

# Seasonal Variation in Hippocampal Volume in a Food-Storing Bird, the Black-Capped Chickadee

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## SUMMARY

Black-capped chickadees (*Parus atricapillus*) in upstate New York show a peak in food-hoarding intensity in October. We caught chickadees at six different times of the year and measured the volume of several brain structures. We found that the hippocampal formation, which is involved in spatial memory for cached food items, has a larger volume, relative to the rest of the brain, in October than at any other time of the year. We conclude that

there is an association between the intensity of food hoarding and the volume of the hippocampal formation and suggest that the enhanced anatomy might be caused by the increased use of spatial memory. © 1995 John Wiley & Sons, Inc.

**Keywords:** food caching, spatial memory, avian hippocampus, seasonal change, brain volume.

## INTRODUCTION

The black-capped chickadee (*Parus atricapillus*), like most other members of the parid family, scatter hoards food items (for an extended review of food hoarding in parids, see Sherry, 1989). In upstate New York, where this study was conducted, hoarding is mainly observed in the fall, especially around the month of October (Odum, 1942). In a laboratory situation, food-storing activity can be induced in black-capped chickadees by simulating fall conditions (Shettleworth et al., 1995). A similar seasonality in behavior has also been described for some close relatives of the black-capped chickadee, such as the willow tit (*Parus montanus*) (Ludescher, 1980; Pravosudov, 1985; Nakamura and Wako, 1988) and the Siberian tit (*Parus cinctus*) (Pravosudov, 1985). It is not clear whether the food is stored for short-term use or acts as a long-term food source to overcome the food shortages of winter. Stevens and Krebs (1985) found that seeds collected from a feeder by marsh

tits (*Parus palustris*) and hoarded in the surrounding territory were all recovered within 3 days, suggesting only a short-term use of hoards. Recently, however, Brodin (1994) found that this is not true for food hoarded by naturally foraging tits. In that situation, seeds may be retrieved from storage sites up to months after storage. In any case, it is clear that seed storage and retrieval are elaborate, important behaviors in this genus that tend to be displayed seasonally.

A problem for animals that scatter their hoards over a large area is how to retrieve them later. Of several possible strategies to solve this problem, parids and corvids use memory to retrieve their hoards (at least for short-term hoarding) (reviewed in Shettleworth, 1990). The type of information used is mainly spatial in nature (Shettleworth and Krebs, 1982; Brodbeck, 1994; Clayton and Krebs, 1994a).

Initial research on the neural basis of this behavior has focused on the avian hippocampal formation (HF). This structure is believed to be homologous to the mammalian hippocampus (Krayniak and Siegel, 1978a, b; Casini et al., 1986; Erichsen et al., 1991; Krebs et al., 1991), which has been implicated in different types of memory: spatial maps (O'Keefe and Nadel, 1978), working memory (Olton, 1983), and declarative memory (Squire et al.,

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**Table 1** Sample Sizes, Subdivided According to Group, Age Category and Sex

Group	1 (Oct 1992)		2 (Dec 1992)		3 (Feb 1993)		4 (Apr 1993)		5 (Jun 1993)		6 (Aug 1993)		7 (Oct 1993)		8 (Dec 1993)	
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Adult	1	1	2	2	2	2	3	3	4	2	5	—	—	2	1	1
Juvenile	2	1	—	—	—	—	—	—	—	4	5	5	—	—	—	—

1993), among others. Ablation of HF in food-storing birds results in an inability to retrieve their caches above chance level (Krushinskaya, 1966; Sherry and Vaccarino, 1989). Black-capped chickadees are impaired in both spatial and working memory tasks after lesions of HF (Sherry and Vaccarino, 1989). Other evidence that suggests an important role for HF in food storing is that it is relatively larger (compared with the rest of the forebrain) in food-storing birds than in their nonstoring relatives (Krebs et al., 1989; Sherry et al., 1989). Similar results linking the HF to spatial tasks have been found in homing pigeons (Rehkämper et al., 1988; reviewed by Bingman, 1990) and cowbirds (Sherry et al., 1993).

In several species of songbird, the volume of the nucleus high vocal center varies seasonally, paralleling the seasonal singing pattern of males (Nottebohm, 1981; Kirn et al., 1989; Brenowitz et al., 1991). It is larger in the spring, when the males sing most, and smallest in the fall, when the males are silent. Given the role of HF in food hoarding and given the seasonality of the behavior, we hypothesize that HF volume might change over the seasons, too, in parallel with the changing demand on spatial memory. We predict a maximum relative volume of HF in the fall (October), because that is when food-storing activity is at its peak.

## METHODS

### Subjects

Subjects were black-capped chickadees, caught near Ithaca, New York, under State and Federal permits. A total of 48 birds were caught at six different times of the year (Table 1). Groups 1 and 7 and groups 2 and 8 are combined in all subsequent analyses, as they were obtained from the same time in the yearly cycle. In the winter months, birds were caught with Potter's traps baited with food, and in the summer with song playback and mist nets. Birds for one sample were typically caught on the same day from the same flock. The samples were large enough relative to flock size for both methods not to have

a bias in age, sex, or social status. All birds were taken into the laboratory on the day they were caught; age and sex were determined after perfusion. The birds were divided into two age classes, based on the ossification of the skull: juvenile (skull not completely ossified) and adult (ossified skull) birds (Smith, 1991). Body weight and gonad weight were recorded.

### Histology

Birds were perfused transcardially with 0.8% saline and 10% formalin in 0.8% saline. The heads were then postfixed in 10% formalin/0.8% saline for at least 1 day, after which the brain was removed from the skull, weighed, and allowed to postfix for at least another day in formalin/saline. The brain was then transferred to 10% formalin in 30% sucrose, until it sank (2 to 3 days). It was weighed again and embedded in 10% gelatin/30% sucrose, which was hardened in 10% formalin/30% sucrose. The brains were then sliced on a freezing microtome at 40  $\mu$ m and transferred to microscope slides. Alternate sections were stained with cresyl-violet stain and coverslips were placed with Permount®.

### Volume Measurements

We measured the volumes of four structures. Our primary nucleus of interest was the HF. Since we are looking for variation specific to HF, we also measured the telencephalon (T), of which HF is part, in order to isolate variation in volume that was specific to HF. We measured two control nuclei that are part of the visual system: the ectostriatum (E), which is a telencephalic nucleus, and the nucleus rotundus (Rt), a mesencephalic nucleus. Sections were scanned with a video camera (COHU) and digitized on a Macintosh IIfx using NIH Image 1.54. The surface area of the target structure was outlined and measured. Volumes were then calculated by multiplying the surface area with the distance between measurements (160  $\mu$ m for HF, T, and E; 80  $\mu$ m for Rt), and adding those numbers. For HF, E, and Rt, we measured left and right hemisphere separately, so we could investigate a possible lateralization in volume. For all other analyses, the sum of both sides was used. Several brains were randomly chosen, their identification numbers were coded, and then they were remeasured to verify that our criteria for regional boundaries were consistent

throughout the study. We found that our HF remeasurements showed a mean variation of 3.3% from the first measurements.

Brain weights changed after immersion in 10% formalin/30% sucrose. In particular, the brains in the June group lost approximately 20% of their weight in this stage, whereas in other groups the weight change was in a random direction and not more than 2% to 3%. This histological effect could be due to differences in perfusion, to a chance difference in the solution's concentration, or to a real difference in the salinity of the brains themselves. To control for this shrinkage in some of the brains, we corrected all the volumes for their weight change. Since we did not have the brain weights for group 3 (February), this group will normally not be included in the analyses that use the corrected brain volumes. For some analyses, we did use all six groups, correcting the brain volumes in group 3 by using the average change in groups 2 and 4. When that occurred, it is mentioned.

### Climate Data

Data about the temperatures and humidity around Ithaca were acquired from the North East Regional Climate Center (Cornell University, Ithaca, New York). We calculated average temperature and humidity (expressed as dew point) on the day the animals were captured and on the day before.

### Statistical Analysis

All statistical analyses were done using the package Systat 5.2.1. on an Apple Macintosh Centris 610. The main statistical technique used was the General Linear Model. This technique allows us to explain a dependent variable by a linear combination of independent variables, which can be continuous (like a volume measure) or discrete (like a grouping variable, e.g., sex). For example, we can set up a model that looks like this (a, b, c, d, and e are constants):

$$[\text{HF volume}] = a [\text{T volume}] + b [\text{age}] + c [\text{sex}] \\ + d [\text{time of year}] + e$$

Such a model tests for effects of each of the independent variables, while keeping the other independent variables constant. When we mention effects of several independent variables on a dependent variable, they are always the result of one such model, unless mentioned otherwise. Results are considered statistically significant for  $p < 0.05$ . When using T size as an independent variable to explain any telencephalic component (here HF or E), only the volume of the T exclusive of the target structure was used, in order to keep both measurements independent of each other.

## RESULTS

### Body Weight

The variation in body weight can be explained by two variables: sex [ $F(1,41) = 39.089$ ;  $p < 0.001$ ] and time of year [ $F(5,41) = 5.994$ ;  $p < 0.001$ ]. Males are on average 10.2% heavier than females. This replicates earlier findings (reviewed by Smith, 1991). Birds are heavier in winter than they are in summer. This seasonal effect is related to temperature. When running a stepwise regression on all climate variables and controlling for sex, both the mean temperature on the day the bird was caught and the mean temperature at that time of year (taken over several years) were found to have a significant effect on body weight [ $F(1,45) = 9.582$ ;  $p = 0.003$  and  $F(1,45) = 17.389$ ;  $p < 0.001$ , respectively]. The birds are heavier when the weather is colder. This is probably due to greater fat reserves in winter.

### Nucleus Rotundus

For the Rt, we found an effect of the time of year, with the April, June, and August groups having a slightly larger Rt than the October and December groups [ $F(4,37) = 2.635$ ;  $p < 0.05$ ], but no age effect [ $F(1,37) = 0.052$ ; NS] or sex effect [ $F(1,37) = 0.013$ ; NS] (Table 2). There is an overall lateralization effect, the left side being 6.6% larger than the right side [repeated measures general linear model with all six groups included in the analysis:  $F(1,40) = 11.533$ ;  $p = 0.002$ ].

### Telencephalon

We found a significant effect of age [ $F(1,37) = 23.108$ ;  $p < 0.001$ ], but not of sex [ $F(1,37) = 0.792$ ; NS] or time of year [ $F(4,37) = 1.805$ ; NS] (Table 2). This result is the same when we include the corrected February group. Juveniles have a larger T than adults (Fig. 1), but there is no difference between males and females, nor does T volume vary significantly throughout the year. The same results were found when we redid the analyses on the T exclusive of HF.

When the analysis is performed on the volumes uncorrected for weight change during fixation, there is a significant seasonal variation, with a volume peak in October. Although correcting for the weight loss makes the significance disappear, the overall pattern is still obvious (Fig. 1). This could still be due to some histological artifact, but we cannot rule out the possibility that there might be a

Table 2 Volumes of the Different Brain Nuclei after Correction for the Weight Loss during Histologic Examination

Group	1 (Oct)	2 (Dec)	3 (Feb)	4 (Apr)	5 (June)	6 (Aug)
Nucleus rotundus						
Adult	1.65 ± 0.36	1.66 ± 0.21	1.89 ± 0.39	1.99 ± 0.21	1.93 ± 0.46	2.22 ± 0.22
Juvenile	1.76 ± 0.36	—	—	—	2.10 ± 0.39	1.98 ± 0.29
Telencephalon						
Adult	397.59 ± 26.34	358.73 ± 40.80	333.58 ± 35.57	387.62 ± 55.22	347.41 ± 65.45	352.47 ± 27.21
Juvenile	440.15 ± 51.77	—	—	—	446.67 ± 19.63	413.21 ± 20.10
Ectostriatum						
Adult	3.90 ± 0.83	4.04 ± 0.47	4.48 ± 0.55	4.76 ± 0.65	4.44 ± 1.17	5.17 ± 0.51
Juvenile	5.22 ± 1.16	—	—	—	4.52 ± 0.59	4.51 ± 0.60
Hippocampal formation						
Adult	21.97 ± 1.59	17.47 ± 1.34	14.02 ± 2.92	18.97 ± 2.74	17.27 ± 2.46	16.34 ± 1.43
Juvenile	19.50 ± 2.51	—	—	—	13.36 ± 0.94	14.64 ± 1.45

Volumes (in mm<sup>3</sup> ± SD) are subdivided according to group (group 3 corrections: see text) and age category.

real seasonal variation in the T volume that is just not picked up by the statistics because of the high variability. Other authors, examining seasonal effects in song control nuclei, have found differences in T volume that followed the variation in song nucleus size (Nottebohm, 1981; Kirn et al., 1989). The variation we see follows the variation in the HF (see later). Since the focus of this article is on specific variation in HF volume, independent of the T, this will not be considered further.

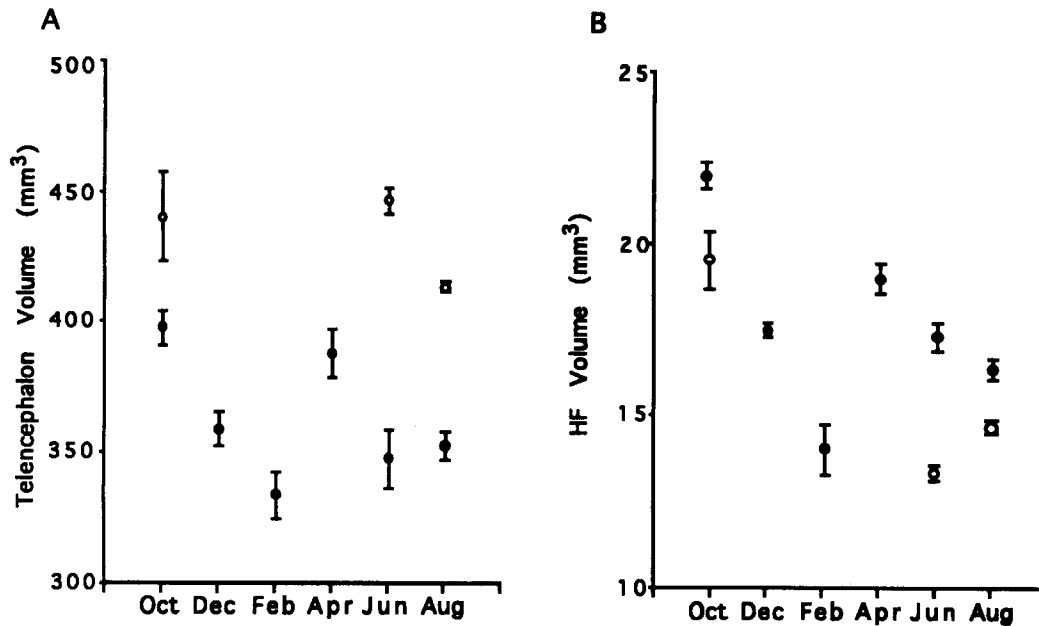
### Ectostriatum

We found a statistically significant effect of T volume (E volume excluded) [ $F(1,36) = 18.490$ ;  $p < 0.001$ ] on the E volume. There was no significant effect of time of year [ $F(4,36) = 1.311$ ; NS], and the effects of age [ $F(1,36) = 3.725$ ;  $p < 0.10$ ] and sex [ $F(1,36) = 3.400$ ;  $p < 0.10$ ] were marginal (Table 2). Redoing the analysis, including the corrected February group, yields virtually the same results. This means that birds with a larger T also have a larger E. There are, however, no differences between the different times of year or between males and females or juveniles and adults. No lateralization effect was found.

### Hippocampal Formation

With HF volume as a dependent variable, we found significant effects of age [ $F(1,36) = 29.980$ ;  $p < 0.001$ ], T volume (HF volume not included) [ $F(1,36) = 14.173$ ;  $p = 0.001$ ], and time of year [ $F(4,36) = 10.752$ ;  $p < 0.001$ ], but not of sex [ $F(1,36) = 0.072$ ; NS] (Fig. 1; Table 2). Again, the same results were found after including the corrected February group. Adult birds have a larger HF than juveniles in the groups for which we can identify both age classes (June through October). When we keep age constant, birds with a larger T also have a larger HF. Chickadees have a larger relative HF in October than they do during the rest of the year, for example, in adults, the relative HF is on average 17% larger in October than during the rest of the year (5.6% of total T volume vs. 4.8% of total T volume) (Figs. 2 and 3).

If we look closer at the age effect in June, August, and October (Fig. 4), there is a significant overall difference in relative HF volume between the three periods and between adults and juveniles, as well as a marginally significant interaction between age and period [two-way ANOVA: month:  $F(2,25) = 12.706$ ;  $p < 0.001$ ; age:  $F(1,25) = 14.275$ ;  $p = 0.001$ ; interaction:  $F(2,25) = 3.177$ ;  $p < 0.06$ ]. In October, the relative HF is about 30% larger



**Figure 1** Mean volumes ( $\pm$ SEM) of telencephalon (A) and hippocampal formation (B), calculated for each age group and corrected for shrinkage during histologic examination. Although juveniles (○) have a larger telencephalon, adults (●) have a larger hippocampal formation.

than it is in August (Bonferroni post hoc test:  $p < 0.001$ ), but there is no difference between June and August.

There is no overall lateralization effect. If we test the groups at each time of year separately for lateralization, using a paired  $t$  test, we only find a significant effect in the June group: at that time of year the right HF is 4.3% larger than the left HF ( $t = 3.443$ ;  $df = 9$ ;  $p = 0.007$ ).

## DISCUSSION

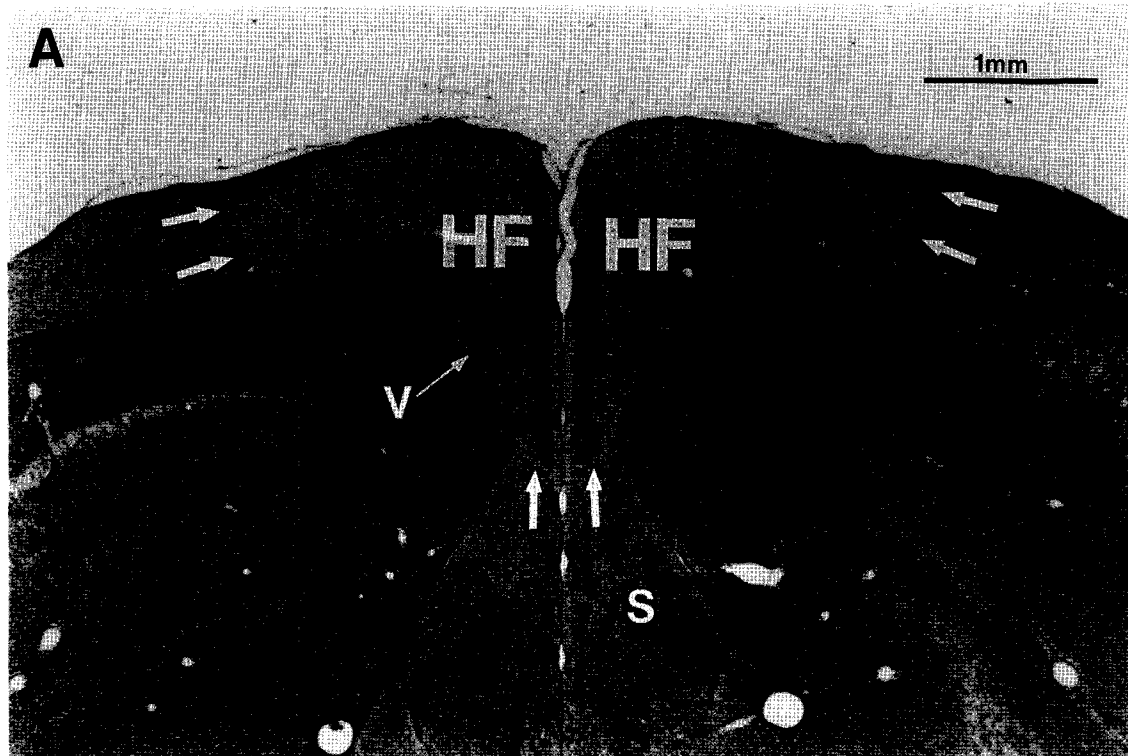
### Lateralization

Clayton and Krebs (1994a) have found evidence that the left eye system of blue tits (*Parus caeruleus*), marsh tits, jays (*Garrulus glandarius*), and jackdaws (*Corvus monedula*) is involved in mainly spatial aspects of memory, whereas the right eye system is more involved in the memory for local configurations. If structural change is tightly coupled to functional change, and if this pattern also applies to chickadees, we would predict that the extensive use of spatial memory by chickadees in October would be associated with especially enhanced anatomy in the right HF (linked to the left eye system). However, we do not find a consistently significant difference between right and left HF. If

there are differences between the two sides related to the nature of the processing that is being carried out, analyses of connectivity or synaptic morphology may be needed to find them. Clayton (1993) cites Watanabe et al. (1986), who showed that the Rt is important for interhemispheric transfer of visual information in pigeons. In that respect, it is interesting that we find that the left Rt is larger than the right Rt. Clayton finds the left side (right eye system) to be involved in longer-term memory. However, as mentioned earlier, this is not the eye system dominant in processing spatial information, making the result difficult to interpret.

### Seasonal Variation in Relative HF Volume

We find a seasonal variation in the volume of the HF, independent of the variation in the rest of the T and independent of the age group and sex of the subjects. Relative HF volume peaks in October, at the time of year when there is also a peak in food-storing behavior in the black-capped chickadee (Odum, 1942). We do not find such a seasonal variation in the E, another T region, which is not thought to be involved in food storing. This suggests that there is a specific link between the peak in storing behavior and the peak in relative HF volume.



**Figure 2** (A) Photomicrograph of a coronal section through the brain of a representative October bird taken at the level of the anterior commissure. The boundaries of the hippocampal formation (HF) are indicated. (V = ventricle; S = septum). (B) Photomicrograph of a coronal section through the brain of a representative bird in August taken at the level of the anterior commissure. The boundaries of the hippocampal formation (HF) are indicated (V = ventricle; S = septum).

### Why Volume?

An often recurring question is why the volume of HF has to increase to increase the function. An increase in volume of a brain nucleus could imply several things. Existing cells could get larger cell bodies or larger dendritic arbors, new neurons or glia could be added, or there could be increased vascularization. An analysis of cell densities in the HF of these birds is presently under way. There is evidence that there is a peak in *de novo* neurogenesis in HF of black-capped chickadees around October (Barnea and Nottebohm, 1994), but that same study does not find differences in total cell number in HF over the season. Both the more cells hypothesis and the larger dendritic arbor hypothesis come down to the same thing: more possible connectivity and, therefore, more brain space, leading to greater capacity or efficiency in processing spatial information (Nottebohm, 1981; Black and Greenough, 1991; Teyler, 1991; Sherry et al., 1992).

### Differences between Juveniles and Adults

In our study the juveniles had a smaller relative HF volume than the adults overall (Fig. 4). From June to August, we find an interaction between age and time of year that is nearly significant. During this interval, adults do not change their relative HF volume, whereas the relative HF volume increases in juveniles. The change in juveniles is likely to be an effect of storing experience during development. Clayton and Krebs (1994b) showed that in marsh tits, HF develops rather late compared with other brain structures and that the development of HF volume is experience dependent. When hand-raised marsh tits were allowed to store and retrieve items, their relative HF was significantly larger than that of birds of the same age that did not have the same experience. This increase was independent of age within the age range tested. We believe that the same processes are going on in chickadees.

We also see that from August to October both

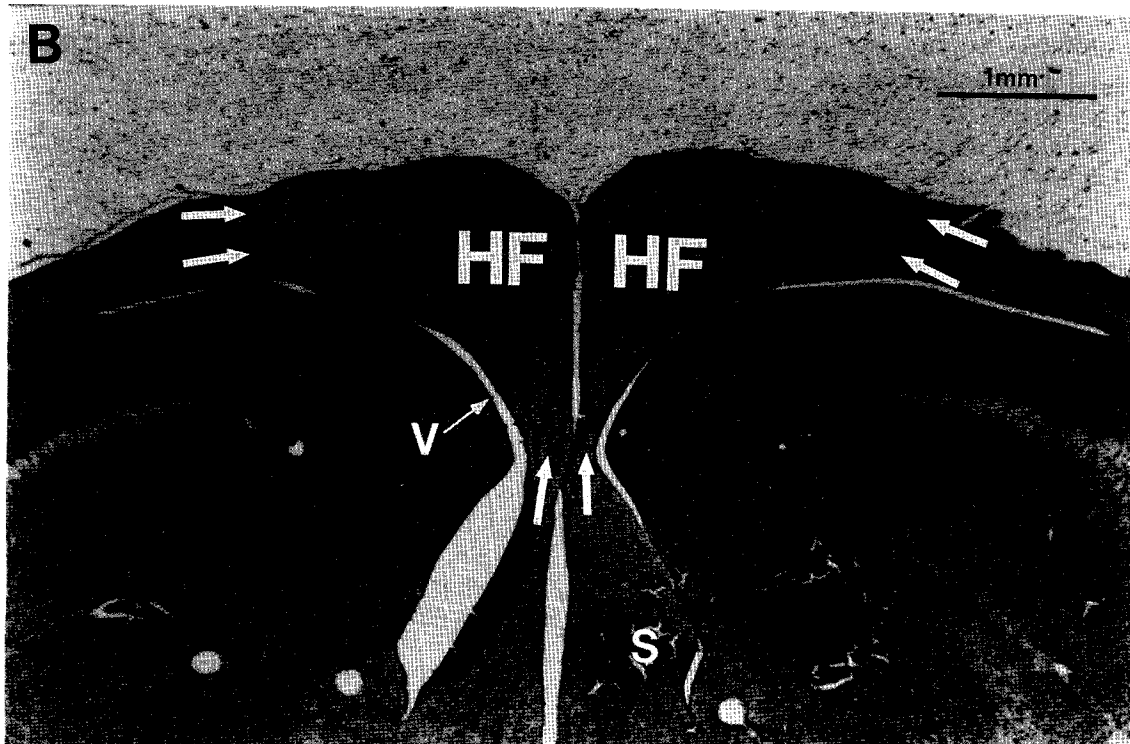


Figure 2 (Continued)

age groups increase the volume of the relative HF, but even in October, juveniles still have smaller relative HFs than adults. This could result from two reasons. Since juveniles start out with a smaller HF, it could be that they cannot reach the full adult HF size in their first fall but must wait until the next fall. Juvenile crested tits (*Parus cristatus*), wil-

low tits, and Siberian tits in the field typically store less food than do adults (Pravosudov, 1985; Lens et al., 1994). Thus, they have less experience with food hoarding, which may keep the HF size smaller than that of adults.

Alternatively, it could be that the experience of juvenile birds with food hoarding is enough to

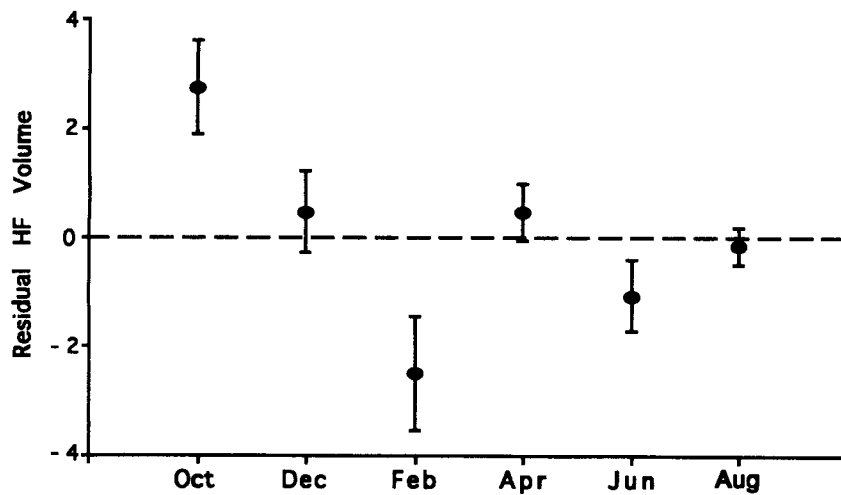


Figure 3 Residuals ( $\pm$ SEM) from the general linear model with HF volume as the dependent variable and telencephalon volume, sex, and age as the independent variables.

bring HF to maximum size, but that the spread on juvenile relative HF volumes is larger than that for adults, with the juveniles at the upper end of the spectrum having the same size HF as adults, but many others having a smaller relative HF. This would bring the mean of juvenile relative HF volumes down below that of adults. During the first winter, then, birds with smaller relative HF could be selected out (possibly because they are not as good at retrieving hoards) so that only the ones with a larger relative HF survive to become adults. No data are available to discriminate between these hypotheses.

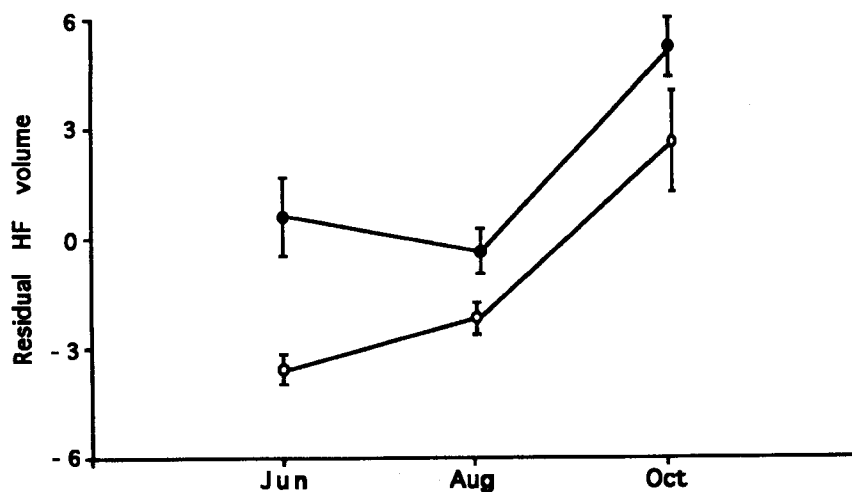
### Mechanisms of HF Seasonal Volume Change

Ludescher (1980) found that in willow tits, like in black-capped chickadees, food-hoarding activity peaks in the fall, even when food supply is kept constant. This means hoarding is not triggered by a sudden overabundant food supply. Shettleworth et al. (1995) found a similar result in black-capped chickadees by varying day length and temperature in a laboratory setting. The increase in storing activity can be linked to the increase in HF volume in two possible ways. First, it could be that the variation in HF volume is triggered by the same change in day length or temperature as the behavior itself. If this is the case, the enlargement of the HF could precede the peak in hoarding behavior, thus setting up the system to be ready for a higher demand on spatial memory. Our study does not have the temporal resolution necessary to determine whether this is true.

Alternatively, the increase in HF size could be a consequence of the increased use of spatial memory that accompanies an increase in hoarding behavior. This would imply that the experience-dependent plasticity seen in development, as already mentioned (Clayton and Krebs, 1994b), continues into adulthood in a cyclical pattern. In a recent study by Krebs et al (unpublished data), one group of black-capped chickadees was artificially induced to store by manipulating day length and temperature, while another group was kept in a nonstoring condition. They were sacrificed at the time of the largest behavioral differences, but no difference in HF size could be found. These animals, however, may not have activated a memory mechanism when storing or retrieving their food, since the hoards were in the individual home cages and always visible. Thus, these results do not argue against the hypothesis that memory use influences the size of HF.

### Why the Peak in October Only?

Why is HF only larger in October, but not during the rest of the winter? Four possible explanations could be given for this, assuming enhanced anatomy is linked to better spatial memory functioning. First, it could be that the variation in HF volume is not linked to food storing at all but is due to some other, unknown reason. It could be linked to another behavior or process that peaks in October. A possible candidate would be having to incorporate new spatial information about a larger home range. Black-capped chickadee flock home ranges



**Figure 4** Residuals ( $\pm$ SEM) from the regression with HF volume as the dependent variable and telencephalon volume as the independent variable, for adults (●) and juveniles (○) in June, August, and October.



are two to three times larger than breeding territories (Glase, 1973). Flocks form in late summer, somewhere between our August and our October data points. The increase in HF volume could therefore be related to the increased need for storing spatial information or for expanding the cognitive spatial map (Bingman and Jones, 1994). Repeating the study for a nonstoring bird with a similar ecology and natural history could resolve this issue.

Second, the change in relative HF volume may be related to a peak in food hoarding and retrieving behavior that is limited to October (Odum, 1942). Increased storing in October has been reported for willow tits (Ludschner, 1980; Nakamura and Wako, 1988) and for black-capped chickadees in northern New York (Odum, 1942). It is less clear whether there is an October peak in retrieval. Experiments with marsh tits (Cowie et al., 1981; Stevens and Krebs, 1985) and willow tits (Brodin, 1992) suggesting that seeds are never stored for more than 2 weeks were based on the speedy disappearance of stored seeds. Those seeds, however, had been supplied to the bird on a feeder table by the experimenter. In a recent study in Sweden, Brodin (1994) showed that willow tits treat naturally foraged food differently than food presented on a feeder. The latter are temporarily hoarded to be able to exploit the food source efficiently but may later be rehoarded in a more permanent location to avoid high cache concentrations. Similar observations were made by Kraft (1990) on a marsh tit, and Nakamura and Wako (1988) on willow tits. Field data from several sources also suggest long-term use of hoards in willow tits (Haftorn, 1954) and varied tits (*Parus varius*) (Higuchi, 1977). Most food-storing parids, therefore, probably do store seeds for longer periods, which suggests that a fall peak in both storage and retrieval is unlikely.

Third, food may be stored for long periods of time, but memory would be used only for short-term retrieval (and possible rehoarding) in the fall. Retrieval in winter would then be accomplished by other mechanisms, such as a separation of hoarding niches between members of the flock. This strategy allows individuals to retrieve mainly their own hoards, without having to remember the exact caching locations. Individual willow tits and crested tits separate their hoarding niches when hoarding items in the fall (Brodin, 1994; Lens et al., 1994). If black-capped chickadees also use other strategies than memory for long-term retrieval, this suggests that the HF is enlarged when spatial memory is needed (for distributing and re-

distributing hoards throughout the territory) but decreases again in volume once a different retrieval mechanism is initiated.

Fourth, memory could be needed even for long-term retrieval, but HF might not be involved in (long-term) memory retrieval, just in memory encoding. Hitchcock and Sherry (1990) showed that black-capped chickadees can retain memories for hoarded seeds for at least 4 weeks in a laboratory situation. Laboratory testing may underestimate the natural persistence of memory, even though the latter may involve many thousands of caches (Pravosudov, 1985), as there are fewer salient cues for orientation, and these are always the same ones, in contrast to the natural situation (Brodbeck et al., 1992). Brodin (1994) finds a higher recovery rate for the first 6 weeks after hoarding of naturally foraged food in willow tits in the field, after which the retrieval rate levels off to a baseline. This suggests a memory span of about the same length as suggested by Hitchcock and Sherry (1990) for black-capped chickadees in the laboratory. Several corvid species have been shown to remember caches in the field (Tombback, 1980; Vander Wall and Hutchins, 1983) and in the laboratory (Balda and Kamil, 1992) for several months.

It remains unknown whether long-term recovery makes use of the HF in the same way as short-term. Krushinskaya (1966) for European nutcrackers (*Nucifraga caryocatactes*) and Sherry and Vaccarino (1989) for black-capped chickadees have demonstrated that the HF is important for remembering the location of stored food items. However, they do not show at which stage of the memory process the HF is crucial. The HF could be important for storing memory, for retrieval of memory, or for both. These experiments cannot resolve this issue because the birds' HFs were ablated before they stored any seeds. If black-capped chickadees use memory to retrieve their caches after several months, our results suggest that enhanced anatomy in HF is not a necessary component of the retrieval mechanism, at least not to the degree that it needs to be sustained all winter long.

These hypotheses are not mutually exclusive. Birds could use the enlarged HF for both storing information about a new, larger home range and for food hoarding. It is possible for birds to separate their hoarding niches ecologically and still use memory to retrieve their hoards.

## CONCLUSIONS

The HF of the black-capped chickadee varies in volume throughout the year, with a peak in Octo-

ber. We conclude that the peak in relative HF volume in October is related to the peak in food-storing behavior at that time of year and that it could be caused by the extensive use of spatial memory.

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## REFERENCES

- BALDA, R. P. and KAMIL, A. C. (1992). Long-term spatial memory in Clark's Nutcracker, *Nucifraga columbiana*. *Anim. Behav.* **44**:761-769.
- BARNEA, A. and NOTTEBOHM, F. (1994). Seasonal recruitment of hippocampal neurons in adult free-ranging black-capped chickadees. *Proc. Natl. Acad. Sci. USA* **91**:11217-11221.
- BINGMAN, V. P. (1990). Spatial navigation in birds. In: *Neurobiology of Comparative Cognition*. R. Kesner and D. Olton, Eds., Erlbaum, Hillsdale, NJ, pp. 423-447.
- BINGMAN, V. P. and JONES, T.-J. (1994). Sun compass based spatial learning impaired in homing pigeons with hippocampal lesions. *J. Neurosci.* **14**:6687-6694.
- BLACK, J. E. and GREENOUGH, W. T. (1991). Developmental approaches to the memory process. In: *Learning and Memory: A Biological View*. J. L. Martinez Jr. and R. P. Kesner, Eds.: Academic Press, San Diego, pp. 61-91.
- BRENEWITZ, E. A., NALLS, B., WINGFIELD, J. C., and KROODSMA, D. E. (1991). Seasonal changes in avian song nuclei without seasonal changes in song repertoire. *J. Neurosci.* **11**:1367-1374.
- BRODBECK, D. R. (1994). Memory for spatial and local cues: a comparison of a storing and a nonstoring species. *Anim. Learn. Behav.* **22**:119-133.
- BRODBECK, D. R., BURACK, O. R., and SHETTLEWORTH, S. J. (1992). One-trial associative memory in black-capped chickadees. *J. Exp. Psych. Anim. Behav. Process.* **18**:12-21.
- BRODIN, A. (1992). Cache dispersion affects retrieval time in hoarding Willow Tits. *Ornis Scand.* **23**:7-12.
- BRODIN, A. (1994). The disappearance of caches that have been stored by naturally foraging Willow Tits. *Anim. Behav.* **47**:730-732.
- CASINI, G., BINGMAN, V. P., and BAGNOLI, P. (1986). Connections of the pigeon dorsomedial forebrain studied with WGA-HRP and <sup>3</sup>H-proline. *J. Comp. Neurol.* **245**:454-470.
- CLAYTON, N. (1993). Lateralization and unilateral transfer of spatial memory in Marsh Tits. *J. Comp. Physiol. A* **171**:799-806.
- CLAYTON, N. S. and KREBS, J. R. (1994a). Memory for spatial and object-specific cues in food-storing and non-storing birds. *J. Comp. Physiol. A* **174**:371-379.
- CLAYTON, N. S. and KREBS, J. R. (1994b). Hippocampal growth and attrition in birds affected by experience. *Proc. Natl. Acad. Sci. USA* **91**:7410-7414.
- COWIE, R. J., KREBS, J. R., and SHERRY, D. F. (1981). Food storing by marsh tits. *Anim. Behav.* **29**:1252-1259.
- ERICHSEN, J. T., BINGMAN, V. P., and KREBS, J. R. (1991). The distribution of neuropeptides in the dorsomedial telencephalon of the pigeon (*Columba livia*): a basis for regional subdivisions. *J. Comp. Neurol.* **314**:478-492.
- GLASE, J. C. (1973). Ecology of social organization in the black-capped chickadee. *Living Bird* **12**:235-267.
- HAFTORN, S. (1954). Contribution to the food biology of tits especially about storing of surplus food. Part I. The crested tit (*Parus c. cristatus* L.). *K. Norske Vidensk. Selsk. Skr.* 1953(4):1-123.
- HIGUCHI, H. (1977). Stored nuts *Castanopsis cuspidata* as a food resource of nestling varied tits *Parus varius*. *Tori* **26**:9-12.
- HITCHCOCK, C. L. and SHERRY, D. F. (1990). Long-term memory for cache sites in the black-capped chickadee. *Anim. Behav.* **40**:701-712.
- KIRN, J. R., CLOWER, R. P., KROODSMA, D. E., and DEVOOGD, T. J. (1989). Song-related brain regions in the red-winged blackbird are affected by sex and season but not repertoire size. *J. Neurobiol.* **20**:139-169.
- KRAFT, M. (1990). Bemerkenswertes Nahrungsdepot einer markierten Sumpfmehse *Parus palustris*. *Anz. Orn. Ges. Bayern* **2**:170-171.
- KRAYNIAK, P. F. and SIEGEL, A. (1978a). Efferent connections of the hippocampus and adjacent regions in the pigeon. *Brain Behav. Evol.* **15**:372-388.
- KRAYNIAK, P. F. and SIEGEL, A. (1978b). Efferent connections of the septal area in the pigeon. *Brain Behav. Evol.* **15**:389-404.
- KREBS, J. R., SHERRY, D. F., HEALY, S. D., PERRY, V. H., and VACCARINO, A. L. (1989). Hippocampal specialization of food-storing birds. *Proc. Natl. Acad. Sci. USA* **86**:1388-1392.
- KREBS, J. R., ERICHSEN, J. T., and BINGMAN, V. P. (1991). The distribution of neurotransmitters and neurotransmitter-related enzymes in the dorsomedial telencephalon of the pigeon (*Columba livia*). *J. Comp. Neurol.* **314**:467-477.
- KRUSHINSKAYA, N. L. (1966). Some complex forms of feeding behaviour of nut-cracker *Nucifraga caryocatactes*, after removal of old cortex. *Zh. Evol. Biokhim. Fisiol.* **11**:563-568.
- LENS, L., ADRIAENSEN, F., and DHONDT, A. A. (1994). Age-related hoarding strategies in the crested tit *Parus cristatus*: should the cost of subordination be reassessed? *J. Anim. Ecol.* **63**:749-755.
- LUDESCHER, F. B. (1980). Fressen und Verstecken von Sämereien bei der Weidenmehse *Parus montanus* im Jahresverlauf unter konstanten Ernährungsbedingungen. *Okol. Vogel* **2**:135-144.

- NAKAMURA, H. and WAKO, Y. (1988). Food storing behavior of willow tit *Parus montanus*. *J. Yamashina Inst. Ornithol.* **20**:21–36.
- NOTTEBOHM, F. (1981). A brain for all seasons: cyclical anatomical changes in song control nuclei of the canary brain. *Science* **214**:1368–1370.
- O'KEEFE, J. and NADEL, L. (1978). *The Hippocampus as a Cognitive Map*. Clarendon Press, Oxford.
- ODUM, E. P. (1942). Annual cycle of the black-capped chickadee-3. *Auk* **59**:499–531.
- OLTON, D. S. (1983). Memory functions and the hippocampus. In: *Neurobiology of the Hippocampus*. W. Seifert, Ed. Academic Press, London, pp. 335–373.
- PRAVOSUDOV, V. V. (1985). Individual differences in foraging and storing behaviour in Siberian Tit *Parus cinctus* Bodd. and Willow Tit *Parus montanus* Bald. *Sov. J. Ecol.* **4**:60–64.
- REHKÄMPER, G., HAASE, E., and FRAHM, H. D. (1988). Allometric comparison of brain weight and brain structure volumes in different breeds of the domestic pigeon *Columbia livia* f.d. (Fantails, homing pigeons, Strassers). *Brain Behav. Evol.* **31**:141–149.
- SHERRY, D. F. (1989). Food storing in the Paridae. *Wilson Bull.* **101**:289–304.
- SHERRY, D. F. and VACCARINO, A. L. (1989). Hippocampus and memory for food caches in Black-Capped Chickadees. *Behav. Neurosci.* **103**:308–318.
- SHERRY, D. F., VACCARINO, A. L., BUCKENHAM, K., and HERZ, R. S. (1989). The hippocampal complex of food-storing birds. *Brain Behav. Evol.* **34**:308–317.
- SHERRY, D. F., JACOBS, L. F., and GAULIN, S. J. C. (1992). Spatial memory and adaptive specialization of the hippocampus. *Trends Neurosci.* **15**:298–303.
- SHERRY, D. F., FORBES, M. R. L., KHURGEL, M., and IVY, G. O. (1993). Females have a larger hippocampus than males in the brood-parasitic Brown-Headed Cowbird. *Proc. Natl. Acad. Sci. USA* **90**:7839–7843.
- SHEFFLEWORTH, S. J. (1990). Spatial memory in food-storing birds. *Phil. Trans. R. Soc. Lond. B* **329**:143–151.
- SHEFFLEWORTH, S. J. and KREBS, J. R. (1982). How marsh tits find their hoards: the roles of site preference and spatial memory. *J. Exp. Psych.: Anim. Behav. Process* **8**:354–375.
- SHEFFLEWORTH, S. J., HAMPTON, R. R., and WESTWOOD, R. P. (1995). Effects of season and photoperiod on food-storing by black-capped chickadees (*Parus atricapillus*). *Anim. Behav.* (in press).
- SMITH, S. (1991). *The Black-Capped Chickadee: Behavioral Ecology and Natural History*. Cornell University Press, Ithaca, NY.
- SQUIRE, L. R., KNOWLTON, B., and MUSEN, G. (1993). The structure and organization of memory. *Annu. Rev. Psychol.* **44**:453–495.
- STEVENS, T. A. and KREBS, J. R. (1985). Retrieval of stored seeds by marsh tits *Parus palustris* in the field. *Ibis* **128**:513–525.
- TEYLER, T. J. (1991). Memory, electrophysiological analogs. In: *Learning and Memory: A Biological View*. J. L. Martinez Jr. and R. P. Kesner, Eds.: Academic Press, San Diego, pp. 299–327.
- TOMBACK, D. F. (1980). How nutcrackers find their seed stores. *Condor* **82**:10–19.
- VANDER WALL, S. B. and HUTCHINS, H. E. (1983). Dependence of Clark's nutcracker (*Nucifraga columbiana*) on conifer seeds during the postfledgling period. *Can. Field Nat.* **97**:208–214.
- WATANABE, S., HODOS, W., BESSETTE, B. B., and SHIMIZU, T. (1986). Interocular transfer in parallel visual pathways in pigeons. *Brain Behav. Evol.* **29**:184–195.