

Females have a larger hippocampus than males in the brood-parasitic brown-headed cowbird

(brain/birds/sex differences)

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ABSTRACT Females of the brood-parasitic brown-headed cowbird (*Molothrus ater*) search for host nests in which to lay their eggs. Females normally return to lay a single egg from one to several days after first locating a potential host nest and lay up to 40 eggs in a breeding season. Male brown-headed cowbirds do not assist females in locating nests. We predicted that the spatial abilities required to locate and return accurately to host nests may have produced a sex difference in the size of the hippocampal complex in cowbirds, in favor of females. The size of the hippocampal complex, relative to size of the telencephalon, was found to be greater in female than in male cowbirds. No sex difference was found in two closely related nonparasitic icterines, the red-winged blackbird (*Agelaius phoeniceus*) and the common grackle (*Quiscalus quiscula*). Other differences among these species in parental care, migration, foraging, and diet are unlikely to have produced the sex difference attributed to search for host nests by female cowbirds. This is one of few indications, in any species, of greater specialization for spatial ability in females and confirms that use of space, rather than sex, breeding system, or foraging behavior *per se*, can influence the relative size of the hippocampus.

Brown-headed cowbirds (*Molothrus ater*) are brood parasites. During breeding, females lay a single egg early in the day and spend the remainder of the morning searching for host nests in which to lay eggs on subsequent days (1–3). Females feed in the afternoon, often leaving the breeding area to do so (1, 4). Females of the eastern subspecies that were the subjects of the present study, *M. ater ater*, lay at least 40 eggs over the course of an 8-week breeding season (refs. 5 and 6; see also ref. 7). Male brown-headed cowbirds do not search for host nests or assist females in gaining access to host nests (7) but associate with females, both monogamously and polygamously, in breeding and feeding habitat. Field studies describe male association with females as consisting largely of following females during their daily activities (4).

Female cowbirds have a variety of methods for locating host nests, including sitting silently and watching nest-building activity by potential hosts, walking on the forest floor while scanning the canopy, and flying into shrubs and low vegetation to flush hosts from their nests (8). Females do not lay in a host nest immediately upon locating it. Search for new host nests follows laying in the daily routine (9), and females are selective in their choice of host nest, preferring to lay in a completed nest containing at least one, but not more than two, host eggs (10, 11). Females must therefore return to the location of a previously discovered host nest in order to lay in it, one or more days after first locating the nest

(2). It is likely that memory for the location of host nests assists females in relocating them.

The avian hippocampal complex, comprising the hippocampus and the area parahippocampalis (HP-APH; ref. 12), plays an important role in the processing of spatial information in birds (13–15). Lesions of the hippocampus disrupt spatial memory for cache sites in food-storing birds and disrupt spatial orientation in homing pigeons. Lesions to the avian hippocampus produce effects on behavior similar to the effects of lesion damage to the mammalian hippocampus. Tasks requiring memory for familiar spatial locations are disrupted, whereas tasks requiring memory for simple associations are not (15). Working memory (16) is likewise disrupted (15). The avian hippocampal complex differs anatomically from the mammalian hippocampus in many ways but evolutionarily is a homologous structure (17). It derives ontogenetically from the same pallial precursors that give rise to the mammalian hippocampal complex (18) and is similar to the mammalian hippocampus in its connections to other parts of the brain (19–21). The distributions of neuropeptides and neurotransmitters in the avian hippocampal complex show a number of similarities to their distributions in the mammalian hippocampus (22, 23).

In both birds and mammals, differences between species and between the sexes in the size of the hippocampus are correlated with reliance on spatial memory (24). The hippocampus of food-storing birds, which use spatial memory to retrieve scattered food caches, is over twice the size of the hippocampus of non-food-storing passerines (25, 26). Homing pigeons likewise have a larger hippocampus than non-homing strains of domestic pigeons (27). In addition, polygamous male voles in the genus *Microtus* have a larger hippocampus than females, probably because of their larger home range (28). Polygamous male voles travel widely in search of females and show superior spatial ability on a number of laboratory tasks (29, 30). Monogamous voles show no sex difference in home range size, spatial ability, or size of the hippocampus (28). Furthermore, hippocampal size among species of kangaroo rats (*Dipodomys*) is correlated with food-storing behavior and sex differences in home range size (31).

The present study compared the size of the hippocampal complex in male and female cowbirds. It was predicted that the hippocampal complex would be larger in females as a consequence of selection for greater spatial ability in females. Male and female red-winged blackbirds (*Agelaius phoeniceus*), and common grackles (*Quiscalus quiscula*) provided comparative data for nonparasitic members of the passerine subfamily Icterinae to which cowbirds belong. All three species are closely related and are members of the same icterine tribe, the Agelaiini. Red-winged blackbirds defend

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Abbreviation: HP-APH, hippocampus and area parahippocampalis.
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small nesting territories, common grackles nest in loose colonial aggregations, and both species exhibit biparental care. In neither red-winged blackbirds nor common grackles did we expect a sex difference in the size of the hippocampus.

METHODS

Subjects and Histology. Adult brown-headed cowbirds [six females, 35.5 g (mean body weight); six males, 43.9 g], red-winged blackbirds (nine females, 39.6 g; seven males, 55.8 g), and common grackles (two females, 77.5 g; two males, 107.3 g) were collected in April and May 1990 in Mississauga, Ontario (43°33'N 79°44'W) and at the Queen's University Biological Station, Elgin, Ontario (44°34'N 76°15'W). Cowbirds were captured by walk-in trap (32), red-winged blackbirds and grackles by walk-in trap and mist net, and held in captivity overnight. Sex was determined by plumage and confirmed by examination of the gonads following perfusion, described below. Birds were carefully transported to the laboratory in individual holding compartments, then anesthetized with sodium pentobarbital (6 $\mu\text{g/g}$) and perfused with 50 ml of buffered 0.85% saline in 0.1 M sodium phosphate buffer (pH 7.4) followed by 150 ml of 4% paraformaldehyde in the same buffer. Brains were stored overnight in fixative at 4°C and then transferred to buffered 25% sucrose for 12–16 hr for cryoprotection. Brains were then frozen at –40°C in isopentane. Frozen sections were cut at 40 μm on a sliding microtome and placed in cold buffer. Alternate sections were mounted on glass slides for Nissl staining with cresyl violet. The remaining sections were placed in acetylcholinesterase incubation medium for 12–16 hr, rinsed, reacted with 1% ammonium sulfide, rinsed well, mounted on glass slides, dehydrated through graded ethanol solutions to xylene, and coverslipped with Permount.

Morphometry. The area of the hippocampal complex (Fig. 1) was digitized at $\times 20$ magnification for every section in which HP-APH occurred, using a Leitz Dialux microscope, a Numonics digitizing tablet connected to a microcomputer, and Jandel JAVA software. The area of the telencephalon, excluding HP-APH, was also digitized for every section in which HP-APH occurred. Nissl sections and alternate acetylcholinesterase sections were examined under higher magnification to determine hippocampal and telencephalic boundaries. Staining for acetylcholinesterase provides a histochemical marker for the rostral and lateral boundaries of HP-APH, determined histologically in previous studies (25, 26). This boundary corresponds approximately to the substance P-containing neuropil boundary identified in the pigeon (22) and to a change in size distribution of neurons described in tits (26). The medial edge of this boundary was taken as the lateral limit of the hippocampal complex (Fig. 1 *Lower*). Area measurements on each section were combined by using the formula for a truncated cone to obtain volume estimates for the hippocampal complex and for the region of telencephalon in which the hippocampal complex occurred. All digitizing was performed blind with respect to species and sex by labeling slides with a numerical code only. The digitizing system was calibrated before each use with the grating on a Neubauer counting chamber. The number of sections digitized for each brain ranged from 21 to 48 (mean = 35.7).

RESULTS

The hippocampal complex and surrounding dorsomedial forebrain of a female brown-headed cowbird and a male red-winged blackbird are shown in Fig. 1. The size relations between the hippocampal complex and the telencephalon are shown in Fig. 2. Analysis of covariance was used to examine the statistical relation between hippocampal volume, telencephalic volume, body weight, species, and sex. This anal-

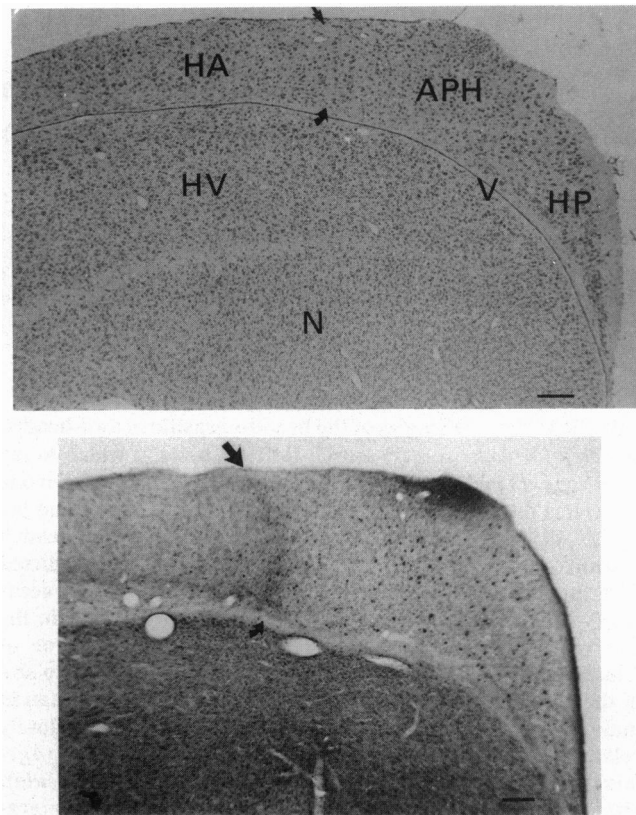


FIG. 1. Photomicrographs of the dorsomedial forebrain showing the hippocampal complex and telencephalic regions of a female brown-headed cowbird in Nissl-stained section (*Upper*) and a male red-winged blackbird in acetylcholinesterase-stained section (*Lower*). Arrows show the lateral boundary of HP-APH. The medial edge of the acetylcholinesterase-containing band was taken as the lateral limit of HP-APH. APH, area parahippocampalis; HA, hyperstriatum accessorium; HP, hippocampus; HV, hyperstriatum ventrale; N, neostriatum; V, ventricle. (Bar = 150 μm .)

ysis included only cowbird and red-winged blackbird data, because the available data on two male and two female common grackles were too few for statistical analysis. HP-APH volume was treated as the dependent variable, telencephalic volume and body weight as covariates, and species and sex as categorical independent variables. The weighted-cell-size method was used to adjust for unequal sample sizes. Preliminary analysis showed that the telencephalon covariate, but not the body weight covariate, accounted for a significant proportion of variation in hippocampal volume. Linearity of regressions and homogeneity of variance were confirmed with scatter plots of residuals of regressions against predicted values from these regressions (33). Tests for heterogeneity of the slopes of regressions showed that there was a significant interaction between the covariate telencephalon volume and species [$F(1,20) = 14.40$, $P < 0.01$]. This interaction indicates that the relation between telencephalon size and hippocampal size differed between the two species, and this can be seen in Fig. 2. Separate analyses of covariance were therefore performed on cowbirds and red-winged blackbirds. These tests showed a significant effect of sex and of the covariate telencephalon volume on HP-APH volume for cowbirds, and no significant effect of sex or the covariate for red-winged blackbirds (Table 1). That is, HP-APH volume depends on both sex and telencephalon size in cowbirds but on neither sex nor telencephalon size in red-winged blackbirds. There is no interaction between sex and telencephalon volume in cowbirds, indicating that changes in telencephalon volume have similar effects on HP-APH volume in both

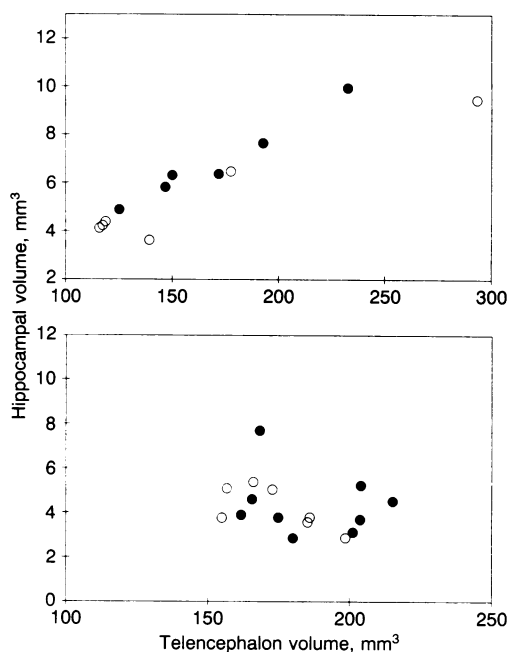


FIG. 2. Volume of the hippocampal complex plotted against telencephalon volume for cowbirds (Upper) and red-winged blackbirds (Lower). See text for details. ●, Females; ○, males.

sexes, but that mean HP-APH volume is greater in females. Mean values for size of the hippocampal complex and telencephalon are shown in Fig. 3. It can be seen that cowbirds possess a greater hippocampal volume than either red-winged blackbirds or grackles, despite being no greater in body size or telencephalon size.

DISCUSSION

These results show that the hippocampal complex is larger in females than in males of the brood-parasitic brown-headed cowbird and that the sexes do not differ in a nonparasitic icterine, the red-winged blackbird. For a smaller sample size of common grackles, there is likewise no indication of a sex difference.

It is notable that the greater hippocampal size occurs in females. Greater hippocampal size in males than in females has been described in voles (28), rats (34), and magpies (35), and reported sex differences in spatial ability tend to favor males in animals and humans (29, 30, 36–40). The occurrence of greater hippocampal size in female cowbirds suggests that it is the use of space, not sex *per se*, that influences relative size of the hippocampus. The results of this study support the conclusion that natural selection for spatial abilities can produce an increase in the relative size of the hippocampus and that selection acting on one sex can produce the further effect of a sex difference in the size of a brain region with

Table 1. Analysis of covariance of hippocampal volume

Source	Sum of squares	df	Mean square	F
Cowbirds				
Sex	3.769	1	3.769	9.179*
Telencephalon covariate	35.451	1	35.451	86.334**
Error	3.285	8	0.411	
Red-winged blackbirds				
Sex	0.654	1	0.654	0.434
Telencephalon covariate	2.504	1	2.504	1.664
Error	9.563	13	1.505	

*, $P < 0.016$; **, $P < 0.001$.

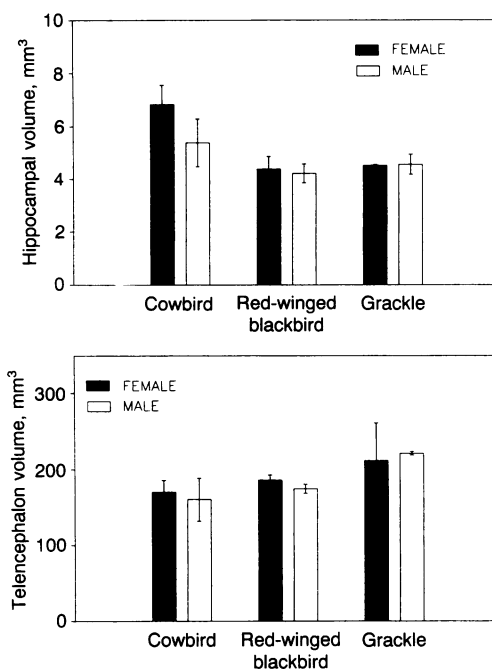


FIG. 3. Mean volumes of the hippocampal complex (Upper) and of the telencephalon (Lower) for male and female cowbirds, red-winged blackbirds, and common grackles.

cognitive function. Although we stress the effects of natural selection in producing the sex difference observed in cowbirds, any such difference must also be the result of a developmental process, and a variety of developmental influences, including the experience of search for host nests, may affect the relative size of the hippocampus in cowbirds.

Size of a neural structure is an admittedly gross measure, with a multitude of possible relations to function and organization. Size differences may be the outcome of differences in cell size (41), cell number (26, 42), synaptic organization (43–45), internal connectivity (46, 47), projections to other brain regions (48), and other variables. The relative size of neural structures can, nevertheless, provide important information on plasticity (49, 50), development (51–54), phylogeny (55, 56), and evolution (57–61).

Uyehara and Nairns[†] have reported somewhat different results for a western subspecies of the brown-headed cowbird *M. ater obscurus*: a linear correlation between hippocampal and telencephalic volumes, as found in the present study, but no sex difference in relative hippocampal size. This may indicate a difference between subspecies of *M. ater* or differences in procedure between the two studies.

An unexpected result in the present study is that hippocampal volume varies with telencephalic volume in cowbirds but not in red-winged blackbirds. Although previous studies have found correlations between hippocampal and telencephalic volumes at the subfamily and family level (25, 26), relations among taxonomic groups are not necessarily a good indication of relations to be found within taxonomic groups (57). Absence of any relation between hippocampal and telencephalic volumes has also been reported for a species of corvid (35). Magpies (*Pica pica*) store food and have a greater hippocampal volume than jackdaws (*Corvus monedula*), which rarely store food. Hippocampal and telencephalic volume are correlated in magpies but not in jackdaws. A possible explanation is that selection for spatial abilities not

[†]Uyehara, J. C. & Nairns, P. M. Proceedings of the Third International Congress of Neuroethology, August 9–14, 1992, Montreal, Quebec, Canada, abstr. 146.

only produces an increase in the size of the hippocampus but also leads to greater interdependence between the hippocampus and the telencephalon, for the processing of spatial information or the execution of spatial behavior (35). An increase in the relative size of the hippocampal complex would thus be accompanied by an increase in the size of the telencephalon, as found in magpies and cowbirds but not jacksnaws and red-winged blackbirds. Intense selection on one sex would be necessary to produce the further outcome of a sex difference, as observed in brown-headed cowbirds (62).

Our prediction of greater hippocampal size in females was based on field observations of search for host nests by female cowbirds. How information about the location of host nests is organized in females and other possible differences in cognitive organization between female and male cowbirds were not addressed in the present study. It has been shown (38) that male and female rats differ not only in their performance on the radial arm maze (with males exhibiting more rapid acquisition) but also in the kind of information they use to orient in the maze. Whether such differences exist between the sexes in cowbirds remains to be determined.

Age and nutritional status are potential confounding variables that could produce an apparent sex difference in cowbirds where none existed. All birds were adults, as determined by plumage and wing chord measurements (63). Cowbirds captured by the method used in the present study tend to be lighter in weight than those captured by mist net, but this effect occurs in both sexes (64). Males, but not females, can be further categorized by plumage into second-year and after-second-year birds, and no age bias occurs in males with the trapping method used in the present study (64). In any case, statistical control for telencephalic size in the present study eliminates the possibility that overall differences in body or brain size are responsible for the sex difference observed in hippocampal volume.

The occurrence of brood parasitism is not the only difference between brood-parasitic cowbirds and nonparasitic red-winged blackbirds. There are other behavioral and ecological differences that could potentially be responsible for the observed sex difference. Cowbirds, for example, provide no parental care. If foraging to feed nestlings makes additional demands on memory, however, then a species difference in hippocampal size between cowbirds and red-winged blackbirds would be expected to favor red-winged blackbirds, and the only indication of such a species difference favors cowbirds (Fig. 3). Furthermore, there is no reason to expect a sex difference to result from the absence of parental care in cowbirds. Another possible confounding variable is migratory behavior. None of the species examined are long-distance migrants. All three stay mainly within North America in winter, with some movement by red-winged blackbirds into Central America, but in general, migratory and local movements differ little among the three species (65, 66). There is no reason to expect a sex difference to result from patterns of migration, because the two sexes winter together in flocks in all three species. Moreover, previous work has shown no systematic relation between hippocampal size and migratory behavior in passerines (25, 67). In homing pigeons, hippocampal lesions do not impair homeward orientation at release sites in experienced birds but do disrupt orientation when birds are within sight of their home loft (13). In a similar fashion, long-distance orientation by migrating birds may occur independently of hippocampal function.

All three species sometimes feed away from their area of breeding activity. Cowbirds travel to short-grass fields, agricultural areas, and livestock yards to feed, though host nests are usually found in forest or woodland. The small nest territories of red-winged blackbirds provide little food, and grackles normally leave the area of the colony to feed. This

aspect of foraging is shared by the sexes, however, and should not lead to a sex difference. Diet in all three species is similar, consisting largely of cereal grains, seeds, and insects over most of their range (68, 69), and provides little reason to expect a sex difference.

The final indication that search for host nests is likely to be the selective pressure leading to the evolution of greater hippocampal volume in female cowbirds is that previously reported sex differences in hippocampal size favor males (28, 34, 35), and as noted earlier, sex differences in spatial ability tend to favor males in animals and humans (29, 30, 36–40). The occurrence of a larger hippocampal volume in females in the case of cowbirds suggests that specialization in this structure does not depend on sex, but on behavioral and ecological factors that influence the use of space and reliance on the cognitive functions of the hippocampus.

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