

Morphological signals of sex and status in Spotted Bowerbirds

Joah R. Madden^{A,B,E}, John A. Endler^C and Francine Jury^{A,D}

^ADepartment of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK.

^BPresent address: Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK.

^CDepartment of Zoology and Tropical Ecology, School of Tropical Biology, James Cook University, Townsville, Qld 4811, Australia, & Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA.

^DCentre for Integrated Genomic and Medical Research, The University of Manchester Medical School, The Stopford Building, Oxford Road, Manchester, M13 9PT, UK.

^ETo whom correspondence should be sent. Email: jrm54@cam.ac.uk

Abstract. The Spotted Bowerbird, *Chlamydera maculata*, appears to be sexually monomorphic. We caught and marked 118 birds in central Queensland, and sexed 88 using molecular methods. We found that our catch was strongly male-biased, both at bower sites and at non-bower feeding sites. We continued to observe the bird's behaviour after their release and so sub-divided males into sexual status groups as either bower-owners or non-owners. We searched for morphological measures, subjectively judged colour differences and quantitatively collected spectral measures of the visual properties of the crest feathers that would allow us to separate birds of differing sex and status. We found that bower owners had larger crests than non-owner males or females and that crest area provided the most accurate predictor of a bird's sex and status in a discriminant function analysis. We studied a cohort of seven males who went from non-owners to bower owners over three years, and found that their change in status was accompanied by a change in crest size – the only significant change in their morphology. Crest size did not relate to the mating success of a bower-owner. Instead, we suggest why the crest may differ between status groups and the implications that this may have for the sexual behaviour of male and female Spotted Bowerbirds.

Introduction

Previous studies of bowerbirds have generally assumed that morphology may be relatively unimportant, and have instead concentrated on aspects of bower architecture, showing that it relates to mate choice (Borgia 1985; Borgia and Mueller 1992; Lenz 1994; Uy and Borgia 2000; Madden 2003). However, many species of bowerbirds are far from drab, instead having bright, sexually dimorphic plumage or erectable crests, and exhibiting a change in plumage or other body parts corresponding with sexual maturation (Marshall 1954; Gilliard 1969). These features suggest that the bower is not the only signalling method used by bowerbirds. Indeed, exclusive dependence on the bower as a basis for mate choice results in several important problems for females trying to make an optimal choice. First, bower design alone does not facilitate accurate species identification. Where Spotted, *Chlamydera maculata*, and Great, *C. nuchalis*, Bowerbirds are sympatric, both species have been seen displaying and attending displays at bowers of the other species (Frith *et al.* 1995; JRM, personal observations) and several examples of resulting hybrids exist (Frith and Frith 1995; JRM, personal observations). Second, the separation of bird and display presents a situation for opportunistic (sneaky) matings, with

potentially lower-quality non-owner birds exploiting an existing bower to display and obtain copulations while the owner is absent. Could a visiting female ascertain the status or quality of her suitor, and hence avoid copulating with a lower-quality, non-owning male? In addition, bower owners are seen to display to other males that appear to mimic female behaviour at the bower and thus incur costs in fruitless display (Borgia and Mueller 1992; JRM and JAE, personal observations). Could an owner use morphological cues to identify the sex of his audience and hence avoid mistaken, costly displays to other males?

In the case of the Spotted Bowerbird, this seems difficult. They appear to be sexually monomorphic (Marshall 1954; Gilliard 1969). One morphological trait that could provide information is the lilac nuchal crest. The crest is made conspicuous during display to both males and females (Warham 1962; Frith *et al.* 1995; JRM and JAE, personal observations; but see Borgia 1995). Museum collection skins of both sexes, identified by dissection, exhibit crests, yet in some specimens, birds identified as males lack crests. Such intra-sexual variation may be due to variation in the sexual status of the birds. In male bowerbirds, this can be divided into two simple classes – whether the bird is a bower-owner or not.

Similarly, male Satin Bowerbirds initially look similar to females, but after 5–6 years they attain a dimorphic mature plumage. This change can be induced by implants of testosterone, corresponding to an attainment of sexual maturity and the onset of bower-focused activity (Collis and Borgia 1992). Mature males are expected to exhibit larger or brighter morphological components than non-owners, and these may correspond to their sexual success in a way analogous to bower components.

Methods

Birds at Taunton National Park (see Miles and Madden 2002 for full site details) were caught in mist-nets, under licence from the Australian Bird and Bat Banding Scheme (Authority no: 2323) and Queensland Parks and Wildlife Service (Permit no: C6/000113/99/SAA). Nets were set either at bowers or at known feeding sites such as clumps of fruit trees. Catching was carried out from August to November, around the time of the breeding season, in 1998, 1999 and 2000.

Morphological measures

We collected a wide range of morphometrics from each bird captured (using callipers unless stated) processing birds within 20 min of capture. All measures used are taken from the right side of the bird. Standard measures including tarsal, wing, tail and hind claw length were measured following Lowe (1990). In addition, bill width was measured at the point above the nostrils. Gape was measured from the rear flange of the gape to the end of the bill. The area of the cloaca was measured as the mean of its width along the head–tail and wing–wing axes (Briskie 1993). Crest length was measured from the point closest to the bird's head to the obvious 'notch' in the crest base (Fig. 1). Crest width was taken at the widest point between the outer feathers when lying par-

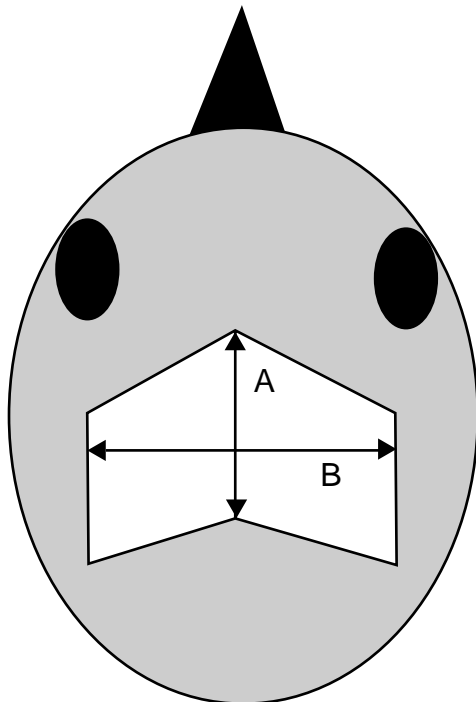


Fig. 1. Method of obtaining the crest area: (A) crest length, (B) crest width. Crest area = $A \times B$.

allel to each other (Fig. 1). Crest area was calculated by multiplying crest length and width.

All morphological measures were highly repeatable when made by a single observer with re-measures made after ~15 min (ANOVAs: wing length $F_{28,29} = 32.33$, r (repeatability) = 94.0; tail length $F_{28,29} = 16.50$, $r = 88.6$; tarsus length $F_{28,29} = 48.9$, $r = 96.0$; crest length $F_{16,17} = 178.1$, $r = 98.9$; crest width $F_{16,17} = 74.5$, $r = 97.4$; gape $F_{6,7} = 37.5$, $r = 94.8$; bill width $F_{6,7} = 11.6$, $r = 84.1$; bill depth $F_{6,7} = 10.2$, $r = 82.1$ (Lessells and Boag 1987)).

Subjective colour measurements

Three measures of colour were made subjectively, before either the sex or status of the bird was known to the observer. Iris colour was scored as either dark or light brown. Gape colour was scored as white or yellow. Cloaca colour was scored as pink or grey. Those colours that were ambiguous were scored as intermediate and excluded from further analysis.

Quantitative colour measurements

Crest spectral properties were measured away from the field, using feathers that we collected (Endler and Théry 1996). Two feathers from the forwards section of the crest were taken and stored away from light. Feathers were observed to comprise three distinct parts, a concealed grey downy base and colourful exposed tip with a blue/purple fringe and a red/orange centre. The spectral properties of these exposed areas were measured to take into account the differences between avian and human visual systems (Endler 1990; Cuthill *et al.* 1999). Plumage reflectance data (Endler 1990; Endler and Théry 1996) were collected at 300–700 nm with an OceanOptics S2000 portable spectrometer and an OceanOptics PX-1 synchronised Xe flash lamp. We laid one feather on top of the other, mimicking their natural orientation and the pair were measured on a matte-black background. We measured the thickest part of the feathers at both the coloured regions (red and blue) separately. The orientation of the shielded probe was always along the long axis of the feathers facing towards the root. Incident and reflected light were at 45° from the feather plane and the sensor was shielded in a matte-black lined tube (Endler 1990; Endler and Théry 1996). The reflectance sensor was calibrated for every bird with an Oriol Spectralon reflectance standard. We calculated the total reflectance (R_t) and the chroma (C) for each spectrum (Endler 1991; Endler and Houde 1995). We calculated C as the maximum relative difference between cone captures of all pairs of each of the four cones, using Starling eye parameters (Hart *et al.* 1998); starlings are typical passerines and there is little variation in cone pigments among passerines (N. Hart, personal communication). In human terms, R_t is proportional to luminance (brightness) and C is proportional to colour 'purity' or 'saturation' (the lower the C the more a pure colour is mixed with white or grey).

Assigning sex and status

Previously, Spotted Bowerbirds could be accurately sexed only by dissection. We determined the sex of birds caught in 1998 and 1999 retrospectively from blood samples using molecular sexing techniques (Griffiths *et al.* 1998). We used Griffiths's primers (also known as P2 and P8) in the PCR process. Samples were then run on polyacrylamide gel and visualised by silver staining, with females being represented by two bands and males having only a single band.

The ownership status of male birds (owner/non-owner) was determined through behavioural observations and video monitoring at bowers (Madden 2003). Bower owners were those birds seen to regularly frequent, maintain and display at a particular bower. They were defined as those males that were in attendance at a bower for >75% of the time for which we recorded at least one bird present. Molecular sexing indicated that all these birds were males. Non-bower owners were birds that molecular sexing revealed as males, but who were not

observed to hold a bower. It is possible that some birds classed as non-owners may have been owners of bowers that were not discovered.

All analyses were performed using SPSS v.11. All results given are two-tailed. Separate multivariate analyses were performed for morphology, subjective and quantitative colour measures due to the large numbers of variables that were being considered and the greatly reduced numbers of birds for whom we had complete data for all measures. The absence of one such data point would preclude a bird from being used in a DFA.

Results

General morphometrics

In all, 55 birds (50 males and 5 females) were caught and measured at Taunton in 1998. In 1999, 33 new birds were caught and 16 individuals were re-caught (39 males and 10 females). The morphology of birds is summarised in Table 1. In 2000, 29 new birds were caught and 17 individuals re-captured. The sexes of these new birds have not been determined. In 1998, the highly biased skew in the sexes caught may be explained by the fact that most of the netting was carried out at active bowers. In 1999, we made special efforts to catch at feeding sites – collections of fruiting bushes and trees where flocks of >10 bowerbirds gathered. We caught 9 females and 17 males at feeding sites compared with only 1 female and 23 males at bowers.

How do morphological measures differ between sex and status groups?

The first encounters with each of 88 birds captured and sexed in either 1998 or 1999 were used in a MANOVA (Table 2). Nine morphological measures were considered (mass, cloaca area, crest area, tarsus length, wing length, hind claw length, tail length, gape and bill width) and year and status were entered as independent factors. Three measures revealed significant differences between status groups when the effect of

year was controlled for (Table 2; Fig. 2). The pattern whereby bower-owning males had larger crests than non-owner males, who, in turn, had larger crests than females, was evident in both 1998 and 1999. This contrasted with the relative ordering of status groups by mass and tail length, which was inconsistent across years with, for example, bower-owners having the longest tails in 1998, but the shortest in 1999.

Colour differences with sex and status

We used the soft part colours and status groupings assigned to 88 birds captured for the first time in 1998 or 1999 and looked to see if such colours could be used to assign a bird to a particular sex or status (Table 3). Cloaca, gape and iris colour were all dependent upon group (Chi-square tests: Table 3). Bower owners were more likely to have pink cloacas, white gapes and chestnut eyes than expected (goodness-of-fit tests: cloaca $G_{adj} = 5.9, P = 0.015$; gape $G_{adj} = 5.9, P = 0.015$; iris $G_{adj} = 11.6, P < 0.001$). Females all had grey, rather than pink, cloacas but showed no significant deviation from random allocation of gape and eye colours (goodness-of-fit tests: gape $G_{adj} = 0.58, P = 0.44$; iris $G_{adj} = 0.06, P = 0.80$). Non-owner males were more likely to have yellow gapes than expected (goodness-of-fit test: gape $G_{adj} = 3.88, P = 0.05$) but showed no deviation from a random allocation of colour for either cloaca or iris (goodness-of-fit tests: cloaca $G_{adj} = 0.03, P = 0.86$; iris $G_{adj} = 0.92, P = 0.34$). When we combined observations from males to allow a comparison between sexes, we found that gape and eye colour were not dependent upon sex (gape $\chi^2_c = 0.32, P = 0.57$; iris $\chi^2_c = 0.26, P = 0.61$) but cloaca colour was significantly dependent on sex ($\chi^2_c = 20.5, P < 0.001$). Independently, soft part colours can tell us little of the sex or status of a Spotted Bowerbird, but our results suggest that any bird with a pink cloaca is unlikely to be a female, whereas a bird with a grey

Table 1. Morphometric measures of Spotted Bowerbirds caught at Taunton National Park in 1998 and 1999

For 1998, bower owners $n = 18$, non-owners $n = 33$, females $n = 5$; for 1999, bower owners $n = 16$, non-owners $n = 23$, females, $n = 10$. Figures show mean measures and range

	Mass (g)	Cloaca (mm ²)	Crest area (mm ²)	Tarsus (mm)	Wing (mm)	Tail (mm)	Hind claw (mm)	Gape (mm)	Bill width (mm)
1998									
Bower owners	141.4 (131–150)	40.0 (60.4–25.5)	292.9 (145.1–551.6)	40.4 (36.7–45.7)	148.7 (143–153)	107.7 (101–112)	11.9 (12.7–11.2)	30.7 (29.6–32.3)	9.3 (8.4–9.8)
Non-bower owners	142.1 (127–157)	32.1 (38.9–25.4)	212.3 (0–416.0)	40.1 (37.5–42.4)	148.5 (144–154)	108.0 (103–112)	12.0 (12.7–11.1)	30.7 (29.3–32.4)	9.3 (7.7–10.7)
Females	144.0 (142–147)	33.6 (41.6–26.5)	185.9 (151.6–239.7)	39.4 (38.1–40.7)	147.5 (145–150)	107.2 (106–109)	11.8 (12.2–11.3)	31.1 (29.5–32.0)	10.0 (9.4–10.4)
1999									
Bower owners	136.9 (117–158)	33.7 (28.1–42.9)	472.9 (235.7–644.9)	40.5 (37.7–42.2)	145.9 (142–150)	105.8 (99–112)	12.3 (11.2–12.8)	31.6 (30.0–33.3)	9.5 (9.1–10.0)
Non-bower owners	144.6 (122–162)	34.8 (25.1–46.8)	170.7 (0–420.0)	40.5 (38.8–42.2)	148.1 (143–154)	112.1 (105–120)	12.4 (11.4–13.2)	31.3 (29.2–32.7)	9.9 (9.1–10.5)
Females	141.7 (131–157)	36.7 (32.9–41.3)	103.0 (0–281.8)	39.4 (38.0–40.7)	147.0 (143–150)	110.7 (105–118)	12.0 (11.6–13.0)	30.9 (29.4–31.9)	9.9 (9.3–10.6)

Table 2. Two-way MANOVA results considering status and year as factors, independently and interacting
*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Dependent variable	<i>F</i>	<i>P</i>
Status		
Mass	4.23	0.02*
Cloaca area	1.37	0.26
Crest	12.98	<0.001***
Tarsus	3.34	0.04*
Wing	0.81	0.45
Hind claw	3.92	0.02*
Tail	11.30	<0.001***
Gape	0.26	0.77
Bill width	2.71	0.07
Year		
Mass	1.62	0.21
Cloaca area	0.97	0.33
Crest	0.13	0.73
Tarsus	2.23	0.14
Wing	3.44	0.07
Hind claw	4.53	0.04*
Tail	0.58	0.45
Gape	2.93	0.09
Bill width	2.92	0.09
Status \times Year		
Mass	3.39	0.04*
Cloaca area	0.71	0.50
Crest	4.75	0.01**
Tarsus	2.77	0.07
Wing	0.48	0.62
Hind claw	0.66	0.52
Tail	7.49	<0.001***
Gape	1.40	0.25
Bill width	2.46	0.09

cloaca, yellow gape and dark brown eye is unlikely to be a bower owner.

Quantitative measures of the visual properties of crests revealed several differences between sex and status groups, although all measures showed some degree of overlap, again making accurate separation impossible (Fig. 3). Bower-owners had purer colours (higher chroma scores) than non-owner males and females in both blue and red regions (*post hoc* Tukey tests: Blue, bower-owners *v.* non-owners $P = 0.022$, bower-owners *v.* females $P = 0.024$; Red, bower-owners *v.* non-owners $P = 0.042$, bower-owners *v.* females

$P = 0.003$). Non-owner males did not differ from females with respect to the chroma of either area (Blue, non-owners *v.* females $P = 0.67$; Red, non-owners *v.* females $P = 0.16$).

Sex and status groups did not differ with respect to the reflectance of red regions, but females had a more highly reflective blue region than bower-owning males (bower-owners *v.* females $P = 0.002$). Again, non-owners did not differ from either bower owners or females (bower-owners *v.* non-owners $P = 0.07$, non-owners *v.* females $P = 0.09$). When we compared the difference in reflectance between the blue and red regions, a form of visual contrast, we found that females had larger differences than either bower owners or non-owners (bower-owners *v.* females $P = 0.005$, non-owners *v.* females $P = 0.037$), who did not differ from each other (bower-owners *v.* non-owners $P = 0.38$). Any such differences in visual properties were not apparent to human observers, but of course may be detected by bowerbirds.

Can sex and/or breeding status be conclusively determined from morphometrics?

Sex could not be conclusively determined using only morphometrics. We used stepwise discriminant frequency (DF) analysis to classify the sex of birds, whose sex we had already determined genetically, based on the morphometrics that we had collected. A stepwise DF model containing tarsus length, bill width and crest area, which prevented any other measures entering, could accurately sex 77.4% of individuals (Table 4a), describing 73.9% of males as males and 93.3% of females as females.

Males who held bowers could not be conclusively separated from those who did not hold bowers purely on the basis of morphological measures. A DF model, considering all males, that only admitted crest area correctly assigned 64.9% of males to the correct status grouping (Wilks' $\lambda = 0.862$, $F_{1,58} = 9.28$, $P = 0.003$). In all, 76.2% of owners were classified as such, compared with 60.4% of non-owners correctly classified.

If neither sex or status was known independently, then predicting a bird's classification on the basis of its morphology became much less accurate. A DF model was constructed, considering all birds and two measures, crest area and tarsus, entered (Table 4b). This model assigned 49.4% of birds into the correct group, which was a significant

Table 3. Colours of soft part of bowerbirds reported from their first capture, grouped according to status at that time

	Cloaca		Gape		Iris	
	Grey	Pink	White	Yellow	Light brown	Dark brown
Bower owners	1	8	16	5	18	3
Non-owners	16	17	19	33	29	23
Females	14	0	9	6	8	7
χ^2_2	18.9		9.9		6.2	
<i>P</i>	<0.001		0.007		0.046	

improvement over the 33.3% expected by chance ($\chi^2_4 = 26.4$, $P < 0.001$). Within the final model, crest area explained 90.1% of the variance and hence provided the best single discriminator. Crest area alone assigned 42.7% of birds into

their correct groups. This was also significantly more accurate than a random allocation ($\chi^2_2 = 20.9$, $P < 0.001$). The DF model correctly assigned 66.7% of actual bower-owners to the grouping of bower-owners, and 80.0% of actual females to the female group. In contrast, 39.6% of non-owners were described as bower-owners, 26.4% as females and only 34.0% correctly as non-owners.

Changes in morphology corresponding to changes in status

Birds who were not bower owners in 1998 but became owners in 1999 or 2000 exhibited an increased crest area as they changed status (Table 5). Non-owner males who did not go on to own a bower in 1999 did not differ in crest size from non-owner males in 1999 who did not go on to hold bowers in 2000 (Table 6). This suggests that a change in crest size of these proto-bower-owners could not be attributed to some environmental factor that would cause a general increase in crest size across the population. Of the four measures that did appear to change over time across the population (hind claw length, tail length, gape and bill width: Table 6), none changed significantly when a single bird changed status (Table 5). We are unsure why these morphometrics should vary between two years.

Using discriminant function analysis, it was possible to predict which individuals would go on to become bower owners from their morphology. We compared 1998 proto-owners (those birds that went on to become bower owners in subsequent years), with their 1998 peers who did not attain bower-ownership. A DF model including mass, which prevented any other measures from entering, correctly assigned 71.9% of birds to either owning or non-owning (Wilks' $\lambda = 0.863$, $F_{1,28} = 4.45$, $P = 0.044$). Surprisingly, proto-owners were somewhat lighter than non-owners (proto-owners (mean \pm s.d.) = 138.0 ± 7.6 , non-owners = 143.1 ± 6.7 ; unpaired $t_{30} = 1.66$, $P = 0.11$).

It was possible to suggest which bower-owning males would subsequently lose their bowers. We compared 1998 males who would lose their bower-owning status in the following years (proto-failures) with fellow bower owners in 1998 who maintained their bowers for the next two years (for 8 proto-failures v. 9 successful peers). A DF model including wing length, which prevented any other measures from entering, correctly assigned 76.5% of birds to either future success or failure (Wilks' $\lambda = 0.658$, $F_{1,15} = 7.80$, $P = 0.014$). Males who would continue to hold bowers for the next two years had shorter wings in 1998 than males who would lose their bowers over the same period (long-term owners (mean \pm s.d.) = 147.2 ± 2.81), losers = 150.5 ± 1.85 ; unpaired $t_{15} = 2.79$, $P = 0.014$).

Relationships between crest size and sexual success

We calculated mating success for each owner using methods described by Madden (2003). There was no significant relationship in either 1998 or 1999 between an owner's crest

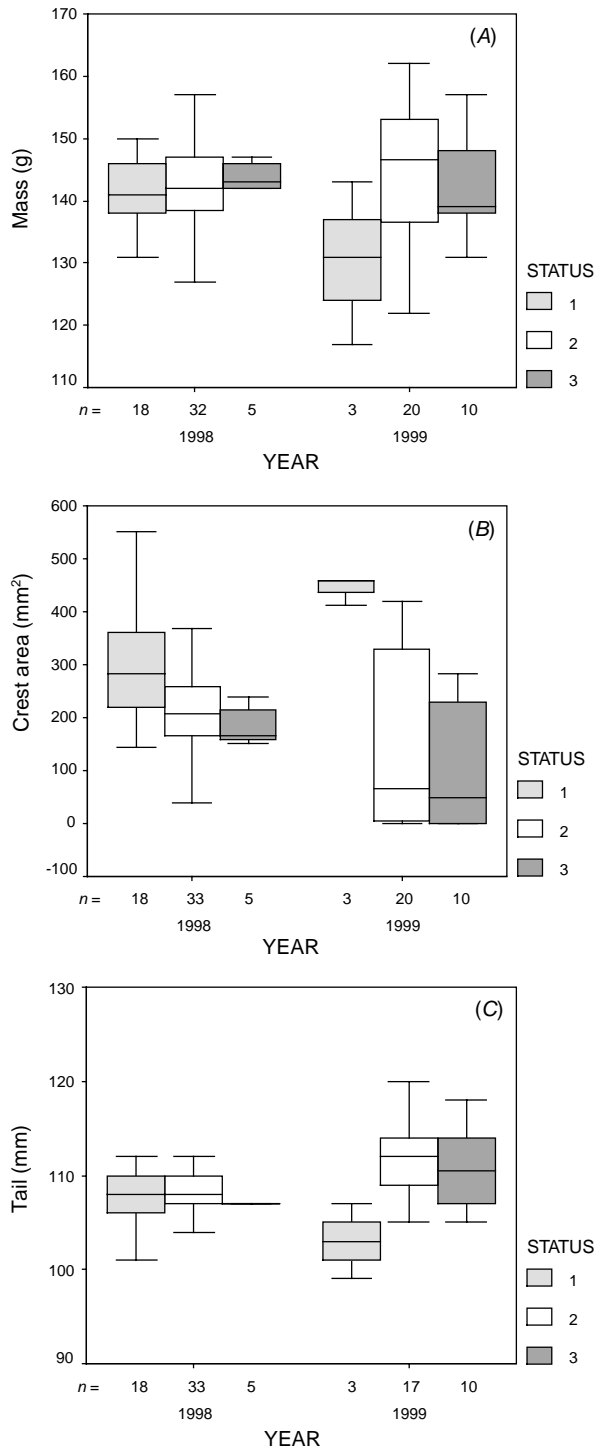


Fig. 2. Morphological measures that differed significantly among status groups when controlling for year: (A) mass, (B) crest area, (C) tail length. Box plots show median, interquartile ranges and 95% CI.

size and his mating success (Spearman rank correlations, 1998: $r_s = 0.22$, $n = 18$, $P = 0.38$; 1999: $r_s = 0.46$, $n = 16$, $P = 0.07$).

Discussion

Skew in sex ratio

The high ratio of captured male to female Spotted Bowerbirds is puzzling. The catch ratio at bowers of 49:5 and 23:1 in 1998 and 1999, respectively, suggests that females spend relatively little time at bowers compared with males. Even when bower owners are excluded from the comparison, due to the very high expectation of finding them at their bower, and the fact that three were recaptured at more than one site, the ratios of 31:5 and 6:1 remain consistently high. Further, they appear to be similar over years, with six times more males being caught at bowers than females. The skew was reduced when we concentrated on feeding sites, to 17:9, yet twice as many males were still caught. Such a skew was not recorded by Lenz (1999), who caught 104 male and 98 female Regent Bowerbirds, or by Borgia and Collis (1990), who caught 350 males and 354 female Satin Bowerbirds. However, great bowerbirds may also exhibit a strong skew in encounter rate (L. Day, personal communication 2002).

We offer three explanations. First, male and females differ both in their attendance of bowers and in their diet, and so their probability of capture. Bowens are the sites of copulations (Borgia and Mueller 1992; Madden 2003), and so females are compelled to visit at this time. Bowens are also the sites of sexual display, where males perform a suite of actions and vocalisations, focused on their bower and its decorations (Marshall 1954; Gilliard 1969). Females stand at the bower, usually within the avenue, to witness such displays (Warham 1962; Borgia and Mueller 1992; Madden 2003). Female Satin Bowerbirds are known to visit several bowens (Uy *et al.* 2001) throughout the breeding season and so are susceptible to capture at this time.

Males obviously attend their own bowens, and in addition, owners may visit neighbours' bowens to maraud them (Borgia and Mueller 1992; Pruett-Jones and Pruett-Jones 1994; Madden 2002). Younger males may also attend established bowens in order to learn correct display techniques or to try to obtain sneaky copulations. However, even if these differences in behaviour between the sexes could account for the 6:1 ratio of encounters at bowens, this alone fails to explain the sex bias away from bowens. If females were not at bowens, they may well be feeding instead. We selected three sites where bowerbirds were seen to gather to feed on concentrations of fruiting bushes (mainly *Myoporum* spp.).

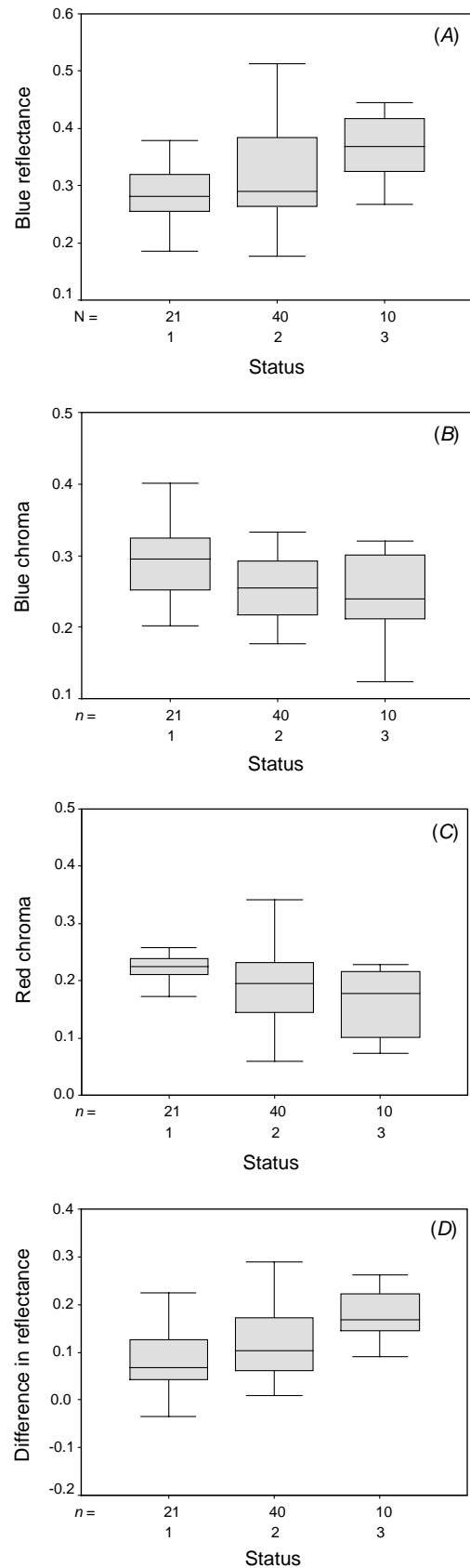


Fig. 4. Significant differences in visual properties of crests among status groups: (A) blue reflectance, (B) blue chroma, (C) red chroma, (D) difference in reflectance. For status class, 1 = bower owner, 2 = non-owning male, 3 = female. Box plots show median, interquartile ranges and 95% CI.

Table 4. Multivariate discriminant function analysis models
Model (A) classified 77.4% of birds correctly. In Model (B) the status groups were categorised as 1 = bower owner, 2 = non-owner male, 3 = female; this model classified 49.4% of birds correctly

Model and variables	Wilks' λ	F	P
(A) Separation of sexes based on morphology			
Tarsus length	0.902	7.60	0.007
Bill width	0.808	8.20	0.001
Crest area	0.757	7.27	<0.001
(B) Separation of birds into sex and status groupings			
Crest area	0.837	6.73	0.002
Tarsus	0.714	6.23	<0.001

The diet of bower owners is much narrower than that of non-owner males (Miles and Madden 2002), but sex differences in diet have not been reported. Spotted Bowerbirds do not show sexual dimorphism in bill measures (see Table 1), which could otherwise reflect differing diets.

A second suggestion is that the sexes differ in their susceptibility to trapping due to behavioural differences. A similar situation may be seen in male-biased catch ratios in marbled murrelets, *Brachyramphus marmoratus* (Vanderkist *et al.* 1999). However, at bowers we expect that the owner, spending a large portion of his day in the vicinity of his bower would have more detailed knowledge of the local area and so be less likely to become trapped in nets, unlike infrequently visiting, naïve females. Uy *et al.* (2001) reported that female Satin Bowerbirds each spent, on average, just under an hour at bowers over the entire breeding season.

Third, Spotted Bowerbirds may truly exhibit a skewed operational sex ratio. This may be due to the polygynous nature of their mating system, with females spending large amounts of time at their nests, and therefore markedly less time at bowers. However, 88% of birds in 1998 and 65% in 1999 were caught before any copulations were recorded. In neither year were any females caught after the first copulation was recorded. Alternatively, the skewed sex ratio may be due

to differential mortality, with sitting females at risk from predators. Finally, the initial sex ratio may be biased, although this has seldom been revealed on a population-wide scale (Oddie and Reim, 2002). No nests were found, so these explanations could not be tested. Such a biased operational sex ratio could be one explanation for the evolution of such an extremely elaborate sexual display by male Spotted Bowerbirds.

Signals of sex and status

Accurately assigning the sex of a Spotted Bowerbird, on the basis of its morphology, was not possible. Although females generally had shorter tarsi, wider bills and smaller crests than males, they could not be reliably separated from non-bower holding males, with much overlap in morphology. No female had pink cloacal protuberances, instead being unanimously grey, but at least some bower-owning and non-owner males also had grey cloacal protuberances. Some previous studies that have suggested that sexing is possible if based on the presence of a crest may be incorrect as we recorded several crested females and uncrested males, as well as substantial overlap between females and both non-owner and owner males.

Spotted Bowerbirds could obtain some information concerning the breeding status of a conspecific from the size of that bird's crest. Males with large crests were likely to be bower owners. It is interesting to note that the crest is made conspicuous during display to both males and females (Warham 1962; Frith *et al.* 1995; JRM and JAE, personal observations; but see Borgia 1995). Of course, our crude measure of crest size, made statically on a stressed bird, differs substantially from the extended crest exhibited during display. The crest colours may provide some information, with bower owners generally having more chromatically pure red and blue regions, or with females having higher contrast in the reflectance of their red and blue areas, but, again, considerable overlap in measures between groups prevents a perfect assignment of sex or status.

Crests are not found in the closely related Fawn-breasted Bowerbird, *Chlamydera cerviniventris*, or Lauterbach's

Table 5. Changes in morphology of seven birds as they progress from being non-owners to bower owners, with accompanying Wilcoxon signed-ranks tests

When a sequential Bonferroni correction is applied to account for multiple comparisons, only changes in crest area remain significant at $\alpha = 0.05$

Variable	Non-owner	Owner	n	Z	P
Mass (g)	139.14	134.86	7	-2.03	0.04
Cloaca area (mm ²)	32.75	29.92	5	-0.67	0.50
Crest area (mm ²)	234.08	420.23	7	2.37	0.02
Tarsus (mm)	39.94	40.55	7	1.89	0.06
Wing (mm)	147.57	146.29	7	-2.21	0.03
Hind claw (mm)	12.16	12.28	7	0.85	0.40
Tail (mm)	108.50	107.64	7	-1.19	0.24
Gape (mm)	30.46	31.26	5	1.75	0.08
Bill width (mm)	9.54	9.56	5	0.40	0.69

Bowerbird, *C. lauterbachii*, but even in these species, males turn their head towards females during display, exposing the site of the presumed ancestral crest at the nape of their neck (Gilliard 1959). The crest of the Spotted Bowerbird may provide information in two ways. First, the crest provides a visiting female with a signal confirming that the bird at the bower is an owner, rather than an opportunistic non-owner who happens to be at the bower while the owner is absent. Thus, she ensures that she does not receive a mating from a low-quality or younger male. In sexually dimorphic bowerbird species, males holding bowers differ markedly from other males. In both Satin and Regent Bowerbirds, males take several years to achieve adult plumage, initially appearing similar to females (Marshall 1954; Gilliard 1969). Moreover, in Satin Bowerbirds, plumage maturation depends on levels of circulating testosterone (Collis and Borgia 1993). Second, the crest provides an intrasexual signal, with bower owners indicating their status to visiting males. This reduces the need to determine status through a series of costly interactions. We did not observe females erecting their crests at bowers but visiting males were seen to erect their crests during male–male display.

However, these signals are susceptible to misinterpretation or deception. We found no discrete crest size threshold between bower owners and other males. This resulted in 33% of bower-owners being misidentified by our best DF model using crest area and tarsal length, as were 20% of females. Crucially, 66% of non-owners were misidentified. This prevents birds from obtaining perfect information regarding the status or sex of another bird from its crest, although, as a rule of thumb, birds with large crests are

probably bower-owners. Non-bower-owning males did not differ significantly from females in crest size. This presents the opportunity for sexual concealment (Rohwer *et al.* 1980) that may reduce intrasexual conflict, enabling young males to interact with bower owners and hence gain opportunities for learning bower-building skills with greatly reduced harassment (Rohwer 1975). Bower owners are frequently seen displaying at the bower towards other known males (JRM, personal observations). In Satin Bowerbirds such behaviour has been interpreted as a form of teaching or practice (Maxwell 1999) but the benefits of such behaviour to the bower owner are unclear. An alternative explanation is that these are misdirected displays, arising because owners find it hard to distinguish males from females. Observant young males gain learning opportunities surreptitiously. Such concealment of sexual identity has also been suggested as an aid, in other species, to obtaining sneaky copulations (Gross 1985) or as a means to reduce sexual competition, with subordinate males concealing their identity more than dominant males (Langmore and Bennett 1999).

Changes in morphology correspond to changes in status

We found that a change in status, moving from non-owner to bower owner, was accompanied by an increase in crest size. Such a change is to be expected if the crest is to signal the status of the bird. Satin Bowerbirds moult from immature plumage to adult plumage at ~6 years, but a premature moult can be induced by testosterone implants (Collis and Borgia 1992). This suggests that plumage in bowerbirds is strongly linked to sexual cycles, and so provides choosy females with a useful signal of a male's suitability as a viable mate.

Table 6. Comparisons of morphological measures between non-owner males in 1998 and 1999 who in the following year did not go on to become bower owners

Accompanying *t*-test statistics are provided. No corrections have been made for multiple comparisons

Variable	Year	<i>n</i>	Mean	s.e.	<i>t</i>	<i>P</i>
Mass (g)	1998	32	142.16	1.24	-0.62	0.54
	1999	22	143.73	2.46		
Cloaca area (mm ²)	1998	32	32.12	0.67	-1.59	0.12
	1999	17	34.53	1.67		
Crest area (mm ²)	1998	33	207.80	16.00	0.55	0.59
	1999	22	187.45	38.73		
Tarsus (mm)	1998	33	40.14	0.20	-1.03	0.31
	1999	22	40.46	0.24		
Wing (mm)	1998	33	148.36	0.44	0.36	0.72
	1999	22	148.09	0.65		
Hind claw (mm)	1998	33	11.99	0.07	-3.20	<0.001
	1999	22	12.37	0.10		
Tail (mm)	1998	33	108.17	0.36	-3.37	<0.001
	1999	19	111.50	1.15		
Gape (mm)	1998	31	30.59	0.13	-2.95	<0.001
	1999	22	31.29	0.21		
Bill width (mm)	1998	31	9.34	0.12	-3.53	<0.001
	1999	22	9.87	0.07		

We were able to predict with some accuracy which males were to change status the following year from their mass. However, we cannot suggest why lighter males should be those who subsequently enjoy bower ownership. Likewise, we cannot suggest why bower owners with shorter wings were likely to continue to hold a bower in subsequent years, although consideration of this measure provided a reasonably accurate means of predicting an owner's future prospects.

The size of the crest did not relate to an owner's mating success. This suggests that it may act as a threshold marker, serving to identify status, rather than as a variable on which sexual success depends. This is a similar conclusion to that drawn by Borgia (1986), who showed that mature-plumaged male Satin Bowerbirds were preferred to immature-plumaged males by choosy females. Mature males carried a low ectoparasite load, yet mature males did not differ among themselves in infection levels, preventing these levels from predicting mating success.

Conclusions

The lack of sexual dimorphism, coupled with the apparently skewed sex ratio, means that studies of Spotted Bowerbirds are problematical. It is recommended that sexing using molecular methods be carried out to allow reliable conclusions to be drawn from the observed behaviour of marked birds. This study also suggests avenues for future research. An investigation of the apparent skewed sex ratio and its causes and consequences may provide an insight into the evolution of elaborate sexual displays. Few previous studies have looked at the role of male bowerbird morphology in determining his mating success (but see Borgia 1986; Borgia and Collis 1990). The crests of male Spotted Bowerbirds may be influential in social and sexual interactions.

This study confirms that Spotted Bowerbirds are sexually monomorphic across almost all conceivable morphological measures. We could find no measurement that consistently and accurately separated all males from females. Instead, we found that bower owners generally possess larger crests than either non-owner males or females, and that the size of the crest increases when birds take on bower ownership. However, we did not find any relationship between crest size and an owner's mating success.

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