Preference for, and spatial arrangement of, decorations of different colours by the Great Bowerbird *Ptilonorhynchus nuchalis nuchalis*

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Summary. Male bowerbirds (Ptilonorhynchidae) build bowers, and adorn them with decorations to attract mates. We investigated preference for, and spatial arrangement of, decorations of different colours at bowers in a population of the western subspecies of the Great Bowerbird *Ptilonorhynchus nuchalis nuchalis*, near Darwin, Northern Territory. Decorations mainly comprised snail shells, stones, pieces of glass, and cycad fruits. The colours of most decorations were white, grey or green. Red materials, preferred in eastern populations of the species, were seldom found in these bowers. The spatial distribution of decorations on the bower platforms had a distinct pattern according to colour. Although both grey and white objects were widely spread over the entire platform, the former tended to be placed near the avenue and the latter towards the outer platform. Green objects were consistently placed separately on both sides of the entrances of the avenue. After decorations were experimentally removed from five bowers, the owners placed the decorations of different colours back again in a configuration similar to that present before removal. As green objects were held in the male's bill during courtship displays, their placement next to the avenue entrance was practical for the male, and the background placement of white and grey objects may serve to make green objects and a male's lavender crest more conspicuous.

Introduction

Male bowerbirds (Ptilonorhynchidae) build bowers on the ground for courtship displays. Bower-building behaviour has attracted much attention from behavioural ecologists because of the insights that it offers into animal mating systems and reproductive strategies (for reviews see Borgia *et al.* 1985; Borgia 1995a; Frith & Frith 2004, 2008). Bowers are of two main types: maypoles and avenues (Frith & Frith 2004). Maypole bowers consist of one or more structures composed of twigs, grass stems or fern in the centre of a display site, whereas avenue bowers consist of two parallel walls made of twigs. Males collect and place various decorations such as snail shells, bones, stones, fruits, feathers or human-made materials (e.g. glass, metal and plastic) in or near the bower (Frith & Frith 2004). To date, studies on the relationship between mating success and bower characteristics, such as the structure and number of decorations, have been conducted mainly on species that build avenue bowers, namely the Satin Bowerbird *Ptilonorhynchus violaceus* (Borgia 1985a,b; Doucet & Montgomerie 2003), Spotted Bowerbird *P. maculatus* (Borgia 1995b; Borgia & Mueller 1992; Madden 2002, 2003a,b), and

Great Bowerbird *P. nuchalis* (Katsuno *et al.* 2010; Okida *et al.* 2010). All of these studies have demonstrated that the mating success of males is correlated with the quality and/or number of particular decorations at their bowers.

Colours of decorations vary among species within the family, but each species usually has a specific colour preference. For example, blue, purple and orange are preferred by the Vogelkop Bowerbird *Amblyornis inornata* (Diamond 1988); blue and yellow by the Satin Bowerbird (Borgia 1985a); and green by the Spotted Bowerbird (Madden 2003a,b). Furthermore, some studies suggest that bowerbirds place particular materials in particular locations within the bower (for review see Frith & Frith 2004). For example, in the Spotted Bowerbird, green *Solanum* fruits are often placed within the avenue, but white snail shells are placed on the periphery of the bower (Madden 2003a). However, relatively little attention has been paid to preferences for colours and the spatial arrangement of decorations among other species and populations.

The Great Bowerbird is widely distributed in northern Australia and comprises two subpsecies, western *P. n. nuchalis* and eastern *P. n. orientalis*. Males build avenue bowers for their courtship displays, and collect many decorations to place on the platforms at each end of the avenue, or more rarely within the avenue (Frith & Frith 2004; Doerr 2009a,b; Katsuno *et al.* 2010; Okida *et al.* 2010). Decorations include many natural materials, such as snail shells, bones, green fruits and green leaves, but also include human-made materials like glass and metal (Frith & Frith 2004). Several authors have described the bower structure and decorations of the Great Bowerbird (Hore-Lacy 1962; Borgia 1995c; Frith *et al.* 1996; Doerr 2009a,b; Katsuno *et al.* 2010; Okida *et al.* 2010). Recently, Endler & Day (2006) experimentally manipulated decorations in bowers of males in a population of the eastern subspecies *P. n. orientalis*, and found that these birds showed a strong preference for, or avoidance of, particular colours. However, information on colour preferences of the western subspecies *P. n. nuchalis* is limited. Although Endler *et al.* (2010) found a size gradient of objects on the bower platform for the eastern subspecies of the Great Bowerbird, there have been no studies to date on the spatial configuration of decorations in the western subspecies.

In this study, we provide data on colour preferences for, and spatial configuration of, decorations in a population of the subspecies *P. n. nuchalis*, and present the results of field experiments in which the arrangement of different decorations at bowers were manipulated.

Methods

Study area

The study was conducted at Coomalie Farm (13°0′S, 131°8′E; 20 km²; 50 m above sea-level), 85 km south of Darwin, Northern Territory, from September to November 2004, during the breeding season of the Great Bowerbird (Frith & Frith 2004; RAN & KE unpubl. data). The dominant vegetation was tall savanna woodland comprising various tree species, including Darwin Woollybutt *Eucalyptus miniata*, *Corymbia polysciada*, Smooth-stemmed Bloodwood *C. bleeseri,* Long-fruited Bloodwood *C. polycarpa,* Kakadu Plum *Terminalia ferdinandiana*, Cooktown Ironwood *Erythrophleum chlorostachys*, Cocky Apple

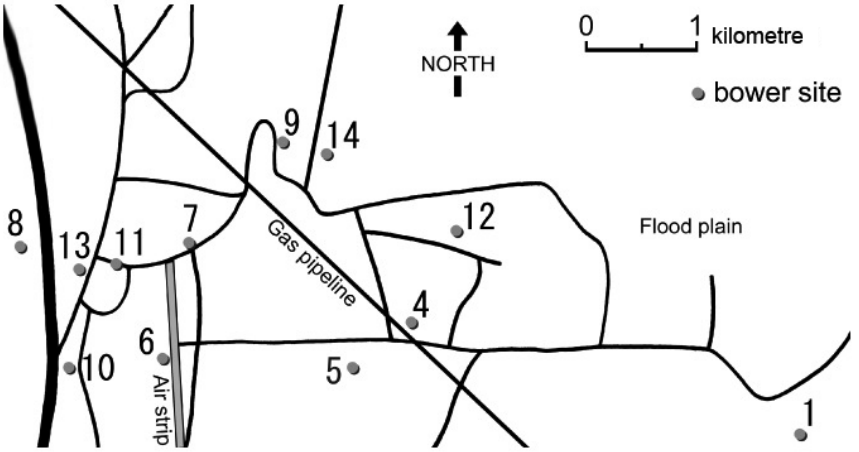

Figure 1. Map of the Coomalie Farm study area, NT, with locations of active Great Bowerbird bower sites during the study period represented by numbered dots. Inactive bowers (2–3) are not shown.

Planchonia careyi and Screw-Palm *Pandanus spiralis*, with a patchily distributed shrub layer including cycad *Cycas armstrongii*, Turkey Bush *Calytrix exstipulata* and *Grevillea decurrens*, and an understory of tall annual spear grass *Sarga* spp. and perennial grasses such as Black Speargrass *Heteropogon contortus*. The climate is monsoon-tropical with a distinct alternation of the dry (May to October) and wet (November to April) season. Mean annual rainfall at nearby Lake Bennett is 1278 mm (Bureau of Meteorology: http://www.bom.gov.au/climate/data/). Temperatures vary little over the year, the highest monthly mean temperature being 33.2°C (November) and the lowest 19.3°C (July). Fires occur annually during the dry season, either from deliberate spot-burning by property owners during the early dry season, or from wildfires lit during the late dry season on neighbouring farms that spread to Coomalie Farm.

Fourteen bowers were located in the study area (Figure 1) and their locations were recorded with a GPS device (GARMIN, FG535). Twelve bowers were active, and two were old and inactive. Of the 12 active bowers, one (No. 11) was under construction and incomplete.

Spatial distribution of decorations

For ten of the 11 active and complete bowers, we recorded the spatial distribution of decorations at each bower by taking a photograph of decorations from just above the bower with a digital camera. One bower (No. 13) was located in dense scrub that precluded photography. Using coloured nails hammered into the ground as markers, we placed 100-cm-scale rulers around the platform on both sides of each bower to form a grid enclosing all of the decorations (Figure 2) and took a photograph. The size of the quadrat varied from 40 cm × 40 cm to 80 cm × 80 cm, depending on the size of the area covered by decorations. To keep light constant during photography, the focal area was shaded with an umbrella.

In the laboratory, the photographs were viewed on a PC monitor, and the quadrat was divided into 6 × 6 cells (see Figure 2). The size of the cells varied, depending on that of the quadrat. Then, in order to measure the relative sizes of the areas covered by white, green and grey materials, 100 dots (10 rows × 10 columns) were superimposed on each cell, and the number of dots covered by each colour was counted to calculate the percentage of coverage.

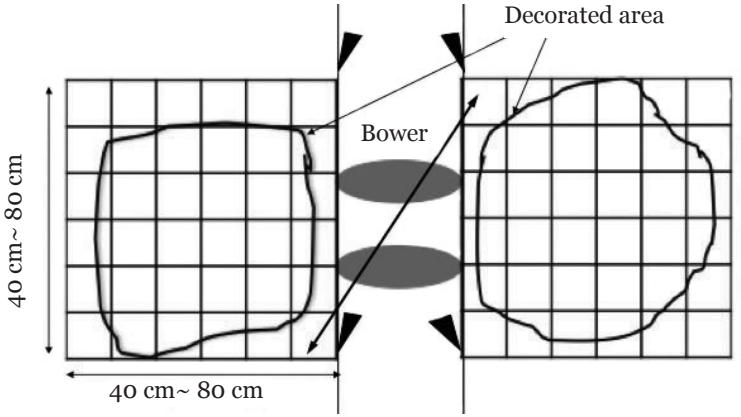

Figure 2. View of virtual grids for measuring the distribution pattern of Great Bowerbird bower decorations at Coomalie Farm, NT. Four small triangles on thin lines indicate marker nails. Data on percentage coverage of each decoration colour in each cell were combined with data for the equivalent cell on the opposite platform as indicated with a bold arrow. Grid size varied from 40 cm × 40 cm to 80 cm × 80 cm according to the size of the decorated area.

As male Bowerbirds performed displays on platforms at both ends of their bowers almost equally frequently (YK pers. obs.), data for each cell on one platform were combined with data for the cell in the equivalent position on the opposite platform (Figure 2).

Type and number of decorations

The type and number of all decorations were recorded at all 11 active bowers. Bower No. 9 was trampled by a Water Buffalo *Bubalus bubalis* during the study period, but within a week, the bower owner built a new bower ~20 m from the original one, from which he transferred almost all of the decorations to the new bower. Data on the spatial distribution of decorations at both the old and new bowers were collected.

Removal and recovery experiments

In order to clarify whether male Great Bowerbirds place decorations in a consistent spatial configuration, we conducted an experiment. We removed all decorations from one of two platforms at each of five bowers (Nos. 4–8), and compared their original distribution with that found after each owner had redecorated his bower. After removal, the decorations were piled at a highly visible location only 2 m from the bower. The bowers were checked and photographed with a digital camera at 3–4-day intervals for 20 or 21 days, when the percentage coverage of each colour was again measured. The Spearman rank correlation test was used to compare the distribution of each decoration type before and after its removal. A significant correlation signified that the male had re-arranged decorations of each colour in the same distribution patterns as before.

Results

Types of decorations

Male Great Bowerbirds gathered natural objects such as snail shells, bones from mammal skeletons, fruits, leaves, macropod dung, and stones, as well as human-

Table 1. Colour of decorations at bowers of Great Bowerbirds at Coomalie Farm, NT.

Colour	*Items of decoration*
White	Snail shells, bones, stones, mortar
Green	Fruits, leaves, glass
Grey	Stones, metal (nails, wire, aluminium sash, cartridges), colourless glass
Other	Dung of macropods, wood chips, charcoal

made objects such as glass and metal (Table 1). The colours of decorations were mainly white, grey and green. White materials comprised snail shells, white stones and bones (Table 1). Green materials comprised green glass, leaves, and fruits, the latter mainly being those of cycads. Grey materials were grey stones and pieces of metal (mainly aluminium). Soiled colourless glass also appeared grey. The most abundant decorations were grey stones, followed by snail shells, white stones, and pieces of colourless and green glass (Table 2). Grey stone decorations could not be counted accurately, as we could not distinguish stones carried by Bowerbirds from those present before the bower was built. All bowers contained all types of objects except for one that lacked green glass and another that lacked green fruits.

Arrangement of decorations

Macropod dung and wood chips were placed on the outer sides of walls, separate from other decorations. Figure 3 shows the spatial distribution of white, grey

Table 2. Number of decorations (mean ± standard deviation) of different types at Great Bowerbird bowers, Coomalie Farm, NT.

Decoration type	*Number*
Grey stones	289.0 ± 163.8
Snail shells	155.0 ± 74.9
White stones, mortar	50.8 ± 44.6
Colourless glass	45.8 ± 43.7
Green glass	41.5 ± 56.3
Bones	19.5 ± 20.4
Green fruits	11.4 ± 10.0
Dung of macropods	6.2 ± 9.5
Wood chips	6.0 ± 14.4
Metal	5.9 ± 9.6
Leaves	4.2 ± 5.5
Other	3.2 ± 8.7

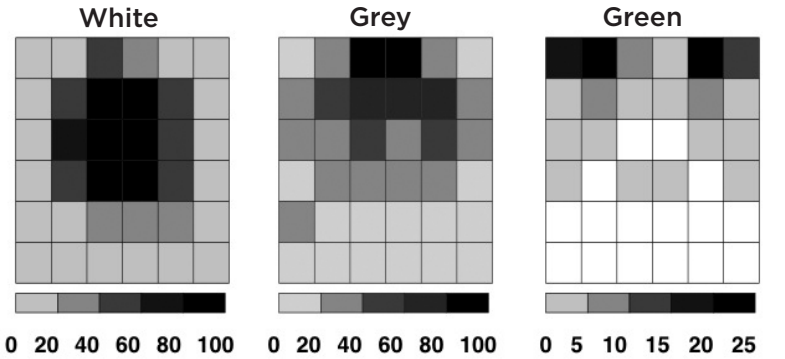

Figure 3. Distribution patterns of white, grey and green objects at bowers of the Great Bowerbird, Coomalie Farm, NT. Mean values of percentage coverage are shown as five shading gradation classes. White cells signify absence of items.

and green objects on the platforms, averaged for all bowers. White objects were mainly clumped around the centre of the platform (Figure 4). Green and grey objects were concentrated towards the entrance to the bower avenue, the former on either side, just outside the avenue walls, and the latter directly in front of the entrance, between the green objects. Grey objects extended all over the platform, but many of them were covered with other objects.

Experiment on removal of decorations

Spearman rank correlations suggested that decorations that had been removed experimentally were re-arranged by the bower owner in a configuration very similar to that existing before their removal. For white materials, correlations were significant at all five bowers; for green and grey materials, correlations were significant at all but one of the bowers (Table 3).

Discussion

Colour preference

In the study population of Great Bowerbirds, the main colours of decorations were white, grey and green (to human eyes), which suggests that male Bowerbirds selectively gather objects of these three colours. As suggested on p. 9, white and grey materials may act as a contrasting background or canvas to highlight coloured objects, and green objects were the only coloured materials collected in the bower. Although this species is known to collect red objects in other regions (Frith & Frith 2004; Endler *et al.* 2005), only one red item was found at a single bower in the present study. Although we placed red plastic materials near a bower in a preliminary study, the owner did not carry them to his bower (YK pers. obs.). Indeed, additional colour-selection experiments in the study area showed that red objects were carried away from the bower (N. Haruyama unpubl. data), strongly suggesting that male Bowerbirds in this population do not seek red objects with which to decorate their bowers.

Table 3. Spearman rank correlations (*Rs*) between percentage coverage of decorations before and 20 days after removal. ** = $P < 0.001$, *** = $P < 0.0001$.

	Colour of decorations		
Bower no.	*White*	*Green*	*Grey*
4	0.74***	−0.041	0.66***
5	0.86***	0.54**	−0.19
6	0.60***	0.74***	0.60***
7	0.63***	0.72***	0.71***
8	0.70***	0.71***	0.81***

There is no consensus on the reasons for species-specific colour preferences in bowerbirds. Madden & Tanner (2003) propounded the sensory bias hypothesis, that male Spotted Bowerbirds collected decorations that were similar in colour to preferred food items in order to attract females, but Borgia & Keagy (2006) found no close relationship between colours of decorations and main foods used by the Satin Bowerbird. As bower decorations are used for stimulating females (Borgia 1995b; Madden 2003a), conspicuous objects may be suitable as decorations. Measuring the spectrogram patterns of plumage, bowers, decorations and the environmental background for Australian bowerbirds, Endler *et al.* (2005) suggested that colour preferences for decorations were chosen to increase the contrast between the bower and its environmental background. This contrast could account for intra- or inter-population variations in colour preference. Indeed, the characteristics of decorations (both colour and material) have been shown to vary both within and between populations (Vogelkop Bowerbird: Diamond 1988; Spotted Bowerbird: Madden *et al.* 2004; Madden 2006). However, a further experimental study is needed to clarify the reasons why the particular colours were preferred or avoided for decorations in an individual population.

Arrangement of coloured objects

The study population showed a consistent spatial arrangement of colours of decorations among bowers of the Great Bowerbird. Although Spotted Bowerbirds place large objects, such as sheep vertebrae, on the periphery of the bower (~2 m from the bower) and small objects like glass fragments and stones in or near the bower, their arrangement was not determined by colour (Borgia 1995b). Borgia (1995b) suggested that large vertebrae may serve as a lure to introduce a female to the bower and that the glass may stimulate her to solicit copulation. As white and grey objects extended all over the bower platforms in our study population of Great Bowerbirds, they may serve as a 'canvas' or 'gesso' (*sensu* Endler & Day 2006). Green objects were conspicuous on this pale canvas, and were placed near the ends of the two bower walls. During his display, the male picks up a piece of glass or fruit from the pile of green decorations at the entrance, and vigorously

bobs his head up and down while exposing his normally concealed, brightly coloured crest (Okida *et al.* 2010). Green objects, to the human eye at least, appear to contrast with the lavender colour of the crest, and this contrast may play a role in impressing the female during the male's courtship display.

Endler *et al.* (2010) found a size gradient in decorations in eastern Great Bowerbirds, wherein small objects like stones were placed near the bower avenue and large objects like snail shells more distant. They proposed that this size gradient made the displaying male appear larger and more conspicuous to the female in the avenue, due to a 'forced perspective'. In the present study such a size gradient was also seen at some bowers where both grey stones and white snail shells were present. In these cases, grey stones were distributed widely on the platform, whereas white objects, mainly snail shells, were placed on the grey stones slightly away from the entrance of the bower, which caused a colour zoning (Figures 4a, c, d). Because the stones were smaller than the snail shells, this colour zoning also resulted in a size gradient similar to that reported by Endler *et al.* (2010). However, although the pattern of the colour zoning was relatively consistent in the present study population, the size gradient pattern varied. In the bower lacking grey stones, almost all decorations were snail shells that were also piled on the platform slightly away from the bower, as seen in other bowers (Figure 4b). There was no size gradient. Furthermore, at another bower, despite all snail shells being of similar size, grey ones were placed near the avenue but white ones were placed towards the outside (Figure 4d).

We believe that the zoning of colours is more important than the size gradient in bower decorations in the study population of Great Bowerbirds. The male Bowerbird displays beside the entrance of the avenue. During the display, he lowers his head and, while holding a green object in his bill, opens his lavender crest to show it to the female in the avenue (Okida *et al.* 2010; KE pers. obs.). Grey and white objects serve not only as a background to highlight green decorations and the lavender crest, but also illuminate the crest and green objects in the bill by reflecting light (Frith *et al.* 1996; Frith & Frith 2004). The size gradient of decorations at some bowers may have been secondarily derived from the colour zoning due to the differences in weight of decorations of different colours. Further research is needed to clarify the relative importance of size and colour.

Characteristics of decorations

It is unclear why particular colours and materials are preferred by each bowerbird species. One explanation is that rare objects provide reliable information about the bower owner's quality (Borgia *et al.* 1985; Diamond 1988). Collecting such rare objects and protecting them from theft by other males are costly behaviours, indicating high male quality. However, although some species collect rare objects, e.g. blue feathers in the Satin Bowerbird, and head plumes of the King of Saxony Bird of Paradise *Pteridophora alberti* in Archbold's Bowerbird *Archboldia papuensis* (Frith & Frith 2004), Madden & Balmford (2004) demonstrated that the decorations predicting mating success in the Spotted Bowerbird were not rare in the environment and not inherently costly to maintain.

Figure 4. Arrangement of decorations at four bowers of the Great Bowerbird, Coomalie Farm, NT. In b–d, the top of the photograph is the end closest to the avenue. Photos: Y. Katsuno

As suggested earlier, green objects may be an important key signal in the display of the western Great Bowerbird. Cycad fruits and green glass comprised the majority of green objects. Glass is presumably an artificial substitute for naturally occurring green fruits, just as blue plastics are substitutes for blue parrot feathers in the Satin Bowerbird. Cycad fruits were abundant and widespread in the environment surrounding the bowers in the study population. Moreover, because cycad fruits are coated with wax, they are durable. Therefore, it appears that the Great Bowerbird (like its congener, the Spotted Bowerbird) does not prefer rare or costly objects. Nor does it feed on cycad fruits; in the study area, the green fruits of Sandpaper Figs *Ficus opposita* were a favoured food item, but Great Bowerbirds did not use them as bower decorations (KE pers. obs.).

White and grey objects formed the majority of bower decorations. Among these objects, snail shells may be relatively rare because we rarely found them in the field, and they were sometimes stolen from bowers by rival males (YK pers. obs.). However, at the bower where white stones were readily available nearby, almost all white objects were stones instead of snail shells (KE pers. obs.). Thus, because their colour was similar, stones and snail shells were apparently used interchangeably. Furthermore, the number of these objects may not matter, because the number of white and grey objects did not affect relative mating success (Katsuno *et al.* 2010). As already discussed, these objects may serve as a background or canvas on which to highlight more valuable objects, or the displaying male himself.

Finally, the preference for green objects and their arrangement to the side of the bower entrance has been observed in other parts of the Northern Territory: the Casuarina campus of Charles Darwin University, Darwin, on the coast, ~70 km directly north-north-west of Coomalie Farm; and inland to Pine Creek, ~120 km south-east of Coomalie Farm; and at Katherine, ~205 km south-east of Coomalie Farm (RAN & KE pers. obs.). Further observational and experimental studies at sites located between western and eastern subspecies of the Great Bowerbird would help to clarify the evolutionary significance of geographic variation in colour preferences and arrangement of decorations in bowerbirds.

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