



Local traditions of bower decoration by spotted bowerbirds in a single population

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Recent work has shown that elaborate secondary sexual traits and the corresponding preferences for them may be transmitted culturally rather than by genetic inheritance. Evidence for such cultural transmission commonly invokes spatial patterns of local similarity, with neighbouring individuals or populations appearing similar to each other. Alternative explanations for local similarity include ecological similarity of neighbouring environments and confounding genetic effects caused by aggregations of kin. We found that bowers built by male spotted bowerbirds, *Chlamydera maculata*, within a single population showed fine-scale similarities between neighbours in the decorations displayed on them. Such similarities did not covary with local decoration availability, local display environment or kinship and could not be explained by stealing behaviour by neighbours. Instead, we suggest that these similarities are products of local tradition, either culturally transmitted by neighbouring males who regularly inspect neighbours' bowers, or as localized responses to variable individual female preferences.

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Female choice for elaborate male sexual traits is well documented (reviewed in Andersson 1994). In many studies, researchers have searched for the genetic heritability of attractive traits in the resulting sons (Petrie 1993; Jones et al. 1998; Brooks 2000) or of other measures of fitness, including survival and fecundity in offspring of one or both sexes (Partridge 1980; Norris 1993; Kempenaers et al. 1997; Sheldon et al. 1997). In some cases, female preferences and male traits are transmitted culturally (reviewed in Freeberg 2000). In particular, studies of birdsong provide numerous examples of local variations and cultural transmission (e.g. Marler & Tamura 1964; Grant & Grant 1996; Payne et al. 2000).

Cultural effects influence both female preferences and male traits. Preferences can be altered either by exposure to novel stimuli at appropriate stages in the life cycle (Freeberg 1996, 1998) or by observations of preferences expressed by other females (Witte & Noltemeier 2002). Much work has concentrated on local spatial patterns of

male traits that may be independent of genetic factors. For example, in Nuttall's white-crowned sparrows, *Zonotrichia leucophrys*, sons produce songs more like those of their neighbours than those of their fathers (Bell et al. 1998). In this study, we followed the line of reasoning based on spatial similarity to suggest that another complex behavioural sexual trait, bowers, may be transmitted culturally rather than exclusively genetically.

Diamond (1987) suggested that bower style is at least in part a culturally transmitted sexual trait that individuals learn from conspecifics. Bowers are extremely elaborate traits, built by males of the family Ptilonorhynchidae, that act as targets of female choice in a nonresource-based mating system (Borgia 1997; Humphries & Ruxton 1999). They are subject to strong sexual selection with high skew in mating success (Borgia 1985; Borgia & Mueller 1992) and therefore are predicted to have a strong genetically heritable component. Species follow general patterns in the form that their bowers take, such that bower design can usually identify the species building it (Marshall 1954; Gilliard 1969; Frith & Frith 2004; but see Frith et al. 1995). However, within a species, populations differ in bower design or decoration usage (Diamond 1986; Hunter & Dwyer 1997; Madden 2003). Such interpopulation differences may be explained by

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differential availability of decorations (Hunter & Dwyer 1997), different display environments (Borgia 2002), genetically isolated populations or local cultural patterns (Uy & Borgia 2000).

In this study, we tested which of these four factors can best explain variation in decorations used on bowers of spotted bowerbirds, *Chlamydera maculata*, within a single study population. This novel intrapopulation approach, compared to previous comparisons between geographically distant populations and possibly over different breeding seasons, allowed us to test all four possible explanations simultaneously.

METHODS

Fieldwork was carried out at Taunton National Park, Queensland, Australia, during 1998–2000 (see Miles & Madden 2002; Madden 2003 for details of the study site, bird banding protocol, bower location, decoration measurements and measures of interbower distance).

Decoration Availability

To assess the local environmental availability of objects at bowers at Taunton, we conducted eight transects from each bower. These started 100 m from the avenue of the bower (to avoid counting objects on unused bowers) and ran for 50 m in the direction of the eight cardinal points (N, NE, E, SE, S, SW, W, NW). All objects encountered within 1 m of the transect line and falling within the size range of decorations naturally used on bowers (7–150 mm) were recorded. Estimates of numbers of three numerous object types, quartz, stones and dung, were obtained from averages of three 1-m² quadrants taken at the beginning, middle and end of each transect. Transects were conducted on 21 November–5 December 1998 ($N = 18$ bowers) and on 29 November–11 December 1999 ($N = 17$ bowers).

For each year, we tested whether decoration usage at bowers depended on the availability of such decorations in the local environment, constructing matrices detailing whether objects were used as bower decorations and whether objects were present or absent in corresponding transects. If usage depended solely on local object availability, then we predicted that a decoration would be both available and used or not available and not used. Alternatively, if usage did not depend on local availability, we predicted either more instances when a decoration was available but unused or unavailable but used, or no significant relation between object use and local availability.

To investigate the relation between object usage and availability at a finer scale, we searched for direct relations between numbers of certain decorations that were both commonly used on bowers and commonly encountered on transects. Our definition of common required that the object was used as a decoration on more than half of the bowers and was encountered on more than half of the transects. In 1998, four objects met our criteria: *Solanum* berries, bones, *Carissa* leaf sprigs and snail shells. In 1999,

three objects met our criteria: *Solanum* berries, *Carissa* leaf sprigs and snail shells.

Bower Bush Architecture

Bowers were built under bushes of a variety and in many cases a mixture of species. We tested whether species of bower bush was related to the type of decorations used on the bower. Bowers were typically built under bushes that conform to a conservative range of dimensions: bush canopy above bowers was thicker, attenuated more light, and covered a greater area than that of randomly selected bushes, and bower location within a bush was associated with a narrow range of canopy heights (Miles & Madden 2002). Bush species provides a proxy measure that encompasses the general physical properties of the bush, the effect of the bush on the local light environment and the visual background against which the bower is viewed. For each bower studied in 1998 and 1999, we recorded which species of bush were present in the canopy. We constructed a presence/absence matrix for each year separately, from which we calculated a distance matrix, using the DISTANCE function in GenALEx (Peakall & Smouse 2001), referring to similarity of canopy composition. For example, two bowers with exclusively *Acacia harpophylla* canopy would be considered more similar to each other than one with both *A. harpophylla* and *C. ovata*, and these three bowers would be more similar to each other than to a bower with a canopy consisting of a mixture of *Eremophila maculata* and *Myporum* spp. If object usage was determined by bush canopy composition, we predicted a significant relation between patterns of bush species and of decoration usage.

Use of AFLP in Calculating Relatedness

Amplified fragment length polymorphism (AFLP) analysis (Mueller & Wolfenbarger 1999) was carried out on blood samples collected from bower owners (Madden et al. 2004). This allowed us to calculate a measure of the relatedness of each bower owner to every other bower owner (Madden et al. 2004).

Constructing Decoration Distance Matrices

We constructed distance matrices that indicated how similar bowers were to each other in the types of decorations that they used. This novel technique was analogous to a calculation of genetic similarity based on band sharing. Each decoration type encountered was comparable to a locus, and for each bower the decoration (allele) was scored as either present or absent. Compiling a presence/absence table for all the bowers measured in each year, similar to a genetic 'fingerprint', allowed us to construct a distance matrix using the DISTANCE programme in GenALEx based on nearest neighbours.

We tested whether such a fingerprint was rigorous in consistently grouping bowers built by known individuals, to determine whether we could be confident that the fingerprint provided meaningful information about an

individual's bower decorations. Subjects were eight males who held bowers in the same location for all 3 years of the study. We tested whether the fingerprint of a single male from one year was more similar to his fingerprint in other years than to the fingerprints of other males. An 'ideal' matrix was constructed, where fingerprints of a single male formed a polytomy of three branches (corresponding to 3 years), each separated by an arbitrary two units. Each of these branches was separated from all branches of all other males by an arbitrary 10 units. The relation between this ideal matrix and the actual matrix was significant (Mantel test: 24×24 , $r = 0.281$, $P = 0.001$). In contrast, a 'random' matrix was constructed, where branches were randomly assigned to two neighbours of an owner, each separated by two units (analogous to two other bowers built by that owner during the study period) and a further 22 neighbours separated by 10 units. There was no relation between this random matrix and the actual matrix (Mantel test: 24×24 , $r = -0.033$, $P = 0.760$). We conclude that our decoration fingerprints provided a robust measure with which to test differences in bower decoration use between owners.

Statistical Tests

Mantel tests to compare relations between spatial, bower and genetic matrices were performed using *zt*, a software tool for simple and partial Mantel tests (Bonnet & Van der Peer 2002). For all analyses, 100 000 randomizations were made. All other analyses were performed using SPSS v.11 (SPSS, Chicago, U.S.A.). All tests are two tailed.

Ethical Note

Birds were caught and blood samples collected under licence from the Australian Bird and Bat Banding Scheme, Queensland Parks and Wildlife Service and the James Cook University ethics committee. One or two haematocrit tubes of blood were collected from the left brachial vein. All ringed birds were released with no signs of injury and several have been resighted up to 6 years later (see also Madden et al. 2004).

RESULTS

Does Local Decoration Availability Relate to Decoration Use?

In 1998, 152 types of objects were recorded; 33 were used as decorations on at least one of the 18 bowers but were not found on any transects, 87 were found on transects but never used on bowers, and 32 were found on both transects and bowers. In 1999, 161 types of objects were recorded; 40 were used as decorations on at least one of the 17 bowers but were not found on any transects, 105 were found on transects but never used on bowers, and 16 were found on both transects and bowers. We constructed contingency tables for each year detailing for each bower whether each object was present or absent on bowers or

Table 1. Objects encountered on transects or their corresponding bowers in 1998 ($N = 18$) and 1999 ($N = 17$)

Year	Used on bower	
	Yes	No
1998		
On transect	99	694
Not on transect	313	1630
1999		
On transect	66	464
Not on transect	280	1927

transects (Table 1). In 1998, objects were more likely to be found on transects but not used as decorations, or to be used as decorations but not available on transects (chi-square test: $\chi_1^2 = 5.5$, $P = 0.02$). In 1999, we found no significant difference between observed and expected occurrences of objects being used or not used depending on their local availability ($\chi_1^2 = 0.005$, $P = 0.94$). Therefore, results for both years failed to support the hypothesis that object usage was related to object availability.

At a finer scale, we found no relations between the rank numbers of specific objects encountered on transects and their usage on the corresponding bower (Table 2). All results were nonsignificant even before correcting for multiple comparisons. Decoration usage did not appear to be determined by decoration availability.

Does Canopy Type Relate to Decoration Use?

In 1998, 10 species of bush featured in the canopies of at least one of 18 bowers. In 1999, eight species of bush, including one not recorded in 1998, featured in the canopies of at least one of 18 bowers. Bush canopy composition was not significantly related either to the bower decoration composition found below it in either 1998 or 1999 (Mantel tests, 1998: 18×18 , $r = 0.075$, $P = 0.32$; 1999: 18×18 , $r = 0.15$, $P = 0.10$) or to bower proximity (Mantel tests, 1998: 18×18 , $r = 0.161$, $P = 0.09$; 1999: 18×18 , $r = 0.163$, $P = 0.08$). Despite this spatial trend, we conclude that decoration usage does not appear to covary with canopy type.

Table 2. Spearman rank correlations between numbers of particular objects encountered on transects and on their corresponding bower

Year	Object	r_s	P
1998 ($N = 18$)	<i>Solanum</i> berry	0.19	0.45
	<i>Carissa</i>	0.18	0.48
	Snail shell	0.04	0.86
	Bone	0.21	0.39
1999 ($N = 17$)	<i>Solanum</i> berry	-0.06	0.81
	<i>Carissa</i>	0.03	0.90
	Snail shell	-0.08	0.75

No corrections were made for multiple comparisons.

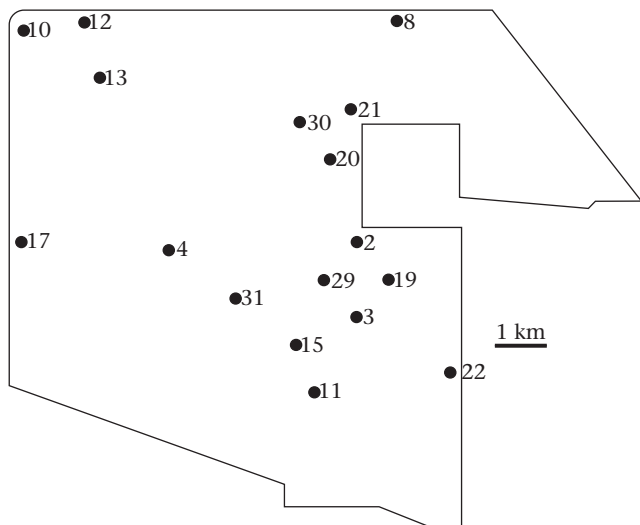
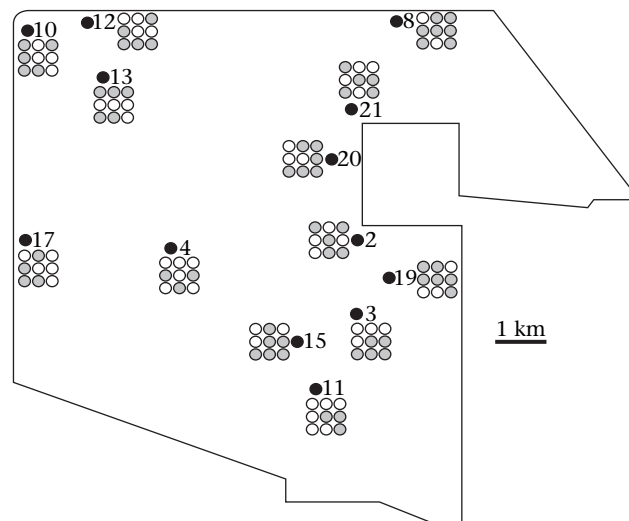


Figure 1. Map of bowers studied in 1998–2000 that were used in partial Mantel tests.

Genetic Versus Geographical Factors?

Madden et al. (2004) found no evidence of geographical clustering of kin at Taunton. Therefore, we used partial Mantel tests (Bonnet & Van der Peer 2002) to investigate relations between geographical, genetic and decoration distance matrices. We first searched for relations between geographical and decoration matrices while controlling for genetic effects. This required genetic, geographical and decoration data for each bower and its owner (1998: 13 bowers, 1999: 12 bowers, and 2000: 11 bowers; Fig. 1). There were significant, positive relations in both 1998 and 1999, but not in 2000, between geographical and decoration matrices (partial Mantel tests, 1998: 13×13 , $r = 0.25$, $P = 0.03$; 1999: 12×12 , $r = 0.33$, $P = 0.02$; 2000: 11×11 , $r = 0.24$, $P = 0.08$). Second, we searched for relations between genetic and decoration matrices when controlling for geographical associations. We found no significant relations in either 1998 or 2000, but a significant, positive relation in 1999 between genetic and decoration matrices (partial Mantel tests, 1998: 13×13 , $r = -0.012$, $P = 0.46$; 1999: 12×12 , $r = 0.27$, $P = 0.04$; 2000: 11×11 , $r = -0.003$, $P = 0.48$). When we combined probabilities from tests of significance made in each year (Sokal & Rohlf 1995), we found an overall significant relation between geographical and decoration distances when controlling for genetic distance (chi-square test: $\chi^2_6 = 19.9$, $P = 0.006$) but no overall relation between genetic and decoration distances when controlling for geographical distance ($\chi^2_6 = 9.5$, $P = 0.30$).

To illustrate this phenomenon, we took the nine objects that appeared on five to nine of the 13 bowers considered in 1998. A visual example including all 65 decorations observed would be complex and problematical. Instead, our subsample of decorations, which is neither ubiquitous nor unusual, provides a simplified illustration of local traditions (Fig. 2). For example, those bowers in the northwest part of the park generally lacked red and black plastic and metal decorations, although these were



- | | | | |
|---|---|---|----------------------------|
| ① | ② | ③ | 1. Freshwater mussel shell |
| ④ | ⑤ | ⑥ | 2. Brown stone |
| ⑦ | ⑧ | ⑨ | 3. White quartz |
| | | | 4. Emu eggshell |
| | | | 5. Red plastic |
| | | | 6. Black plastic |
| | | | 7. Vine stem |
| | | | 8. Blue glass |
| | | | 9. Metal |

Figure 2. Examples of local decoration similarity based on the nine decoration types found on five to nine bowers of the 13 bowers considered in 1998. Each grid of nine circles indicates the presence (●) or absence (○) of a decoration type at each bower.

commonly used in the southeast part of the park. Bowers in the north part of the park frequently used white quartz, which was seldom used on those bowers in the south part. Bowers in the west part of the park all used blue and/or purple glass, which was absent from the four eastern most bowers. We constructed a distance matrix based on the presence and absence of these nine decoration types and plotted contours of association, joining bowers with those most similar to each other in decoration type (Fig. 3). The separation of western and eastern bowers is clearly visible, as is fine-scale spatial structuring, particularly in the western bowers.

DISCUSSION

Bowers that were geographically close to each other were highly similar in their usage of decorations. These patterns cannot be explained simply by similarities in the availability of object in neighbouring areas, because decoration usage did not relate to potential availability in the local environment. Neither did the type of decoration used relate to the canopy structure of the bush under which the bower was built (i.e. similar display environments), although there was some evidence that geographically close bowers were more likely to be built under similar species of bushes. Similarity of decoration usage also cannot be predicted by genetic similarity of the owners, because relatives do not display close to each other (Madden et al. 2004), and, in the present study, did not use similar suites of decorations. Instead, the

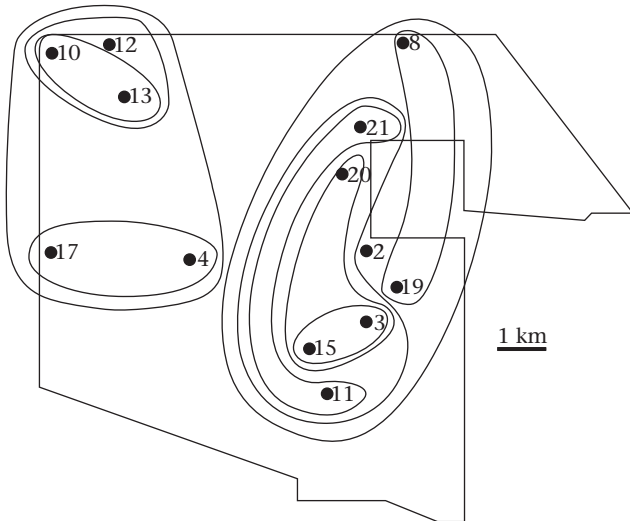


Figure 3. Clusters of bowers in 1998 based on a between-groups linkage distance matrix constructed using the nine decorations described in Fig. 2. Similarity contours contain bowers with similar suites of decorations.

similarities in the decorations patterns of neighbouring bowers suggests local traditions.

Bower owners are more likely to visit neighbours' bowers, often to maraud (Borgia 1985; Pruett-Jones & Pruett-Jones 1994; Madden et al. 2004). Thus, geographically similar decoration usage may be entirely because neighbouring males are more likely to steal decorations from neighbours, creating a local homogeneity of decoration use. This explanation is unlikely to explain the strength of the pattern that we observed. Stealing rates in spotted bowerbirds are relatively low (Borgia & Mueller 1992; Madden et al. 2004). At Taunton, over 1000 manmade objects were marked and their movements tracked for 4 years (Madden et al. 2004). Manmade objects accounted for approximately one-third of the number of decoration types on a bower. Over the 4 years of monitoring, 27 items were recorded on bowers other than those where they were first marked, representing interactions between 16 pairs of bowers. The total numbers of decorations on a spotted bower at Taunton averaged over 500 (J. R. Madden, unpublished data), making the contribution of stolen objects to the overall composition of bower decorations insignificant.

An alternative explanation suggests that visiting neighbouring bowers provides an opportunity for males to assess novel decoration usage regularly and so learn by instruction. Males pay close attention to the displays of peers, rapidly increasing their rate of destruction of bowers that have been artificially improved (Madden 2002). This evidence suggests that males have some concept of what each is 'allowed' to display, in effect, an appreciation of his social standing. Therefore, males may recognize that certain males are successful and so copy their choice of decorations, leading to male-driven tradition development, with attractive males acting as role models for less successful neighbours.

A third explanation is that males learn what attracts females by trial and error, and moderate their display in

response to experience (Diamond 1986). Uy et al. (2000, 2001) suggested that female satin bowerbirds, *Ptilonorhynchus violaceus*, visit geographically close bowers over several years. This practice could provide an opportunity for developing local traditions, with males responding to an individual female's preferences. Reasons for variation in individual female preferences are unclear, but could depend on local variations in object rarity (Borgia et al. 1987; Hunter & Dwyer 1997), indicating male quality (but see Madden & Balmford 2004), regular fluctuations in expressed sensory biases (Madden & Tanner 2003), varying display environments (Borgia 2002) or a general female preference for novelty (Borgia et al. 1985). Under these conditions, females could drive tradition development by altering or refining trait preferences at a more rapid rate than can be matched by purely genetic variation in male phenotype.

Bower style as a culturally transmitted trait has attracted previous attention, particularly in studies by Diamond (1982, 1986, 1987, 1988) who concentrated on differences in bower architecture and decoration usage in five populations of Vogelkop bowerbirds, *Amblyornis inornatus*. Such differences between these populations were not explained solely by varying availabilities of coloured decorations, demonstrated both by casual inspection of local decoration availability and more rigorously by offering equal numbers of differently coloured poker chips and recording differing patterns of acceptance (Diamond 1986). Neither does there appear to be significant genetic differences between at least two of these populations (Uy & Borgia 2000). These studies did not test ecological differences between populations; Uy & Borgia (2000) favoured the explanation of nonarbitrary changes in female preferences, and suggested a coordinated change between environmental conditions and male display. Hunter & Dwyer (1997) reported that bowers within two populations of satin bowerbirds were more similar to each other than to those of another population. However, they concluded that their observations of such a gross, interpopulation difference resulted from differences in object availability between the populations. Madden (2003) found that objects that best predicted male mating success in spotted bowerbirds at Taunton were different from those at another population of spotted bowerbirds (Borgia & Mueller 1992; Borgia 1995). Spatial differences in song have also been reported. Male golden bowerbirds, *Prionodura newtonia*, from within a population sang a song similar to each other, but distinct from that of males from other locations (Westcott & Kroon 2003). Males responded more strongly to playbacks of songs of local dialects than of foreign dialects (Westcott & Kroon 2003). Other studies of satin, spotted and golden bowerbirds have not considered genetic relatedness. Our study excludes three explanations for spatial similarity in bower decoration usage: decoration availability, display environment and exclusively genetic factors. Instead, we found support for Diamond's (1987) suggestion that bower style is at least partly culturally transmitted.

Culture can be ascribed to any species in which one community can readily be distinguished from another by its unique suite of behavioural characteristics (de Waal

1999). Such a definition has been applied in response to the observation of spatial aggregations of complex behavioural repertoires in chimpanzees, *Pan troglodytes* (Whiten et al. 1999), and orangutans, *Pongo pygmaeus* (Van Schaik et al. 2003). The term 'culture' has been applied less freely to nonprimate species (Fragaszy & Perry 2003). Members of one population of a bowerbird species can be distinguished from another, not morphologically, but by components of their sexual display. We found in the present study that individuals within a single population can also be assigned to geographically specific groupings, and propose two broad mechanisms, neighbour interactions or localized variation in female choice, that could explain the existence of such cultural identifiers. The general form of display for spotted bowerbirds and other species of bowerbirds, i.e. bower building, gross colour preferences, broad-scale decoration positioning (e.g. white objects at the avenue entrances), remains highly conserved within the species (Marshall 1954; Warham 1962; Borgia & Mueller 1992; Borgia 1995; Madden 2003), suggesting at least an underlying genetic determinism of display form. Despite this broad genetic framework, fine-scale, nongenetic, culturally mediated variations in bower decoration appear to be possible.

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