

BRIEF COMMUNICATIONS

Sexual Dimorphism and Species Differences in HVC Volumes of Cowbirds

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Cowbirds exhibit extensive variation in their social, territorial, and reproductive behaviors. Nissl-stained brain sections of specimens from a previous study (J. C. Reboreda, N. S. Clayton, & A. Kacelnik, 1996) were used to study the gross anatomy of a song control nucleus in 3 South American cowbirds (bay-winged, *Molothrus badius*; shiny, *M. bonariensis*; and screaming, *M. rufoaxillaris*). Cowbird high vocal center (HVC) volumes were consistently higher in males than in females in all 3 species. The largest HVC size of females found in bay-winged cowbirds is consistent with observations that females of this species, but not of the other 2 species, occasionally sing. The extent of the sexual dimorphism of relative HVC size was highest for the sexually dichromatic and promiscuous shiny cowbirds and smaller for the monochromatic and monogamous bay-winged and screaming cowbirds, suggesting that selection pressures associated with morphological traits and social systems are reflected in brain architecture.

The brain regions involved in learning and producing avian songs have provided an exciting model system to study the development, mechanism, function, and evolution of the neurobiological basis of a complex yet specific behavior (Brenowitz, 1991, 1997; DeVoogd & Szekely, 1998). Although much of the research has focused on the

detailed understanding of the neural control of singing in a few species of birds, several of the conclusions and predictions drawn from previous reports have been successfully applied and tested in comparative studies (DeVoogd & Szekely, 1998). A potential use of the strong correlations between brain architecture and behavioral traits is to reverse the behavior-to-neurons approach and to apply results of neuroanatomical studies as a tool to predict behavioral patterns that have not yet been studied in detail.

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This reverse approach makes use of relations between those aspects of singing and song system anatomy that have been observed in previous studies. For example, there is often a strong correlation between the amount and quality of female song and the degree of sexual dimorphism in the volume of the oscine high vocal center (HVC), both within and across species (Ball, Casto, & Bernard, 1994; Brenowitz & Arnold, 1986; MacDougall-Shackleton & Ball, in press; Nottebohm & Arnold, 1976; but see Gahr, Sonnenschein, & Wickler, 1998). In addition, several studies have found a positive relationship between the relative volume of the HVC and the repertoire size of individuals within a species (e.g., Canady, Kroodsma, & Nottebohm, 1984; Kroodsma & Canady, 1985; Nottebohm, Kasparian, & Pandazis, 1981; Ward, Nordeen, & Nordeen, 1998; but see Bernard, Eens, & Ball, 1996; Hamilton, King, Sengelaub, & West, 1997; MacDougall-Shackleton, Hulse, & Ball, 1998). These findings suggest that individual differences in HVC size confer individual differences in the ability to acquire long and/or

complex songs (Brenowitz, Lent, & Kroodsma, 1995). In contrast, in at least one study it was found that individual differences in exposure to song variability did not affect HVC volume but did affect synaptic density on HVC neurons (Airey, DeVoogd, & Kroodsma, 1994).

Associations between brain nuclei and specific aspects of singing behavior appear stronger in interspecific comparisons. Relative HVC volume is positively correlated with song complexity in males across a wide range of songbird species (DeVoogd, Krebs, Healy, & Purvis, 1993), as well as within a group of closely related species (e.g., Szekely, Catchpole, DeVoogd, Marchl, & DeVoogd, 1996). These interspecific correlations between singing behavior and neural architecture may allow us to use neurobiological data to predict qualitative variation in vocal complexity. When detailed descriptions and observations from the field are lacking or difficult to collect, this reverse approach may be particularly powerful for generating testable hypotheses about behavior patterns, such as singing, that should be subject to sexually selective pressures (Andersson, 1994; Catchpole, 1987; DeVoogd & Szekely, 1998).

In conjunction with a previous study (Reboreda et al., 1996), we collected data on HVC volumes in three sympatric South American species of cowbirds during their breeding season, when singing behavior is probably under the strongest selective pressure (DeVoogd & Szekely, 1998). These molothrine cowbirds are closely related icterids (see Freeman & Zink, 1997; Lanyon, 1992, for discussion of their phylogenetic relationships) but show marked differences in their reproductive behaviors (Friedmann, 1929; Ortega, 1998). The shiny cowbird (*Molothrus bonariensis*) and the screaming cowbird (*M. rufoaxillaris*) are obligate brood parasites. In the shiny cowbird, only females search for nests to parasitize, whereas in the screaming cowbird, both males and females seek out potential hosts to parasitize (Friedman, 1929). In contrast to these two species, the bay-winged cowbird (*M. badius*) is not parasitic and provides biparental care for its own young (Friedmann, 1929; Ortega, 1998). Screaming and bay-winged cowbirds are sexually monochromatic and appear to be monogamous, as they form lasting pair-bonds, whereas shiny cowbirds are sexually dichromatic and appear to be promiscuous, as they lack prolonged pairbonds (Fraga, 1991; Mason, 1987).

Although several specific aspects of the reproductive and social biology of South American cowbirds have been documented by various authors (e.g., Fraga, 1991; Kattan, 1997; Mason, 1987; summarized by Ortega, 1998), to date no detailed comparative studies exist on the vocal behavior of these three species. According to Friedmann (1929), in shiny and screaming cowbirds, only males sing during the breeding season, whereas in bay-winged cowbirds both sexes produce song. Friedmann also characterized the song of the bay-winged cowbird as the most simple and primitive, followed by the more variable song and call types of the screaming cowbird, and the even more diverse vocalizations of the shiny cowbird. However, these comparisons were not based on systematic recordings of songs and may not be comparable to any of the quantitative classification systems of song-repertoire complexity used in more recent studies

(Kroodsma, 1982). For example, a formal comparison of song between bay-winged and brown-headed cowbirds (*M. ater*) suggested no significant interspecific difference in the relatively small number of syllable types (Irwin, 1990), even though the brown-headed cowbird has been described by Friedmann (1929) as a species with a particularly large repertoire size, at least among the cowbirds.

In this investigation, we measured the volume of the HVC song nucleus in males and females of the three species. We predicted that relative HVC size would be highest in female bay-winged cowbirds because females of this species sing, unlike females in the other two species. We also predicted that species in which relative HVC volume is large would produce more elaborate songs than species in which HVC volume is small. Finally, we examined whether the mating system, the presence of sexually dimorphic plumage, and the patterns of parental investment (all of which correlate with the potential strength of sexual selection; Andersson, 1994) covary with the extent of neuroanatomical sexual dimorphism among these species. Specifically, we predicted that the magnitude of sexual dimorphism should be greater for the sexually dichromatic shiny cowbirds than for other two monochromatic cowbird species.

Method

Three species of cowbirds (see Table 1) were collected during the austral breeding season, and brain sections from males and females of each species were prepared as described in detail by Reboreda et al. (1996). The brains were sectioned at 40 μ m, and every fifth section was Nissl stained and mounted on microscope slides. Slides with sections were coded and data collection was carried out by researchers unaware of the subjects' sex and species.

To measure the volume of the HVC in our sample, we applied the spatial and cytoarchitectural criteria commonly used to delineate this nucleus in other oscine species in previous studies (see Gahr, 1997). The profiles of the "HVC proper" (Foster & Bottjer, 1998; Kim, Clower, Kroodsma, & DeVoogd, 1989) were then traced by one of us (M. E. H.) by using a camera lucida. The areas of the HVC in each section and for each hemisphere were determined with NIH Image 1.61 (National Institutes of Health, 1996). The HVC volumes were computed by summing the areas of HVC on the sections and multiplying by the sampling interval (200 μ m). Observer error in tracing the HVC of the same individuals

Table 1
Species Difference and Sexual Dimorphism in Three Species of South American Cowbirds Collected During the Breeding Season (M \pm SD)

Species and sex	<i>n</i>	Body weight (g)	Telencephalon volume (mm ³)	HVC volume (mm ³)
Bay-winged				
Female	4	41.5 \pm 1.43	1,022 \pm 21.1	0.112 \pm 0.028
Male	4	46.3 \pm 1.53	976 \pm 75.2	0.290 \pm 0.068
Screaming				
Female	6	52.3 \pm 1.05	857 \pm 24.0	0.038 \pm 0.0047
Male	6	55.5 \pm 1.53	861 \pm 27.0	0.098 \pm 0.014
Shiny				
Female	8	46.8 \pm 1.40	808 \pm 29.3	0.024 \pm 0.0041
Male	8	50.7 \pm 1.20	923 \pm 16.3	0.167 \pm 0.012

Note. HVC = high vocal center.

repeatedly was estimated to be 12% (i.e., the average difference in volumes of five nuclei that were drawn twice). When possible, HVC volumes were averaged between the right and left hemispheres for each subject, but in 10 of the 36 samples, only one hemisphere was sufficiently intact. For these birds, we used the HVC measurement from one side only. There was no evidence for lateralization of HVC volumes in any of the three species (Wilcoxon signed rank tests, $ps > .200$).

To control for allometric relations, we calculated relative HVC volume as the ratio of log-transformed HVC and telencephalon volumes for each subject. Analyses of variance (ANOVAs) were carried out on these values, but we used nontransformed proportions for illustration in the figures. Because we used brain sections from a previous study, there was no need to kill additional subjects. However, this approach limited the sample size within each species–sex group (see Table 1).

Results

Relative HVC volumes varied significantly between species and were largest in both females and males of the bay-winged cowbird (see Figure 1), two-way ANOVA, $F(2, 30) = 20.10$, $p < .0001$. Relative HVC volume was consistently larger in males than in females, $F(1, 30) = 79.90$, $p < .0001$ (see Figure 1A). The extent of sexual dimorphism was most extreme in the shiny cowbird and less extreme and similar in both the bay-winged and screaming cowbirds, Sex \times Species interaction: $F(2, 30) = 8.68$, $p < .0012$, (see Figure 2).

In addition, HVC and telencephalon volumes were, but HVC volumes and body weight were not, positively correlated for all species and sexes pooled, Spearman rank correlation, $r_s = 0.469$, $p < .0056$; and $r_s = 0.079$, $p > .641$, respectively. Log-transformed body weights and telencephalon volumes also varied significantly across species, two-way ANOVAs: $F(2, 30) = 21.60$, $p < .0001$; and $F(2, 30) = 11.20$, $p < .0006$, respectively. Body weight was greater in males than in females, $F(1, 30) = 11.60$, $p < .0020$, but telencephalon volume did not differ between the sexes, $F(1, 30) = 0.98$, $p > .332$, (see Table 1). There was a significant

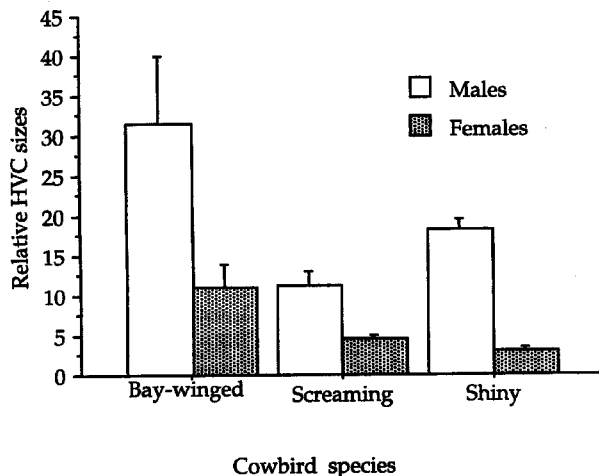


Figure 1. Relative high vocal center (HVC) size ($10^5 \times [\text{HVC volume} \div \text{telencephalon volume}]$) in three species of cowbirds ($M + SEM$, see Table 1 for sample sizes).

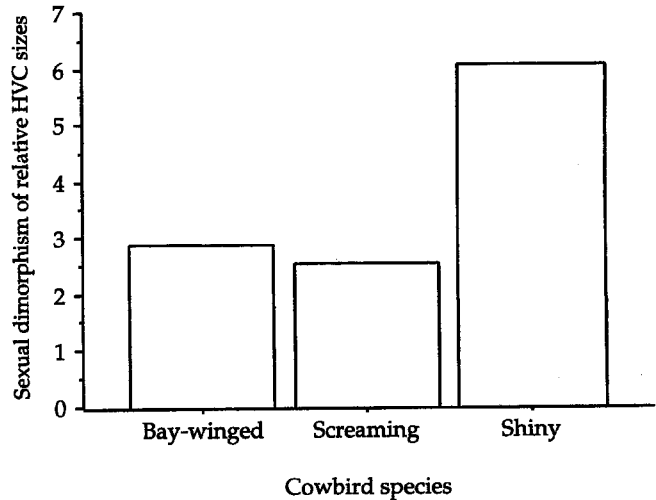


Figure 2. Sexual dimorphism of relative high vocal center (HVC) sizes in three species of cowbirds. Dimorphism values are calculated for each species as: (mean conspecific male relative HVC) \div (mean conspecific female relative HVC). Bay-winged and screaming cowbirds are monogamous and have sexually monochromatic plumage. Male bay-winged cowbirds show both nest search and feeding behavior, and male screaming cowbirds exhibit nest search behavior. Shiny cowbirds are promiscuous and have sexually dichromatic plumage; only females show nest search behavior.

Species \times Sex interaction for telencephalon size, $F(2, 30) = 0.40$, $p < .0291$, but not for body weight, $F(2, 30) = 0.31$, $p > .732$. Post hoc analyses showed that neither body weight nor telencephalon volumes were significantly different between sexes within each species (one-way ANOVAs, corrected $ps > .05$) with the exception of the sexually dimorphic telencephalon size in shiny cowbirds ($p < .005$; see Table 1).

Discussion

A number of previous studies have shown that the HVC is larger in males than in females, a difference that is most pronounced in species in which females do not sing (Ball et al., 1994; Brenowitz, 1997; Brenowitz & Arnold, 1986; Gahr et al., 1998). In our study, we found that the HVC is larger in males than in females in all three cowbird species. Relative HVC size is also larger in male brown-headed cowbirds than in females (Cleal, Allan, King, Sengelau, & West, 1996; Hamilton et al., 1997). In this congeneric species, female mate choice is based, in part, on male singing performance. These findings are consistent with the idea that male singing behavior and its neural substrate are sexually selected traits in cowbirds (Andersson, 1994; DeVoogd & Szekely, 1998; but see Gahr et al., 1998). Relative HVC size among females was largest in bay-winged cowbirds, the only species of this study in which females sing (Brenowitz & Arnold, 1986; Friedmann, 1929).

Comparative studies have found positive correlations between relative HVC volume and song repertoire size in males (DeVoogd et al., 1993; Szekely et al., 1996), whereas intraspecific comparisons have yielded positive correlations

in some species and the lack of these trends in others (e.g., compare Canady et al., 1984; Nottebohm et al., 1981 with Bernard et al., 1996; Hamilton et al., 1997; Kim et al., 1989; MacDougall-Shackleton et al., 1998). The largest relative HVC size in male bay-winged cowbirds (Figure 1) suggests that song complexity should be greatest for this species. Alternatively, it is possible that differences in song characteristics other than complexity or repertoire size may be reflected in the different relative HVC sizes (e.g., DeVoogd, Houtman, & Falls, 1995; MacDougall-Shackleton et al., 1998).

That song complexity may be the greatest for bay-winged cowbirds is interesting because, although no systematic comparisons of repertoire size in South American cowbirds have been published, Friedmann (1929) qualitatively characterized the song of the bay-winged cowbird as the simplest of all cowbirds. Even without quantitative data on song complexity, the large HVC in males of the bay-winged cowbirds is intriguing because the correlation of relative HVC volume with song complexity seems to relate to the strength of sexual selection (DeVoogd & Szekely, 1998), and the latter is normally negatively associated with monogamy and with the extent of male parental care (Andersson, 1994; Clutton-Brock, 1991). We can use two aspects of what is known of the reproductive behaviors in cowbirds to make predictions about the neural effects of sexual selection.

First, according to current theory, the strength of sexual selection and thus the magnitudes of sexually selected traits are positively correlated with variance in mating success (Andersson, 1994). Variance in reproductive success, in turn, is likely to be higher for promiscuous than for monogamous mating systems because in promiscuous species some males could monopolize the majority of matings while others never mate at all. In contrast, in monogamous species most males are mated and may sire similar numbers of young (Andersson). Bay-winged and screaming cowbirds form relatively stable, monogamous pairbonds during the reproductive period, unlike the promiscuous shiny cowbirds (Ortega, 1998). This theory then predicts that the magnitude of sexually selected characteristics should be greater in male shiny cowbirds than in males of the other two species.

Second, current theories also predict that there is less opportunity for sexual selection in species in which levels of parental investment between males and females are more similar than in species in which parental investment is carried out exclusively by one sex (Andersson, 1994; Clutton-Brock, 1991). Male shiny cowbirds do not appear to provide any form of parental investment, unlike males in the other two monogamous cowbird species (nest-searching and feeding in bay-winged cowbirds and nest-searching in screaming cowbirds, Ortega, 1998). Thus, to the extent that HVC volume is a sexually selected character in males, both observations suggest that it should be greater in shiny cowbirds than in the other two species. These predictions were not upheld by our data, suggesting that either the theories are incorrect or the HVC volume of males may not be an accurate indicator of sexual selection.

Perhaps a more appropriate measure of the potential strength of sexual selection is the extent of sexual dimorphism, that is, the ratio of the relative sizes of the male and

female HVC. Unlike the male trait sizes alone, this measure does not assume that female trait size is constant and similar across species. To control for relative female HVC size is especially relevant in these cowbird species because of the significant interactions between sex and species (see Results section and Figure 1). The extent of sexual dimorphism in relative HVC volume is expected to be higher in species with larger potential for sexual selection (Andersson, 1994) and, indeed, we found that the HVC is about twice as dimorphic in shiny cowbirds as in the other two species (Figure 2). This scenario is also supported by the presence of sexual dichromatism of plumage in shiny cowbirds (a trait that is often sexually selected, Andersson, 1994) and by the lack of plumage dichromatism in bay-winged and screaming cowbirds (Ortega, 1998, Figure 2). Patterns of sexual dimorphism in body weight, another trait that is frequently sexually selected (Andersson, 1994), are more equivocal. In previous studies, male screaming, bay-winged, and shiny cowbirds weighed more than females (6.6%, 26%, and 24%, respectively; Ortega, 1998). In our sample, although males were generally heavier than females among the captured birds, the sexes did not differ significantly in body weight within any of the three species (see Results section and Table 1). Because of the small sample sizes in our study and the extensive intraspecific geographic variation of weight dimorphism (Ortega, 1998), it remains unclear whether body size is strongly correlated with other sexually selected traits in cowbirds.

Despite the striking differences in the extent of sexual dimorphism in the three cowbird species, some caveats are inevitable in interpreting our results. First, a comparison of only three species is insufficient to assess the statistical significance of the resulting trends. Second, a recent meta-analysis of comparative data (Gahr et al., 1998) questioned whether the extent of sexual dimorphism of the HVC and the robust nucleus of the archistriatum can reliably predict sex-specific variation in song complexity in species of songbirds in which both sexes sing. Many of these suggestions will not be solved until large-sample meta-analyses controlling for phylogeny are performed (Brenowitz, 1997; see DeVoogd & Szekely, 1998; MacDougall-Shackleton & Ball, in press).

In conclusion, our results support the hypothesis that differences in brain architecture reflect differences in the vocal behavior of female cowbirds. Intriguingly, our cross-species comparisons leads to the expectation of greatest song complexity in the nonparasitic bay-winged cowbird, which is monogamous and exhibits paternal care. We also suggest that the extent of sexual dimorphism in relative HVC size may indicate the relative potential strengths of sexual selection of cowbirds. Comparative neuroanatomy, therefore, may complement behavioral and morphological studies in assessing selective pressures and adaptations of some species, especially when direct observations on correlated behavioral traits are lacking or hard to collect. Future neuroanatomical comparisons within cowbirds, however, need be complemented by detailed observations of the vocal behaviors and genetic mating systems of these species to better understand the relationship between realized selection pressures and brain architecture.

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