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Evolution of Bower Complexity and Cerebellum Size in Bowerbirds

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Key Words
Birds · Bowerbirds · Cerebellum · Hippocampus · Sexual selection

Abstract
To entice females to mate, male bowerbirds build elaborate displays (bowers). Among species, bowers range in complexity from simple arenas decorated with leaves to complex twig or grass structures decorated with myriad colored objects. To investigate the neural underpinnings of bower building, we examined the contribution of variation in volume estimates of whole brain (WB), telencephalon minus hippocampus (TH), hippocampus (Hp) and cerebellum (Cb) to explain differences in complexity of bowers among 5 species. Using independent contrasts, we found a significant relationship between bower complexity and Cb size. We did not find support for correlated evolution between bower complexity and WB, TH, or Hp volume. These results suggest that skills supported by the cerebellum (e.g., procedural learning, motor planning) contribute to explaining the variation in bower complexity across species. Given that male mating success is in part determined by female choice for bower design, our data are consistent with the hypothesis that sexual selection has driven enlargement of the cerebellum in bowerbirds.

Introduction

Males of the bowerbird family (Ptilonorhynchidae), except three monogamous species, build elaborate display sites (bowers) used to entice females to mate [Marshall, 1954; Kusmierski et al., 1997]. Bower design appears to have been sexually selected through female choice as females of several species are known to select mates based at least partially on the quality of the bower or the number of particular items used to decorate the bower [Borgia and Mueller, 1992; Madden, 2003a]. Each species of bowerbird has a particular bower style and preference for decorations of certain types or colors [Marshall, 1954; Madden, 2003b]. Some species build simple or rough-hewn bowers, whereas others build intricate, complex, precisely decorated structures [Marshall, 1954; Kusmierski et al., 1997].

Previous research has shown that endocranial volume in bowerbirds is associated with bower complexity, suggesting that the diversity of skills associated with bower building has led to the evolution of size increases in several brain regions concomitantly with increasing bower complexity [Madden, 2001]. This might reflect the expansion, in concert, of several independent neural regions to support a complex suite of behaviors, or may suggest that selection for general intelligence and thus larger brains has allowed for the behavior. In other species, increases

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in whole brain size are associated with behavioral suites that are thought to demand general intelligence, such as sociality and tool use [Lefebvre et al., 2002; Reader and Laland, 2002]. Independent of Madden [2001], we hypothesized that brain size might be related to bower complexity. Given that changes in whole brain (WB) are often the result of changes in telencephalon volume we also examined relationships between telencephalon size and bower complexity. To go beyond these general measures and in order to begin to explore more specific neural underpinnings of bower building, we also hypothesized that the size of particular neural regions, the hippocampus (Hp) and cerebellum (Cb), might be related to bower complexity.

If variation in bower design is associated with differences in the size of particular brain regions, we may infer that a known function of that brain region could be critical for bower building. Brain region/behavior relationships have been found in other species. For instance, in avian species relationships have been found between hippocampal volume and food storing, HVC volume and song complexity, and mesopallium volume and innovative feeding styles [Sherry et al., 1992; Brenowitz, 1997; Timmermans et al., 2000; Day 2003].

Our study had two aims: First, we sought to determine if bower building is generally associated with an increase in volume of WB, Telencephalon minus Hp (TH), Hp or Cb by comparing four bower building bowerbirds (family Ptilonorhynchidae) with a bowerbird that does not build a bower, the spotted catbird (family Ptilonorhynchidae, *Ailuroedus crassirostris*). Secondly, we tested the hypothesis that the volumes of WB, TH and neural regions known to be involved in spatial or procedural skills, hippocampus and cerebellum respectively, are associated with variation in bower design. As the hippocampus is known to support avian spatial memory [Sherry et al., 1992], we predicted that hippocampal volume would be greater in species that use larger numbers and types of ornaments and whose nearest neighbor distances are greatest, as this would demand memory for more locations in order to collect ornaments and for memory of greater distances to steal from and destroy neighbors' bowers. The cerebellum is involved in learning procedures by observation [Graziano et al., 2002]. We predicted that cerebellum volume would be related to the structural complexity and precision of bower design, as this feature appears to be at least partially learned by observation and practice [Collis and Borgia, 1993]. Our work is the first to compare the size of particular brain regions among bowerbirds and offers a unique opportunity to infer which brain regions might be involved in aspects of bower building.

Materials and Methods

Subjects

Sixteen male breeding, bower-owning bowerbirds (or giving territorial calls in the case of spotted catbirds) were captured in North Queensland, Australia using mistnets or cagetraps (4 golden bowerbirds *Prionodura newtonia*, 4 toothbill bowerbirds *Scenopoeetes dentirostris*, 4 great bowerbirds *Chlamydera nuchalis*, 2 satin bowerbirds *Ptilonorhynchus violaceus*, and 2 spotted catbirds *Ailuroedus crassirostris*). Bower ownership was determined by long term observations in banded populations or focal observations for non-banded populations. Breeding status was judged by behavior at the bower and confirmed by testis size and histological condition (bunched spermatozoa). Only one bowerbird of a species was collected from any one geographic region. All species used are listed as common in their range [Simpson and Day, 1996] and are not listed in any threat category [IUCN, 2003; Centre, 2004]. All protocols were approved by the relevant animal care and use committees of the University of California, Santa Barbara, James Cook University, Townsville, Queensland and CSIRO Atherton, Queensland and appropriate permits were acquired from Queensland Parks and Wildlife Services.

Bower Traits

The five species studied offered a range of bower types (fig. 1) as we personally observed (L.B.D and D.A.W.) and as described in published accounts. Spotted catbirds do not build a bower. Toothbill bowerbirds clear a patch of ground and decorate this court with upturned leaves [Marshall, 1954]. Golden bowerbirds build a one- or two-tower 'maypole' bower that varies greatly in design and size among individuals [Frith and Frith, 2000b]. A display stick is decorated with lichen and whitish-yellow bracts or flowers. Satin bowerbirds build a small avenue bower (approximately 20 cm long by 30 cm wide) with thin sticks and decorate a single court. The court is covered with straw and decorated with mainly yellow and blue natural and manmade objects such as feathers, flowers, insect elytra, and plastic objects [Borgia, 1985]. Finally, great bowerbirds build a large avenue bower (approximately 70 cm long by 50 cm wide), decorated with color/location specificity on the front, the rear, one side and the interior (unpublished observations). These decorations are natural or manmade, principally gray, green and red objects, such as snail shells, glass, fruits, seeds, and plastic [Marshall, 1954].

Scoring Bower Characteristics

We constructed an index to score bowers for general complexity. We used the guidelines described by Madden [2001], considering the bowers' structural complexity (size and number of walls or towers) and ornamentation (number, diversity). These bower characteristics were obtained by a combination of personal observations and consensus reports from other authors [Marshall, 1954; Kusmierski et al., 1997; Frith and Frith, 2000a]. In addition, we considered elements of the display that would be related to the particular skills and brain areas of interest. Figure 1 lists bower attributes

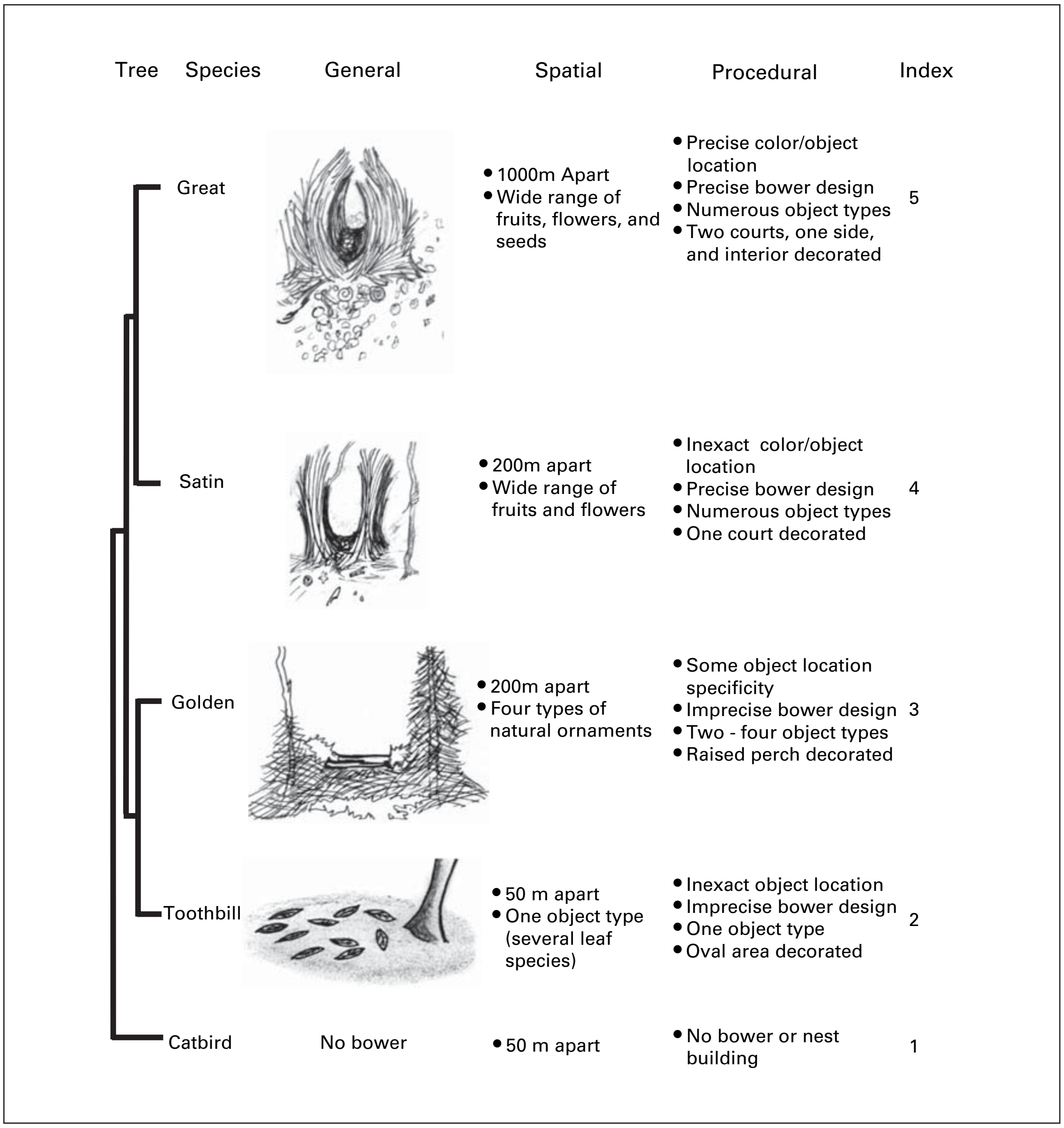

Fig. 1. Phylogenetic tree, pictorial representation of general bower complexity, and spatial and procedural elements of bower building for the five species of bowerbirds examined.

that we believe are indicative of the animals' spatial or procedural skills. Nearest neighbor distance and the numbers and types of fresh plant materials used on the bower would reflect spatial skills requiring memory of more locations, both to collect ornaments and to steal or destroy other males' bower. The precision of color/object location, precision of bower design, numbers of object types to sort, and distinct locations decorated reflect the use of procedural skills. Catbirds were given a score of one and each additional level of complexity added a point to the species score. This method allowed us to come up with an index similar to that for general complexity.

When we compared assignment of scores for general complexity with the spatial and procedural skills required, we found that each of these dimensions resulted in identical indices. The identical indices suggest that the dimensions of general complexity and the need for spatial and procedural skills are interrelated for the species studied. As these dimensions are not uniquely identifiable in our scoring system, we refer to relationships found between brain regions and bower variables at the most conservative level, i.e., as relationships between brain and general bower complexity.

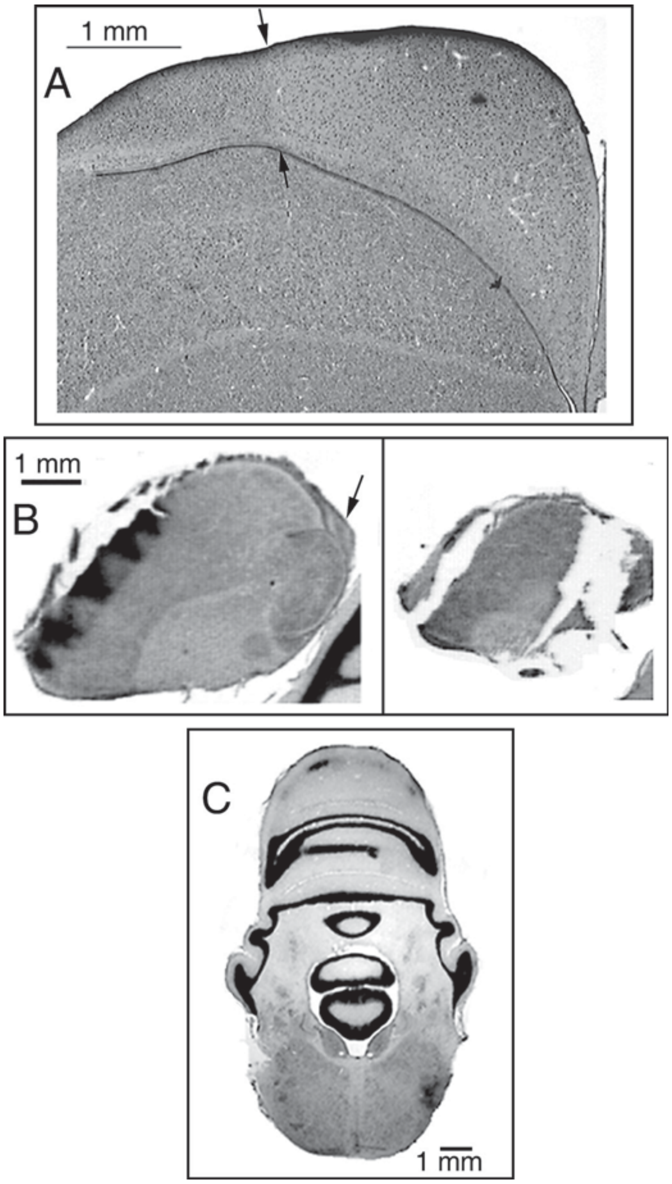

Fig. 2. Photomicrographs depicting location of neuroanatomical markers used for estimates of brain region volume. **A** Boundary between hippocampus and the apical part of the hyperpallium indicated by arrows. **B** Left panel, example of a telencephalon slice that would have been measured as hippocampal tissue is still recognizable (arrow). Right panel, candidate slice following that in the left panel showing caudal end of the telencephalon that would not have been included in measurements. **C** Cerebellum at point where lingula separates from the cerebellum.

Table 1. The estimated volume of brain regions (log, mm^3) and weight (log, g) for five species studied

	Whole brain	Telencephalon	Cerebellum	Hippocampus	Body weight
Catbird	3.100	2.972	2.005	1.297	2.220
Golden	2.926	2.792	1.877	1.696	1.821
Great	3.269	3.161	2.122	1.350	2.276
Satin	3.252	3.155	2.076	1.399	2.208
Toothbill	3.077	2.956	1.972	1.304	2.162

Histology and Neuroanatomy

Bowerbirds were weighed, given a lethal, intracoelomic dose of sodium pentobarbital (10 mg/kg), and perfused transcardially with heparinized (5 IU/ml) saline (0.85%), followed by neutral buffered formalin (NBF). Brains were postfixed in NBF for a minimum of four weeks and placed in 20% sucrose until sinking (approximately three days). The brains of great bowerbirds were cut in half and the right half was used in another study. All whole brains and the left half of great bowerbird brains were cut frozen in the coronal plane at 40 μm; every 6th section was mounted and stained with cresyl violet. An effort was made to produce a consistent angle of sectioning for all brains. Brains were collected in the field and a scale fine enough to weigh brains accurately was not available.

Slides were coded and individuals performing measurements did not know species identity. Researchers were kept blind to the identity of great bowerbirds by the inclusion of left hemispheres of additional bowerbird brains not included in the final analysis. Areas of the WB (estimated; see below), TH, Cb and Hp were measured on alternate, stained sections using NIH Image. When estimating volume for neural regions, ventricular and blood vessel areas were subtracted prior to calculating volumes. Sampling procedures, measurements of area, and volume calculations followed standard methods of stereology [Gundersen et al., 1988].

Standard neuroanatomical landmarks were used to delineate the boundaries of the brain areas selected for measurement. Measurements of WB started from the first section in which the pallial-subpallial lamina appeared and continued until the cerebellar lingula separated from the rest of the cerebellum (fig. 2C). In bowerbirds, this is observed in approximately the caudal fifth of the cerebellum and thus much of the hindbrain was included. The WB measurement is an estimate, as the caudal optic tectum was lost during processing of several brains, and thus was not included for any of the animals. Telencephalon measurements started as for WB and ended at the last section in the caudal pole of the telencephalon in which any hippocampal tissue was recognizable (fig. 2B). On sections in which the telencephalic hemispheres were joined with the diencephalon, prominent markers such as the occipito-mesencephalic tract and the anterior commissure were used to determine telencephalic boundaries [Brenowitz et al., 1995]. The Hp is bounded by the mid-line, the lateral ventricle, and the brain surface. Laterally it can be distinguished from the apical part of the hyperpallium (HA) by an obvious increase in cell density on the HA side (fig. 2A) [Sherry et al., 1989]. The Cb was measured from first appearance until the lingula separated from the remainder of the cerebellum. To accurately divide the Cb into left and right sides, a line was drawn down the midline of the ventricular space and paired structures in the midbrain and hindbrain.

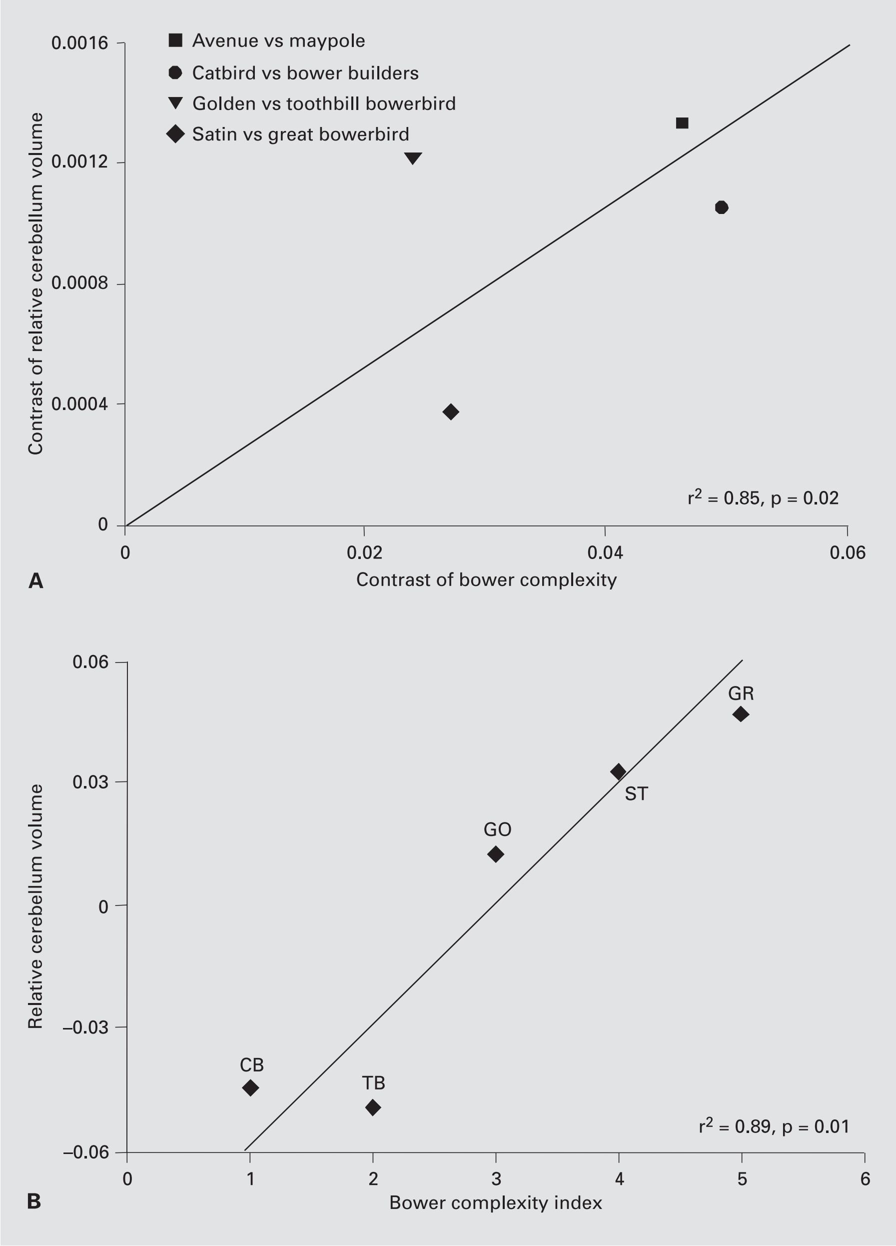

Fig. 3. Phylogenetically corrected and unmodified analyses of relationship between cerebellum volume and bower complexity. **A** Regression between contrasts for relative cerebellum volume and bower complexity. Species diverging at each node are given in legend. **B** Regression between relative cerebellum volume and bower complexity uncorrected for phylogenetic relatedness. GR = Great bowerbird, ST = satin bowerbird, GO = golden bowerbird, TB = toothbill bowerbird, CB = spotted catbird.

Left and right sides of the brain were measured for all species except great bowerbirds. t tests (n = 12) showed no significant difference between the volume of left and right sides for any of the regions measured. Only left hemispheres were used in data analyses. Hippocampus, and thus TH measurements, from two toothbill bowerbirds were not included in the analyses because tissue damage precluded accurate measurement of these areas.

Data Analyses

Brain region volumes and body weights were log transformed (table 1) to improve fit to normality (Shapiro-Wilks tests, for each species $p > 0.12$). Because it is already known that endocranial volume scales with bower complexity [Madden, 2001], use of brain size for scaling other brain regions would mask selection for any changes in other brain regions that may be related to bower complexity [Deaner et al., 2000]. In addition it is known that brain mass increases with body mass in birds [Martin, 1981], thus volumes were corrected for body size by performing regressions with log-transformed weight as the estimator variable. All sets of residuals from the regression using body weight as the estimator were normally distributed (Shapiro-Wilks, $p > 0.25$). Residuals from this analysis were corrected for phylogenetic relationships using independent contrasts [Harvey and Pagel, 1991] calculated using CAIC which showed no violations of its assumption checks [Purvis and Rambaut, 1994]. The phylogeny and branch lengths were estimated from available mitochondrial cytochrome b sequences [Kusmierski et al., 1997] using maximum likelihood (nucleotide composition a = 0.28, c = 0.32, g = 0.15, t = 0.25; gamma alpha = 1.419, estimated proportion of invariant sites = 0.51), assuming a molecular clock and GTR + gamma + invariant sites model implemented in PAUP [Swofford, 2003]. Maximum likelihood models estimated a tree topology identical to published results [Kusmierski et al. 1997] and a likelihood ratio test did not reject a molecular clock. Independent contrast for brain regions (WB, TH, Cb, and Hp) and bower complexity were analyzed using simple regression forced through the origin, as recommended for tests of correlated traits in independent contrast analyses [Purvis and Rambaut, 1994]. To determine whether a larger brain – as well as more specific regions – are associated with bower building in general, one-sample t tests were used to compare WB, TH, Hp and Cb volumes (normalized for body weight) of the four bower builders to those of the non-bower-building spotted catbird. In all cases, $p < 0.05$ was the criterion for statistical significance.

Results

Comparison of the non-bower-building spotted catbird to the four other species revealed that the spotted catbirds had smaller WB and TH than bower builders (WB $t(3) = 3.24$, TH $t(3) = 3.52$), one-sample t tests, $p < 0.05$). In contrast, the volumes of the Hp and Cb were not smaller in spotted catbirds compared to the bower builders. The independent contrast analysis, used to detect correlated evolution between bower complexity and the volume of brain regions, revealed a strong relationship between bower complexity and Cb volume ($p = 0.027$, $r^2 = 0.85$, n = 4 contrasts; fig. 3A). However, we found no statistically significant relationship between independent contrasts for WB, TH, or Hp and contrasts for bower complexity indices ($p > 0.10$; fig. 4).

Discussion

As we predicted, bower building bowerbirds have larger WB and TH than the non-bower-building spotted catbirds. Thus, on average, being a bower builder is associated with the enlargement of several brain regions. We found no association between increases in size of the WB, TH, or Hp and increasing bower complexity among species. But we did find a strong association between increases in Cb size and increasing bower complexity, suggesting a link between cerebellum function, i.e., procedural learning or motor planning, and the skills necessary for bower building.

Our data on WB estimates versus bower complexity differ from those reported by Madden [2001], who found evidence for correlated evolution between endocranial volume and bower complexity. This discrepancy could be accounted for by a number of methodological differences, including the measure of brain size (i.e., endocranial volume vs. whole brain volume estimates), the body size measure against which brain size was normalized (tarsus cubed vs. body weight), the species examined and the number of independent contrasts. Moreover, we calculated branch lengths for our model, whereas Madden [2001] used a model that assumes punctuated evolution [Purvis and Rambaut, 1994]. Our model should be more accurate if changes in character traits accumulated prior to complete species diversification and thus differing branch lengths represent a more accurate model of evolution [Diaz-Uriarte and Garland Jr., 1998]. However, reanalysis of our data using Madden's model [2001] does not alter the outcome, suggesting that the use of different models cannot fully account for the discrepancy in results.

We did find that, on average, the volume of WB is larger for the bower builders than for the non-bower-building spotted catbird, as previously reported [Madden, 2001]. In addition we found that the volume of TH was larger in bower builders than in the spotted catbird. Thus, bower builders as a group have larger brains and telencephalons than non-bower-builders, although there was not a consistent relationship between shifts in the magnitude of bower complexity and shifts in the magnitude of WB or TH volume at the nodes of species divergence in the species we examined.

We also did not find a significant relationship between hippocampal size and bower complexity; nor did we find that the Hp was larger in bowerbirds than in the non-bower-building spotted catbird. This is somewhat surprising given that hippocampal volume is correlated with a need to locate distributed resources in a variety of non-bowerbird species and because many bowerbird species including the spotted catbird cache food near nests or bowers [Pruett-Jones and Pruett-Jones, 1985; Frith and Frith, 2001, Day and Westcott, pers. obs]. The percentage of hippocampus relative to telencephalon volume reported by Sherry et al. [1992] for food-storing subfamilies is 3.9% and for non-storing families is 1.6%. In this study the percentage of hippocampal volume relative to telencephalon volume ranged from 1.6 to 2.6 % for bower-builders (mean = 2.1%) and was 2.2% for spotted catbirds.

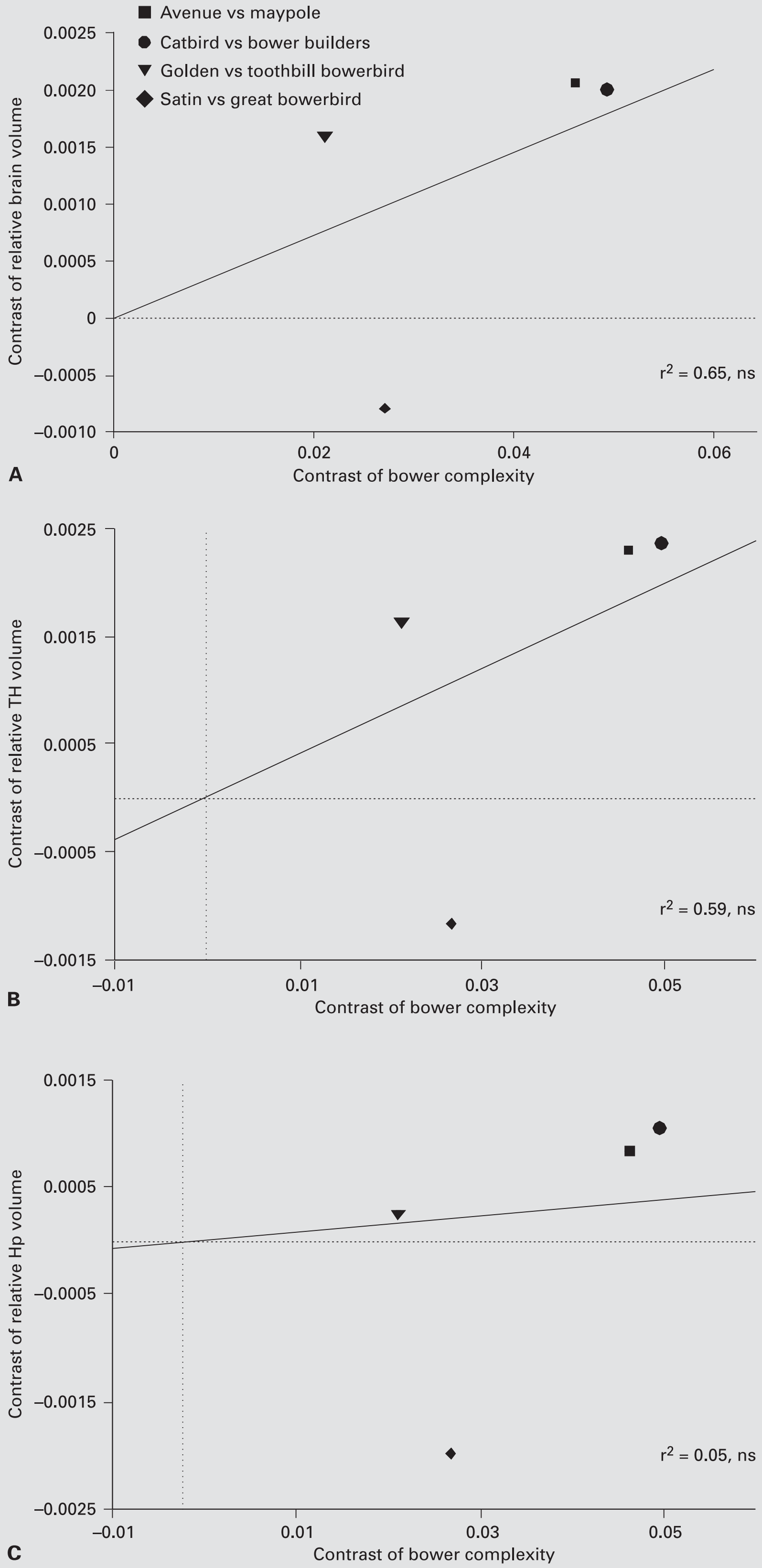

Fig. 4. Regression between contrasts for relative volume of WB (**A**), TH (**B**), and Hp (**C**) and bower complexity. Species diverging at each node are given in legend.

Thus, the hippocampus does not occupy as large a percentage of the telencephalon in bowerbirds as it does in food-storing birds, and the average for bower builders is much the same as for the spotted catbirds. More detailed assessment of the spatial skills used by bowerbirds for bower building and defense and other needs, such as foraging, could shed light on the evolution of the hippocampus in this family.

We did find a significant relationship between cerebellum volume contrasts and bower complexity contrasts even though the non-bower-building spotted catbird did not, on average, have a significantly smaller cerebellum volume than those observed in bower-building species. The latter observation appears to be due to similar cerebellum volumes in toothbill bowerbirds and spotted catbirds (fig. 3B, non-phylogenetically-corrected values). Interestingly, the contrast analyses similarly reveal that the largest contrast in cerebellum volume is not at the node of divergence between catbirds and bower builders, but at the node of divergence between avenue builders and maypole builders (fig. 3A). Perhaps such relationships exist because an important shift in cerebellar structure is associated with the transition from clearance of a patch of ground and simple decoration of this court, as done by the toothbill bowerbirds, to actual bower construction as performed by the other bower-building species studied.

To interpret the role of the cerebellum in bower construction we need to consider that the sexual display of bowerbirds includes not only the construction of the bower, but also postural displays, and that the cerebellum may contribute to these motor behaviors as well [Whitlock, 1952; Pearson, 1972; Butler and Hodos, 1996]. However, many bowerbirds have similar postural displays that do not vary in congruence with bower complexity. For instance, the displays of toothbill, satin, and great bowerbirds are similar in style if not in duration [Frith and Frith, 1993], whereas toothbill bowerbirds do not build bowers, and satin and great bowerbirds build relatively complex bowers. Thus it is unlikely that the evolution of a larger cerebellum occurred in order to support the different postural displays in these bowerbird species.

Overall, because the phylogenetic analyses suggest that cerebellar size has increased with increasing bower complexity, we can cautiously infer that the cerebellum is important to some aspect of bower building. Although we cannot be certain what role the cerebellum plays in building intricate bower structures, consideration of this brain region's function in other behaviors is instructive. Recent work in rats has shown that lesions of the cerebellum interfere with observational and experiential learning of the procedural components of tasks [Leggio et al., 2000; Graziano et al., 2002]. The cerebellum might play a similar role in observational learning in bowerbirds, as the development of bower building skills appears related to learning by observation [Neville, 1988; Collis and Borgia, 1993]. Differences in cerebellum volume or morphology also appear to relate to the performance of other types of tasks [Thach, 1996]. For example, the volume of the cerebellum is smaller in humans that are relatively slow at finger and foot tapping as compared to other individuals [Bekkelund et al., 1999]. The volume of the cerebellum molecular layer predicts individual variability in rats' tendency to explore novel stimuli [Anderson, 1994]. In mice, the number of Purkinje cells is correlated with the number of trials to learn the association between a tone and a following puff of air to the eye [Spath and Woodruff-Pak, 2003]. What is common to each of these cerebellar related activities, i.e., procedural learning, rapid motor movements, and attention to novelty, is the ability to learn to associate a particular context with a specific motor sequence [Thach, 1996]. This ability to learn how to move and in what context would also be integral to learning how to construct and maintain complex bowers. Our results suggest that in bower building, as in other domains where complex motor sequences must unfold under particular conditions, the cerebellum could play a role. However, this suggestion must be tempered by the fact that the role of the cerebellum in 'cognitive' aspects of motor performance, such as motor learning and observational learning, has not, yet, to our knowledge been demonstrated in birds.

The basic neuroanatomical organization and connectivity of the cerebellum in birds has been well studied [reviewed by Portmann and Stingelin, 1961] and is similar in many respects to mammals. Although some differences in connectivity between mammals and birds have been observed, the functional consequences of these differences are not fully understood [Necker, 1992]. The most striking difference between mammals and birds is the lack of cerebellar hemispheres in birds compared to mammals and the related possibility that there may be less advanced ipsilateral control by the cerebellum in birds [Pearson, 1972]. Direct stimulation and activation of the cerebellum by peripheral stimuli have demonstrated that different folia of the cerebellum serve different parts of the body in birds (wing, legs, neck), and also serve different functions, resulting in multiple topographically organized maps of the body and regional specificity for such things as deep and cutaneous proprioceptive stimuli [Pearson, 1972; Schulte and Necker, 1998]. Differences in bird species' behaviors are sometimes related to the size of particular folia, such as a reduction in folia II and III with relative disuse of hind limbs (such as in hummingbirds) or expansion of folia VII in visual guided predators [Pearson, 1972; Iwaniuk et al., 2004]. However, not all folia pattern differences across species can be accounted for by obvious differences in behavior and general conclusions drawn from these comparisons, such as assignment of folia VII to visual processing, can be at odds with electrophysiological data [Pearson, 1972; Clarke, 1974; Schulte and Necker, 1998]. Thus, although it may be instructive to observe folia patterns in bowerbirds in comparison with other passerines, interpretations of differences will necessarily be mostly ad hoc until there is a more complete understanding of folia function.

Studies involving lesions of the cerebellum in birds appear to agree with the initial studies done in mammals which show that the cerebellum plays a role in motor control and balance and also appears to be sensitive to the general state of the animal in a way that is not easily explained by simple reference to motor control [Pearson, 1972]. The greatest impediment to replicating mammalian lesion studies in birds is that mammalian studies typically involve hemicerebellectomy from which the animal recovers almost all obvious motor impairments in a short time such that cognitive impairments can be revealed. Because birds lack bilateral hemispheres this cannot be done, but small cerebellar lesions in birds have been shown to result in only temporary motor impairments [Pearson, 1972]. Thus, it should be possible to validate our general inference that a role of the avian cerebellum in learning procedures by observation underlies the relationship we found between cerebellar volume and bower complexity among bowerbird species.

Although we studied only males, our data raise the question of what we expect with regard to the size of the cerebellum in female bowerbirds. Sexual selection of a trait does not necessarily result in sexual dimorphism of the trait. Females may pass pleiotropic genes coding for the selected trait and other traits on to both male and female offspring that will be maintained as long as the gene codes for a selectively neutral trait in females. Madden [2001] suggested this as a possible reason for finding that both male and female bowerbirds showed a similar relationship between bower complexity and endocranial volume. A second possibility is that bower complexity is also related to larger brains in females but for different reasons than in males [Madden, 2001], such as demands for sensory processing of the signal. However, if we are correct that the cerebellum is playing a role in males' ability to learn the procedures necessary for bower building, we predict that females will have a smaller cerebellum than males in bowerbirds, similar to the sexual dimorphism that has been found for the size of song control nuclei in passerines in which males sing more than females [Brenowitz, 1997], and to the larger size of the hippocampus in the sex that requires more spatial ability [Gaulin, 1992; Sherry et al., 1993]. Indeed, as discussed below, the presence of androgen receptors in the cerebellum of great bowerbirds suggests the potential for hormonal adjustment of cerebellar morphology in bowerbirds, as is found for the song control nuclei in many passerines [Brenowitz, 1997; Smith et al., 1997].

Our study is one of the first to suggest that sexual selection might result in adaptations of the cerebellum to behavioral characteristics. Interestingly, this particular behavior, i.e., bower building, is supported by androgen action [Marshall, 1954; Collis and Borgia, 1993] and circulating testosterone levels are related to bower quality and copulation success [Borgia and Wingfield, 1991]. We have recently shown that there are abundant androgen receptor (AR) immunoreactive cells in all layers of the great bowerbird cerebellum [Day and Olster, 2003]. Additionally, intense labeling of AR mRNA has been found in the Purkinje cells and the deep cerebellar nuclei of golden-collared manakins, a bird with an acrobatic mating display [Fusani et al., 2003]. The distribution and quantity of androgen receptors in the cerebellum of great bowerbirds and golden-collared manakins appear to be greater than in other birds that have been examined [Metzdorf et al., 1999]. These observations, taken together with the data obtained in this study, are consistent with the notion that the cerebellum is an androgen-responsive brain region that has adapted to a role in androgen-triggered sexual displays.

In sum, our results suggest that, in general, bower building is associated with a larger brain and telencephalon but that whole brain, telencephalon and hippocampus do not uniformly increase in size with increases in bower complexity across species. Of the regions studied, only cerebellum volume is associated with species differences in bower complexity, suggesting that the skills necessary to build a more intricate and precisely decorated bower are supported by increases in cerebellum volume.

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