

## The Hippocampal Complex of Food-Storing Birds

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**Key Words.** Hippocampus · Hippocampal complex · Memory · Food storing · Hoarding · Caching · Birds · Passerines

**Abstract.** Three families of North American passerines – chickadees, nuthatches and jays – store food. Previous research has shown that memory for the spatial locations of caches is the principal mechanism of cache recovery. It has also been previously shown that the hippocampal complex (hippocampus and area parahippocampalis) plays an important role in memory for cache sites. The present study determined the volume of the hippocampal complex and the telencephalon in 3 food-storing families and in 10 non-food-storing families and subfamilies of passerines. The hippocampal complex is larger in food-storing birds than in non-food-storing birds. This difference is greater than expected from allometric relations among the hippocampal complex, telencephalon and body weight. Food-storing families are not more closely related to each other than they are to non-food-storing families and subfamilies, and the greater size of the hippocampal complex in food-storing birds is therefore the result of evolutionary convergence. Natural selection has led to a larger hippocampal complex in birds that rely on memory to recover spatially dispersed food caches.

### Introduction

Three families of North American passerines – chickadees (Paridae), nuthatches (Sittidae), and jays and crows (Corvidae) – store food in widely dispersed cache sites. An individual bird can establish several hundred cache sites in a single day and several thousand in the course of a year. Each cache is in a novel spatial location, and cache sites are not re-used in the wild. Cached food may be retrieved after a few days or after many months, depending on the species. Food storing of this kind occurs in no other North American passerines. Shrikes (Laniidae) store food in a different way, impaling small numbers of prey at a few sites to assist in handling the prey rather than to establish a reserve of stored food [1, 2].

A number of studies have examined how food-storing birds recover their caches of food and have shown that memory for the spatial locations of caches is the

principal mechanism. Chickadees and their European counterparts, the tits, readily recall the locations of caches [3–8], as do a number of species of corvids [9–14]. These findings are reviewed in Sherry [15] and Balda et al. [16]. It can be shown that cache recovery accuracy is consistently greater than expected by chance and greater than expected from preferences to use particular kinds of cache sites. There is no evidence that birds mark their cache sites or use mnemonics based on the sequence of storing to relocate caches. Although magpies (*Pica pica*) are able to smell buried food [17], cache recovery remains highly accurate in other species when they are prevented from smelling stored food.

In mammals, the hippocampus plays an important role in memory and information processing. Two dominant theories of the function of the hippocampus deal with the processing of spatial information [18, 19] and working memory [20], though a variety of

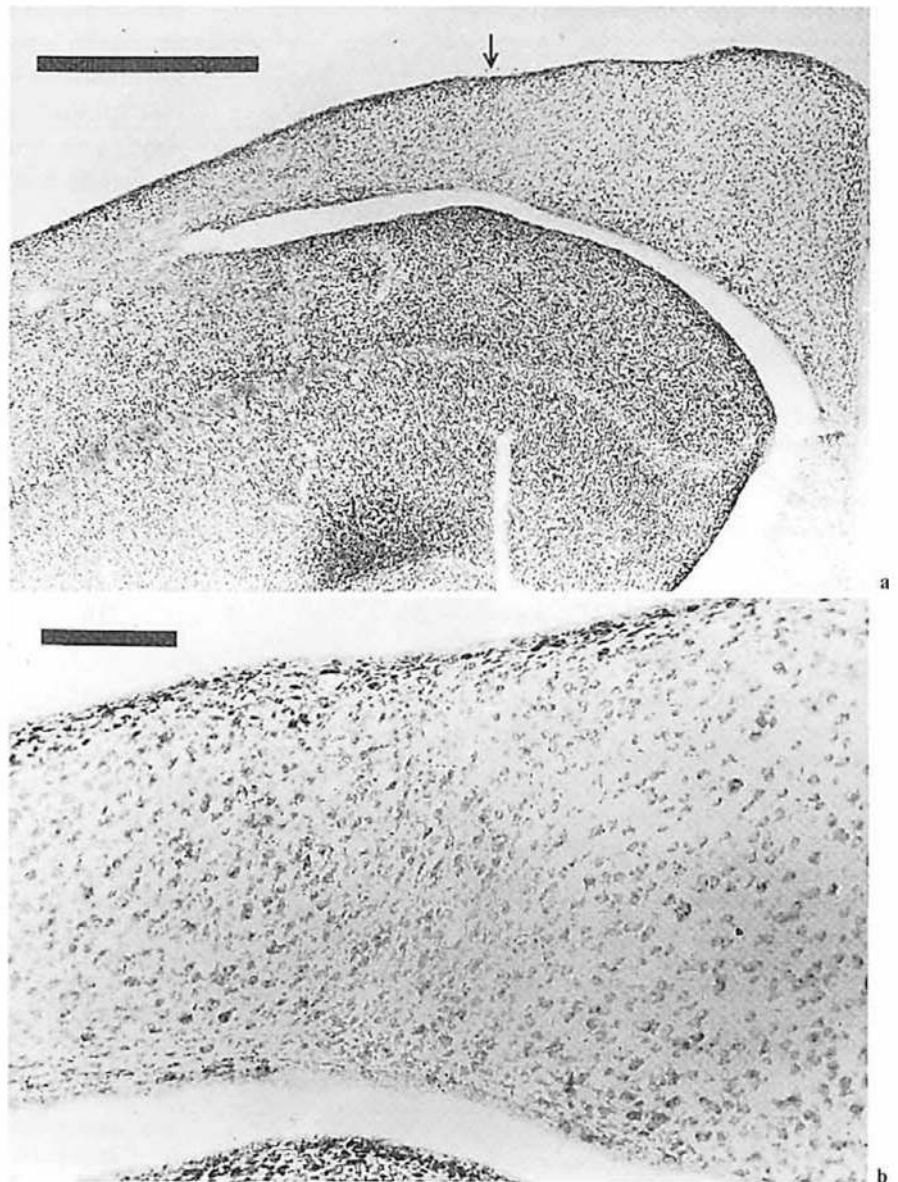


Fig. 1. Boundary used to define the lateral extent of the hippocampal complex. a Left Hp-APH of black-capped chickadee. Section at about the level of Section b in figure 2. Arrow indicates lateral margin. Scale bar = 1 mm. b Enlargement of region indicated by arrow in a. Scale bar = 100  $\mu$ m.

other theoretical accounts have also been offered [e.g. 21]. It has been demonstrated that the hippocampal complex of birds (hippocampus and area parahippocampalis; Hp-APH) is homologous to the hippocampal formation of mammals, on the basis of ontogenetic [22] and neuro-anatomical similarities [23–27]. The detailed relation between structures within the hippocampal formation of mammals and those within the Hp-APH of birds, however, are not yet clear.

Lesions of the hippocampal complex disrupt cache recovery in black-capped chickadees (*Parus atricapillus*) [28]. Damage to Hp-APH produces deficits in

memory for spatial locations and deficits in working memory. Lesions of the hyperstriatum that include the hippocampus also disrupt cache recovery in a corvid food-storer, the Eurasian nutcracker (*Nucifraga caryocatactes*) [29]. In homing pigeons, lesions of Hp-APH impair orientation and recognition of the home loft [30, 31]. The hippocampal complex of birds thus shares some functions with the homologous structure in mammalian brains.

Morphometric analysis of brains from a variety of passerines had previously indicated that there exist differences in the size of the Hp-APH between food-storing and non-food-storing species [32]. The present

Table 1. Species and measured variables

		n	Body weight g	Hp-APH volume mm <sup>3</sup>	Telencephalon volume mm <sup>3</sup>
Corvidae <sup>1</sup>					
<i>Cyanocitta cristata</i>	blue jay	1	113.32	45.68	996.91
Paridae <sup>1</sup>					
<i>Parus atricapillus</i>	black-capped chickadee	3	12.4	9.58	278.68
Sittidae <sup>1</sup>					
<i>Sitta canadensis</i>	red-breasted nuthatch	1	11.5	7.52	180.01
Troglodytidae					
<i>Troglodytes aedon</i>	house wren	2	10.2	3.84	263.71
Sylviinae					
<i>Regulus calendula</i>	ruby-crowned kinglet	1	7.3	1.51	120.55
Turdinae					
<i>Turdus migratorius</i>	American robin	1	79.0	10.42	681.61
Mimidae					
<i>Dumetella carolinensis</i>	gray catbird	1	40.7	6.86	506.82
Sturnidae					
<i>Sturnus vulgaris</i>	European starling	1	96.5	17.80	950.83
Parulinae					
<i>Dendroica magnolia</i>	magnolia warbler	1	8.2	1.66	124.41
<i>Dendroica coronata</i>	yellow-rumped warbler	1	12.4	2.41	158.82
<i>Dendroica striata</i>	blackpoll warbler	1	11.9	2.60	175.74
<i>Setophaga ruticilla</i>	American redstart	1	7.2	0.99	89.16
<i>Seiurus aurocapillus</i>	ovenbird	1	16.9	3.67	279.02
<i>Seiurus noveboracensis</i>	northern waterthrush	1	19.6	1.51	144.06
<i>Geothlypis trichas</i>	common yellowthroat	1	9.4	2.55	215.43
		mean	12.2	2.20	169.52
Cardinalinae					
<i>Cardinalis cardinalis</i>	northern cardinal	1	44.0	16.48	695.46
<i>Pheucticus ludovicianus</i>	rose-breasted grosbeak	1	43.2	3.99	374.11
		mean	43.6	10.24	534.79
Emberizinae					
<i>Melospiza melodia</i>	song sparrow	1	20.6	3.80	364.69
<i>Melospiza georgiana</i>	swamp sparrow	1	18.1	3.96	311.10
<i>Zonotrichia albicollis</i>	white-throated sparrow	1	24.2	5.40	390.11
<i>Junco hyemalis</i>	dark-eyed junco	1	19.5	6.66	312.41
		mean	20.6	4.96	344.58
Fringillidae					
<i>Carduelis tristis</i>	American goldfinch	1	12.5	3.85	181.07
Passeridae					
<i>Passer domesticus</i>	house sparrow	3	25.32	6.99	384.22

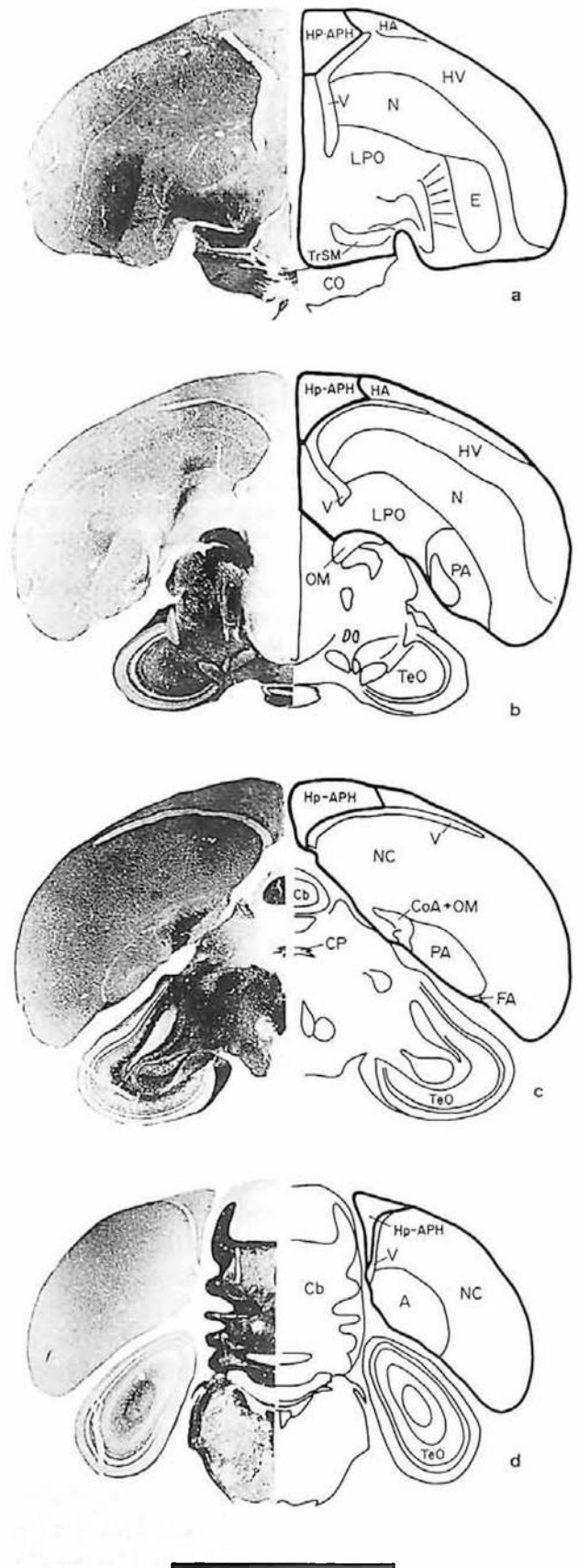
<sup>1</sup> Food-storing families.

paper describes a comparative analysis of the size of the hippocampal complex in 23 species of North American passerines drawn from the 3 food-storing families and from 10 non-food-storing families and subfamilies. Results on food-storing and non-food-storing European passerines are described elsewhere [33].

In the present study, the volume of the hippocampal complex and telencephalon were determined from serial sections. The relation of Hp-APH volume to body weight, telencephalon volume and caching behaviour was determined by multiple regression. Additional analyses were performed to examine the influence on Hp-APH volume of a number of other variables that might be expected to affect brain evolution: migratory behaviour, diet and social organization.

### Materials and Methods

Twenty-eight birds from 23 species in 13 passerine families and subfamilies were collected (table 1). Birds were collected under Canadian Wildlife Service permit at the Erindale campus of the University of Toronto and at the Long Point Bird Observatory on the north shore of Lake Erie. All procedures followed guidelines established by the Canadian Council on Animal Care. Body weight was recorded, the bird was anaesthetized with sodium pentobarbital (Nembutal, 7 µg/g) and perfused with 0.9% physiological saline followed with 10% formalin. The brain was removed and placed in 10% sucrose formalin for 24 h, followed by storage in 30% sucrose formalin until sectioning. Frozen sections were made in the coronal plane at either 25- or 40-µm intervals and stained using Auleta stain for cells and fibres. Brains were mounted for sectioning to maintain, as far as possible, comparable section planes in different species, although because the data of interest were volume estimates perfect alignment was not necessary. Every 6th section in the case of 25-µm sections and every 4th section in the case of 40-µm sections was enlarged 15× using a Bausch & Lomb slide enlarger, and outlines of the Hp-APH, telencephalon and other structures were traced. Sections were viewed by light microscope (Nikon Op-



**Fig. 2.** Hippocampal complex and telencephalon of black-capped chickadee. Regions included in hippocampal complex and telencephalon are indicated with heavy outline. Sections a-d are ordered rostrocaudally. Scale bar = 5 mm. A = Archistriatum; Cb = cerebellum; CO = chiasm opticum; CoA = commissura anterior; CP = commissura posterior; DSV = decussatio supraoptica ventrale; E = ectostriatum; FA = tractus fronto-archistriatalis; HA = hyperstriatum accessorium; HV = hyperstriatum ventrale; LPO = lobus parolfactorius; N = neostriatum; NC = neostriatum caudale; OM = tractus occipito-mesencephalicus; PA = paleostriatum augmentatum; Rt = nucleus rotundus; TeO = tectum opticum; TrSM = tractus septomesencephalicus; V = ventricle. [Nomenclature follows ref. 50 and 51.]

tiphot) at 10× to confirm and to add anatomical details. Tracings were digitized using a Numonics 2210 tablet, microcomputer and Jandel software. Accuracy of the tracing tablet was  $\pm 0.025$  mm.

The dorsal, ventral and medial extent of the hippocampal complex in coronal sections correspond to the surface of the brain, the ventricle and the mid-line, respectively. The lateral extent of Hp-APH was taken as the boundary at which there is a marked increase in cell density, compared to Hp-APH, and a change in cell type from large neurons characteristic of Hp-APH to a mixture of both large and small neurons (fig. 1). Lateral to this boundary, cells show an oblique or curving alignment, while on the medial or Hp-APH side of the boundary cells are distributed in no apparent alignment. These criteria can be used throughout the rostral to caudal occurrence of the Hp-APH. Figure 2 shows the regions included in the hippocampal complex and telencephalon at various points in the rostrocaudal extent of Hp-APH. The Hp-APH of passerines, in contrast to that of pigeons, retains a dorsomedial position with respect to the telencephalon even at its caudal limit, and in sections remains attached to the larger body of the telencephalon, as shown in figure 2d. Staining, sectioning, enlarging and tracing were performed blind with regard to food storing, migration and other behaviour of each species.

The volume contained between successive sections was calculated using the formula for volume of a truncated cone:

$$V = \frac{1}{3} (h_1 + \sqrt{h_1} \cdot \sqrt{h_2} + h_2),$$

in which  $h_1$  and  $h_2$  are the areas from successive sections, and  $l$  is the interval between successive sections, in this case 150  $\mu\text{m}$  for 25- $\mu\text{m}$  sections and 160  $\mu\text{m}$  for 40- $\mu\text{m}$  sections.

The relation between Hp-APH volume, body weight, telencephalon volume and behaviour was determined by multiple regression [34].

## Results

Figure 3 shows sections through the Hp-APH for several food-storing and non-food-storing species. Hippocampal complex volumes, telencephalon volumes and body weights for each species are presented in table 1. Logarithmic transformations of these data were used in all subsequent analyses to normalize the data for statistical treatment and because the relation among morphological variables is expected to be exponential [35]. With comparative data of this kind it is also necessary to control for non-independence among taxonomic groups [35–37]. For example, because of their evolutionary affinity the many species of warblers (table 1) should probably not be regarded as providing independent data on the relation of Hp-APH to brain and body weight. Instead, they probably provide many replicate instances of the relation among these variables as it exists in warblers. We followed the method of Clutton-Brock and Harvey [35,

36] to determine at what taxonomic level observations could be regarded as independent. Analysis of variance for an unbalanced design with genus nested within subfamily and subfamily nested within family showed a significant effect for subfamily [log Hp-APH volume:  $F(3,6) = 6.09$ ,  $p < 0.05$ ; log telencephalon volume:  $F(3,6) = 11.00$ ,  $p < 0.01$ ; log body weight:  $F(3,6) = 16.08$ ,  $p < 0.01$ ] and no significant effect for either genus or family. Subfamily was therefore chosen as the taxonomic level for all analyses, and mean values for subfamilies were calculated from all species in each subfamily. In cases where there is only a single subfamily represented in a family, that subfamily is given its family name in table 1. Taxonomy and nomenclature follow the American Ornithologists' Union (AOU) check-list [38].

Multiple regression was used to examine the relation between the variable log Hp-APH volume and the three variables log body weight, log telencephalon volume and food-storing behaviour [34]. When variables were entered in the regression in a stepwise fashion, telencephalon volume accounted for a substantial proportion of the variance in Hp-APH volume ( $r^2 = 0.755$ ) and was found to have a coefficient significantly greater than zero [ $F(1,11) = 33.81$ ,  $p < 0.01$ ]. This relation between the hippocampal complex and the telencephalon shows that, as expected, birds with larger brains have a larger hippocampal complex. Body weight accounted for no additional variance in Hp-APH volume beyond that accounted for by telencephalon volume and did not have a coefficient significantly different from zero. Food storing, in contrast, did account for additional variance in Hp-APH volume, raising the proportion of variance accounted for ( $r^2 = 0.968$ ) and was found to have a significantly non-zero coefficient [ $F(1,10) = 67.73$ ,  $p < 0.01$ ]. The regression of Hp-APH volume on telencephalon volume and food-storing behaviour minimized Mallow's  $C_p$  ( $C_p = 2.32$ ) compared to regressions on all possible subsets of variables and produced an overall regression significantly greater than zero [ $F(2,10) = 153.3$ ,  $p < 0.01$ ].

The relation of Hp-APH volume to body weight and telencephalon volume is illustrated in figure 4. It can be seen that for each food-storing family the hippocampal complex is larger than expected from the relation between hippocampal complex volume and telencephalon volume. The same is true for the relation between hippocampal complex volume and body weight. The relation between telencephalon volume

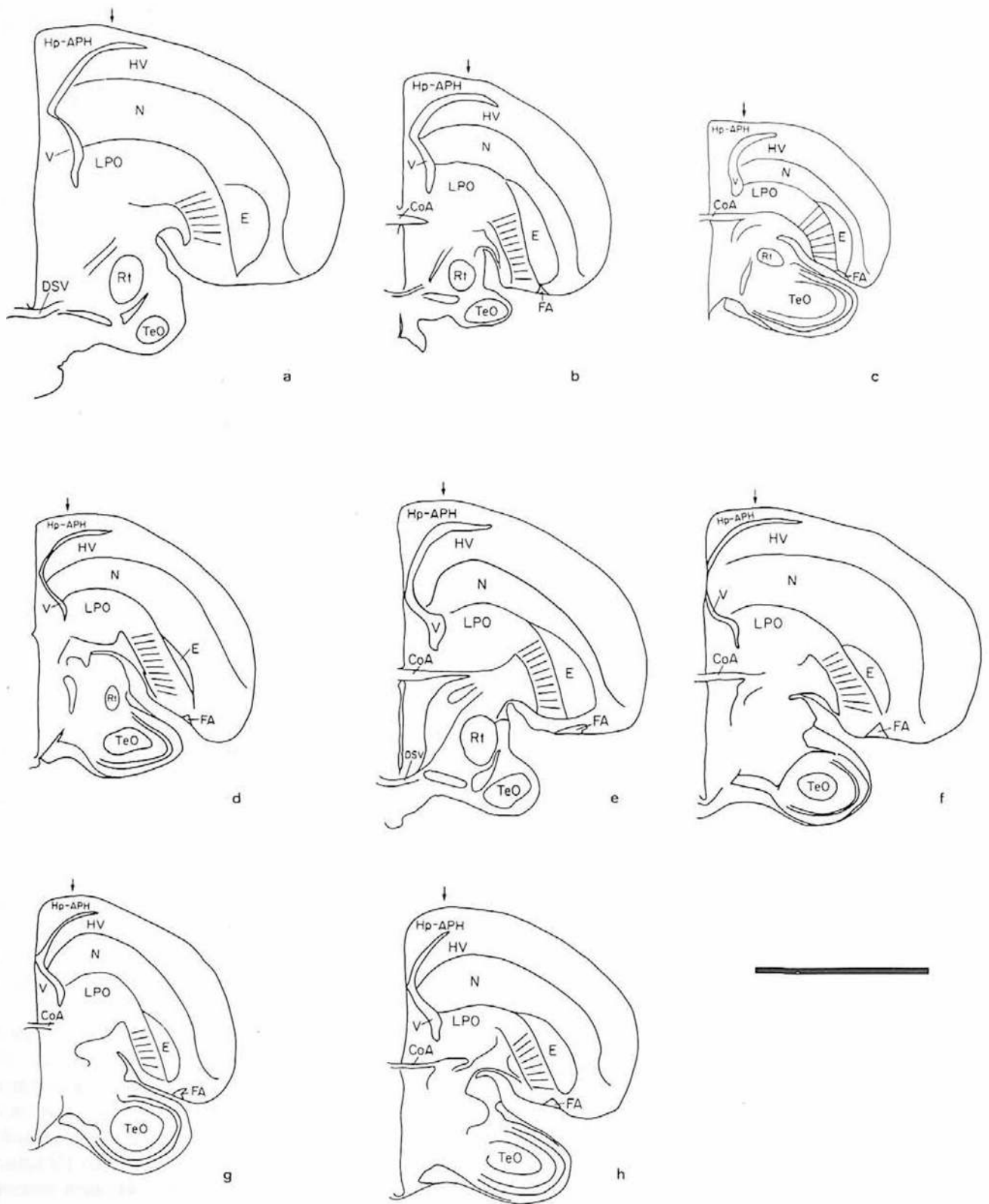
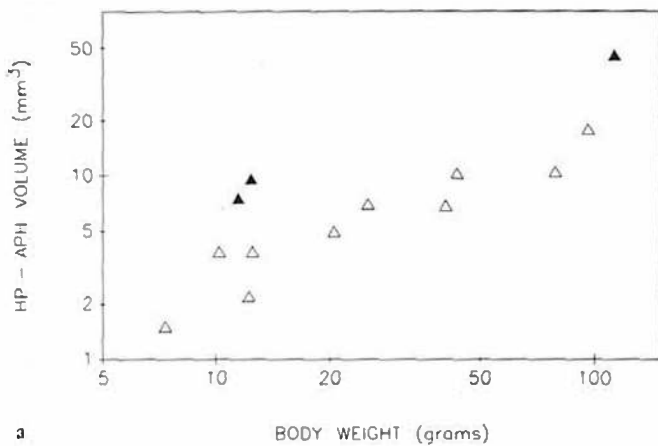
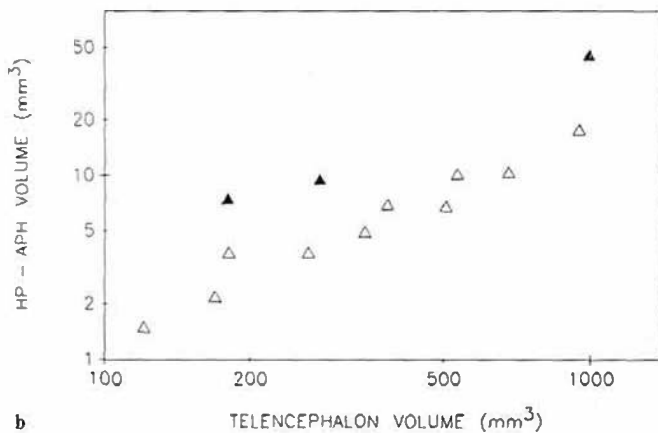


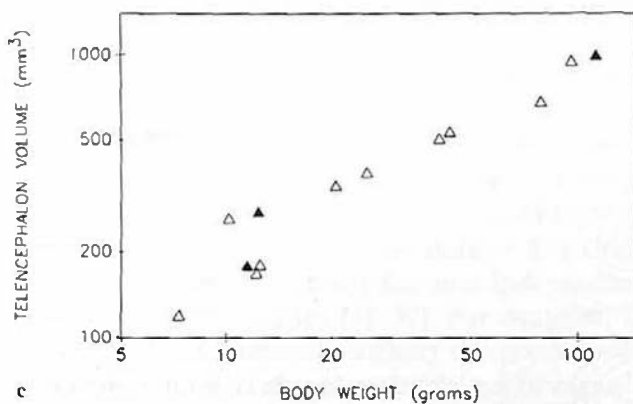
Fig. 3. Coronal sections through the hippocampal complex at the level of the anterior commissure for 3 food-storing species, blue jay (a), black-capped chickadee (b) and red-breasted nuthatch (c), and 5 non-food-storing species, house wren (d), Northern cardinal (e), rose-breasted grosbeak (f), dark-eyed junco (g) and house sparrow (h). Arrow indicates lateral margin of Hp-APH. Scale bar = 5 mm. Abbreviations as in figure 2.



a

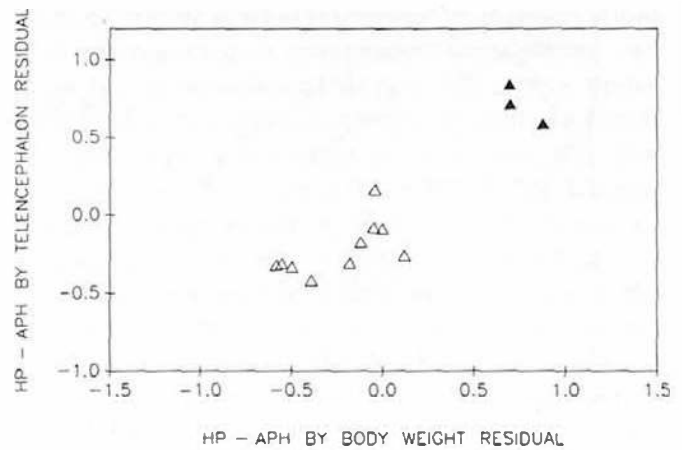


b



c

**Fig. 4.** Relations between Hp-APH volume and body weight (a), Hp-APH volume and telencephalon volume (b) and telencephalon volume and body weight (c).  $\blacktriangle$  = Food-storing subfamilies;  $\triangle$  = non-food-storing subfamilies. All variables are plotted on logarithmic axes.



**Fig. 5.** Residuals of the regression between Hp-APH volume and telencephalon volume plotted against residuals of the regression between Hp-APH volume and body weight.  $\blacktriangle$  = Food-storing subfamilies;  $\triangle$  = non-food-storing subfamilies.

and body weight is the same for food-storing birds as it is for other birds. The relation between Hp-APH volume, telencephalon volume and body weight can be seen more clearly in figure 5, which plots the residuals from regressions fitted to the data shown in figures 4a and b. These residuals show the difference between observed Hp-APH volume for a subfamily and that predicted from the regression calculated for all subfamilies. Residuals for non-food-storing families cluster near zero. Residuals for the 3 food-storing families are all positive, and are the largest residuals in the data set.

Multiple regression was repeated, replacing food-storing behaviour with either migratory behaviour (migrant - non-migrant), diet (omnivore - specialist) or social organization (solitary - social), but none of these variables accounted for significant variation in Hp-APH volume in addition to that accounted for by telencephalon volume.

A subset of migratory species, for which estimates of the distance traveled during migration were available [39], was analyzed further (table 2). Telencephalon volume accounted for substantial variation in hippocampal complex volume ( $r^2 = 0.911$ ) and had a coefficient significantly greater than zero [ $F(1,6) = 62.05$ ,  $p < 0.01$ ], but no additional variation was accounted for by either body weight or the distance traveled during migration. The relations between Hp-APH volume and migratory distance in these birds are shown in figure 6.

Table 2. Migrants and migration distance

		Migration distance km
Sylviinae		
<i>Regulus calendula</i>	ruby-crowned kinglet	825
Parulinae		
<i>Dendroica magnolia</i>	magnolia warbler	3,199
<i>Dendroica coronata</i>	yellow-rumped warbler	1,211
<i>Dendroica striata</i>	blackpoll warbler	4,235
<i>Setophaga ruticilla</i>	American redstart	3,767
<i>Seiurus aurocapillus</i>	ovenbird	3,784
<i>Seiurus noveboracensis</i>	northern waterthrush	5,768
<i>Geothlypis trichas</i>	common yellowthroat	1,782

Distances are means from figures 10 and 11 of Keast [39], which give approximate distance between centres of breeding and wintering ranges.

A final possibility is that, despite the statistical independence among subfamilies, food-storing birds differ from other passerines for reasons that are purely phylogenetic. That is, birds in the families Paridae, Sittidae and Corvidae may be similar in Hp-APH size, and different from other passerines, because the 3 families are closely related. The fact that they store food too may be just a further similarity. Paridae, Sittidae and Corvidae, however, are not more closely related to each other than they are to other passerine families and subfamilies. The AOU check-list [38], the arbiter of North American avian taxonomy, places all of the families analyzed in the passerine suborder Passeres. Families within Passeres are not grouped into higher-order categories, such as superfamilies. Sibley and Ahlquist [40] have presented a phylogeny and classification of passerines based on DNA hybridization. Their results differ somewhat from the AOU [38] classification. They do not, however, indicate that Paridae, Sittidae and Corvidae are more closely related to each other than they are to other passerines. Paridae and Sittidae are placed in the parvorder Muscicapae and Corvidae in the parvorder Corvi. Within Muscicapae the family regarded as closest to the Sittidae is the Troglodytidae, and members of the Paridae are regarded as more closely related to the kinglets [family Regulidae in ref. 40; subfamily Sylviinae in ref. 38] than to members of the Sittidae.

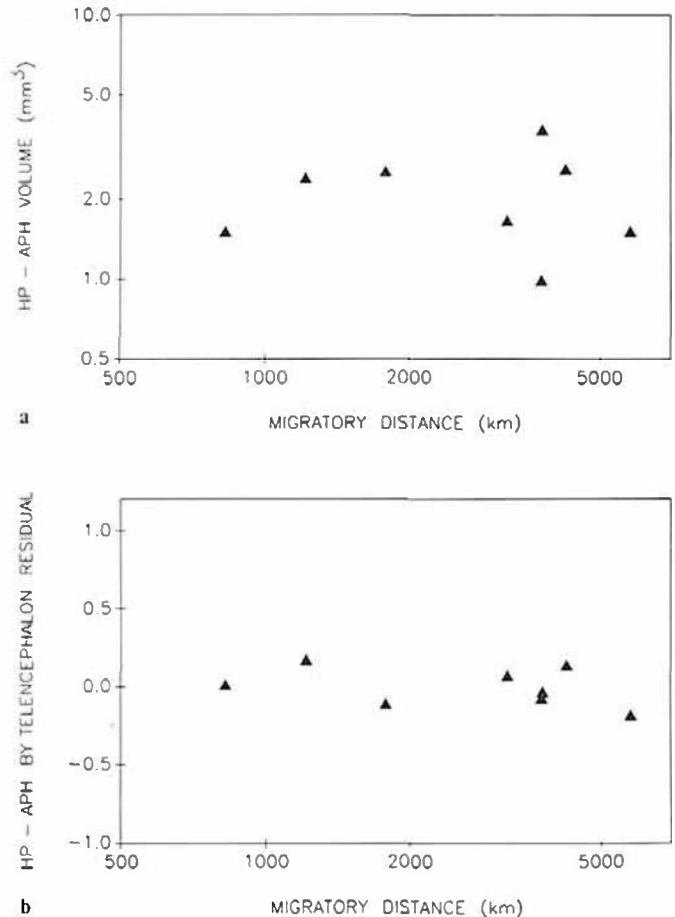


Fig. 6. a Relation between Hp-APH volume and migratory distance for the 8 migratory species shown in table 2. Migratory distances are from Keast [39]. Both variables are plotted on logarithmic axes. b Residuals of the regression between Hp-APH volume and telencephalon volume for 8 migratory species plotted against migratory distance. Distance axis is logarithmic.

## Discussion

The results show that food-storing passerines have a larger hippocampal complex than do non-food-storing passerines. This effect is in addition to the expected size relations between the hippocampal complex and the brain and between the hippocampal complex and body weight. The 3 food-storing families with a large hippocampal complex are not closely related, indicating that the changes in hippocampal size are the result of evolutionary convergence. The details of Hp-APH structure were not examined in the present study. Thus, adaptive modification of the hippocampal complex may differ in the 3 food-storing families. There may be more than one way in which



Hp-APH can be modified to achieve long-duration memory for large numbers of spatial locations.

There are many cases in which differences among species of birds in the structure of the brain can be clearly related to the effects of natural selection on brain and behaviour. Among scolopacid shorebirds, reliance on a sensitive probing bill for feeding has resulted in a dramatic increase in the size of the fore-brain region receiving trigeminal input [41]. There is considerable variation in the size of the olfactory bulbs in birds, and these can be related to reliance on olfaction [42]. Differences in size of the song repertoire are correlated with differences in size of the song control nuclei [43, 44].

With regard to the hippocampus, Rehkämper et al. [45] have shown that the structure is larger in homing pigeons than in two other non-homing breeds of pigeon, fantails and strassers. The larger size of the hippocampus, and larger size of some other telencephalic structures including the olfactory bulbs, may be related to homing ability. The role played by the hippocampus in homing, however, is not a simple one. Bingman et al. [30, 31] have shown that homing pigeons with hippocampal lesions are correctly home-ward oriented at the release site but are slower to reach home than controls and encounter difficulties when within sight of the home loft. Nonetheless, the results of Rehkämper et al. [45] show that selection by man can produce differences in hippocampal size that correlate with orientation abilities. Artificial selection has also produced differences in the fine structure of the hippocampal formation in mammals. For example, strains of mice which show greater habituation to a novel environment have larger mossy fiber termination fields [46].

In mammals, the hippocampal formation increases in size from the insectivores to the prosimians and from the prosimians to the higher primates, after allowing for differences in body size [47], but this general trend is difficult to relate to specific selective pressures. Other neuro-anatomical structures in mammals, however, are clearly correlated with ecological and social variables. Indices of cerebral cortex size are correlated in prosimians with troop size, in New World monkeys with size of the troop home range and in Old World monkeys with size of the individual home range [48], suggesting that different selective pressures have influenced the evolution of the cortex in different primate taxa. Armstrong et al. [49] have shown that the anterior thalamic nuclei are relatively

larger in primates with single-male social groups than in primates with multi-male social groups.

The greater size of the hippocampus in food-storing birds provides a clear case in which natural selection has modified a brain region involved in a cognitive component of behaviour. The increased size of the hippocampus in 3 unrelated families of food-storing passerines indicates that natural selection favouring food storing has resulted in modification of the brain region that plays a central role in memory for cache sites. Although the discussion has stressed that the observed differences are the result of natural selection, this does not discount the possibility that individual experience in storing and retrieving food may play a role in the development of this size difference in the hippocampus.

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