Sex, bowers and brains

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Inter- and intraspecific variations in the sizes of specific avian brain regions correspond to the complexity of the behaviour that they govern. However, no study has demonstrated a relationship between gross brain size and behavioural complexity, a hypothesis that has been proposed to explain the unusually large human brain. I show, using X-rays of museum specimens, that species of bowerbirds that build bowers have relatively larger brains than both related and ecologically similar but unrelated species that do not build bowers. Bower design varies across species from simple cleared courts to ornate, hut-like structures large enough to contain a small child. Furthermore, species building more complex bowers have relatively larger brains, both within each of the two different bower-building clades and across the family as a whole, controlling for phylogeny. Such gross differences in brain size are surprising and may reflect the range of cognitive processes necessary for successful bower building. The relationships are strongest for males, the bower-building sex, although there is a similar trend in females. Because the size and complexity of bower design is targeted by female choice, the observation that relative brain size is related to bower complexity suggests that sexual selection may drive gross brain enlargement.

Keywords: bowerbirds; brain size; behavioural complexity; sexual selection

1. INTRODUCTION

Bowers, built by males of the family Ptilonorhynchidae, are extravagant traits that incur costs due to natural selection and benefits via inter-sexual selection (Borgia 1997). Within bowerbird species, females preferentially mate with males who construct larger, better quality and more highly decorated bowers (Borgia 1985; Borgia & Mueller 1992; Lenz 1994; Uy & Borgia 2000). Furthermore, female choice can drive substantial changes in intraspecific bower design, potentially leading to speciation (Uy & Borgia 2000). Bower complexity, in terms of size and design, the range of objects used as decorations and the layout of decorations in discrete, colour-defined groupings, varies widely across the Ptilonorhynchidae (Marshall 1954; Gilliard 1969). Maypole bowers, built by *Prionodura* and *Amblyornis*, consist of a central sapling onto which sticks and decorations are woven; the base of the sapling is often also surrounded with decorations. Court-clearing species, including *Scenopoeetes* and *Archboldia*, decorate their chosen display site but do not build a stick structure, yet they have been shown to be members of the maypole-building clade of bowerbirds (Kusmierski *et al.* 1997). Avenue bowers, built by *Chlamydera*, *Sericulus* and *Ptilonorhynchus*, are typified by the presence of two or more parallel walls of grass or sticks at the centre of a display court on which a variety of decorations is laid. Catbirds of the genus *Ailuroedus* do not build bowers.

The construction of high-quality bowers appears to require experience, learning and practice. Immature satin bowerbirds, *Ptilonorhynchus violaceus*, were found to bring inappropriately coloured objects and thick sticks to practice bower sites where third-, fourth- and fifth-year males appeared to play a role in the education of the younger

birds (Vellenga 1986). Maxwell (1999) confirmed that young immature satin bowerbirds spend time with older immature birds learning aspects of bower design and display. A spotted bowerbird, *Chlamydera maculata*, living sympatrically with satin bowerbirds outside its normal range, built a structure similar to the local satin bowerbirds' bowers and decorated it with blue objects rather than the more usual red, green and white objects (Neville 1988). Spotted bowerbirds from a population in central Queensland, Australia, built bowers similar to the sympatric great bowerbird, *C. nuchalis* (Frith *et al.* 1995). In addition to a learnt aspect of the behaviour, building a bower may also require a well-developed spatial memory, used to remember the location of supplies of decorations or neighbouring bowers, and an ability to innovate by using novel decorations or producing abnormally elaborate bower designs (Frith *et al.* 1994).

Learning, spatial memory and innovation have been shown to correspond to the sizes of the relevant brain regions in several other species of birds. Populations of the marsh wren, *Cistothorus palustris*, differ in the numbers of songs that they learn. When two such populations were compared, it was found that the volumes of two specific areas of the brain involved in song were 30–40% larger in the population learning around 150 songs than in the population learning only about 50 songs (Canady *et al.* 1984). A positive correlation was found between hippocampal volume and the estimated amount of food caching (a behaviour involving spatial memory) exhibited by seven corvid species (Healy & Krebs 1992). In an exhaustive study of feeding innovations in birds, Lefebvre *et al.* (1997) demonstrated a positive relationship between two measures of forebrain size and absolute and relative levels of innovation frequency. If, as seems likely, bower building is a cognitively complex task involving elaboration of a variety of brain regions then total brain volume may vary with the complexity of the bower that the bearer builds.

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2. METHODS

(a) *Calculating relative brain size*

Collecting fresh specimens for brain analysis was not feasible. Several species are listed under a range of threat categories (Collar *et al.* 1994). This lack of tissue precluded the measurement of individual brain components, although fine-scale differences are likely to prove important. However, good numbers of skins are held at the Rothschild Collection, Tring, UK. These skins often contain complete skulls, allowing examination by X-ray photography. The skulls of 37 avenue builders and 33 maypole builders, along with those of ten catbirds and eight unrelated, medium-sized frugivores of Australo-Papuan forest or open woodland, were sufficiently complete to be measured (see Appendix A). These included ten species of bowerbirds and four non-bowerbird species.

The X-ray source was aligned to ensure a constant angle for photography. Two orthogonal images were taken of each skull: lateral and dorso-ventral. A scale was obtained by using a metal bar of known length placed along the centre of the skull in each image. Three measures were taken, blind to the species' identity. Length described the greatest dimension of the brain cavity along an axis passing from the bill to the back of the skull. Height described the greatest distance perpendicular to the length of the brain cavity, from skull roof to skull base. Width described the greatest distance from one side of the brain cavity to the other, perpendicular to the axis along which length was measured.

An index of brain-cavity volume, intuitively linked to maximal brain volume, was calculated by approximating the brain cavity to an ellipsoid using the formula $(\pi/6) \times \text{length} \times \text{height} \times \text{width}$. Avian brain mass increases with body mass (Martin 1981). Reliable body masses were not available for several species, so instead I used skeletal information. The cube of the tarsus length provided a measure of body size (Freeman & Jackson 1990). Mean tarsus lengths and brain-cavity volumes were calculated for each species and log transformed to achieve approximate normality (Kolmogorov–Smirnov tests, all $p > 0.2$). Taking residuals from a regression of transformed mean tarsus lengths against transformed mean brain-cavity volumes yielded measures of relative brain size, controlling for body size. For the comparison between bowerbirds and non-bowerbirds, the regression was restricted to males and included all four non-bowerbird species. For all other analyses, I used residuals derived from regressions that included only the bowerbird species, but considered mean values for males and females separately. All sets of residuals were normally distributed (Kolmogorov–Smirnov tests, all $p > 0.2$).

(b) *A bower-complexity index*

Five species of avenue builders and four species of maypole builders/court clearers offered a range of bower complexities (figure 1). A bower-complexity index, considering both bower structure (number and size of walls or maypoles) and bower ornamentation (number, diversity and orderly arrangement of decorations), was constructed based on independent descriptions (Marshall 1954; Gilliard 1969; Diamond 1982; Borgia 1997; Kusmiński *et al.* 1997). Catbirds, which do not build bowers, scored one. Species that clear courts or build simple bowers with a narrow range of decorations scored two or three. Species that build ornate structures decorated with a wide range of objects arranged in discrete groupings scored four or five. Comparing two highly differing types of structures (avenues and maypoles)

was problematical. Therefore, an index was constructed for each clade allowing intra-clade analyses. In order to consider phylogenetic effects across the whole family, the two indexes were combined, retaining the intra-clade scores. This produced an anomaly. The simple avenue of the regent bowerbird, *Sericulus chrysocephalus*, was given the same score as the cleared and decorated court of the toothbilled bowerbird, *Scenopoeetes dentirostris*. I repeated the cross-family analysis with *S. chrysocephalus* assigned scores of both two and three, and present here only the most conservative results. Bower-building species were compared with the closely related catbird *Ailuroedus melanotis*, which does not build bowers.

3. RESULTS

(a) *Does the bowerbird family exhibit a propensity towards large brains?*

I compared the mean relative brain sizes of a selection of male, medium-sized, woodland/forest frugivores representing four different passerine families from the Australo-Papuan region (specifically, *Philemon novaeguineae*, *Sphecotheres viridis*, *Dicrurus bracteatus* and *Ptiloris magnificus*) with those of male catbirds (ancestral, non-bower-building bowerbirds) and bower builders (figure 2). Non-bowerbird species did not differ from catbirds in relative mean brain size (one-sample *t*-test, $t = 0.19$, d.f. = 3, $p = 0.86$), suggesting that the family Ptilonorhynchidae does not have a predisposition for abnormally large brains. However, both catbirds and non-bowerbirds had significantly smaller brains for their body size than bower-building species (catbird versus nine bower builders: one-sample *t*-test, $t = 8.48$, d.f. = 8, $p < 0.01$; nine bower builders versus four non-bowerbirds: Mann–Whitney *U* test, $W = 16.0$, $p = 0.04$).

(b) *Do species that build more complex bowers possess correspondingly larger brains?*

I examined this question in two ways, searching for consistency in results between methods. Initially, I looked at patterns within the two separate clades: maypole builders and avenue builders. Male avenue builders, constructing more complex bowers, had significantly larger brains for their body size than those constructing simpler bowers ($r^2 = 0.83$, $n = 6$ species, $p < 0.01$) (figure 3a). This relationship was repeated in females, although the level of significance decreased ($r^2 = 0.48$, $n = 6$ species, $p = 0.08$). Maypole builders mirrored these results. The relative brain size of males was significantly correlated with bower complexity ($r^2 = 0.81$, $n = 5$ species, $p < 0.05$) (figure 3b). The relationship in females was not significant ($r^2 = 0.47$, $n = 5$ species, $p = 0.12$). This last result may be confounded by the fact that only one female specimen was available for each of *Archboldia papuensis* and *S. dentirostris*.

A problem with this method is that species cannot be considered to be truly independent (Harvey & Pagel 1991), yet the numbers in each clade (five and six) were low, making corrections for phylogenetic relatedness impractical. Therefore, I controlled for the effects of relatedness by using comparative analysis of independent contrasts (Purvis & Rambert 1994), considering the family as a whole whilst retaining the same bower-complexity scores, basing my analyses on a molecular

Figure 1. Relationships between the ten species of bowerbird considered in this study, based on a phylogeny constructed from mitochondrial cytochrome *b* sequences by Kusmierski *et al.* (1997). Bower and habitat descriptions are taken from Kusmierski *et al.* (1997). BCI: bower complexity index.

phylogeny (Kusmierski *et al.* 1997). For males, I found a strong relationship between contrasts in relative brain size and contrasts in bower complexity ($p < 0.01$, $r^2 = 0.61$, $n = 10$ contrasts) (figure 4a). For females, the relationship

was apparent but less strong ($p = 0.06$, $r^2 = 0.31$, $n = 10$ contrasts) (figure 4b).

To put these results in context, the size-corrected average brain size of males of the complex bower builder

Figure 2. Mean relative brain sizes of bower builders, catbirds and non-bowerbirds. Error bars indicate ± 1 s.e.m. (non-bowerbirds: $n = 4$; catbirds: $n = 1$; bower-builders: $n = 9$).

Figure 3. Plots of mean standardized residuals measuring relative brain size against bower complexity for (a) avenue builders and the catbird and (b) maypole builders and the catbird (males: solid diamonds; females: solid squares).

C. lauterbachii was 80.6% larger than that of the male catbird *A. melanotis*.

4. DISCUSSION

Birds building bowers have relatively larger brains than both related and unrelated species that do not build bowers. Within the bowerbird family, species that build more complex bowers possess correspondingly relatively larger brains. This is seen separately in both avenue

Figure 4. Regressions between contrasts for (a) male and (b) female relative brain size and bower complexity with the lines forced through the origin.

builders and maypole builders, as well as across the family as a whole, and appears to be independent of potentially confounding phylogenetic effects. Moreover, all bowerbirds inhabit woodland or forest, are frugivorous and develop altricially, and the bower builders are all polygamous (the catbird is assumed to be monogamous) (Marshall 1954; Donaghey 1981; Borgia & Mueller 1992; Lenz 1994). These similarities reduce, but of course do not entirely eliminate, the possibility that variation in brain size is driven by differences in the species' ecology, developmental history or mating strategy (Bennett & Harvey 1985; Healy & Krebs 1992). That catbirds do not differ from ecologically similar birds in relative brain size indicates that the bowerbird family does not have an inherent propensity for large brains. I suggest that the differences in brain size between bower builders and catbirds, and amongst bower-building bowerbirds, are not driven primarily by ecological factors but rather by the most striking behavioural differences between the species, namely the complexities of bower construction.

These results are somewhat surprising. Whilst important studies have revealed links between behaviours and specific brain regions (e.g. Kirn *et al.* 1989; Healy & Krebs 1992; Székely *et al.* 1996), no other work has related behavioural differences to variations in gross brain size. Several other studies have demonstrated sex differences in brain-region size and related these to sexual selection targeting such traits as song (reviewed in Catchpole 1987). In this study, I have shown that although the relationship between brain size and bower complexity (a sexually selected trait) is stronger in male bowerbirds, the same trend is also seen in females. This finding can be

explained in two ways. First, females may benefit from a corresponding increase in brain size for similar reasons to males, specifically, an increased ability to analyse and compare more innovative or complex bower structures and improved spatial memory to facilitate returning to chosen bower sites after initial assessment (Uy *et al.* 2000). Second, a non-exclusive alternative is that female brain size may have co-evolved alongside male brain size due to pleiotropy, yet remains selectively neutral (Lande 1980; Lindenfors & Tullberg 1998). Fine-scale neuro-anatomical studies may clarify this by revealing sex differences in specific brain regions.

This relationship between brain size and a sexually selected trait provides some indirect support for the hypothesis put forward by Miller (2000) that sexual selection may drive the evolution of the abnormally large

human brain in response to female choice targeting novel, complex male behaviours. Bowerbirds provide one of the very few examples in biology of the building of ornate physical structures purely for the purposes of sexual display. I have demonstrated here a correlation between the complexity of such a display and relative brain size.

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APPENDIX A

Specimens used in this work and their Natural History Museum, Tring, UK, identification numbers are given below.

species	sex	identification number	species	sex	identification number
<i>Ailuroedus melanotis</i>	F	1964.60.1400	<i>C. lauterbachii</i>	M	1949.62.101
<i>A. melanotis</i>	F	1964.60.1403	<i>C. lauterbachii</i>	M	1953.17.228
<i>A. melanotis</i>	F	1964.60.1405	<i>Chlamydera maculata</i>	F	1964.60.1419
<i>A. melanotis</i>	F	1964.60.1407	<i>C. maculata</i>	F	1964.60.1421
<i>A. melanotis</i>	F	1964.60.1410	<i>C. maculata</i>	M	1964.60.1420
<i>A. melanotis</i>	M	1964.60.1399	<i>C. maculata</i>	M	1964.60.1422
<i>A. melanotis</i>	M	1964.60.1401	<i>C. maculata</i>	M	1964.60.1423
<i>A. melanotis</i>	M	1964.60.1404	<i>C. maculata</i>	M	1964.60.1424
<i>A. melanotis</i>	M	1964.60.1411	<i>C. maculata</i>	M	1964.60.1425
<i>A. melanotis</i>	M	1964.60.1412	<i>C. maculata</i>	M	1964.17.658
<i>Amblyornis m. macgregoriae</i>	F	1904.4.19.29	<i>Dicrurus bracteatus</i>	M	1916.5.30.877
<i>A. m. macgregoriae</i>	F	1911.12.22.71	<i>D. bracteatus</i>	M	1916.5.30.901
<i>A. m. macgregoriae</i>	F	1913.3.6.155	<i>Philemon novaeguineae</i>	M	81.5.1.4161
<i>A. m. macgregoriae</i>	M	1913.3.6.153	<i>P. novaguineae</i>	M	1925.11.1.689
<i>A. m. macgregoriae</i>	M	1949.62.88	<i>Ptilonorhynchus v. violaceus</i>	F	1900.6.11.41
<i>A. m. macgregoriae</i>	M	1949.62.89	<i>P. v. violaceus</i>	F	1939.12.9.2134
<i>A. m. macgregoriae</i>	M	1949.62.90	<i>P. v. violaceus</i>	F	1939.12.9.2135
<i>A. m. macgregoriae</i>	M	1953.17.224	<i>P. v. violaceus</i>	F	1969.41.1054
<i>A. m. macgregoriae</i>	M	1953.17.225	<i>P. v. violaceus</i>	M	4
<i>Amblyornis subularis</i>	F	1911.12.22.70	<i>P. v. violaceus</i>	M	81.11.7.367
<i>A. subularis</i>	F	1913.3.6.146	<i>P. v. violaceus</i>	M	93.4.4.60
<i>A. subularis</i>	F	1913.3.6.147	<i>P. v. violaceus</i>	M	1900.6.11.40
<i>A. subularis</i>	F	1970.2.42	<i>P. v. violaceus</i>	M	1969.49.51
<i>A. subularis</i>	M	1911.12.22.66	<i>Ptiloris magnificus</i>	M	1916.5.30.1328
<i>A. subularis</i>	M	1913.3.6.152	<i>P. magnificus</i>	M	1916.5.30.1331
<i>A. subularis</i>	M	1932.12.21.69	<i>Scenopoeetes dentiostriis</i>	F	85.11.19.2
<i>A. subularis</i>	M	1969.41.807	<i>S. dentiostriis</i>	M	85.11.19.1
<i>A. subularis</i>	M	1969.41.809	<i>S. dentiostriis</i>	M	90.9.19.21
<i>Archboldia papuensis</i>	F	1953.17.222b	<i>S. dentiostriis</i>	M	90.9.19.22
<i>A. papuensis</i>	M	1953.17.217	<i>S. dentiostriis</i>	M	93.4.4.132
<i>A. papuensis</i>	M	1953.17.218	<i>S. dentiostriis</i>	M	1964.60.1413
<i>A. papuensis</i>	M	1953.17.219	<i>S. dentiostriis</i>	M	1964.60.1414
<i>A. papuensis</i>	M	1953.17.220	<i>Sericulus chrysocephalus</i>	F	72.2.10.21
<i>A. papuensis</i>	M	1953.17.221	<i>S. chrysocephalus</i>	F	81.11.7.371
<i>A. papuensis</i>	M	1953.17.222	<i>S. chrysocephalus</i>	F	1955.6.n6.26
<i>A. papuensis</i>	M	1965.29.32	<i>S. chrysocephalus</i>	M	45.3.15.26
<i>Chlamydera cerviniventris</i>	F	1939.12.9.1537	<i>S. chrysocephalus</i>	M	72.2.10.20
<i>C. cerviniventris</i>	F	1970.2.23	<i>S. chrysocephalus</i>	M	95.4.5.58
<i>C. cerviniventris</i>	M	1925.11.1.332	<i>S. chrysocephalus</i>	M	1900.6.11.43
<i>C. cerviniventris</i>	M	1939.12.9.2731	<i>S. chrysocephalus</i>	M	1943.4.19.2
<i>Chlamydera lauterbachii</i>	F	1916.5.30.1013	<i>S. chrysocephalus</i>	M	1955.6.n6.25
<i>C. lauterbachii</i>	F	1953.17.229	<i>S. chrysocephalus</i>	M	1969.41.784
<i>C. lauterbachii</i>	F	1953.17.230	<i>Sphecotheres viridis</i>	M	60.9.5.77
<i>C. lauterbachii</i>	M	1949.62.100	<i>S. viridis</i>	M	1969.29.493

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