

## ABSTRACT

Title of Thesis: ALLOMETRIC COMPARISON OF BRAIN STRUCTURE VOLUMES IN THREE SPECIES OF BOWERBIRD: SATIN BOWERBIRDS (*PTILONORHYNCHUS VIOLACEUS*), SPOTTED BOWERBIRDS (*CHLAMYDERA MACULATA*), AND GREEN CATBIRDS (*AILUROEDUS CRASSIROSTRIS*).

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In three species of Australian bowerbirds the volumes of several brain structures were determined based on areal measurements of fixed tissue. Allometric comparisons, i.e., those that take into account the gross interspecies and intersexual differences in body mass and overall size, were made among these three species. Sexual dimorphisms were detected in the vocal control nuclei of each species. Most intriguingly, a putatively novel nucleus in the dorsal hyperstriatum of all three species has been identified. These findings are discussed in a functional context, in which the bower-building habits of these three species of bowerbird are considered.

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BOWERBIRDS (*CHLAMYDERA MACULATA*), AND GREEN CATBIRDS (*AILUROEDUS  
CRASSIROSTRIS*).

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# Dedication

To Saskia.

## Acknowledgements

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## Chapter 1: Introduction

The most fundamental tenet underlying the practice of the neurosciences is that for any behavior, there is a corresponding constellation of brain regions. As such, the fundamental task of the neurosciences lies, broadly, in the attribution of functional roles to the infinitely varied concatenations of activation of different brain regions. While it is true that no organismic behavior is underwritten by the activation or suppression of a single brain nucleus, it is nonetheless true that some regions maintain critical executive roles for the behaviors with which they are most closely functionally related. In this manner, particular brain regions are colloquially construed to be "for" certain behaviors. As such, the cytoarchitectural constitution of these regions is bound to differ as the behaviors differ. This should be especially true of behaviors that are specific to particular taxa.

For many years, the behavior of bower building in the family Ptilonorhynchidae has been intensively studied (e.g., Marshall, 1954; Diamond, 1982; Borgia, 1985; Borgia et al., 1987; Frith et al., 1996; Lenz, 1999), but



there has been virtually no study of bowerbird neuroanatomy. The present investigation aims to fill that gap, representing the first look into the fine neuroanatomy of bowerbirds<sup>1</sup>.

Bowerbirds are relatively large passerines native to the Australo-Papuan region. They are remarkable in their behavior - males construct stick structures (bowers) from twigs and sometimes straw. Vines, mushrooms, arthropod skeletons and other diverse materials such as feathers and fruit are used to decorate bowers (Gilliard, 1969; Diamond, 1982). There is a great variety of bower types (Gilliard, 1969; Cooper & Forshaw, 1979). Green catbirds (*Ailuroedus crassirostris*) do not build display courts; tooth-billed bowerbirds (*Scenopoeetes dentirostris*) and Archbold's bowerbirds (*Archboldia papuensis*) do not build bowers but do minimally ornament a forest floor clearing with overturned leaves and use diverse decorations respectively. Regent bowerbirds, (*Sericulus chrysocephalus*), satin bowerbirds (*Ptilonorhynchus violaceus*), spotted bowerbirds (*Chlamydera maculata*) great bowerbirds (*C. nuchalis*), fawn-breasted bowerbirds

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<sup>1</sup> However, see Madden (2001) for a brief overview of the relationship between *gross brain size* and bower complexity.

(*C. cerviniventris*) and Western bowerbirds (*C. lauterbachii*) all construct avenue-type bowers. Avenue bowers consist of two vertical walls built near a court on which collected ornaments are displayed. In these species, bowers are decorated with variously colored ornaments: flowers, snail shells, fruits, even manmade objects and detritus such as coins, shotgun shells, and broken glass (Figure 1).

In this first look at the fine neuroanatomy of the bowerbird, we set out to identify regions of the bowerbird brain that appear to differ markedly from similarly situated brain regions in other, more well-known avian species. Moreover, in view of the striking differences in behavior between males of different bowerbird species, it seems logical to ask if there are also differences in brain organization in satin & spotted bowerbirds and green catbirds. This question presupposes that differences in gross behavior across species are underwritten by organizational or cytoarchitectural neural differences across species. Such differences may manifest in various ways: differences in the density of receptor sites for steroid hormones or in the concentration of synapses specific to different neurotransmitters or simply in the gross size of brain



**Figure 1.** Photograph of a typical avenue-type bower. Note the two vertical walls, center passage and display court, amply adorned with plastic, sheep vertebrae and green citrus fruit. This is the bower of a spotted bowerbird (*Chlamydera*) found in rural New South Wales.

structures. It is the lattermost prospect that we evaluate here. The following brain nuclei were measured: lateral magnocellular nucleus of the anterior neostriatum (LMAN), high vocal center (HVC), robust nucleus of the archistriatum (RA), and nucleus rotundus (Rt). Nucleus Rt is known to vary in volume as a result of naturally-occurring changes in testosterone titers (Smulders, 2002). An additional, putatively novel nucleus in the dorsal hyperstriatum was identified and measured as well.

## Chapter 2: Materials and Methods

Satin bowerbirds, spotted bowerbirds and green catbirds were captured live<sup>2</sup> in cage traps baited with food (bread, fruit, etc.) from four different locales in New South Wales, Australia. Satin bowerbirds were also lured into traps by the presence of blue trinkets. Spotted bowerbirds were also trapped in mist nets erected at or very near the bower. Birds were caught one at a time. Immediately upon capture, the bird was retrieved from the trap and anesthetized with urethane (ethyl carbamate; 0.2cc/kg). Brain mass was obtained from the dry weight of post-fixed brains and body mass was obtained at the time of capture. The perfusion technique described below was used for all birds. At such time as a bird had reached a surgical plane of anesthesia (determined by the absence of a pedal withdrawal reflex), the abdomen and thorax were depilated and an abdominothoracotomy was performed by incising the upper abdominal cavity and cutting through the ribs, pectoral

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<sup>2</sup>All procedures involving live animals were performed with the express approval of the Institutional Animal Care and Use Committee of the University of Maryland, the Animal Ethics Committee of Griffith University (Queensland, Australia), Environment Australia, and the New South Wales Parks and Wildlife Service.

muscles, and clavicle just lateral to the sternum. Heparin (an anticoagulant agent) was injected into the heart with a 23-gauge needle via the left ventricle. The pericardium was cut so as to expose the cardiac muscle; a 16-gauge needle was then inserted into the left ventricle of the heart, and the right atrium was cut. A gravity-fed system was used to perfuse the circulatory system with physiological saline, followed by 4% paraformaldehyde (PFA). Following perfusion with PFA, the head was removed and placed in a jar with PFA, which was then sealed and labeled. After at least 24 hours, the calvarium was removed and the head was returned to the PFA solution and the jar re-sealed. Brains thus processed were shipped back to the University of Maryland, where they were immersed in a cryoprotectant solution (30% sucrose-PFA) for at least 24 hours prior to sectioning. The sex of each bird was determined by manual and visual examination of the testes or oviduct.

Brain mass and body mass were collected for each bird used in this study. An index of the relationship between brain mass and body mass was derived from these data. This brain-mass index (BMI) is calculated as a ratio of brain mass to body mass. Brain weight is

plotted against body weight in a log:log system for interspecies comparisons (Rehkämper et al., 1988<sup>3</sup>):

$$\text{BMI} = \frac{\log \text{ brain mass (g)}}{\log \text{ body mass (g)}} .$$

BMI is an unbiased indicator of relative brain size. A higher BMI value represents a higher relative brain-to-body mass ratio. In other words, BMI is an indicator of the proportion of body mass that is composed of brain. Additionally, the overall brain volume of fixed brains was determined by multiplying the brain mass by the specific weight of brain tissue (specific weight of brain tissue = 1.036; from Rehkämper et al., 1988).

Brains were mounted on the copper sectioning stage of a freezing microtome, then flash-frozen with powdered dry ice (CO<sub>2</sub>). The brains were then sectioned at a thickness of 40µm into plastic wells filled with phosphate-buffered saline (PBS). After the whole brain had been sectioned, the tissue was then mounted on gelatin-submerged glass slides, and left to dry for at least 24 hours. Dried slides were subjected to thionin

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<sup>3</sup>Log:log ratio is used in order to dampen the broad variability observed in insterspecific brain and body mass values.

stain for up to one minute. The mounted tissue was then dehydrated in a series of graduated alcohols and cleared in hemo-deoxygenase prior to being cover-slipped. Areal volumetric reconstruction of brain sections was performed in the following manner. Scion Image (Frederick, Maryland) was used to render digital images of individual brain sections. The perimeters of selected nuclei were calculated throughout their rostral-caudal extent. The sum of these areal measurements was then multiplied by the thickness of the section (in all cases, 40 $\mu$ m). By this method, a projection of the absolute brain volume of brain regions was calculated as a ratio of absolute nuclear volume to overall brain volume.

The transformation of relative regional or nuclear brain volume as a result of domestication, speciation or sexual selection appears to manifest most robustly in the telencephalon rather than in the brain stem (Rehkämper et al., 1988). For this reason, the present investigation has as its focus several well-known telencephalic nuclei, and one mesencephalic nucleus. These nuclei were selected for a number of reasons. Specifically, the nuclei chosen are generally well-defined and identifiable in Nissl-stained tissue. The song control nuclei -HVC, LMAN, and RA- are well known and there are many

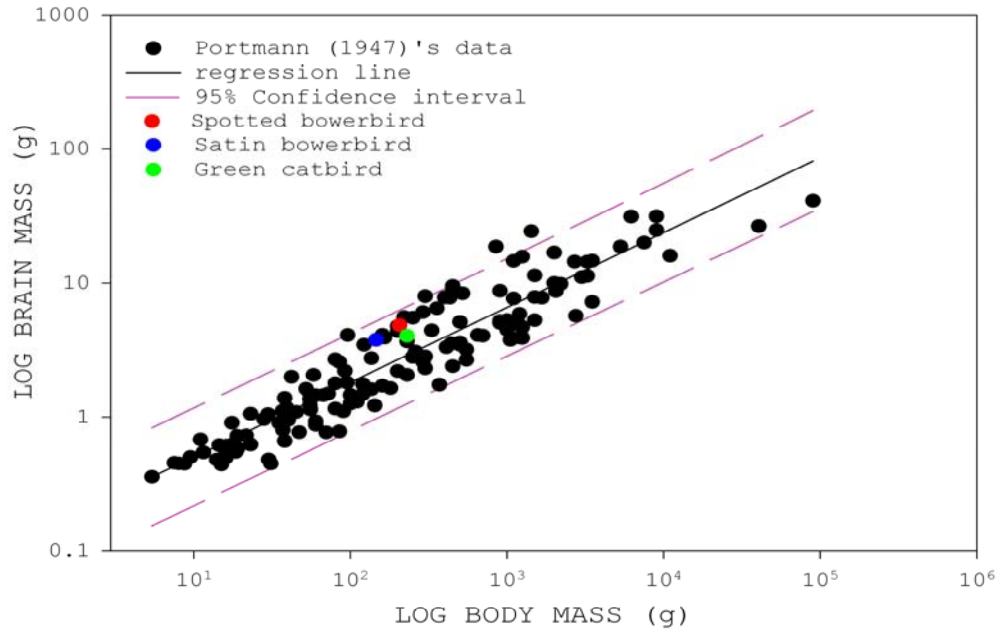


preexisting data concerning their appearance and constitution in males of other species; these preexisting data provide a reference point for interspecies and intersexual comparisons among bowerbirds. The mesencephalic nucleus Rt is presumptively a non-dimorphic nucleus and is used as a control nucleus for intersexual comparisons.

## Chapter 3: Results

Bowerbird brains appeared to be typical in relative brain volume and gross morphology for passerine species. Brains weighed between 137g (*C. maculata*) and 255g (*A. crassirostris*). Green catbirds, which build no bowers, have a relatively low BMI (0.256); spotted bowerbirds' BMI is 0.265, and satin bowerbirds' BMI is 0.296. A preliminary test to see whether the brains of bowerbirds are exceptional is to compare bowerbird BMIs against the BMIs of many other species. Taken from over 150 species of birds from 14 avian families, Portmann (1947)'s data provide a background onto which these new bowerbird data can be cast.

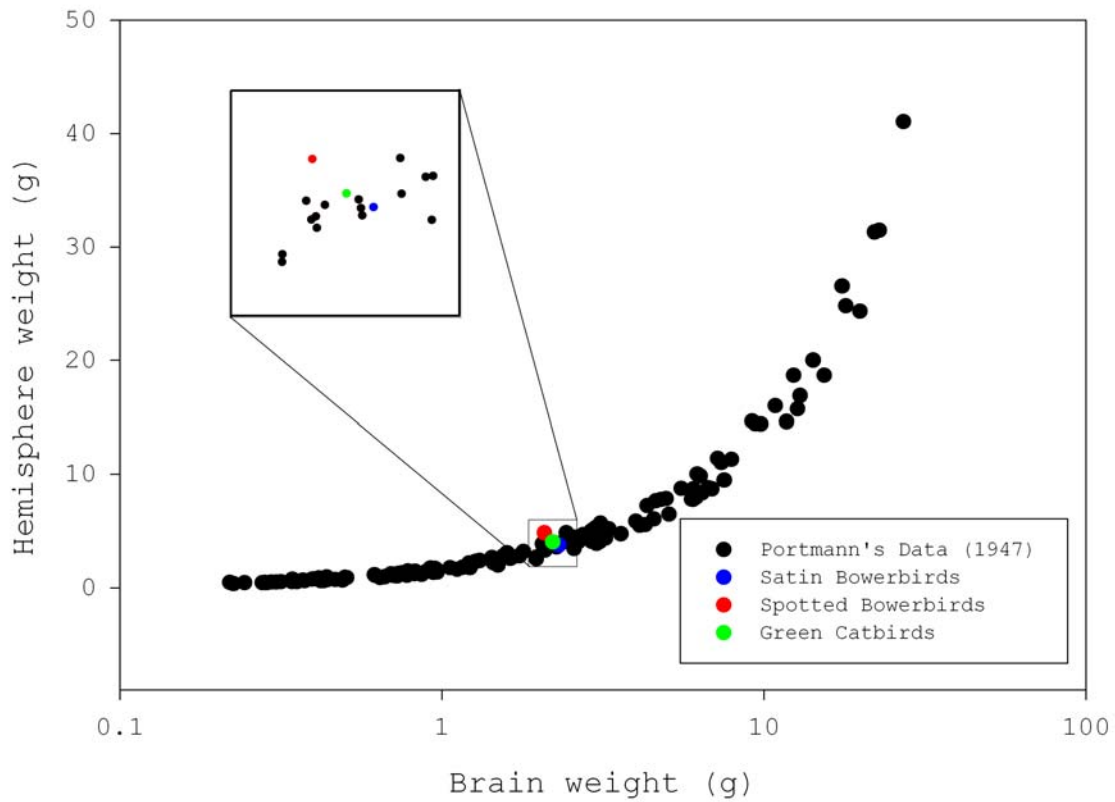
Figure 2 is a scatter-plot of the BMI of Portmann's birds (in black) along with the green catbird, spotted bowerbird and satin bowerbird (in green, red and blue, respectively). Bowerbirds' BMIs lie within the range of the BMI of all the other birds, meaning that the bowerbird brain is not, in allometric terms, particularly larger or particularly smaller than the brains of other birds. The BMI values for bowerbirds do lie on the higher side of the cluster in which they are situated,



**Figure 2.** Scatter plot of Brain Mass Indices (i.e., log brain mass versus log body mass). Data points in black are from Portmann (1947); red, green and blue data points represent the species average for spotted bowerbird, green catbird and satin bowerbird, respectively. Purple dashed lines delimit a 95% confidence interval. Raw data presented in tabular form in Appendix 1B.

but they nonetheless appear to be unremarkable compared to the whole.

As mentioned earlier (viz. Rehkämper et al., 1988), the degree to which speciation and other factors transform brain volume is manifested most robustly in the telencephalon. Accordingly, we compared bowerbird telencephalon measurements to Portmann's data to determine whether there is a difference in the relative contribution of telencephalon to overall brain mass between bowerbirds and non-bowerbirds. Figure 3 shows Portmann's data with data points for satin bowerbirds, spotted bowerbirds and green catbirds added. These data show how relatively large the telencephalon is in each species. Satin bowerbirds, spotted bowerbirds and green catbirds are superimposed onto Portmann's data in blue, red and green, respectively; what this superimposition illustrates is that the telencephalon is not abnormally large in each of these species. Thus, as in the case of BMI, the bowerbird brain does not appear larger overall or more allometrically biased towards a larger telencephalon than other birds in Portmann's sample. This does not support the hypothesis that bowerbird brains are especially large. Satin and spotted bowerbirds have slightly larger BMIs, but a comparable



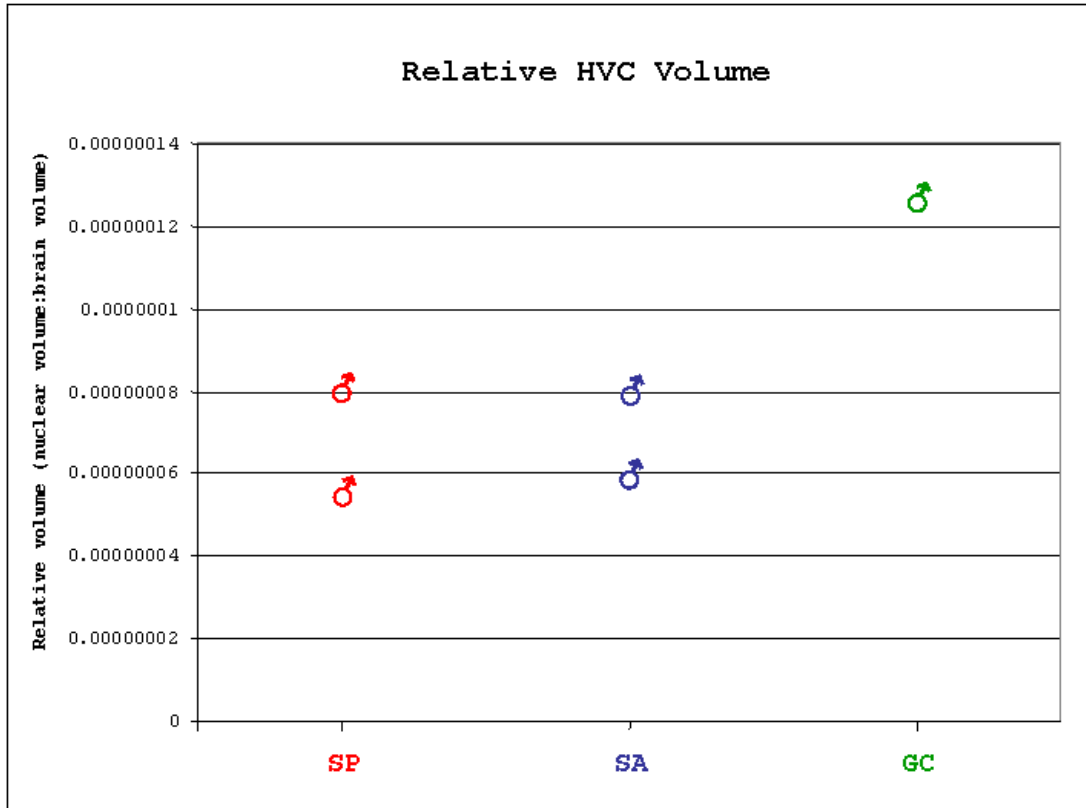
**Figure 3.** Scatter plot of brain weight versus hemisphere (telencephalon) weight. Data points in black are from Portmann (1947); red, green and blue data points represent the species average for spotted bowerbird, green catbird and satin bowerbird, respectively. The box inset shows an exploded view of the relationship between the bowerbirds and Portmann's birds. Raw data presented in tabular form in Appendix 1B.

allometric measurement for the telencephalon does not obtain in catbirds, which are intermediate in size.

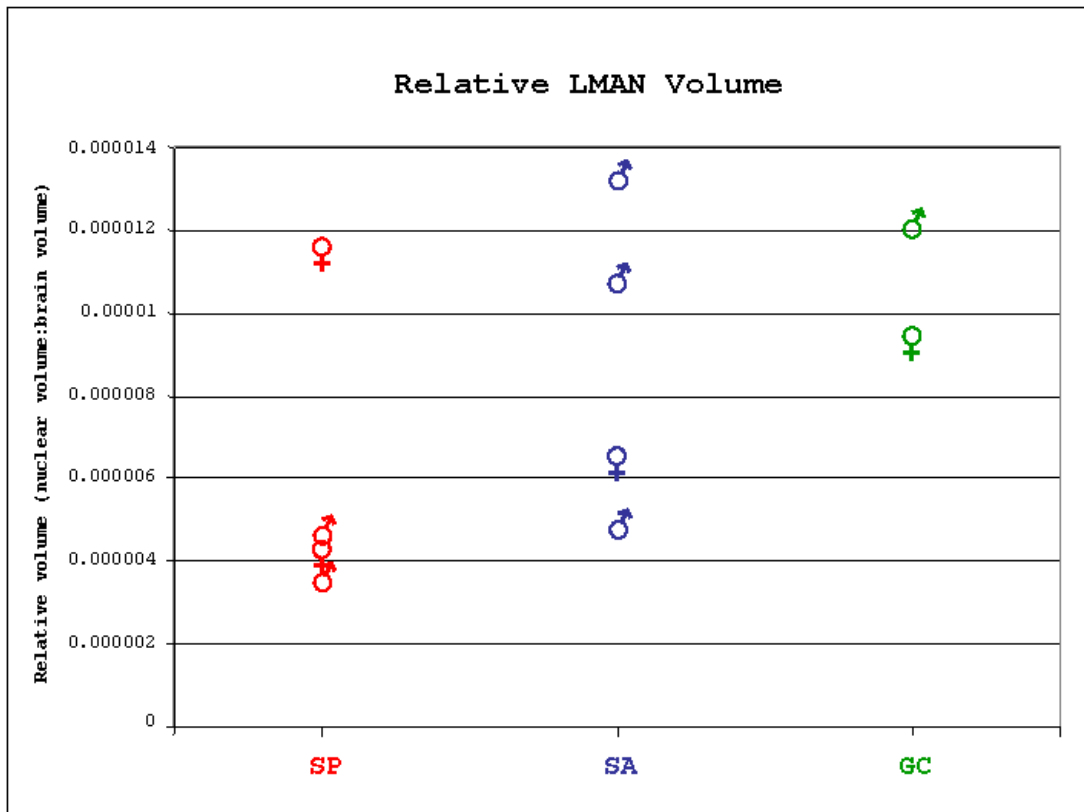
The relative volumes of telencephalic nuclei HVC, LMAN and RA and the mesencephalic nucleus Rt are shown in Figures 4 through 7. In Nissl-stained sections, HVC does not appear in the female bowerbird brain. In corresponding sections in the male bowerbird brain, there is a prominent nuclear group that can be readily identified as HVC. Accordingly, the plotted values in Figure 4 are for males only.

Relative LMAN values show no tendency towards sexual dimorphism (Figure 5). This lack of dimorphism is expected, given that female bowerbirds evaluate potential mates at least in part based on the quality of the males' song (Loffredo & Borgia, 1986) and that LMAN has been identified as an important nucleus for song discrimination in other passerine species (Burt et al., 2000).

Nucleus RA showed an expected sexual dimorphism, with a higher relative volume in males than in females (Figure 6). This dimorphism was expected, given the fact that RA is an integral component of the motor pathway for song (Wang et al., 1999) and that females tend to sing

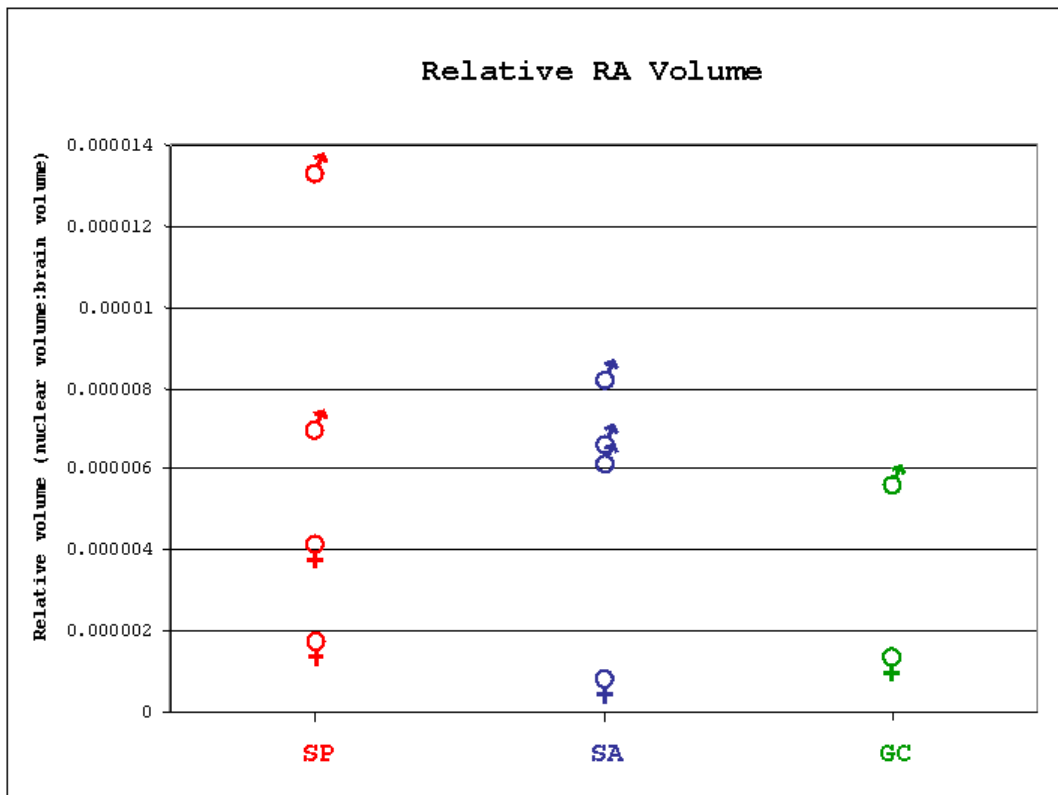


**Figure 4.** Graph displaying the relative volume of nucleus HVC in the brain of three species of bowerbird (SP=spotted bowerbird, SA=satin bowerbird, GC=green catbird). Values obtained are the ratios of nuclear volume to overall brain volume. HVC was not evident in Nissl-stained tissue of any female brains. Raw data presented in tabular form in Appendix 1C.



**Figure 5.** Graph displaying the relative volume of nucleus LMAN in the brain of three species of bowerbird (see Figure 4 for abbreviations). Values obtained are the ratios of nuclear volume to overall brain volume. Raw data presented in tabular form in Appendix 1C.





**Figure 6.** Graph displaying the relative volume of nucleus RA in the brain of three species of bowerbird (see Figure 4 for abbreviations). Values obtained are the ratios of nuclear volume to overall brain volume. Raw data presented in tabular form in Appendix 1C.

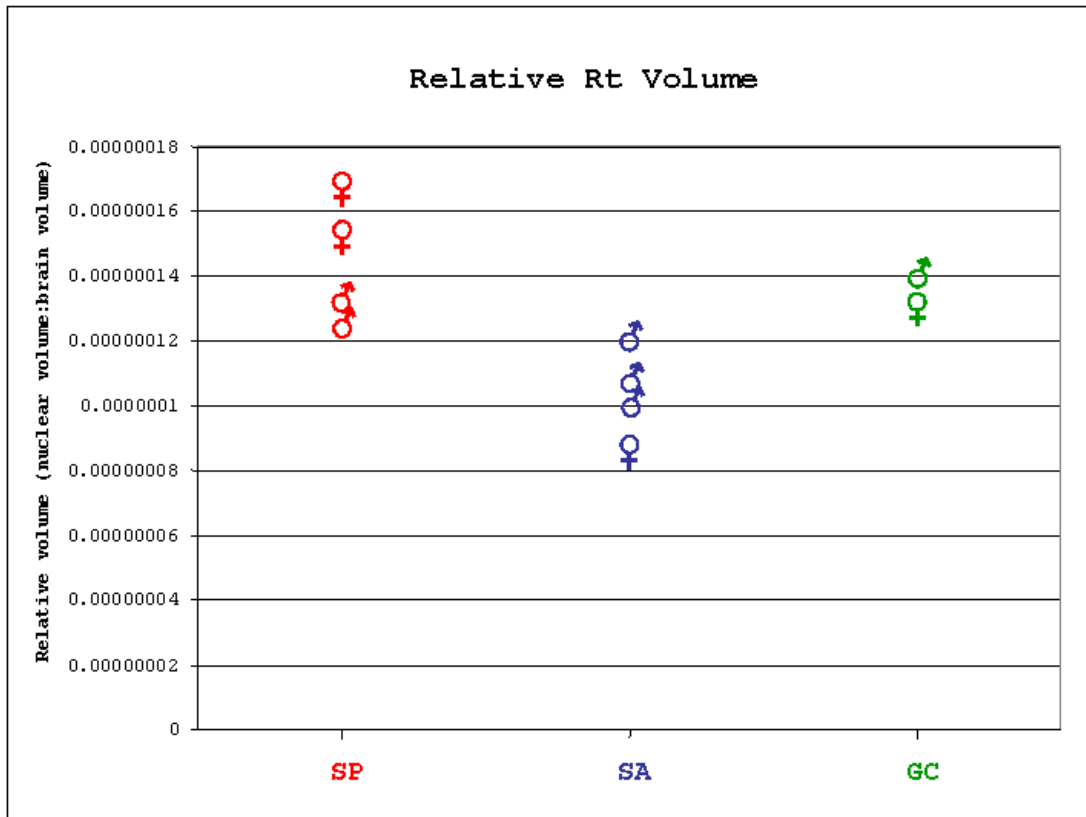
less than males in passerines generally and in bowerbirds specifically.

The relative volume of Rt appears intraspecifically homogeneous, although there do appear to be differences in relative Rt volume between species (Figure 7).

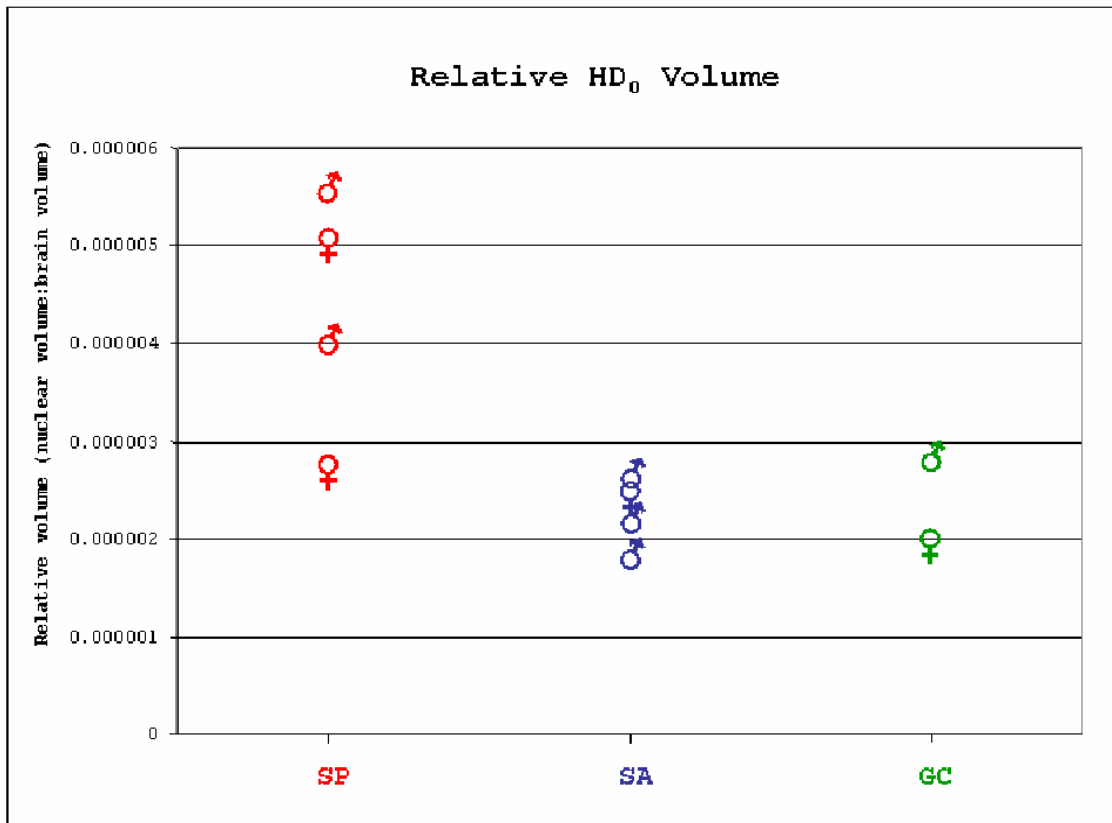
Examination of all bowerbird brains has revealed the presence of a nucleus not previously observed in any avian taxa. Situated in the ventral and lateral aspect of the dorsal hyperstriatum (HD), somata are compactly contained within this nucleus by a thin encapsulation of fibers (Figure 8). This putative obovate<sup>4</sup> nucleus of the dorsal hyperstriatum (HD<sub>0</sub>) appears rostrally just anterior to the emergence of the lobus parolfactorius (LPO) and extends caudally past LMAN and disappears just anterior to the emergence of the optic chiasm. The relative volumes of HD<sub>0</sub>, as shown in Figure 9, are relatively closely clustered in satin bowerbirds and green catbirds, but less so in spotted bowerbirds. The relative HD<sub>0</sub> volumes do not show a clear sexual dimorphism in our sample. Although the sparseness of green catbird data makes it difficult to assess whether there is a true difference between relative HD<sub>0</sub> volume in

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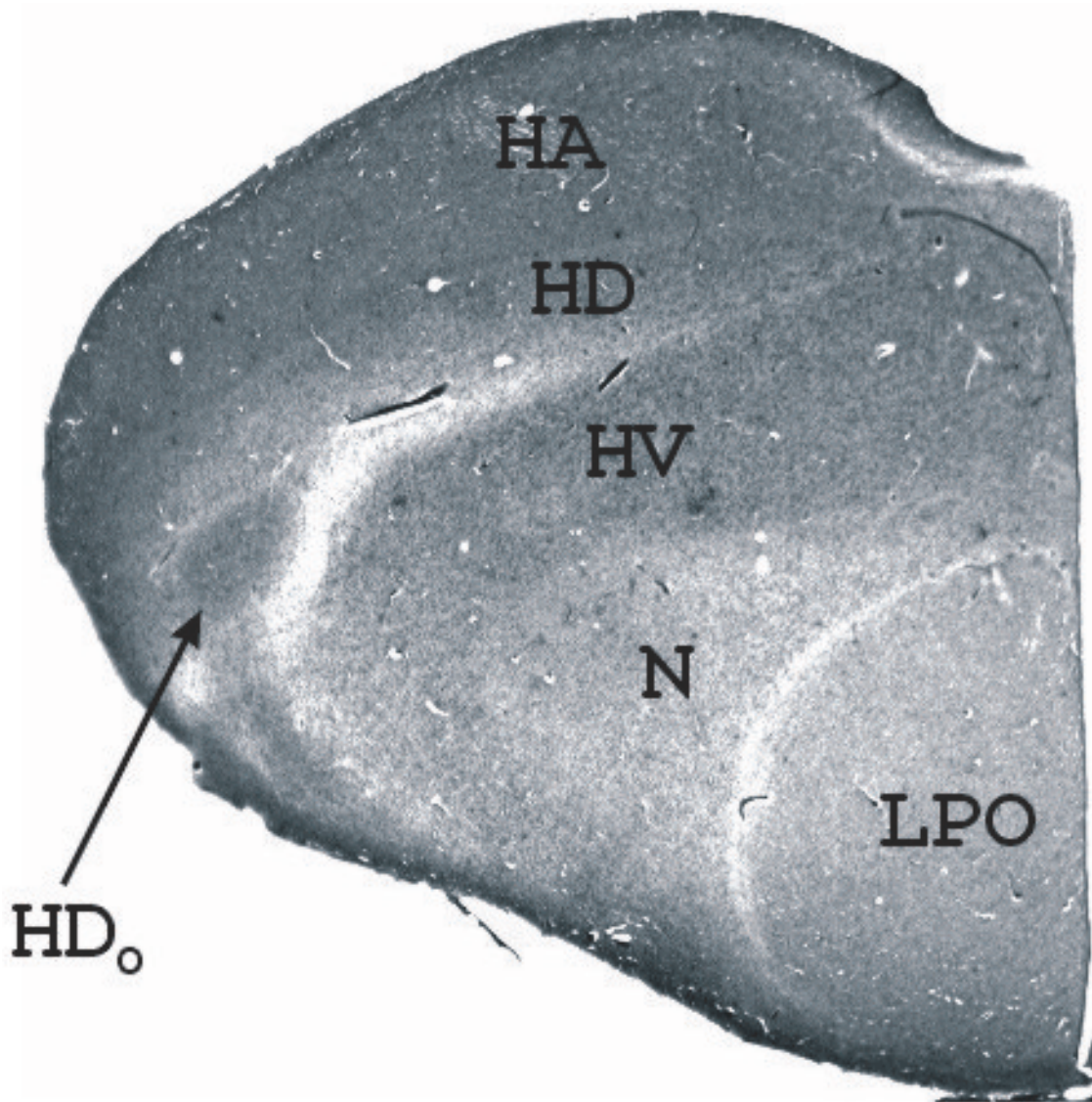
<sup>4</sup>I.e., broad and rounded about the lateral aspect and tapering towards the midline



**Figure 7.** Graph displaying the relative volume of nucleus Rt in the brain of three species of bowerbird (see Figure 4 for abbreviations). Values obtained are the ratios of nuclear volume to overall brain volume. Raw data presented in tabular form in Appendix 1C.



**Figure 8.** Graph displaying the relative volume of nucleus HD<sub>0</sub> in the brain of three species of bowerbird (see Figure 4 for abbreviations). Values obtained are the ratios of nuclear volume to overall brain volume. Raw data presented in tabular form in Appendix 1C.



**Figure 9.** Cross-sectional (coronal) view of Nissl-stained tissue from a satin bowerbird. HD<sub>0</sub> appears as a distinct islet of cells more darkly stained and more densely packed than the surrounding neuropil. HD<sub>0</sub>, as such, appears in satin bowerbirds, spotted bowerbirds and green catbirds. (Abbreviations: HA, accessory hyperstriatum; HD, dorsal hyperstriatum; HD<sub>0</sub>, obovate nucleus of the dorsal hyperstriatum; HV, ventral hyperstriatum; N, neostriatum; LPO, parolfactory lobe).

green catbirds and satin bowerbirds, there appears to be negligible overlap between the ranges of spotted bowerbirds' and satin bowerbirds' relative  $HD_0$  volumes.

## Chapter 4: Discussion

The relative volumes of HVC and LMAN appear in bowerbirds much as they would in any other passerine. HVC was not evident in the Nissl-stained tissue of any female bowerbird. The one sense in which HVC appears different in bowerbirds than it might in other songbirds is that in the green catbird, a species that does not have nearly as complex and varied a vocal repertoire as spotted or satin bowerbirds, relative HVC volume is considerably higher than in the other two species. HVC volume increases as a function of song repertoire (Airey & DeVoogd, 2000; MacDougall-Shackleton et al., 1998; Ward et al., 1998). Given catbirds' limited repertoire, the relative size of HVC in the male green catbird was not expected.

One explanation for the particularly large relative contribution to overall brain mass of HVC in the male green catbird is that males and females call antiphonally (Marshall, 1954). Avian species that practice antiphonal vocalizations tend to have larger and sexually monomorphic HVC volumes (Brenowitz et al., 1985; Brenowitz & Arnold, 1985; Brenowitz & Arnold, 1986). However, HVC was not evident in the female green catbird

brain. This ambiguity can only be resolved with a larger number of specimens and perhaps by assessing HVC volume according to steroid receptor density or some other cytological marker.

The relative volumes of LMAN in male and female green catbirds appeared similar, but the degree of variation in the other two species is enigmatic. In spotted bowerbirds, the relative LMAN volumes of two males and one female are tightly clustered ( $3.54 \times 10^{-6}$  to  $4.52 \times 10^{-6}$ ), with one female outlier substantially higher ( $1.16 \times 10^{-5}$ ). As mentioned earlier in the context of HVC measurements, there may yet be a more illuminating means (e.g., alternative cytological markers) of measuring the relative volume of LMAN in bowerbirds. The overall distribution of relative LMAN values in spotted bowerbirds is roughly equal to that seen in satin bowerbirds.

Although RA is clearly sexually dimorphic, its dimorphism is not as marked as that of HVC. RA is evident in males and females, but in each species, the female relative RA volume is lower. It is expected that RA should be sexually dimorphic in all species (such as satin and spotted bowerbirds) in which males sing more than females. This is certainly the case for satin and



spotted bowerbirds, but perhaps less so for the antiphonally-calling green catbirds. It remains to be seen whether the difference between the relative RA volume of the male and female green catbird is a true dimorphism or if the difference exists within a broader range of monomorphy.

There are known to be volumetric increases in the adult male songbird Rt as a result of naturally occurring variation in testosterone titers (Smulders, 2002). Lesions to nucleus Rt contribute significantly to impairment of stimulus discrimination (Güntürkün & Hahmann, 1999). So, for much the same reason that we predicted LMAN relative volumes to be monomorphic, we expected Rt to be monomorphic. The reasoning behind this presumption is straightforward and has much to do with the peculiar mating habits of satin and spotted bowerbirds. Insofar as bower quality is a determinant of male quality (Borgia, 1985; Borgia et al., 1987), both the males *and* females of bower-building species are required to perform fine visual discriminations: the males in order to construct the bower and make appropriate corrections, additions and alterations; and the females in order to recognize the high-quality bower.

The relative Rt volume for spotted bowerbirds is situated somewhat higher than that for satin bowerbirds. It is tempting to suggest that this may have some relationship with the habits of bower-building peculiar to those species. Spotted bowerbirds build larger bowers and incorporate a greater variety of color than do satin bowerbirds. However, the relative volume of Rt in green catbirds (which *do not* build bowers) lies within the range of spotted bowerbirds and above the range of satin bowerbirds. Once again, we suppose that a greater number of green catbird brains would be instrumental in resolving this ambiguity. Moreover, the relative volume of Rt in species that build even more complex bowers might shed yet more light on the proposed relationship between bower complexity and the birds' ability to perform fine visual discriminations -a task that is underwritten in significant part by nucleus Rt.

An unexpected finding is that of a nucleus in the bowerbird dorsal hyperstriatum that has never been observed in any other species. The most unique aspect of bowerbirds' behavior is, of course, the construction of bowers. Therefore, it is our tentative assumption that the uniquely ptilonorhynchid suite of behaviors associated with bower building (e.g., building,

decorating and appraising bowers) are at least in part underwritten by HD<sub>0</sub>. There is nominal support for this idea. Bischof and Rollenhagen (2000) describe increases in dendritic spine density in a region of the zebra finch (*Poephila guttata*) forebrain that corresponds to the bowerbird HD, and Sananda and Bischof (2002) describe increases in the expression of the immediate early gene, *c-fos*, in the same area. The area where these changes take place includes HD generally and corresponds to the region of the bowerbird brain in which HD<sub>0</sub> is found. In the absence of electrophysiological or other data that might reveal the functional significance of HD<sub>0</sub>, we must rely on the data from the zebra finch. The conditions under which these structural and biochemical changes were induced in the zebra finch suggest the role of the newly found bowerbird nucleus.

The developmental process of sexual imprinting was concomitant with the changes seen in the zebra finch HD. Bischof and Rollenhagen (1999) define sexual imprinting as a biphasic process by which young animals first learn the social environment and characteristics of conspecifics that will eventually make suitable partners. Later under the guidance of the previously acquired species-specific social and multisensory stimuli, the

preference for a sexual partner stabilizes, so that it cannot be altered again subsequently.

The location of the zebra finch HD and the changes that occur in it during sexual imprinting suggest that HD<sub>0</sub> serves the same role as (or one similar to) the sensory and integrative role of the zebra finch's HD region during sexual imprinting. This is to say that the multisensory HD area (HD<sub>0</sub> in bowerbirds) may acquire an aptitude towards responding to certain stimuli, but not others. Additionally, this may help explain why there appears to be no marked sexual dimorphism in HD<sub>0</sub>. If it were the case that HD<sub>0</sub> critically subserves *bower construction* (exclusively), then we would expect to see a marked sexual dimorphism for this nucleus, as is seen, for example, in HVC and RA. If, however, HD<sub>0</sub> more generally subserves the process(es) of sexual imprinting -which is common to males *and* females- it follows that HD<sub>0</sub> would not be sexually dimorphic.

Madden's bower complexity index (2001) provides a framework within which to evaluate the possibility that HD<sub>0</sub> in part subserves the many behaviors that go into bower construction and appreciation. Bower complexity as indicated by this Bower Complexity Index (BCI) is based on structural characteristics and the degree of

ornamentation found in different species' bowers. Comparing the relative volume of HD<sub>0</sub> in spotted bowerbirds (BCI=4), satin bowerbirds (BCI=3) and green catbirds (BCI=1) shows a generally higher relative HD<sub>0</sub> volume in the spotted bowerbird. Satin bowerbirds have a relative HD<sub>0</sub> volume lower than that of spotted bowerbirds. Green catbirds, the males of which species build no bowers, have a relative HD<sub>0</sub> volume similar to that of satin bowerbirds (Figure 10). The coefficient of correlation of relative HD<sub>0</sub> volume and BCI is  $r=0.72$ . That there is no significant difference between the relative HD<sub>0</sub> volume of satin bowerbirds and green catbirds may be a reflection of reality, or it may be an artifact of the small number of green catbird specimens (n=2) used in this investigation.

Bower Complexity Index (BCI)  
and Relative Volume of HD<sub>0</sub>

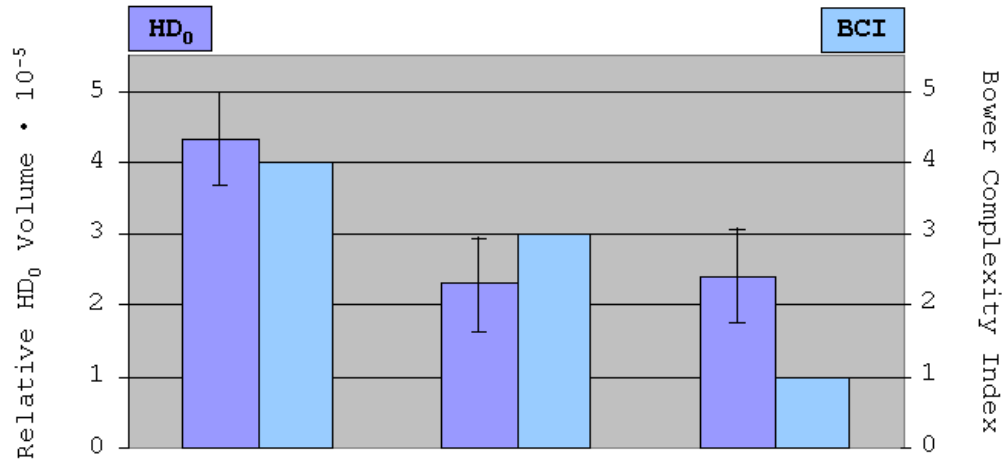


Figure 10. Bower Complexity Index (in aqua) of spotted bowerbirds, satin bowerbirds and green catbirds plotted against their respective relative HD<sub>0</sub> volumes (in blue). Raw (brain) data presented in tabular form in Appendix 1D.

## Chapter 5: Conclusions

It is not possible to determine unequivocally from the present findings whether the putative nucleus HD<sub>0</sub> is in fact related to the bower-building life history of the Ptilonorhynchidae family. It is significant, however, that this feature is unique to bowerbirds. The putative nucleus HD<sub>0</sub> is not evident in any other avian brain thus far studied (Craigie, 1928, 1930; Karten and Hodos, 1967; Brown, 1971; Pearson, 1972; Stokes et al., 1974; Morenkov and Hun, 1977; Kuenzel and Masson, 1988; Matochik et al., 1991; Dubbeldam et al., 1997; Voronov and Alekseev, 2001). Some critical questions arise as the result of the discovery of a novel nucleus in the passerine hyperstriatum: what afferent and efferent pathways to and from HD<sub>0</sub> connect it with the rest of the brain? What is the developmental trajectory of HD<sub>0</sub> throughout the process of sexual imprinting? Does HD<sub>0</sub> indeed vary systematically with bower complexity, as is suggested by the present findings? The answer to these questions as well as the identification of a more specific functional role for HD<sub>0</sub> are tasks that will be best suited to electrophysiological and neuroanatomical tract-tracing experiments.

## Appendices

**Appendix 1A** shows body mass, brain mass and telencephalic mass for individual bowerbirds used in the present investigation.

<b>Scientific Name</b>	<b>Sex</b>	<b>Body Mass (g)</b>	<b>Brain Mass (g)</b>	<b>Telencephalon Mass (g)</b>
<i>Ailuroedus crassirostris</i>	Male	255	4.38	3.37
<i>Ailuroedus crassirostris</i>	Female	204	3.7	2.81
	avg.	229.5	4.04	3.090

<i>Chlamydera maculata</i>	Male	160	4.28	3.03
<i>Chlamydera maculata</i>	Male	139	4.02	2.96
<i>Chlamydera maculata</i>	Female	147	3.14	2.208
<i>Chlamydera maculata</i>	Female	137	3.67	2.619
	avg.	145.75	3.7775	2.704

<i>Ptilonorhynchus violaceus</i>	Male	215	5.05	3.89
<i>Ptilonorhynchus violaceus</i>	Female	178	4.49	3.49
<i>Ptilonorhynchus violaceus</i>	Male	208	5.42	4.15
<i>Ptilonorhynchus violaceus</i>	Male	222	4.43	3.42
	avg.	205.75	4.8475	3.738



**Appendix 1B** contains body mass, telencephalic mass and whole brain mass data from 133 of the avian species used by Portmann (1947), as well as from 3 bowerbird species.

	Scientific Name	Body wt (g)	Telencephalon wt (g)	Total brain wt (g)	<i>n</i>
1	<i>Dromeius noveaehollandiae</i>	40500.0	17.472	26.551	1
2	<i>Struthio camelus</i>	90000.0	27.072	41.058	1
3	<i>Coturnix chinensis</i>	31.0	0.243	0.450	2
4	<i>Coturnix coturnix</i>	85.0	0.401	0.783	16
5	<i>Perdix perdix</i>	370.0	0.921	1.747	12
6	<i>Chrysolophus pictus</i>	550.0	1.792	3.194	4
7	<i>Gallus gallus</i>	550.0	1.429	2.676	2
8	<i>Phaisanus colchicus torquatus</i>	1200.0	2.258	3.922	5
9	<i>Lophura nychtemera</i>	1250.0	2.743	4.676	1
10	<i>Lyrurus tetrix</i>	1250.0	2.050	3.890	2
11	<i>Tetrao urogallus</i>	2750.0	3.102	5.698	1
12	<i>Pavo cristianus</i>	3500.0	4.338	7.238	5
13	<i>Anas crecca</i>	300.0	1.739	2.832	1
14	<i>Anas penelope</i>	700.0	2.649	4.050	2
15	<i>Mergus serrator</i>	900.0	2.909	5.034	1
16	<i>Anas platyrhynchos</i>	1200.0	4.001	5.881	4
17	<i>Somateria mollissima</i>	2050.0	6.040	8.722	1
18	<i>Anser anser</i>	3250.0	7.914	11.316	4
19	<i>Cygnus olor</i>	11000.0	10.836	16.000	4
20	<i>Jynx torquilla</i>	37.0	0.495	0.804	4
21	<i>Dendrocopos medius</i>	58.0	1.490	2.061	1
22	<i>Dryocopus schulzi</i>	80.0	1.964	2.703	7
23	<i>Picus canus</i>	122.0	2.569	3.465	2
24	<i>Picus viridis</i>	200.0	3.220	4.384	3
25	<i>Dryocopus martius</i>	300.0	6.153	7.979	1
26	<i>Upupa epops</i>	55.0	0.821	1.233	4
27	<i>Merops apiaster</i>	60.0	0.415	0.878	2
28	<i>Alcedo atthis</i>	35.0	0.505	0.909	1
29	<i>Cuculus canorus</i>	100.0	0.825	1.462	4
30	<i>Melopsittacus undulatus</i>	36.7	0.777	1.111	11
31	<i>Agapornis fischeri</i>	42.0	1.492	1.997	2
32	<i>Calopsitta novae hollandiae</i>	85.0	1.964	2.579	4
33	<i>Psittacula eupatria</i>	96.0	3.090	4.091	1
34	<i>Trichoglossus novaehollandiae</i>	136.0	1.659	2.749	1
35	<i>Amazona versicolor</i>	400.0	5.957	7.818	5
36	<i>Cacatua sulphurea</i>	450.0	6.891	8.720	1
37	<i>Psittacus erythacus</i>	450.0	7.525	9.502	4
38	<i>Ara arauna</i>	850.0	15.383	18.693	2
39	<i>Ara chloroptera</i>	1430.0	19.879	24.343	1
40	<i>Apus apus</i>	38.0	0.370	0.665	14
41	<i>Tachymarptis melba</i>	90.0	0.620	1.107	10
42	<i>Caprimulgus europaeus</i>	70.0	0.343	0.769	1

43	<i>Otus scops</i>	92.0	1.445	2.208	1
44	<i>Athene noctua</i>	165.0	3.019	3.923	6
45	<i>Asio otus</i>	250.0	4.110	5.513	10
46	<i>Tyto alba</i>	290.0	4.548	6.068	16
47	<i>Strix aluco</i>	450.0	6.698	8.820	10
48	<i>Bubo bubo</i>	2000.0	12.930	16.894	7
49	<i>Geopelia cuneata</i>	30.0	0.219	0.483	3
50	<i>Streptopelia risoria</i>	143.0	0.696	1.224	2
51	<i>Columba livia</i>	300.0	1.272	2.312	1
52	<i>Columba palumbus</i>	450.0	1.308	2.399	7
53	<i>Porzana porzana</i>	80.0	0.617	1.158	4
54	<i>Crex crex</i>	110.0	0.750	1.305	3
55	<i>Rallus aquaticus</i>	120.0	1.060	1.763	8
56	<i>Gallinula chloropus</i>	230.0	1.206	2.062	3
57	<i>Fulica atra</i>	410.0	2.089	3.326	15
58	<i>Porphyrio porphyrio</i>	500.0	3.270	5.131	3
59	<i>Grus virgo</i>	2000.0	6.205	10.018	1
60	<i>Balearica pavonina</i>	3250.0	9.768	14.413	3
61	<i>Grus antigone</i>	7500.0	14.210	20.024	1
62	<i>Actitis hypoleucos</i>	47.0	0.394	0.772	2
63	<i>Limnocryptes minimus</i>	60.0	0.500	0.930	1
64	<i>Capella gallinago</i>	100.0	0.730	1.264	2
65	<i>Philomachus pugnax</i>	180.0	0.956	1.647	7
66	<i>Vanellus vanellus</i>	200.0	1.216	2.208	7
67	<i>Scolopax rusticola</i>	290.0	1.629	2.593	6
68	<i>Buhinus oedicephalus</i>	440.0	2.081	3.540	4
69	<i>Hematopus ostralegus</i>	500.0	2.267	3.602	2
70	<i>Numenius arquatus</i>	650.0	2.442	4.087	1
71	<i>Sterna albifrons</i>	40.0	0.438	0.952	1
72	<i>Sterna hirundo</i>	120.0	0.784	1.486	1
73	<i>Larus ridibundus</i>	250.0	1.549	2.812	11
74	<i>Larus argentatus</i>	1000.0	2.577	4.467	1
75	<i>Larus marinus</i>	1670.0	4.788	7.775	1
76	<i>Fratercula artica grabae</i>	330.0	2.536	4.432	4
77	<i>Tachybaptus ruficollis</i>	160.0	0.950	1.715	8
78	<i>Podiceps cristatus</i>	1050.0	2.124	3.764	6
79	<i>Colymbus stellatus</i>	1200.0	2.432	4.856	1
80	<i>Spheniscus demersus</i>	2700.0	9.403	14.450	1
81	<i>Phoenicopiterus ruber roseus</i>	3000.0	7.371	11.058	9
82	<i>Ixobrychus minutus</i>	136.0	0.949	1.616	2
83	<i>Egretta garzetta</i>	500.0	2.072	3.468	7
84	<i>Botaurus stellatus</i>	900.0	3.294	5.207	1
85	<i>Egretta alba</i>	1000.0	3.192	5.298	1
86	<i>Ardea cinerea</i>	1500.0	4.967	7.867	10
87	<i>Ciconia ciconia</i>	3500.0	9.176	14.676	6
88	<i>Leptoptilus crumeniferus</i>	6200.0	22.041	31.319	1
89	<i>Phalacrocorax carbo</i>	2200.0	6.337	9.872	12

90	<i>Pelecanus onocrotalus</i>	9000.0	22.812	31.467	1
91	<i>Alauda arvensis</i>	39.0	0.865	1.176	9
92	<i>Melanocorypha calandra</i>	55.0	0.941	1.361	4
93	<i>Delichon urbica</i>	15.0	0.282	0.442	5
94	<i>Hirundo rustica</i>	18.5	0.342	0.551	12
95	<i>Anthus pratensis</i>	16.0	0.316	0.533	3
96	<i>Motacilla alba</i>	23.0	0.374	0.626	5
97	<i>Cinclus cinclus</i>	60.0	0.904	1.454	4
98	<i>Troglodytes troglodytes</i>	9.5	0.305	0.504	6
99	<i>Erithacus rubecula</i>	16.2	0.346	0.613	6
100	<i>Turdus ericentorum</i>	67.0	0.895	1.459	8
101	<i>Turdus merula</i>	95.0	1.161	1.808	10
102	<i>Regulus regulus</i>	5.4	0.225	0.357	5
103	<i>Acrocephalus scirpaceus</i>	14.0	0.282	0.483	5
104	<i>Sylvia borin</i>	19.0	0.353	0.586	3
105	<i>Muscicapa striata</i>	16.0	0.295	0.498	2
106	<i>Lanius collurio</i>	29.7	0.719	1.053	2
107	<i>Bombycilla garrulus</i>	55.5	0.710	1.142	6
108	<i>Sturnus roseus</i>	55.2	0.960	1.476	4
109	<i>Sturnus vulgaris</i>	80.0	1.221	1.787	10
110	<i>Oriolus oriolus</i>	72.0	0.906	1.498	2
111	<i>Garrulus glandarius</i>	160.0	2.911	4.101	9
112	<i>Coloeus monedula</i>	200.0	3.593	4.758	6
113	<i>Pica pica</i>	220.0	4.269	5.581	12
114	<i>Pyrrhocorax pyrrhocorax</i>	356.0	5.066	6.489	1
115	<i>Corvus frugilegus</i>	430.0	6.005	7.790	8
116	<i>Corvus corone</i>	520.0	6.429	8.383	21
117	<i>Corvus corax (fem)</i>	1100.0	11.762	14.624	5
118	<i>Corvus corax (male)</i>	1250.0	12.697	15.732	7
119	<i>Aegithalos caudatus</i>	7.5	0.283	0.456	7
120	<i>Parus coeruleus</i>	11.0	0.491	0.682	7
121	<i>Parus major</i>	17.5	0.642	0.909	7
122	<i>Sitta europaea</i>	23.0	0.726	1.060	5
123	<i>Certhia familiaris</i>	8.7	0.277	0.447	3
124	<i>Prunella modularis</i>	18.9	0.440	0.725	1
125	<i>Serinus canaria</i>	8.0	0.286	0.451	3
126	<i>Carduelis spinus</i>	11.5	0.354	0.546	9
127	<i>Carduelis cannabina</i>	18.0	0.429	0.636	8
128	<i>Carduelis carduelis</i>	14.5	0.421	0.619	13
129	<i>Fringilla coelebs</i>	21.6	0.466	0.731	9
130	<i>Passer domesticus</i>	28.0	0.664	0.968	10
131	<i>Loxia curvirostra</i>	38.0	0.966	1.389	2
132	<i>Montifringilla nivalis</i>	45.0	0.704	1.093	2
133	<i>Coccothraustes coccothraustes</i>	52.0	1.115	1.626	7
134	<i>Ailuroedus Crassirostris</i>	229.5	3.090	4.036	2
135	<i>Chlamydera maculata</i>	145.8	2.704	3.772	4
136	<i>Ptilonorhynchus violaceus</i>	205.8	3.738	4.848	4

**Appendix 1C** contains allometric (i.e., nuclear volume per whole brain volume  $\times 10^{-8}$ ) data for five brain nuclei in three bowerbird species. Values given are in arbitrary units. Dashed lines indicate that the nucleus was not observed in that bird. (Abbreviations: HD<sub>o</sub>, obovate nucleus of the dorsal hyperstriatum; HVC, used as a proper name by convention; LMAN, lateral magnocellular nucleus of the anterior neostriatum; RA, robust nucleus of the archistriatum; Rt, rotund nucleus; SP, spotted bowerbird; SA, satin bowerbird; GC, green catbird).

	<b>SP1<sup>♂</sup></b>	<b>SP2<sup>♂</sup></b>	<b>SP3<sup>♀</sup></b>	<b>SP4<sup>♀</sup></b>
<b>HD<sub>o</sub></b>	3986	5527	5085	2757
<b>HVC</b>	55	79	--	--
<b>LMAN</b>	4521	3542	11602	4373
<b>RA</b>	6987	13243	1800	4113
<b>Rt</b>	124	131	170	154

	<b>SA1<sup>♂</sup></b>	<b>SA2<sup>♀</sup></b>	<b>SA3<sup>♂</sup></b>	<b>SA4<sup>♂</sup></b>
<b>HD<sub>o</sub></b>	2583	2472	1817	2346
<b>HVC</b>	79	--	58	--
<b>LMAN</b>	4770	6527	10711	13233
<b>RA</b>	6639	778	6177	8182
<b>Rt</b>	105	87	102	119

	<b>GC1<sup>♂</sup></b>	<b>GC2<sup>♀</sup></b>
<b>HD<sub>o</sub></b>	2774	1983
<b>HVC</b>	126	--
<b>LMAN</b>	11994	9391
<b>RA</b>	5612	1343
<b>Rt</b>	139	132

**Appendix 1D** contains the average relative volume of HD<sub>0</sub> (HD<sub>0</sub> rel. vol.) for each bowerbird species, bower complexity index for each bowerbird species (**BCI**) and the correlation (**r**) between the two sets of data.

	<b>SP</b>	<b>SA</b>	<b>GC</b>	<b>r</b>
<b>HD<sub>0</sub> rel. vol.</b>	4.326	2.289	2.412	0.720
<b>BCI</b>	4	3	1	

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