicating that fruit and flowers were not the predominant decorations on ancestral bowers (Fig. 3a). A similar reconstruction of the ancestral character state for acceptance of inedible man-made objects offered to males as bower decorations showed a value close to one (0.88 ± 0.35; Fig. 3b), suggesting that the ancestor did not require decorations that were edible. The readiness of most bowerbird species to use inedible objects, the low occurrence of fruits on bowers, and evidence that these are ancestral traits does not support the hypothesis that bower decoration preferences are derived from food preferences.

DISCUSSION

The significant negative correlation between food and experimental decoration preferences and the trend in the same direction between food and natural colour preferences that we found is opposite to the relationship predicted by the FCD hypothesis. These results support neither the FCD hypothesis nor the hypothesis that decoration preferences drive food colour choice in satin bowerbirds. These relationships suggest that there are different rules for food colour preferences and for decoration colour use, making it unlikely that food preferences have driven the evolution of decoration preferences. Our results are also inconsistent with a more general sensory drive hypothesis (see Endler 1992), under which sensory biases resulting from the sensory system (e.g. McDonald & Hawryshyn 1995) or environment (e.g. Endler & Houde 1995; Boughman 2001) has caused parallel evolution of food and decoration preferences. The distinctly different preferences associated with decoration colour and food colour suggest that there are different mechanisms affecting the evolution of each of these preferences.

What is less clear is why food and decoration colour preferences have this negative relationship. We were not certain that we would find a consistent food colour

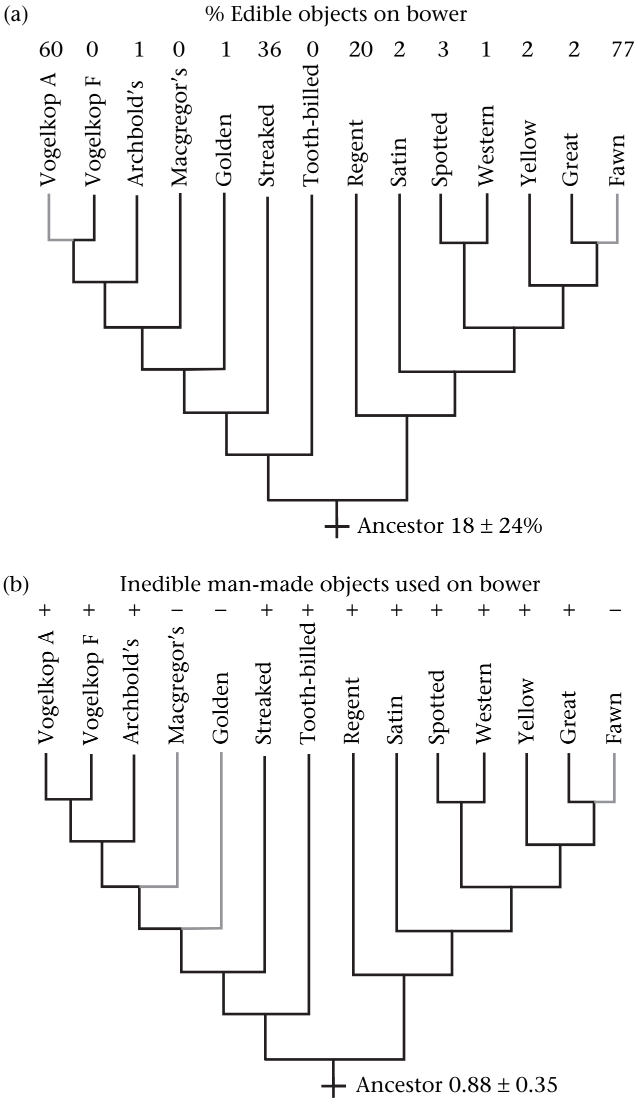

Figure 3. (a) Reconstruction of ancestor character state at the time bower decoration evolved for the percentage of edible objects used as bower decorations. Percentage of edible objects is mapped onto the bowerbird phylogeny, with black lines showing lineages having less than 50% edible objects on their bowers and grey lines showing lineages having greater than 50% edible objects on their bowers (percentages for extant species are also reported for each species). Source or location (G. Borgia, personal observations) for field studies: Arfak Vogelkop, *Amblyornis inornatus* A, Fak Fak Vogelkop, *Amblyornis inornatus* F (Uy & Borgia 2000); Archbolds', *Archboldia papuensis* (Frith et al. 1996); MacGregor's, *Amblyornis macgregoriae* (Sinove, Central Province, Papua New Guinea); golden, *Prionodura newtoniana* (Mt Baldy, Atherton, Queensland, Australia); streaked, *Amblyornis subalaris* (Kagi, Central Province, Papua New Guinea); regent, *Sericulus chrysocephalis* (Lenz 1994); satin, *Ptilonorhynchus violaceus* (Borgia 1985; Kagi, Central Province, Papua New Guinea); spotted, *Chlamydera maculata*, great, *Chlamydera nuchalis* (Borgia 1995b); toothbilled, *Ailuroedus dentirostris* (Mt Baldy, Atherton, Queensland, Australia); western, *Chlamydera guttata* (Exmoth, Western Australia); fawn-breasted, *Chlamydera cervinventris*, yellow-breasted, *Chlamydera lauterbachi* (Dumpu Station, Madang Province, Papua New Guinea). (b) Reconstruction of the tendency for ancestral bowerbirds to accept inedible man-made objects as bower decorations. Extant species received a score of one if they used inedible man-made objects (+, black lines) or a score of zero if they did not (−, grey lines).

preference because strong food colour preferences could limit food intake by causing individuals to reject valuable food items, and because field observations of satin bowerbirds show no evidence of strong food colour preferences (Donaghey 1996; Lenz 1999). Our observation that food items of all colours were consumed in experimental trials suggests that food colour preferences in satin bowerbirds may function in prioritizing food consumption rather than causing any particular colour of food to be rejected with its nutritional benefits lost. Preferred food colours had the highest light reflectance values, suggesting the possibility that birds chose the brightest food items first (Fig. 4). This bias may allow satin bowerbirds to forage more efficiently by causing them to select the most easily detectable foods first. It is also possible that the wavelength of reflected light for food items is correlated with carotenoid content and that satin bowerbirds select these items because they prefer high-carotenoid items in their diet. Carotenoids are found in orange, yellow and red fruits, and satin bowerbirds showed the strongest preference for these food colours, which is consistent with a preference for carotenoid-indicating colours. However, more information, including carotenoid content of different coloured food items eaten by satin bowerbirds, would be needed to effectively test this hypothesis.

Our decoration preference results are consistent with other studies of satin bowerbird decoration preferences in which males show a strong male preference for blue decorations and a dislike for red decorations (Morrison-Scott 1937; Marshall 1954; Chaffer 1984; Borgia et al. 1987; J. Keagy, unpublished data) and females show a preference for blue decorations (Borgia 1985, 1993; Patricelli et al. 2003; Coleman et al. 2004). Naturally white hibiscus flowers were offered to males along with others that were dyed blue and red; males consistently chose blue and white and rejected red (Borgia et al. 1987). Coleman et al. (2004) found that males readily added large amounts of blue plastic chips to their bower platforms when the chips were placed in piles nearby. Male satin bowerbirds also preferentially steal blue decorations from other males (Marshall 1954; Borgia & Gore 1986; Hunter & Dwyer 1997). The ranking of decoration colours based on their frequency of use on bowers where only natural objects were available (Wallaby Creek, Table 1) was not significantly correlated with our experimental measure of bower decoration preferences ($r_S = 0.58$, $t = 1.42$, $P = 0.23$), possibly because of the relative rareness of blue objects in the natural habitat (Borgia et al. 1987), which may account for the inability of most males to amass large numbers of blue decorations on their bowers. Near picnic areas man-made blue plastic objects are common and are used in abundance on bowers (Hunter & Dwyer 1997), and can be the most common decoration colour on satin bowerbird bowers (G. Borgia, personal observation).

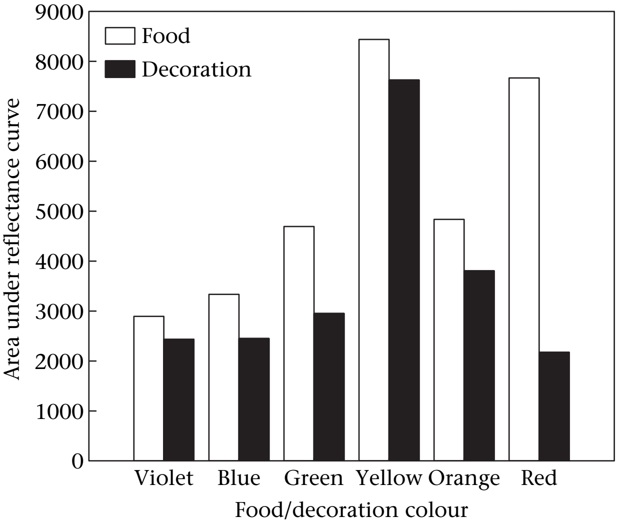

Figure 4. Brightness as indicated by area under the reflectance curve for six colours of bower decorations and cereal used in satin bowerbird bower decoration and food colour choice experiments.

The blue objects used on satin bowerbird bowers typically have relatively low reflectance, so it appears that the criteria used for choosing bower decorations in this species are different from those used in food choice. In a survey of the availability of putative decorations of different colours in habitat adjacent to satin bowerbird bowers, Borgia et al. (1987) found that blue decorations were extremely rare, and they hypothesized that blue objects are preferred as decorations by satin bowerbirds because they are scarce. Borgia & Gore (1986) suggested that males that are able to accumulate blue decorations on their bowers under the threat of theft by competing bower holders are able to signal aggressive dominance to females, which may be an important indicator of male genetic quality. In support of this hypothesis, Hunter & Dwyer (1997) found that less stealing of blue objects occurred at locations where blue was more common. Rareness of natural blue objects, in part, may be due to their low relative reflectance, so few other plants or animals use blue as a signal. Male satin bowerbirds may compensate for the use of blue display items of low reflectance by placing them on a relatively bright yellow carpet of straw and leaves, thus enhancing contrast and increasing the visibility of blue decorations laid on top. This manipulation of decorations of particular colours may allow satin bowerbirds to construct a unique and highly visible signal that also conveys information about male status and possibly genetic quality.

Male reaction to less preferred bower decoration colours (e.g. red) is very different from that to less preferred food items. Males do not use red objects on their bowers and often dump and sometimes hide them far away from the bower (G. Borgia, personal observation). Removal of less preferred colours may allow males to develop consistent colour schemes for bowers that serve as highly visible and recognizable signals not disrupted by other colours. The common tendency of male bowerbirds from a variety of species to consistently use particular colours of decorations at specific locations around the bower (e.g. Borgia 1995a) supports the hypothesis that it is critical to present a reliable pattern of colour-based signals to females.

Cross-species comparisons that reconstruct ancestral characters related to food colour preferences are valuable because bower decoration has a long history in the bowerbirds (Kusmierski et al. 1997). The most direct test of the FCD hypothesis would have been to reconstruct ancestral food colour preferences and ancestral bower decoration colour preferences and determine whether the results of these reconstructions matched. However, the high degree of lability in colours used as bower decorations when mapped onto the bowerbird phylogeny (G. Borgia, unpublished data) indicates that reconstruction of this trait would be highly unreliable. This, combined with the lack of information on food colour preferences across bowerbird taxa (e.g. see Frith & Frith 2004) and the difficulty of interpreting results in a captive setting (Madden & Tanner 2003; also see above) did not allow this test. We were, however, able to use comparative information to test another hypothesis consistent with the FCD hypothesis, that ancestral bower decorations were dual-use traits that functioned both in display and as food. Under this hypothesis, preferences for food and decorations should be similar because the same objects are used for both. Our results suggest that a relatively small proportion of decorations on bowers of extant and ancestral species are and were edible (e.g. flowers and fruits, and that these are only rarely eaten; G. Borgia, personal observation). Also, a high proportion of extant species use inedible man-made objects, and our reconstruction suggests that this would also have been likely for the bowerbird ancestor, suggesting that colour and durability may have been more important than food value in the initial choice of bower decorations.

A possible criticism of this and previous (e.g. Madden & Tanner 2003) studies is that we used male decoration colour preferences to infer female decoration colour preferences. Direct assessment of female decoration colour preference is difficult because female bowerbirds typically do not pick up or otherwise manipulate decorations around the bower, nor do they bring or steal decorations, thus precluding the kind of experiments we did with males. While we cannot validate the entire ranking of male colour preferences in females, there is evidence indicating strong preference in both sexes for the colour blue, the colour most preferred in our tests of males. First, male satin bowerbirds strongly compete for blue decorations (Borgia & Gore 1986), which function only in mate attraction. Second, females prefer males with more blue decorations on their bowers (Borgia 1985, 1993; Patricelli et al. 2003; Coleman et al. 2004). In addition, although none of the hypotheses considered here suggest that male and female colour preferences should differ in species in which males collect display items, evidence that males use decorations to attract females suggests that their colour preferences should be similar.

In conclusion, several lines of evidence indicate that the FCD hypothesis does not explain decoration preferences in satin bowerbirds. First, we did not find the predicted positive correlation between food colour preferences and male decoration colour preferences, but instead found a significant relationship in the opposite direction. Second, the FCD hypothesis should lead to similar reactions to preferred and less preferred colours of decorations and food items, but we found that while no food items were rejected, less preferred decorations were consistently rejected. Third, our reconstruction of ancestral character states suggests that food items were not likely to have been used in a dual-use role as food and decorations, and thus, our results do not support a mechanism by which food colour preferences might drive decoration colour preferences. Fourth, other experimental studies of decoration colour preferences in male satin bowerbirds have shown that colour preferences of young males differ from those of adult males (S. W. Coleman & G. Borgia, unpublished data). Here we found a positive correlation of food colour preference for juvenile and adult males, suggesting different age-specific patterns of decoration and food colour preferences, which is not consistent with the FCD hypothesis. The negative correlation between food and decoration colour preferences that we found is also inconsistent with the hypothesis that female colour preferences for male display traits affect food colour preferences and the hypothesis that a generalized sensory drive mechanism produced common decoration and food colour preferences. The significant inverse correlation between food and decoration colour preferences provides strong evidence against a common causal link between these preferences. Our results are most consistent with the conclusion that different mechanisms have produced food and decoration colour preferences in satin bowerbirds.

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