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Patterns of food storing by black-capped chickadees suggest a mnemonic hypothesis

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Abstract. There is no general theory of cache dispersal in food-storing animals. The present study of free-ranging black-capped chickadees, *Parus atricapillus*, was undertaken to determine whether caches were deployed in ways that might reduce the overall memory load required for cache recovery. Birds were studied in natural habitats of New York state's Hudson Valley during the time of the year when they lived in flocks. Birds were offered sunflower seeds at feeders during the autumn and winter. Storing flights ended usually at short distances from the feeder and tended to cluster around a preferred orientation. This orientation often persisted on subsequent days and overlapped with that of other flock members. The behaviour observed may reflect a compromise between the need to minimize the energy cost for food storing (close to source), to minimize the risk of thievery (scatter-hoarding), and to optimize the memorization of caching sites. One hypothesis offered to explain this behaviour is that cached sites clustered in a particular direction will be remembered with reference to a common set of landmarks, and thus pose less of a memory load than items cached over a broad area using all directions away from a food source.

Two years ago we noticed that individual colour-banded black-capped chickadees, *Parus atricapillus*, carrying sunflower seeds away from a feeder tended to depart in a narrowly defined direction. What could be the significance of this behaviour? We report here the results of the study that followed.

Our observations of chickadees were prompted by an interest in understanding the behavioural and neural mechanisms used by small animals trying to acquire a lot of information. Brain space may limit how much can be learned (Nottebohm et al. 1981; Canady et al. 1984). The hippocampus is thought to be involved with the acquisition of spatial memories (O'Keefe & Nadel 1978; Bingman et al. 1984) and it has been suggested that the amount and complexity of spatial information that an animal can remember is related to the size of the hippocampus. Birds that engage in food storing have a relatively larger hippocampus than those that do not (Krebs et al. 1989; Sherry et al. 1989). Similarly, female brown-headed cowbirds, *Molothrus ater*, a nest parasite, have a larger hippocampus than males, possibly related to the females' need to remember the location of the various nests where they will lay their eggs (Sherry et al. 1993).

The amount of information about external events that a brain can acquire and remember is probably limited not just by the brain space available but also by the way in which memories are acquired and linked. Data organized in 'chunks' are more readily remembered than random collections of data (Miller 1956; Mandler 1967; Simon 1974; Wickelgren 1979; Terrace 1987). However, we know very little about the nature of the information that wild animals living in their natural surroundings acquire and how they 'chunk' it. Food storing by animals may allow us to look at the way in which some animals chunk spatial memories.

Many mammals and birds store food and use it later. They follow different strategies for storing this food, ranging from highly distributed (scatter-hoarding) to highly clumped (larder-hoarding) stores (Vander Wall 1990). However, there is no theory of cache dispersal that predicts what each species will do. The strategy evolved by each species should combine a number of requirements. Specifically, it should (1) minimize the cost of

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caching, defending and retrieving food; (2) minimize the chances of spoilage; (3) minimize the risk of losing access to the stored food, for example, by snow, ice or floods; (4) minimize the risk of theft; and (5) maximize the animal's ability to remember where each food item was stored.

Optimal cache dispersal by scatter-hoarders has been addressed by two models, both based on costs and benefits of spacing caches (Stapanian & Smith 1978; Clarkson et al. 1986). These models predict, among other things, that caching should occur in a 360° arc around the source, unless some of the area is unsuitable for caching. However, field experiments (Stapanian & Smith 1978; Cowie et al. 1981; Kraus 1983; Clarkson et al. 1986; Hurly & Robertson 1987) used to test these models showed that caches are rarely distributed in a uniform manner around the source. For example, individual fox squirrels, *Sciurus niger*, grey squirrels, *S. carolinensis*, red squirrels, *Tamiasciurus hudsonicus*, marsh tits, *Parus palustris*, and magpies, *Pica pica*, transport food items to only a portion of the area surrounding the food source, resulting in a cache dispersion that is strongly directional. These scatter-hoarders live in pairs (marsh tits), solitarily (squirrels), or with varying levels of conspecific intrusion (magpies). Individuals living or foraging in close proximity may avoid using overlapping caching areas and thus not use the full 360° arc around a food source to store food (Cowie et al. 1981; Clarkson et al. 1986). In addition, some of the clumping of storage sites may reflect substrate properties that are important to the animals but are not obvious to the observer. Some site clumping could result, too, from individuals transferring food to core areas of their home range or territory where it can be more readily defended.

The use of space for food storing has not been studied in scatter-hoarders that live in flocks. These animals share the same territory or home range for long periods of time. In a case where a group is moving and foraging together, competition between members of the group is probably intense and continuous, and one might predict, from this alone, that individuals might try to minimize the overlap between the space they use for caching and that used by other members of the flock. That is, individuals might feel encouraged to have exclusive use of caching sectors while the flock as a whole might make full use of all sectors around a rich food source.

The aim of the present study was to describe the use of space for food storing by free-ranging flocks of black-capped chickadees and by individual members of a flock. It was our hope that our collection of data would tell us something about the rules that organize food caching and, as a result, give us some feeling for the complexity of the memories underlying cache retrieval. Maximal complexity would occur if each food item were stored in a random direction from where it was found, so that its retrieval would require a rather complete description of each storage site. Minimal complexity would result from storing all items in a same place. Intermediate levels of complexity would result from storing food items according to simple rules that reduce the amount of information that had to be remembered. For example, a bird might choose to store seeds from a particular tree in sites clustered in a particular direction away from this tree. Observations on the directionality of storing activity can help us discriminate between these various strategies.

Black-capped chickadees are omnivorous and found year-round in much of temperate North America. These birds are very common in the Hudson Valley, where the present study was conducted. During autumn and winter black-capped chickadees live in flocks, consisting of 5–12 individuals. Such flocks have an average home range of about 15 ha (Butts 1931; Odum 1942; Smith 1967). During the day the flock moves around the home range, foraging on invertebrates and seeds. Some of the food is eaten immediately, while the rest is stored in cracks, beneath bark, moss or lichens, or on branches and tree trunks, with one or a very few items per cache site (Sherry 1989).

We addressed the following general question. Do members of a chickadee flock or the entire flock direct their storing activity towards a restricted area of the home range? To answer this question we observed the direction of food-storing flights of chickadees coming to feeders. The specific questions we asked were as follows.

(1) Is food storing activity around a feeder oriented towards a particular direction?

(2) If activity is oriented, does the preferred direction stay the same on different days, or can it change?

(3) If activity is oriented, do individuals within the same flock overlap in their preferred caching directions?

(4) Is it possible to use data on food-storing directions to discern the strategy used by black-capped chickadees and understand how it relates to specific selective pressures?

Study Site

The study was conducted at The Rockefeller University Field Research Center for Ecology and Ethology in Millbrook, New York. Millbrook is 130 km to the north of New York City, in rural Hudson Valley. The Field Research Center comprises 492 ha of natural habitats consisting of woodlands, meadows and marshes.

METHODS

Characterization, Quantification and Localization of Storing Activity

Field observations were done on two flocks of black-capped chickadees. These flocks were part of a broader banded population (five flocks) which had been observed for 2 years prior to this study. The home range of each flock was determined by prior field observations. Each bird was banded with a unique combination of colour and aluminium bands. We placed our feeders well within a flock's home range, thereby increasing the likelihood that all birds observed at a feeder belonged to the same flock. Moreover, feeders were placed in wooded areas; they were surrounded by vegetation in all directions, affording many potential food-storing sites.

We observed the birds at feeders baited with sunflower seeds during December 1991 and February, September and October 1992. We baited the feeders with seeds one day before observations were made. All observations were done between 1000 and 1500 hours, using binoculars, at a distance of about 10 m from the feeder, for at least 0·5 h at each location. A landmark close to each feeder was chosen to be 'direction zero' (or 12 o'clock) and space around the feeder was accordingly divided by eye, in clockwise order, into 12 equal arcs of 30° each. The identity of birds taking seeds from the feeder and the directions of their 'storing flights' were determined to the closest 'clock hour' and recorded on a tape-recorder. As far as possible each bird was followed visually until it landed to either eat or store the seed.

Field workers are familiar with the dilemma of what to observe. If one tries to observe everything, this may be at the expense of focusing on any one feature. If one tries to observe all animals in a group, this may be at the expense of having enough entries for meaningful statistical comparisons between any two individuals. Moreover, one has to be careful not to intrude into the very behaviour that one is trying to observe. For these reasons, we chose to gather data on just one variable, direction of storing fights.

In most cases the observer (always A.B.) did not see the actual storing site, as when the storing activity occurred high up in trees, or in very dense vegetation, or on the backside of tree trunks. However, 'storing' and 'eating' behaviour were different and therefore it was possible to discriminate between them. When eating a seed the bird usually landed on a branch close to the feeder, held the seed between its feet and pecked at the husk to open it. Once the husk had been opened the bird took bites of the seed's inner part, still holding it down between its feet, until the shell was empty. A bird showing storing behaviour landed and started hopping with the seed in its beak, presumably looking for a storing site. We scored this as 'storing activity'. In some cases it was possible to see the actual storing; the bird wedged the seed under bark, in moss, or into cracks of branches or trunks. But even then we did not try to inspect and verify the storing site. As a result, all our data concern the direction of storing flights, not the location of storing sites. Attempts to verify storing sites would have interfered with the birds' behaviour, and would have been time consuming and often physically difficult.

At the beginning of our study we tried to estimate the horizontal distance of all flights in which a banded chickadee carried a seed away from the feeder, regardless of how the flight ended. These observations (e.g. those of 18 December 1991) showed that three-fourths or more of all these flights ended with the bird landing within a radius of 15 m from the feeder. The observation range varied from feeder to feeder, depending on the surrounding vegetation, but it was never less than 15 m. The direction of storing flights was given by the line connecting the feeder and the place where the bird landed to start its storing activity. The birds flew directly from the feeder to the landing site, in what looked like a fairly straight line. We compared the direction

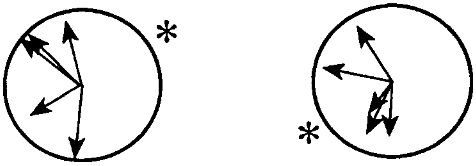

Figure 1. Mean vectors (r_c) of departing food-storing flights of black-capped chickadees from the same flock, observed on 20 December 1991 at feeder 4 for two consecutive 0·5-h periods from each of two different locations. Each vector stands for the mean direction of storing flights for a single bird; when a bird was observed only once the direction of the vector represents that flight. *Indicates position of observer.

of all seed-carrying flights away from the feeder with the direction of those that ended in observable storing activity. We did not record the substrate on which the bird landed to start its 'storing activity', nor the height above the ground where this happened. In short, we focused on the one behavioural variable, the direction of storing flights, that we felt could be recorded in an objective and quantitative manner with a minimum of disturbance to the birds' ongoing behaviour.

To ensure that the observer's presence and position relative to the feeder did not affect the birds' flight directions we carried out a simple experiment. A certain feeder was observed for two consecutive 0·5-h periods from each of two different locations. The outcome of this test (Fig. 1) satisfied us that the orientation of the storing flights was not related to the position of the observer. In addition, we show in all other figures the position of the observer with respect to the feeder and direction of the storing fights.

Protocols and Statistical Analysis Used to Study Storing Activity

Is there a preferred single area for food storing within the flock's home range?

Three feeders were set along a narrow trail, about 50 m apart, within the home range of the same flock (feeders 1, 2 and 3). All feeders were baited at the same time and observed in succession for 0·5-h periods, on four dates: 18 and 30 December 1991 and 18 and 28 February 1992. If there had been a single preferred place within the flock range where members of a flock stored their food, birds would have gone there from all three feeders.

We calculated the mean vector for each bird at each feeder using the methods of circular statistics described by Batschelet (1981, pp. 7 and 37). A mean vector incorporates sine and cosine data from each individual observation, that is, the mean obtained is a geometrical, not arithmetical mean. A mean vector was defined by direction ($\bar{X}^{\circ}$=mean angle of sample) and strength (r_c=mean vector length). We define significant directionality of flights as a clustering of directions that would occur by chance with a probability of 5% or less. The following examples demonstrate how this works. (1) If a bird flies in two directions, 0° and 180° to store its food, the mean of these two flights will be 90°, but this mean will come with a vector length of zero, i.e. no directionality. (2) If a bird flies in two directions, at 85° and 95°, the mean again will be 90°, but this time the vector length is very close to 1, indicating strong directionality.

To test whether birds departing on storing flights from several feeders within the flock's range converged on a common storing area, we included all birds observed, regardless of the number of flights observed for each bird at any one feeder. The 'mean vector' for this test equalled the mean of several flights away from a particular feeder by a particular bird, or for the single flight observed. However, when testing whether a bird that stored food obtained at various feeders used a single storage area, we only used data from five birds for which we had a minimum of five storing flights from each feeder on that particular date. Therefore, for the latter situation the 'mean vector' represents a minimum of five flights.

Is food-storing activity around each feeder oriented or random?

All feeders and dates included above were also used to test this question. In addition, one more feeder was set in another flock's home range, and more observations were done on other dates (14–15 September and 24–27 October 1992). Each feeder was observed on at least three dates, every time for 0·5 h.

We calculated for each bird at each feeder the mean vector, using the methods described above. When testing for directionality of storing flights at the flock level, we included all birds observed, each represented by a 'mean vector', regardless of number of flights. Our data for each feeder did not show a bivariate normal distribution, and therefore we used the Moore non-parametric test for directionality (Batschelet 1981) to test for flock orientation. This test requires that mean vectors be based on first-order samples of equal sizes, but in our case different number of flights were included for different birds. However, it has been shown before that violation of this condition (i.e. the use of samples of unequal size) does not have serious statistical consequences (Batschelet 1981). To confirm this, we chose one case randomly (Fig. 3a, 15 September) and tested it twice: once with our samples of unequal size, and then with mean vectors based on samples of equal size ($N=5$ flights, chosen randomly for each bird). We repeated the latter test 10 times, using different combinations of the five randomly chosen flights per bird. All tests yielded similar results.

Results for single individuals included only those birds for which we had observations on the direction of at least five storing flights. We used the Rayleigh test (Batschelet 1981) to determine whether any directedness that might be shown by the storing flights of these individuals was significant.

Do food-storing flights from a feeder show similar orientation on different days?

We only used birds observed on several days at the same feeder whose food-storing flights showed a significant orientation on each of these days. Nine individuals from two different flocks met these conditions. The data allowed us to make 25 comparisons. The rank-sum test (Batschelet 1981) was used to determine whether a bird's preferred direction of storing flights was the same on different dates. However, this test is designed for small sample sizes where neither N_1 nor N_2 is greater than 12. Therefore, when sample sizes exceeded that limit (up to $N_1=15$; $N_2=14$) we applied the run test (Batschelet 1981), also designed to test two samples with respect to the mean angles. Both tests require a continuous circular distribution of data. Because our single data points were grouped (class interval of 30°), we transformed data for each bird by breaking ties and spacing them evenly within the class interval (we did this following the advice of mathematician Joel Cohen, The Rockefeller University, personal communication). For example, in the case of two observations to direction 30° (1 o'clock) for a particular bird at a particular feeder, these observations were transformed into 25° and 35°, and in case of three observations to the same direction transformation was to 22·5°, 30° and 37·5°. The effect of this transformation would be to counter the very strong directionality that a particular bird might have shown, as would be the case if all its flights had actually been at 30°. As a result, estimates of means and statistical comparisons of means obtained in this manner are conservative.

Do members of a flock overlap in the direction of their storing flight?

This question was studied whenever two or more individuals were observed at the same feeder on the same day and were found to have preferred orientations in their food storing flights. In such cases (45 comparisons, made among 20 birds tested on nine dates and at four different feeders) we compared the mean angles of the oriented individuals to determine whether they overlapped in their preferred food-storing direction. Each comparison was tested by either rank-sum or run test, depending on sample size (see above).

RESULTS

The Orientation of Food-carrying Flights Away from a Feeder

Observations conducted on 18 December 1991 included the direction of all food-carrying flights away from feeders 1, 2 and 3. We compared for each bird the orientation of food-storing flights versus the orientation of all food-carrying flights. We used for our comparison only birds that had a minimum of five storing flights away from any one feeder and for whom these flights yielded a significant orientation. Four of the 10 birds observed on that date met these criteria (Fig. 2). Fifty-eight per cent of all their food-carrying flights were observed to end with food-storing activity. The mean direction of the food-storing flights was very close to that of all food-carrying flights, the mean divergence of the two vectors being 5°, with a range from 4° to 8°. We concluded from this that the direction of the observed food-storing flights away from a feeder was representative of that of all of the food-storing flights away from that feeder. Subsequently, we kept track only of

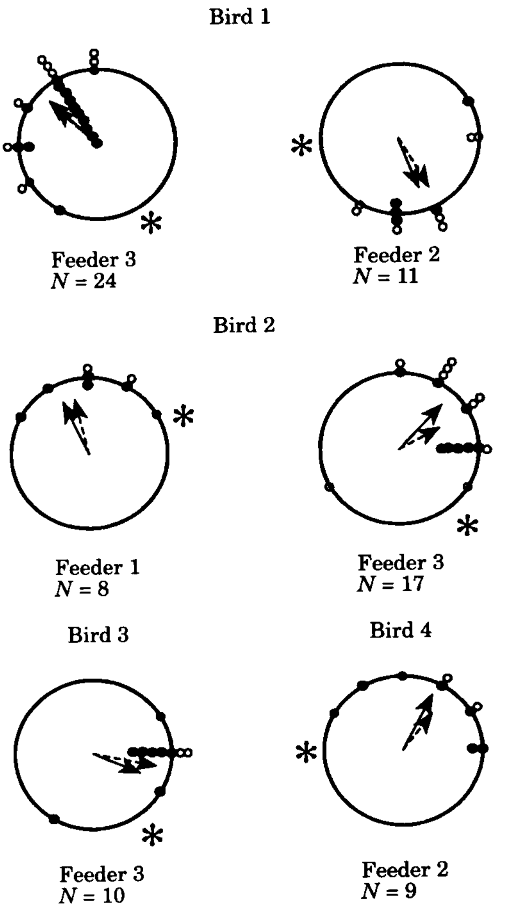

Figure 2. Mean vectors (r_c) of all food-carrying flights (– – –) and of storing flights (——) of four black-capped chickadees observed on 18 December 1991 at feeders 1, 2 or 3. N equals the number of total flights observed. *Indicates position of observer. ○: Food-carrying flights; ●: storing flights. Spatial relations between feeders are not shown.

the direction of flights that we saw end with food-storing activity.

Is There a Single Preferred Area that is Used for Storing?

Flock level

The direction of food-storing flights of individuals from one flock was observed at three feeders within the flock's home range on four different dates (Fig. 3). The results suggest that there was no single place that was preferred by the flock because storing flights from all feeders did not converge on a common point. Furthermore, in most cases the birds did not fly far away from the feeder, but tended to store seeds in the close vicinity of the feeder. For example, on 18 December we scored the direction of all food-carrying flights away from the feeder, regardless of whether the observer saw the bird land and store the seed. When observing feeder 1, only nine (38%) flights out of 24 were to distances of more than 15 m away from this feeder. The proportion of longer flights from the two other feeders was 10 (26%) out of 38 from feeder 2, and eight (22%) out of 36 from feeder 3.

Individual level

In most cases where a bird was observed on the same day at two feeders that were 50 or 100 m apart, its food-storing flights did not converge on a common point (Fig. 4). This suggests that individuals did not store their food at a single place within their home range, but tended to fly to different directions from different food sources.

Is Activity Around Each Feeder Concentrated in a Particular Sector?

Flock level

Thirteen (62%) out of 21 arrays of food-storing flights (Figs 3, 5; each feeder on each day provided one array) showed orientation, while the rest were not significantly oriented (Table I). These results indicate that in most cases the flock was not making full use of the 360° available. Furthermore, when looking at the data from each feeder for the various days sampled, the great majority of storing flights used only 180° of contiguous orientation. The clustering of directions favoured by individuals in a flock suggests that the same spatial cohesiveness shown by chickadee flocks when moving through their home range in search of food (Glase 1973) is also maintained during food caching.

Individual level

Seventy-three cases were recorded in which a bird was observed more than five times at a certain feeder on a specific day. Rayleigh tests for directedness were performed on these cases and of these tests, 54 (74%) were significant ($P<0{\cdot}05$),

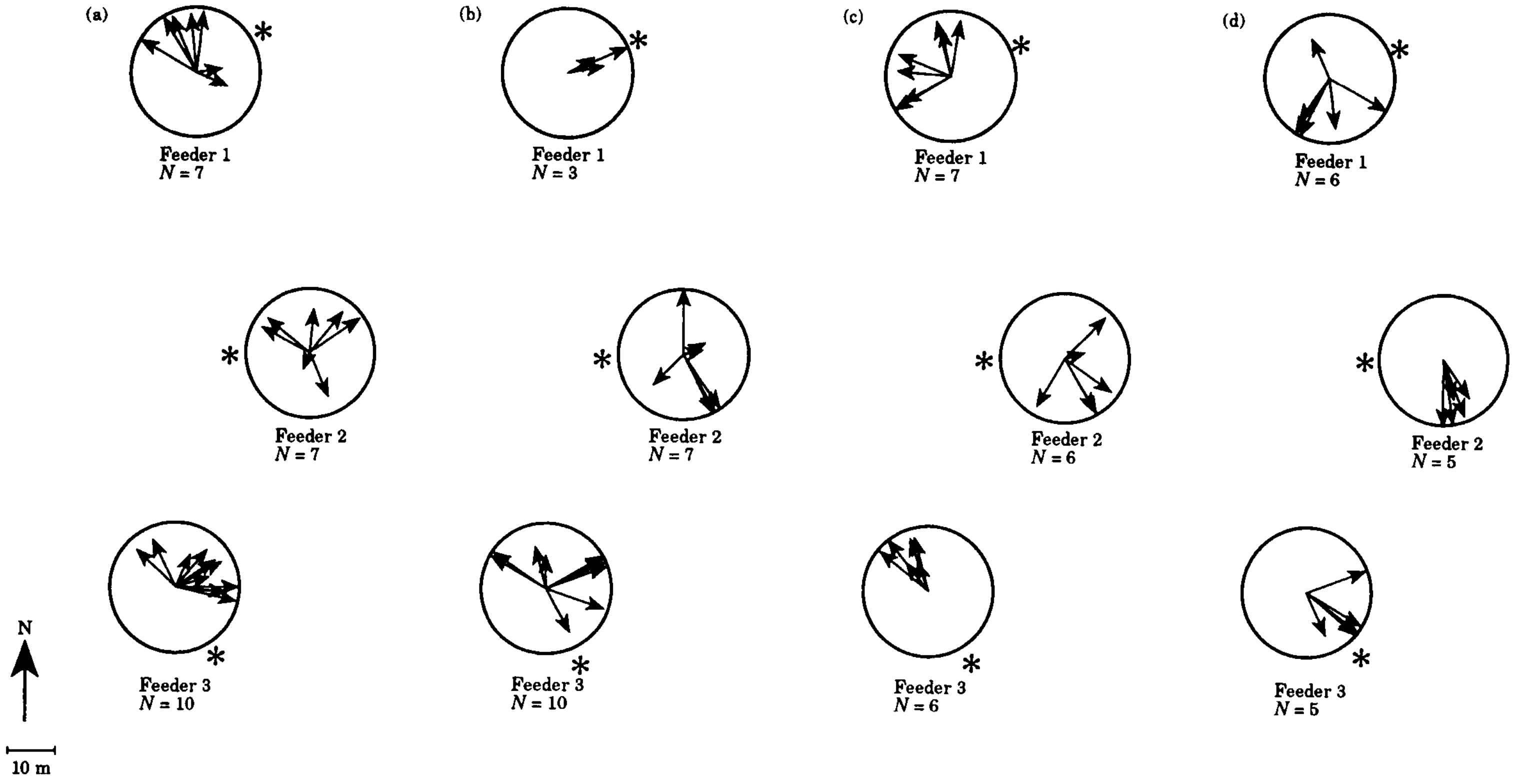

Figure 3. Mean vectors (r_c defined as in Fig. 1) of departing food-storing flights of black-capped chickadees from the same flock, observed at feeders 1, 2 and 3, on (a) 18 December 1991, (b) 30 December 1991, (c) 18 February 1992, and (d) 28 February 1992. The relative distances and compass directions between feeders are accurately represented. *N* equals the number of birds observed at each feeder. *Indicates position of observer.

indicating that the bird flew to a preferred direction to store seeds. These 73 cases, however, were based on observations of 27 individuals, 18 of which had been observed on more than 1 day. Therefore, to assure independence in the data tested, one case per individual (i.e. observations including a minimum of five flights from the same feeder on the same day) was drawn randomly, to form a sample of 27 cases. Of these 27 cases, 21 birds (78%) showed significant orientation in their storing flights away from the feeder, while only six (22%) were not found to be oriented. The probability of such a ratio occurring by chance is small (two-tailed P=0·006) suggesting that most of the black-capped chickadees we observed did not store food randomly, but tended to use a preferred direction away from a feeder.

When Activity is Oriented, Does the Preferred Direction Stay the Same on Different Days?

Out of 25 comparisons of the differences in mean angles towards which nine individuals oriented their food-storing flights from a certain feeder on different days (not same feeder for all birds), 19 birds (76%) showed no significant differences in mean angles, and only six (24%) gave significant differences (P<0·05; Table II). However, five birds were compared on more than two occasions and some of the replicates were dependent. Therefore, we repeated the calculation, this time including results of only one comparison per individual, chosen randomly. We tested nine comparisons this way and of these, seven (78%) were not significantly different and two (22%) were. The probability of this outcome occurring by chance is P=0·09, which does not meet the usually accepted criterion for significance (P<0·05). All we can say is that birds did not necessarily retain on different days the same preferred direction when storing seeds away from a feeder. In terms of our

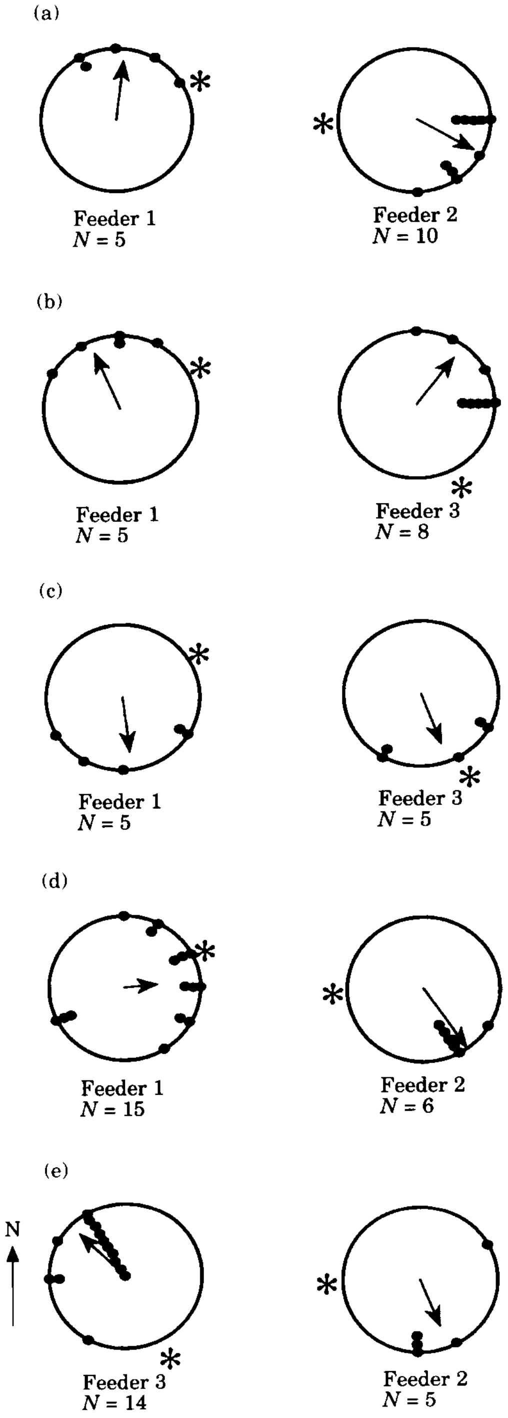

Figure 4. Mean vectors (r_c defined as in Fig. 1) of departing food-storing flights of five individual black-capped chickadees, each bird was observed at two feeders on a same day. (a) Bird 1, 18 February; (b) bird 2, 18 December; (c) bird 3, 28 February; (d) bird 4, 30 December; (e) bird 5, 18 December. Spatial relations between feeders are not shown, but the mean vectors of storing flights are true to actual compass directions. Each dot indicates a single flight direction. N equals the number of flights observed. *Indicates position of observer.

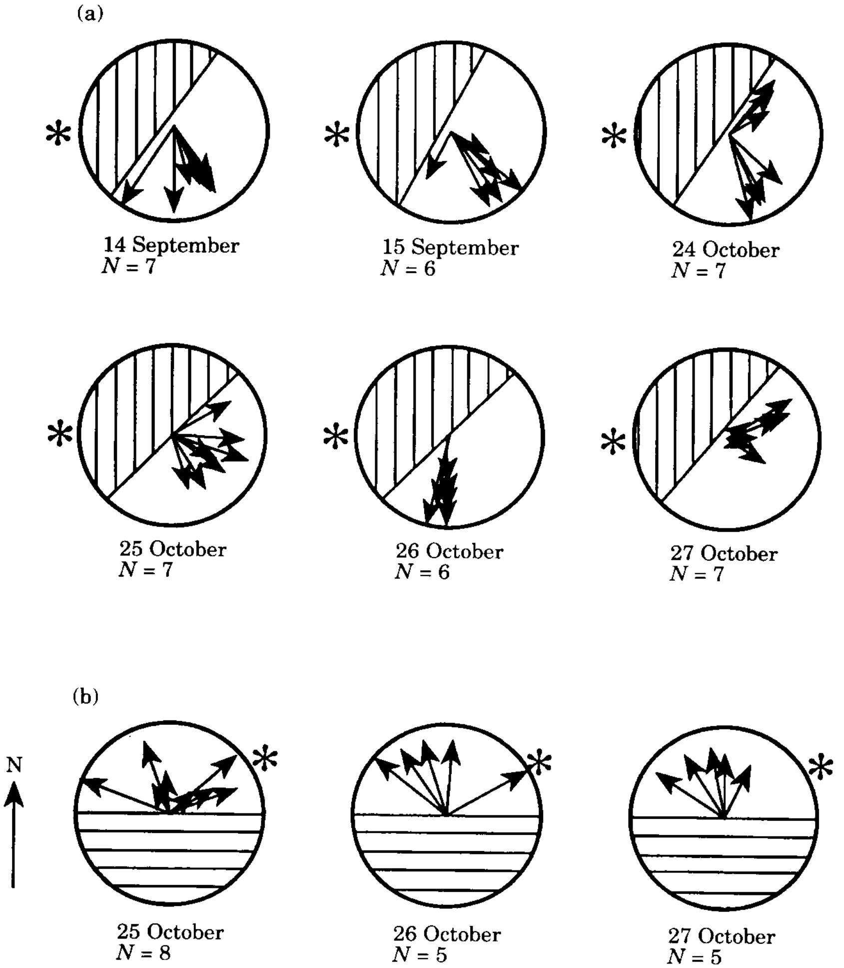

Figure 5. Mean vectors (r_c defined as in Fig. 1) of departing food-storing flights of black-capped chickadees from feeders 2 (a) and 4 (b), each within the home range of a different flock. Notice that during the period of sampling, half of the potential 360° distribution (shaded area) was grossly underused. N equals the number of birds observed. *Indicates position of observer.

original sample of 27 different birds, our results suggest that 61% ($0{\cdot}78 \times 0{\cdot}78$) of the birds showed a pattern of consistent orientation when storing food away from the same feeder on different days.

If the Storing Activity of Individuals Within a Flock is Oriented, Do They Show Overlap in the Directionality of Their Storing Flights?

We compared pairs of birds that were oriented from a particular feeder on the same day, to test whether the mean angles of their preferred food-storing directions differed or overlapped (Table III). Out of 45 comparisons, 39 (87%) did not show any significant difference in mean angles while only six (13%) yielded significant results. The probability for such a ratio occurring by chance is very small (two-tailed $P<0{\cdot}00001$), indicating that generally birds that found seeds in a particular feeder overlapped in the direction of their food-storing flights.

Table I. Results of the Moore test for directionality of two flocks of black-capped chickadees on 10 dates (one flock was observed at feeders 1, 2 and 3, and another flock was observed only at feeder 4)

Date	Feeder 1	Feeder 2	Feeder 3	Feeder 4
18 December	*	NS	*	
30 December	*	NS	NS	
18 February	NS	NS	*	
28 February	NS	*	*	
14 September		*		
15 September		*		
24 October		NS		
25 October		*		*
26 October		*		NS
27 October		*		*

NS: Flock was not oriented; *flock was oriented, $P<0{\cdot}05$.

DISCUSSION

General

We observed the directionality of the food-storing flights of chickadees carrying sunflower seeds away from a feeder to determine whether food caching by black-capped chickadees follows recognizable rules that might reduce the memory load required to retrieve each food item. We suggest that our feeders resembled natural situations of high local concentration of food, as normally used by chickadees during autumn and winter. For example, Odum (1942) reported that hemlock seeds, *Tsuga canadensis*, were an abundant item in the autumnal and winter diet of black-capped chickadees, and that the birds had been observed to both feed on and store these seeds. Odum (1942) reported that this same population fed in the autumn on the seeds of plants such as goldenrods (*Solidago juncea* and *S. graminifolia*), asters and other Compositae; all of these plants grow in patches. Glase (1973) also observed chickadee flocks foraging on goldenrod patches. Concentrated food sources are also exploited by other Paridae (tits) that feed on spruce and pine cones (Haftorn 1954, 1956a, 1960; Alatalo & Carlson 1987).

We set up feeders and observed storing behaviour during September, October, December and February. It might be argued that this period is longer than the one during which black-capped chickadees normally store food. There is evidence that storing intensity in tits varies considerably with the time of year: Odum (1942) observed black-capped chickadees storing many hemlock seeds during October and November. No storing was observed after December although birds continued to feed on these seeds. Haftorn (1956b, 1974) had similar observations for Scandinavian tits, whose storage season is mainly late summer and autumn. However, there are also some records of food storing by black-capped chickadees later in winter, for example, storing seeds of Trumpet creeper, *Campsis radicans*, in February (Brewer 1963). In our study area seeds of hemlock, yellow birch, *Betula alleghaniensis*, and Chinese sumac, *Ailanthus altissima*, were still on the trees in late winter and at that time they were also observed lying on the snow under these trees. Black-capped chickadees hopped on the snow and picked up these seeds. However, we do not know whether any of these items were stored in late winter. Nevertheless, even if we prolonged the occurrence of this behaviour by providing artificially abundant food in late winter, there are no grounds for suspecting that the nature of food storing observed in late winter would be different from that observed in the autumn, and we did not observe differences in the use of space for storing between autumn and winter.

Use of Space for Food Storing by Flocks and Individuals

Our data indicate that within the flock home range, there was no single preferred place for food storing, and that most of the storing was done within a radius of 15 m from where the seeds were offered. In addition, our data suggest that the directionality of the food-storing flights that we observed was representative of the overall storing activity of a bird. Intriguingly, this same directionality may be shared by the food-carrying flights that ended in eating behaviour, although we do not have enough data to make a strong claim on this. It seems possible, though, that the directionality of food-carrying flights is a primary tendency that affects all of these flights, regardless of whether they end in eating or storing. That is, black-capped chickadees may be following a simple rule that does not discriminate according to its consequences.

A pattern of dispersed storing areas, each near a given food source, makes sense as the flock's home range is relatively large. For small birds like

Table II. Results of rank-sum and run tests for differences in mean angles towards which individuals were oriented from the same feeder on different days

Bird	Dates tested and results					
1	14 September/15 September NS					
2	14 September/15 September NS					
3	24 October/25 October NS	24 October/26 October NS	25 October/26 October NS			
4	14 September/25 October $P=0{\cdot}014$	14 September/26 October NS	14 September/27 October NS	25 October/26 October $P=0{\cdot}007$	25 October/27 October NS	26 October/27 October $P=0{\cdot}007$
5	14 September/24 October NS	14 September/26 October NS	24 October/26 October NS			
6	25 October/26 October $P=0{\cdot}005$	25 October/27 October NS	26 October/27 October NS			
7	18 December/18 February $P<0{\cdot}001$					
8	14 September/15 September NS	14 September/25 October NS	14 September/26 October NS	15 September/25 October NS	15 September/26 October NS	25 October/26 October NS
9	18 December/28 February $P=0{\cdot}04$					

chickadees, with a body mass of about 11 g, flying from different parts of their home range to one or very few places where food is cached would be costly (in terms of calories spent) and dangerous (exposure to predators). Other studies on other Parids also report that transport distances are usually short, averaging 7 m for boreal tits (Haftorn 1974), 10·8 and 6 m for two different populations of willow tits, *Parus montanus*, and 5·7 m for Siberian tits, *P. cinctus* (Alatalo & Carlson 1987). However, these may be underestimates. A study of food storing by marsh tits that mapped the storing sites of radioactively labelled seeds revealed that some of these seeds were stored at distances of more than 40–50 m from a source (Cowie et al. 1981). Our observations do not exclude the possibility that at least some of the seeds carried away by our black-capped chickadees were stored at distances well in excess of 15 m.

Our results indicate that on any one day a chickadee flock used only a limited portion of the 360° arc around a food source. On that same day different flock members tended to show a consistent and even narrower orientation in their departing food-storing flights. These individual orientations often persisted on subsequent days. Comparisons between the preferred orientations shown by the storing flights of most individuals observed at a feeder on a particular day yielded considerable overlap. However, this subset of preferred orientations can shift in time. So, when one overlays all data from the four dates shown in Fig. 3 for each feeder, one gets a rather broad distribution of directions (Fig. 6). This, combined with the relatively wide space used around a feeder by the flock as a whole on some days (e.g. Fig. 3), suggests, but does not prove, that suitability of the surrounding area for caching was not a limiting factor. The criterion for choosing sites for our feeders was that each feeder be surrounded on all sides by rather homogeneous vegetation.

If the directional distribution of potential caching sites was not a limiting factor, then the tendency for directional storing activity must have been influenced by other factors. Perhaps

Table III. Results of rank-sum and run tests for differences in mean angles towards which different individuals were oriented from the same feeder on the same day

Date	Comparison tested	Result	Feeder
18 February	1:2	NS	1
18 February	3:4	NS	2
28 February	4:5	NS	2
14 September	6:7	NS	2
14 September	6:8	NS	2
14 September	6:9	NS	2
14 September	6:10	NS	2
14 September	7:8	NS	2
14 September	7:9	NS	2
14 September	7:10	NS	2
14 September	8:9	NS	2
14 September	8:10	NS	2
14 September	9:10	NS	2
15 September	6:7	P=0·037	2
15 September	6:10	NS	2
15 September	7:10	NS	2
24 October	12:9	P=0·018	2
25 October	11:10	NS	2
25 October	11:13	NS	2
25 October	11:9	NS	2
25 October	11:10	NS	2
25 October	8:13	NS	2
25 October	8:9	NS	2
25 October	8:10	NS	2
25 October	13:9	NS	2
25 October	13:10	NS	2
25 October	9:10	NS	2
25 October	14:15	NS	4
25 October	14:16	NS	4
25 October	15:16	NS	4
26 October	14:15	P=0·007	4
26 October	8:9	P=0·04	2
26 October	8:10	NS	2
26 October	9:10	NS	2
27 October	15:16	NS	4
27 October	15:17	NS	4
27 October	16:17	NS	4
18 December	6:18	P=0·009	3
18 December	6:2	NS	3
18 December	6:19	NS	3
18 December	18:2	P=0·03	3
18 December	18:5	NS	3
18 December	2:5	NS	3
18 December	4:5	NS	1
18 December	6:9	NS	1

Each number under 'comparison tested' represents a bird. For example, 1:2 means that bird 1 was compared with bird 2.

individuals used a smaller arc for caching than that potentially available so as to avoid competition for caching sites with other flock members.

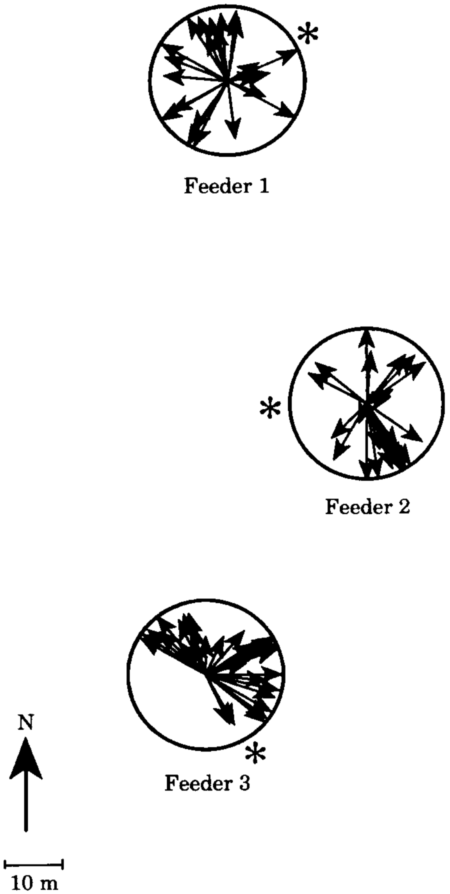

Figure 6. Mean vectors (r_c defined as in Fig. 1) show the departing food-storing flights of black-capped chickadees observed at three feeders on four dates (18 and 30 December 1991; 18 and 28 February 1992). Data are the same as in Fig. 3. The relative distances and compass directions between feeders are accurately represented. Each bird can be represented up to four times at a particular feeder because of the four dates during which observations were done, each time by a different mean vector. *Indicates position of observer.

The idea of competition avoidance was first suggested by Stapanian & Smith (1978) who reported that individual fox squirrels cached in nearly exclusive areas but that the composite distribution of the caches of the local population approached a more uniform distribution. A similar phenomenon had been shown for magpies (Clarkson et al. 1986) and marsh tits (Cowie et al. 1981). Use of exclusive caching areas might be possible when two or very few individuals share a home range, as in the cases mentioned above. However, this type of 'space exclusion' might be impossible with a flock situation, when there are sometimes up to a dozen birds feeding and storing simultaneously around the same food source. A bird trying to avoid overlap would have to know where each of the other members of the flock had stored its food. And indeed, our data show that although individual birds tended to be oriented towards a certain direction when flying to store seeds, they often overlapped in the directions used. We do not know whether the storing sites of birds sharing the same orientation from the feeder did in fact overlap.

While overlap of storing orientations might be unavoidable for scatter-hoarders living in flocks, reduction of competition for cache sites and reduction of predation on caches by other birds can still be achieved by storing at different distances from the feeder or by using different substrates. Haftorn (1956b) has shown that there is considerable interspecific variation in types of sites that different Norwegian tits (*Parus atricapillus, P. cristatus* and *P. ater*) select to cache food. One important difference was the distribution of cache sites along branches from trunk to branch tip in conifer trees. Alatalo & Carlson (1987), who studied two tit species in Sweden, also showed that when the two species were sympatric, interspecific competition influenced the choice of hoarding substrate. Such a pattern of substrate preference was also suggested by Cowie et al. (1981) at the species level: when studying food storing by marsh tits, these authors noticed that individual birds tended to store in different types of substrate (one bird was 'a moss specialist', another favoured nettle stems and a third preferred balls of dead leaves and twigs). Black-capped chickadees might face an even more complicated situation, as very often the flock forages together with other food hoarders such as white-breasted nuthatches, *Sitta carolinensis*, and tufted titmice, *Parus bicolor*. However, no one has studied whether black-capped chickadees use choice of substrate as a way to achieve niche separation and thereby reduce robbery and competition for caching sits. Interestingly, birds that watch other individuals of the same species cache food are not good at remembering the location of these caches (Bossema 1979; Vander Wall 1982; Baker et al. 1988). Thus, the memory of caching sites may result from the act of caching and so a bird may be better served by caching its own food than by spying on other birds.

A Hypothetical Framework for Understanding the Neural Basis of Food Caching

The use of directionality of food-storing flights away from a food source might be related to the neural mechanisms underlying caches memories; recent field and laboratory experiments suggest that food-caching birds remember information related to storage and that they use memory to find the sites of their hoards (Cowie et al. 1981; Sherry 1984; Kamil & Balda 1990; Shettleworth et al. 1990). Remembering the location of hundreds of caches scattered through a large three-dimensional home range, and the status of each (full or empty) may pose a daunting memory load on a bird's brain (that of black-capped chickadees weighs 0·5 g). A directional clumping of storage sites would still require that birds remember the location of each hidden item, but now each storage site no longer has to be remembered with reference to the entire home range.

A bird that clumps its storing sites in a particular direction away from a food source would also strengthen its memory of that particular sector and its landmarks. In fact, strength of memory for that sector would be directly related to the density of seeds stored there. Thus, directional clumping increases the number of opportunities to memorize the general area of food storing, thus making it easier to remember the location of each stored item.

The idea that caching patterns may be a mnemonic aid for future recovery of caches was first suggested by Kraus (1983), working with grey squirrels. However, grey squirrels are not an ideal species to make this case because the clumping of storage sites he observed could have resulted from the squirrel's attempts to reduce site overlap with other individuals caching in the same general area. Kraus' (1983) suggestion was overlooked by subsequent workers who continued to insist that caches should be dispersed randomly around a source to reduce the cost of travel and the risk of theft, respectively (Stapanian & Smith 1978; Clarkson et al. 1986). Our results force a re-evaluation of this widely held view. We believe, as does Kraus, that individual preferences for directionally clumped storing sites are best explained as a mnemonic aid. That is, we suggest that scatter-hoarders should clump their hoarding sites in a particular direction away from the source because caching sites organized in this manner are easier to remember. This hypothesis would explain why territorial red squirrels have directional, clumped caches even though they have exclusive use of the area surrounding the food source (Hurly & Robertson 1987).

The mnemonic hypothesis is more easily appreciated by dwelling on how animals remember the location of objects in space. Familiar space is not an empty volume, but a recollection of the relative directions and distances between prominent landmarks. Tinbergen (1951) showed many years ago that wasps provisioning their nests homed on the entrance to the nest guided by its relation to a few simple landmarks. When these landmarks were displaced in a particular direction, the wasp's approach and search for the nest's entrance was also displaced (reviewed by Tinbergen 1951, pp. 97–100; Carthy 1956, pp. 27–41). Black-capped chickadees may also remember each individual cache site by its relation to a few prominent landmarks. Such an effect has been demonstrated for black-capped chickadees storing seeds in aviaries (Sherry 1992). In addition, clustered cache sites may be remembered more easily than scattered ones because the spatial memories were acquired with reference to a same set of prominent landmarks. This hypothesis might be tested by studying retrieval efficiency in large aviaries in which tits are offered the opportunity (by restricting substrate availability) to store in a clumped or dispersed manner.

The fact that the preferred-hoarding orientation shown by an individual often aligns with that of the flock is probably not coincidental. Black-capped chickadee flocks move through the vegetation as a group (Glase 1973) and this cohesiveness is apparently kept during hoarding. Chickadees may also search for cached food simultaneously with other flock members. An individual's memory regarding storing orientation for a particular source of food would be reinforced by the memories of the other flock members, so that the flock would act as a communal repository of this shared information. Of course, each individual still has to remember where it placed individual items. This idea might also be tested by keeping birds in aviaries singly or in flocks and comparing retrieval efficiency when caching and retrieving under either of these two conditions.

This brings us back to our motivation for doing the present study. We know that black-capped chickadees store food, but we did not know how these stores were dispersed, and therefore how much of a memory load they might present. We conclude from our behavioural observations that the distribution of food caches made by black-capped chickadees reflects a compromise between the need to minimize the energy costs of food storing (close to source), to minimize the risk of thievery (scatter-hoarding), and to optimize the memorization of caching sites (clustered). Some of the main seed sources within the home range of a chickadee flock are clumped together, and usually remain available for periods of weeks, and even months. Therefore, each individual may have only to remember a limited number of main food sources, nearby landmarks and associated caching locales (defined by direction and distance away from the food source), plus the position of each cache site within these locales. A restriction of caching areas to a preferred direction from a food source, and its coincidence with caching areas used by other flock members, may help each individual remember where it has stored food within the home range.

Our emphasis on the need to manage the memory load and thus maximize retrieval suggests that food storage by black-capped chickadees might favour, by and large, items that are super-abundant and bear a clear spatial association with their easily recognizable source (hemlocks, pine trees, goldenrod patches, etc.). In this manner, the location of caching sites need not be memorized with reference to a three-dimensional grid of the entire home range, but can be remembered just in terms of a relatively few, major food sources and hiding locales, perhaps on a particular substrate, at a particular distance and orientation from conspicuous objects. Identification of these food sources may occur in the autumn, when the majority of the seed crops within the home range are readily identified. Memories of food stores organized in this manner may be less daunting than a full and detailed inventory of haphazardly scattered caching sites. If memory is organized this way, then each autumn, as chickadees join a flock and become established in a home range, there may be a major restructuring of the map that an individual will use to store and retrieve food items, and this too is a prediction that can be tested in aviary-held birds.

Daily rhythms in caching and retrieving have been noted in some food-storing species. For example, crested tits (Haftorn 1954) and nuthatches (Löhrl 1958) store more in the morning, and marsh tits were observed to retrieve more in the afternoon than at other times of the day (Stevens & Krebs 1986). This strategy might ensure that these small birds have a secure source of food before entering the long, cold night (Grubb & Waite 1987; Powlesland 1980). If black-capped chickadees follow this pattern and if they restrict their caching to food items that are abundant and occur in well-defined, clustered sources, then stomach contents of birds feeding in the morning would include a cross-section of all food items encountered during this foraging period; stomach contents of birds feeding late in the day, predominantly on cached food, would show an overrepresentation of seeds from the major, conspicuous food sources, which, we hypothesize, would be the ones preferentially cached and retrieved.

We hope that the observations and hypotheses included in this paper will offer a frame of reference for future work on the ethology, ecology and neurobiology of food-storing behaviour. A companion paper will deal with the neurobiology of the chickadee hippocampus.

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