

REPORT

The evolution of hippocampus volume and brain size in relation to food hoarding in birds

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Abstract

Food-hoarding birds frequently use spatial memory to relocate their caches, thus they may evolve a larger hippocampus in their brain than non-hoarder species. However, previous studies testing for such interspecific relationships provided conflicting results. In addition, food hoarding may be a cognitively complex task involving elaboration of a variety of brain regions, even outside of the hippocampus. Hence, specialization to food hoarding may also result in the enlargement of the overall brain. In a phylogenetic analysis of distantly related birds, we studied the interspecific association between food hoarding and the size of different brain regions, each reflecting different resolutions. After adjusting for allometric effects, the relative volume of the hippocampus and the relative size of the entire brain were each positively related to the degree of food-hoarding specialization, even after controlling for migration and brood parasitism. We also found some significant evidence for the relative volume of the telencephalon being associated with food hoarding, but this relationship was dependent on the approach we used. Hence, neural adaptation to food hoarding may favour the evolution of different brain structures.

Keywords

Behaviour, brain size, cognitive ecology, comparative analysis, evolution, food hoarding, hippocampus, telencephalon.

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INTRODUCTION

Several avian species, such as many Corvids (crows, jays, nutcrackers, etc.) and Parids (tits, titmice, chickadees, etc.), hide food for later consumption and recover their caches when supplies are less abundant (Vander Wall 1990). Typical food hoarders may store food items in hundreds or thousands of sites for periods of days or months. Such birds may undergo an adaptive neural specialization because remembering the locations of caches probably demands an extensive spatial memory capacity.

The hippocampal formation in the brain has been implicated in spatial learning in birds and mammals (review in Colombo & Broadbent 2000). This has generated the hypothesis that the adaptation to a specialized memory capacity in food-hoarding birds is accompanied by an evolutionary enlargement of the hippocampal region relative to the rest of the forebrain (Krebs *et al.* 1989, 1990; Sherry *et al.* 1989; Healy & Krebs 1992, 1996; Brodin & Lundborg 2003). However, tests of this hypothesis have produced conflicting results. Several studies reported that

hoarding species or families possess larger hippocampi than non-hoarding relatives, and that species classified as large-scale hoarders have larger hippocampi than less specialized hoarders (Krebs *et al.* 1989, 1990; Sherry *et al.* 1989; Healy & Krebs 1992, 1996; Hampton *et al.* 1995; Basil *et al.* 1996). On the other hand, a recent study using a larger dataset revealed no significant relationship between food hoarding and the volume of the hippocampus among species (Brodin & Lundborg 2003). Moreover, the relative hippocampal volumes in two non-storing *Picoides* woodpeckers were similar to a scatter hoarder *Melanerpes* species (Volman *et al.* 1997). Previous appraisals relied on comparisons of closely related species and were restricted to certain avian families, or compared different taxonomical groups at higher levels. Only few of these studies considered that the apparent interspecific relationship between traits may be confounded by the similarity because of common descent (e.g. Krebs *et al.* 1989; Healy & Krebs 1992; see also Sherry 1997). However, none of the earlier tests controlled accurately for the confounding effects of phylogeny by applying modern comparative

methods in combination with information on phylogenetic relationships across a wide range of species.

The complex neuronal control of a behaviour potentially involves closely and distantly connected neural substrates and their synaptic connections. Hence, the neural adaptation to a specialized behaviour may favour the evolution of several neural structures affecting the evolution of the entire brain (e.g. Gittleman 1994; Lefebvre *et al.* 1997; Madden 2001; Garamszegi *et al.* 2002; Reader & Laland 2002). Arising from the complexity of the behaviour (Vander Wall 1990), it is plausible that adaptation to food hoarding may not only require superior spatial memory, but also special sensory and motor skills. For example, experiments showed that the majority of food-hoarding birds rely on visual information from nearby landmarks, sometimes in combination with sun-compass information, to locate concealed caches, whereas some species can smell hidden food (review in Sherry & Duff 1996). In addition, food hoarding appears to require experience, learning and practice. Juvenile mountain chickadees *Poecile gambeli* increased the number of seeds stored as time progressed (Clayton 2001), whereas experience of storing and/or retrieving caches is required for marsh tits *Parus palustris* to develop the spatial preference as seen in adults (Clayton 1995). If specialization to food hoarding selects for the enlargement of different neural structures responsible for the learning, and the sensory and motor control of this behaviour, we hypothesize that it also selects for large brains. Although the relative size of the hippocampus may appear small, simultaneous neural specializations to food hoarding may occur in other regions of the brain with significant volumetric importance. Therefore, if food hoarding is a cognitively complex task involving elaboration of a variety of brain regions, then total brain volume may vary with the specialization of this behaviour.

Using 55 bird species belonging to different taxonomical groups, in a phylogenetic analysis, we tested the hypothesis that adaptive specialization to food hoarding leads to the enlargement of neural regions of different scales. We related the volume of the hippocampus relative to the volume of the telencephalon, the volume of the telencephalon relative to body size, and the size of the overall brain relative to body size to food hoarding among species. According to the hypotheses posited above, we predicted that food hoarding would be positively related to the size of these neural areas.

METHODS

We obtained from the literature information on the volume of the hippocampus and the telencephalon, and on the mass of the brain (see Table 1 for references). To calculate the relative volume of the telencephalon we controlled for body mass that was taken from the same sources. Estimates of the volumes of different neural substrates may vary to some

degree within species for biological reasons, but also for other reasons. For example, individuals of the same species may differ in the size of a neural area, but differences between measurements of different laboratories may also raise noise in the data (we note that such lab differences may raise type I errors in the data independent of the hypothesis at hand and not consistent bias). However, when we assessed the reliability of different neural measures by calculating the repeatability of these traits across studies, we found that the mean volumes are highly repeatable within species (Hippocampus: $F_{18,114} = 53.103$, $P < 0.001$, $R = 0.902$; Telencephalon: $F_{18,114} = 97.999$, $P < 0.001$, $R = 0.945$; Brain mass: $F_{30,92} = 126.42$, $P < 0.001$, $R = 0.977$). High repeatability of different brain volumes may indicate that their intraspecific variation for any reason may be small compared to the interspecific variation. Therefore, when multiple reports for these traits were available for a single species, we calculated their averages, which can be considered species-specific attributes in an interspecific context. Based on the high repeatability of traits, we also assumed that single measurements are highly representative for particular species.

Previous studies appear to use randomly the volume of telencephalon involving or excluding the volume of the hippocampus. However, consulting the original sources, we were unable to obtain the relevant information on the definition of telencephalon for all species. Therefore we used data on the telencephalon as reported in the original sources irrespective whether they involved or not the volume of the hippocampus. This approach may raise some noise in the data. However, as the size of the hippocampus is usually less than 5% of the entire telencephalon, the heterogeneity caused by differences in the definition of the volume of the telencephalon is of a minor importance that is independent of the hypothesis under test. Note that Brodin & Lundborg (2003) also disregarded this source of noise, and that telencephalic volume is highly repeatable.

We followed the general practice to characterize the extent of food hoarding by using a 3-point scale (see Brodin & Lundborg 2003). Species with no evidence of food hoarding were considered as non-hoarders (score of 1), whereas species that store small amounts of food for short time intervals were categorized as non-specialized hoarders (score of 2) and those that exhibit typical caching behaviour by storing thousands of items in the autumn for later recovery were treated as specialized hoarders (score of 3). We controlled for migratory habit and brood parasitism, because these behaviours have been suggested to require space in the hippocampus or in the brain (Krebs *et al.* 1989; Healy *et al.* 1991, 1996; Clayton *et al.* 1997; Winkler *et al.* 2004), thus potentially confounding the interspecific relationship between food-hoarding behaviour and the volume of the hippocampus. Migratory behaviour was scored on a 3-point

Table 1 The volume of the hippocampus, the volume of the telencephalon, brain mass, body mass, food hoarding, brood parasitism and migration in birds. References for hippocampus, telencephalon and body mass are also given

Species	Hippocampus (mm ³)	Telencephalon (mm ³)	Body mass (g)	Reference ^a	Brain mass (g)	Body mass (g)	Food hoarding ^b	Brood parasitism ^c	Migration ^d
<i>Agelaius phoeniceus</i>	4.3	180	47.7	1	1.76	67.2	1	0	2
<i>Apbelocoma coerulescens</i>	24.9	848.5	75.5	See Ref. in 2	2.95	76	2	0	1
<i>Apbelocoma ultramarina</i>	34.1	1166	114	See Ref. in 2	3.74	128.4	2	0	1
<i>Baeolophus wollweberi</i>	9.7	257.2	10.4	See Ref. in 2			2	0	1
<i>Carduelis chloris</i>	18.6	599.8	27.8	3	0.91	25.8	1	0	2
<i>Certhia familiaris</i>	15.8	242.1	9	3	0.48	8.8	1	0	1
<i>Corvus corone</i>	136.8	4988.3	417	See Ref. in 2	8.28	522.6	2	0	1
<i>Corvus frugilegus</i>	116.3	5679.6	335.5	See Ref. in 2	7.93	466.8	2	0	2
<i>Corvus monedula</i>	59.3	2921.4	208.8	See Refs in 2 and 3	4.94	219.1	1	0	2
<i>Cyanocitta cristata</i>	45.7	996.9	113.3	See Ref. in 2	3.01	84.6	3	0	2
<i>Emberiza schoeniclus</i>	12.5	339.6	18.3	3	0.69	19.8	1	0	2
<i>Erethacus rubecula</i>	17.6	366.4	18.2	3	0.66	18	1	0	2
<i>Ficedula albicollis</i>	7.4	181.6	12.2	3	0.47	10.3	1	0	3
<i>Fringilla coelebs</i>	16.3	544.5	21.4	3	0.77	22.1	1	0	2
<i>Fulmarus glacialis</i>	17.4	1067.1	525	4	6.68	622	1	0	2
<i>Garrulus glandarius</i>	94	1701.8	172.6	See Refs in 2 and 3	4.11	163	3	0	1
<i>Gymnorhinus cyanocephala</i>	30.9	1101	102.4	See Ref. in 2	3.64	103	3	0	1
<i>Junco hyemalis</i>	14.4	402.8	19.8	5, 6	0.86	18.2	1	0	2
<i>Lonchura striata</i>	6.7	213.3	12.3	3	0.77	12.3	1	0	
<i>Melanerpes carolinus</i>	71.6	1349.6	61.7	7	2.24	68.5	3	0	1
<i>Melanerpes erythrocephalus</i>	30.5	861.7	71.6	7	1.84	71.6	3	0	2
<i>Melospiza melodia</i>	20.7	653.5	20.8	8	0.99	21.3	1	0	2
<i>Molothrus ater</i>	6.1	165	39.7	1	2.19	57.9	1	1	2
<i>Molothrus badius</i>	24.9	1003	43.9	9	1.53	44.5	1	0	
<i>Molothrus bonariensis</i>	25.9	823.8	47.9	10			1	1	1
<i>Molothrus rufoaxillaris</i>	26.4	852.5	52.4	10			1	1	1
<i>Nucifraga columbiana</i>	44.7	1322.3	130.8	See Ref. in 2			3	0	1
<i>Oceanodroma leucorhoa</i>	8.6	372.5	49.9	4	0.92	39.6	1	0	2
<i>Parus ater</i>	14.3	293.3	9.1	See Refs in 2 and 3	0.59	8.8	2	0	2
<i>Parus caeruleus</i>	12.4	293.3	13.3	See Refs in 2 and 3	0.66	10.4	1	0	2
<i>Parus major</i>	14.9	412.4	19	See Refs in 2 and 3	0.86	17.2	1	0	2
<i>Parus montanus</i>	26	247.7	10.2	See Ref. in 2	0.79	13	3	0	2
<i>Parus palustris</i>	19.3	307.6	10.6	See Refs in 2 and 3	0.68	12	2	0	1
<i>Phylloscopus collybita</i>	7.6	139.6	7.5	3	0.31	7.6	1	0	3
<i>Phylloscopus trochilus</i>	9	183.2	8.7	3	0.34	9.2	1	0	3
<i>Pica pica</i>	97.4	2893.1	182.7	See Ref. in 2	5.49	206.1	2	0	1
<i>Picoides pubescens</i>	34.5	634.3	27	7	1.25	25.3	2	0	1
<i>Picoides villosus</i>	73.5	1509.5	66.3	7	3.06	82.8	2	0	1
<i>Poecile atricapillus</i>	12.8	278.6	10.8	See Refs in 2 and 11	0.79	12	2	0	1
<i>Poecile gambeli</i>	12.1	307.5	10.8	See Ref. in 2	0.78	11.3	3	0	1
<i>Poecile sclateri</i>	10.5	278.5	11	See Ref. in 2			2	0	1
<i>Prunella modularis</i>	20	425.6	20.3	3	0.75	19.4	1	0	2
<i>Pyrrhocorax graculus</i>	60.3	1601.3	163	See Ref. in 2	3.2	150	1	0	1
<i>Quiscalus quiscula</i>	4.4	217.5	92.4	1	2.84	91.4	1	0	2
<i>Saxicola torquata</i>	10.4	268.5	13.3	3	0.63	15.3	1	0	3
<i>Sitta europaea</i>	34.2	537	19.8	12	1.09	22.5	3	0	1
<i>Sturnus vulgaris</i>	28.8	849.2	82.3	3	1.99	81.5	1	0	2
<i>Sylvia atricapilla</i>	13	367.3	15.5	3	0.71	17.6	1	0	3
<i>Sylvia borin</i>	14.6	271	13.9	3	0.62	19.2	1	0	3
<i>Taeniopygia guttata</i>	5	183.7	12	3	0.44	11.5	1	0	1
<i>Troglodytes troglodytes</i>	12.4	314.1	9.6	3	0.5	9.4	1	0	2

Table 1 continued

Species	Hippocampus (mm ³)	Telencephalon (mm ³)	Body mass (g)	Reference ^a	Brain mass (g)	Body mass (g)	Food hoarding ^b	Brood parasitism ^c	Migration ^d
<i>Turdus merula</i>	39.2	977.2	113	3	1.63	98.8	1	0	2
<i>Turdus philomelos</i>	33.3	829.9	67.8	3	1.59	67.5	1	0	2
<i>Urocissa erythrorhyncha</i>	77.8	2293.6	202.7	See Ref. in 2	3.8	214	2	0	
<i>Vidua paradisaea</i>	14.6	331.9	22.2	3	0.66	22.2	1	1	

As we used data on brain mass from other sources, the corresponding body mass were also taken from those sources itself (Crile & Quiring 1940; Armstrong & Bergeron 1985; Mlikovsky 1990; Garamszegi *et al.* 2002; Iwaniuk & Nelson 2003).

^a1, Sherry *et al.* (1993); 2, Brodin & Lundborg (2003); 3, DeVoogd *et al.* (1993); 4, Abbott *et al.* (1999); 5, Smulders *et al.* (2000); 6, Cristol *et al.* (2003); 7, Volman *et al.* (1997); 8, Lee *et al.* (2001); 9, Reboreda *et al.* (1996); 10, Clayton *et al.* (1997); 11, MacDougall-Shackleton *et al.* (2003); 12, Krebs *et al.* (1989).

^bFood hoarding: 1, non-hoarders; 2, non-specialized hoarders; 3, specialized hoarders.

^cBrood parasitism: 0, non-parasitic; 1, parasitic.

^dMigration: 1, resident; 2, partially migratory; 3, fully migratory.

scale as follows: resident (a score of 1), partial migrant (species having resident and migratory populations; a score of 2) or migrant (a score of 3). In our dataset there were four well-known brood parasitic species. Because intermediate states are biologically meaningful, food hoarding and migration were used as continuous variables in the phylogenetic analysis, as was done in the majority of previous studies (e.g. Healy & Krebs 1992, 1996). However, these variables can be viewed as categorical variables, and their use in approaches that require continuous variables with normal distribution is questionable. Therefore, in a second set of analyses we performed statistics by using food hoarding, migration and brood parasitism as categorical variables. Because the chosen phylogenetic framework does not allow the use of categorical variables, we performed analyses with categorical variables on the raw species data. The relevance of this second approach was subsequently verified, as the phylogenetic analyses revealed weak roles for the confounding effect of the common descent (see Results). A priori, we did not predict differences between the outcome of the categorical and continuous approaches. The entire database together with references is provided in Table 1.

Information on food-hoarding behaviour was obtained from Volman *et al.* (1997); Brodin & Lundborg (2003) and from standard ornithological handbooks (Cramp & Perrins 1985–1994; Poole *et al.* 1993–2002). We used Cramp & Perrins (1985–1994) and Poole *et al.* (1993–2002) in combination with field guides (Heinzel *et al.* 1997; National Geographic 2000) to assess migratory habit. Brood-parasitism in cowbirds was scored according to Reboreda *et al.* (1996) and Clayton *et al.* (1997), whereas *Vidua paradisaea* is known as a typical brood-parasite species (e.g. Sorenson *et al.* 2003). After checking Cramp & Perrins (1985–1994) and Poole *et al.* (1993–2002) other species were treated as non-parasitic birds.

To control for phylogenetic effects, we tested for potential interspecific association between hippocampal volume, telencephalic volume, brain size and food hoarding by using a maximum likelihood approach implemented in the program *Continuous* (Pagel 1997). This approach characterizes evolutionary changes along each branch of a phylogenetic tree through the variance components of traits (Pagel 1997, 1999). It controls for similarity because of common descent and allows investigation of correlated evolution between pairs of characters while assessing the mode of trait evolution and the importance of phylogenetic corrections. Hypotheses are tested with likelihood ratio statistics. This compares the log-likelihood of the model corresponding to a null hypothesis (H_0) over the model for an alternative hypothesis (H_1), where the likelihood ratio = $-2 \log_e[H_0/H_1]$. The likelihood ratio statistic is asymptotically distributed as a chi-squared variate with degrees of freedom equal to the difference in the number of parameters between the two models. We first assessed sequentially the contribution of scaling parameters, κ : branch length scaling factor, and λ : phylogeny scaling factor for the pairs of traits in focus. Once an appropriate model with adjusted scaling parameters had been selected, we studied correlated evolution of traits of interest. We compared the goodness-of-fit of model H_0 fitted to the data by allowing only independent evolution with that alternative H_1 model that permits correlated evolution of the characters. The associated likelihood ratio statistic reveals the significance of the correlated trait evolution. We assumed that the evolution of traits follows standard constant-variance random walk evolutionary model, thus we used the corresponding settings in *Continuous* (Model A). For each evolutionary model, we present the appropriate scaling parameters, phylogenetic correlations and the corresponding log-likelihood ratio statistics testing

for correlated trait evolution. To control for the potentially confounding effects of migration, we entered this variable together with the traits of interest in the same phylogenetic model, and calculated partial phylogenetic correlations. To control for brood-parasitism, we excluded the four parasitic species from our analysis. Prior to the analyses, we calculated the volume of the hippocampus relative to the telencephalon by adopting the approach for analogue allometric adjustment as recommended by Purvis & Rambaut (1995). First, we entered the \log_{10} -transformed volume of the hippocampus and \log_{10} -transformed volume of the telencephalon in a phylogenetic model. Then relying on the parameter estimates of *Continuous*, we calculated the slope of the phylogenetic regression line between these traits. Next, we fitted this slope to the raw species dataset, and took residuals from the line. We used these residuals as the magnitude of hippocampal volume relative to the volume of the telencephalon, which were entered in subsequent evolutionary models. We applied similar procedures to calculate the relative volume of the telencephalon, and the relative size of the overall brain mass controlling for body mass. However, when we used an alternative approach for allometric adjustments by entering three traits (e.g. hippocampus, telencephalon and food hoarding) in a single phylogenetic model, and calculated the partial phylogenetic correlation between the traits of interest (hippocampus and food hoarding) by controlling for the third variable (telencephalon), the results were very similar to those we report here. This was also the case, when we scaled the volume of the hippocampus relative to body size instead of the volume of the telencephalon.

The phylogenetic hypothesis presented in Fig. 1 was based on a composite phylogeny reported by Sibley & Ahlquist (1990), combined with information from other sources (Goodwin 1986; Gill *et al.* 1989; Sheldon *et al.* 1992; Suhonen *et al.* 1994; Cibois & Pasquet 1999; Johnson & Lanyon 1999; Klicka *et al.* 2000). We applied branch lengths from the tapestry tree of Sibley & Ahlquist (1990) for higher taxonomic levels. Within families the distance between different genera was set to $3.4 \Delta T_{50}H$ units, and between species within genera to $1.1 \Delta T_{50}H$ units (Sibley & Ahlquist 1990; Bennett & Owens 2002).

The phylogenetic method does not produce phylogenetically transformed data. For illustrative purposes we present figures based on the raw species data on which we superimpose the phylogenetically corrected regression lines.

RESULTS

We found significant and positive phylogenetic associations between food hoarding and the relative size of the hippocampus ($\kappa = 0.414$, $\lambda = 0.822$, LR = 3.799, d.f. = 1, $P = 0.006$, $n = 55$, phylogenetic correlation: 0.359;

Fig. 2a), and between food hoarding and relative brain size ($\kappa = 1.000$, $\lambda = 0.871$, LR = 2.416, d.f. = 1, $P = 0.028$, $n = 50$, phylogenetic correlation: 0.303; Fig. 2c), but not between food hoarding and relative telencephalic volume ($\kappa = 0.415$, $\lambda = 0.771$, LR = 0.091, d.f. = 1, $P = 0.669$, $n = 55$, phylogenetic correlation: 0.058; Fig. 2b). When we excluded brood-parasitic species and calculated partial phylogenetic correlations between food hoarding and different neural volumes by controlling for migration, the previous relationships remained unchanged (hippocampus: overall model testing for the coevolution of three traits, $\kappa = 0.142$, $\lambda = 0.816$, LR = 3.518, d.f. = 3, $P = 0.071$, $n = 48$; partial phylogenetic correlation between hippocampus and food hoarding: 0.292, $P = 0.024$; telencephalon: overall model testing for the coevolution of three traits, $\kappa = 0.254$, $\lambda = 0.902$, LR = 1.471, d.f. = 3, $P = 0.401$, $n = 48$; partial phylogenetic correlation between telencephalon and food hoarding: -0.057 , $P = 0.695$; brain size: overall model testing for the coevolution of three traits, $\kappa = 0.253$, $\lambda = 0.867$, LR = 5.331, d.f. = 3, $P = 0.014$, $n = 45$; partial phylogenetic correlation between brain size and food hoarding: 0.342, $P = 0.009$).

We previously detected minimal roles for phylogenetic effects ($\lambda < 1$). Hence, we also applied statistical approaches on the raw species data to test for similar associations by using categorical variables. This approach revealed significant differences in the volume of different brain regions among food-hoarding categories (hippocampus: $F_{2,54} = 5.086$, $P = 0.010$; telencephalon: $F_{2,54} = 6.352$, $P = 0.003$; brain size: $F_{2,49} = 15.586$, $P < 0.001$). When we used binary states for food hoarding by collapsing non-specialized and specialized hoarders (scores 2 and 3) into a single category, these results remained identical (hippocampus: $t_{53} = 2.656$, $P = 0.010$; telencephalon: $t_{53} = 3.443$, $P = 0.001$; brain size: $t_{48} = 5.642$, $P < 0.001$). To control for the potentially confounding variables, we performed analyses in which we used food hoarding as a three-state variable together with migration and brood parasitism categories as independent variables with brain volumes as dependent variables. This approach revealed very similar results to the phylogenetic correlations that were based on continuous variables (hippocampus: overall model, $F_{5,49} = 2.080$, $P = 0.086$, effect for food hoarding $F_{2,49} = 2.970$, $P = 0.061$; telencephalon: overall model, $F_{5,49} = 2.380$, $P = 0.053$, effect for food hoarding $F_{2,49} = 1.462$, $P = 0.243$; brain size: overall model, $F_{5,44} = 10.646$, $P < 0.001$, effect for food hoarding $F_{2,44} = 9.504$, $P < 0.001$).

DISCUSSION

Here we showed that food-hoarding species have a larger hippocampus than non-hoarding species. The interspecific

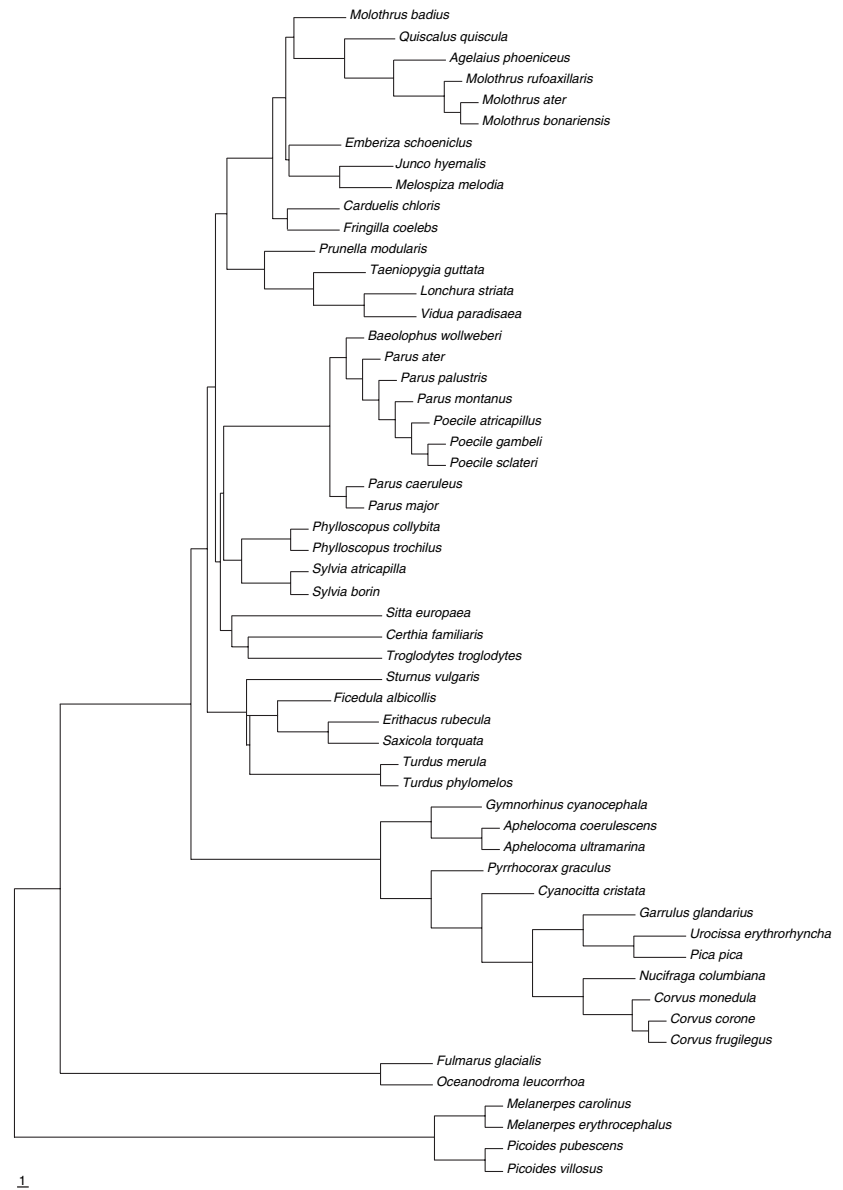


Figure 1 The phylogeny of birds used for the phylogenetic analysis of food hoarding in association with relative volumes of the hippocampus, and of the telencephalon and also relative overall brain size. The scale for branch length is given in the bottom left.

association between hippocampal volume and food hoarding is likely to be related to the special constraints that food hoarding imposes on spatial memory, and the role played by the hippocampus in spatial memory (Krebs *et al.* 1989). Our results in relation to the hippocampus are consistent with previous studies reporting similar relationship within (Krebs *et al.* 1990; Healy & Krebs 1992, 1996; Hampton *et al.* 1995; Basil *et al.* 1996) and among avian families (Krebs *et al.* 1989; Sherry *et al.* 1989). However, the evidence we report is in conflict with a recent comparative study of bird species, which found no significant interspecific relationship between food hoarding and the relative volume of the hippocampus (Brodin & Lundborg 2003). Compared with

these studies, our analysis is novel in two respects. First, we used a larger dataset than previous investigations, thus covering a broad taxonomical range of species (13 families, of which two are non-passerines). Second, we controlled for phylogenetic associations. We suspect that the first-named difference is of major importance. Reanalysing the dataset of Brodin & Lundborg (2003), who used 21 bird species, under our phylogenetic framework, we came to similar findings to theirs in terms of no significant relationship between food hoarding and the relative volume of the hippocampus ($\kappa = 0.000$, $\lambda = 0.000$, LR = 0.384, d.f. = 1, $P = 0.381$, $n = 21$, phylogenetic correlation = 0.199). On the other hand, when we implemented the approach of Brodin &

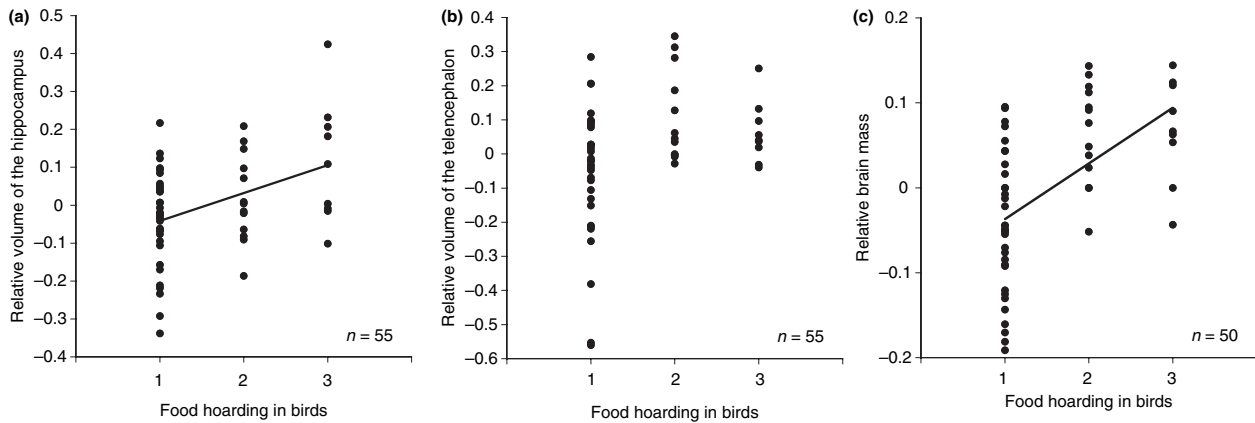


Figure 2 The relationship between food hoarding and the volume of the hippocampus relative to the volume of the telencephalon (a), the volume of the telencephalon relative to body size (b) and brain mass relative to body size (c), all based on the raw species data. Lines are phylogenetically corrected linear regression lines and presented only if the corresponding phylogenetic associations were significant (see text).

Lundborg (2003) on our raw species data, and calculated categorical differences in relative hippocampal volume among different food-hoarding categories while neglecting phylogenetic associations, our conclusions were unchanged. In addition, when we used a bivariate variable for food hoarding by collapsing non-specialized and specialized hoarders into a single category the results remained identical. Thus, our findings seem to be unaffected whether we use phylogenetic control or categorical variables for food hoarding. In our study, we used 55 species belonging to different taxonomical groups, and thus examined evolutionary transitions in food hoarding and hippocampal volume across a broad evolutionary spectrum. Our sample of birds included relatively more non-hoarder species than that of Brodin & Lundborg (2003) or of others. This difference may have also increased the power of our analysis implying the importance of non-hoarding species when assessing the correlative evolution of neural volumes and food hoarding. Considering the phylogenetic distribution of food hoarding, it is more parsimonious that food-hoarders evolve from non-hoarders than *vice versa*. Our results therefore suggest that evolutionary change towards specialization of food hoarding has been accompanied by evolutionary changes in hippocampal volume during the long-term phylogenetic history of birds. These evolutionary changes may be robust when non-hoarding species evolve some degree of food hoarding.

We also showed that the relative size of the overall brain was positively and significantly related to food hoarding among birds unaffected by the approach used. According to our knowledge, this study is the first to show such an evolutionary association. When we used categorical approaches, we found some role for the relative size of the telencephalon in association with food-hoarding specializa-

tion, although Healy & Krebs (1992) reported no significant interspecific correlation between these traits. In our study, the difference between the results of the correlative and categorical approaches for the telencephalon may be because of the small difference between non-specialized and specialized hoarders. The inspection of the corresponding figure (Fig. 2b) suggests that the volumetric augmentation of the telencephalon may be important when non-hoarding species switch to food hoarding on an evolutionary scale. Hence, food-hoarding specialization may not only favour the evolution of the size of the hippocampus, but apparently it also affects the size of larger regions in the brain.

Although investigations of food-hoarding birds assumed that the hippocampus is the key neural substrate for information stored in spatial memory, there has been a recent debate on the exact localization of such neural structures (Bolhuis & Macphail 2001). In fact, little is known about the role of neural structures outside of the hippocampus in mediating food-hoarding behaviour. Shiflett *et al.* (2002) have shown among Parids that the septum, a medial forebrain structure that shares reciprocal connections with the hippocampus, may be specialized for some aspects of food hoarding. They found that relative septum volume was larger in food-hoarding chickadees than in related non-hoarding species. However, the size of the hippocampus and the septum may still be of minor volumetric importance, thus it remains difficult to disentangle which structures are responsible for the detected evolutionary patterns concerning overall brain size. Tracing studies have found efferent projections from the hippocampal formation to the hyperstriatum, midbrain nuclei and basal ganglia (e.g. Székely & Krebs 1996; Atoji *et al.* 2002), whereas the hippocampus may receive afferent

innervations from the visual system (Wylie *et al.* 1999). Although it remains difficult to apply this functional evidence in an ecological context, the rich connectivity of the hippocampus may suggest that food hoarding relies upon multiple neural systems and the hippocampus is just a part of it.

The interspecific correlations we present do not provide insight into the exact mechanism that generates an evolutionary link between food hoarding and brain size. However, our results may imply that the neural specialization to food hoarding may be complex, as its integration into the brain may require a general neural augmentation. In addition to a well-developed spatial memory, food hoarding potentially involves several cognitive tasks that help individuals to cope with the environment when hiding and retrieving food. The complex neuronal government of these tasks may not only necessitate the variety of different brain regions, but it may also require their synaptic connections. The simultaneous evolution of these neural substrates in association with food hoarding may lead to an increase of the entire brain.

Overall, relying on a wide range of species, we found strong evidence that food hoarding is associated with volumetric augmentation of the hippocampus. Additionally, larger brain regions, most importantly the overall brain, seem to adapt to such a complex cognitive task on an evolutionary scale. Our results thus indicate that the concerted evolution of different brain structures with volumetric importance may have occurred in response to the increased demand that food hoarding imposes on neural capacity.

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