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Spatial memory in food-storing birds

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SUMMARY

In the wild, several species of birds among the parids (tits and chickadees) and corvids store food in scattered locations and find it again days or months later. The food storers that have been tested use memory to recovery their stores in the laboratory. The importance of memory to a food-storing way of life suggests that these birds possess an adaptive specialization of some aspect or aspects of memory. Recent work has focused on analysing how memory is involved in recovering stored food, discovering how this memory can be tested in tasks that do not involve food storing, and comparing the memory of storing birds with that of their non-storing relatives in a variety of tasks.

1. NATURAL HISTORY OF FOOD-STORING

Species in 12 of the 170 families of birds store food (Sherry 1985). From the viewpoint of this meeting, those that hoard in a large number of scattered locations are of most interest, because the possibility exists that they use an extensive spatial memory to recover their stores. In recent years, systematic data from field and laboratory have begun to accumulate on food-storing in two families, the tits (Paridae) and the corvids (Corvidae). Although much has been learned about memory and other aspects of food-storing in these birds, a number of questions remain unanswered or even unasked, and one aim of this review is to point out some of them.

Some northerly species of tits and corvids spend large proportions of their time in the late summer and autumn harvesting food and storing it where it will be accessible when snow blankets the ground and ice caps the treetops. Pravosudov (1985) estimated that Siberian tits (*Parus cinctus*) may store up to 500 000 items per year; in the autumn they spend most of the daylight hours foraging and storing. In years with a good crop of pine cones, Clark's nutcrackers (*Nucifraga columbiana*) can cache up to 33 000 pine seeds in about 6600 separate locations (Vander Wall & Balda 1977). The nutcrackers' storing is highly organized in space: seeds are pried out of unripe cones and carried in the capacious sublingual pouch, a specialized seed-transporting structure, as many as 22 km to 'storing slopes'. These are open south-facing areas higher up the mountains that will be relatively bare of snow in the winter. During August and September the birds may make two or three round trips a day. Similarly, but on a smaller spatial scale, tits may gather food in some parts of trees and store it in others (Haftorn 1956; Pravosudov 1985).

Among both tits and corvids there is wide inter-species variation in the amount of food stored and the birds' apparent reliance on successfully recovering it.

In contrast to the tits of Scandinavia and Siberia, marsh tits (*P. palustris*) in southern England store food for only a few hours or days (Stevens & Krebs 1986). The blue tit and great tit (*P. caeruleus* and *P. major*) store very little or not at all (Sherry 1989), yet their distributions overlap with those of the marsh tit and the food-storing coal tit (*P. ater*), among others. Likewise, two other corvids living in similar areas of the American Southwest store much less than Clark's nutcracker and do not travel so far to do their storing (Vander Wall and Balda 1981). The pinyon jay and scrub jay (*Gymnorhinus cyanocephalus* and *Aphelocoma coerulescens*) also lack the morphological specializations of the nutcrackers, the long sharp bill, sublingual pouch, and strong flight muscles. They are constrained to harvest pine seeds after the cones have opened, and, having fewer stored seeds to feed potential young, they do not breed so early in the spring. The corvids also include one species, the northwestern crow (*Corvus caurinus*) (James & Verbeek 1983), that stores just a few items for a few hours or days.

Among the corvids, at least in the community described by Vander Wall & Balda (1981), there are clear species differences in morphology and life history related to storing. Among the tits, these differences are not so marked, nor is it clear why some species store while others do not. To benefit from storing, a bird must stay in the same area, and among the species in southern England, the storing tits are more sedentary than the non-storing species (Cowie *et al.* 1981). Another suggestion is that storing is a way to make the most of an ephemeral food source that cannot be dominated. Thus the smaller tits fly back and forth, storing items, while the bigger tits simply try to chase others away from the food (Cowie *et al.* 1981). Storing can also function to counteract seasonal or daily fluctuations in food supply. Thus the more northerly tit species, like some of the corvids, seem to do the most storing. They also do it seasonally (Haftorn 1956; Pravosudov 1985). Species in less severe climates also

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store seasonally (Ludescher 1980) and exhibit a daily rhythm of storing. Food encountered during the day is stored and then eaten in the late afternoon, when it is critical to accumulate enough reserves to survive the night (Lucas & Walter 1990; D. F. Sherry & J. R. Krebs, personal communication; Stevens & Krebs 1986). Two detailed functional models of storing have been developed to account for the daily pattern of storing within a storing species (McNamara *et al.* 1990; Lucas 1990). However, speculations about the cross-species distribution of storing still need to be tested with data from other tit and corvid communities as well as with data from other families.

2. IS MEMORY USED TO RECOVER STORES IN THE FIELD?

(a) *Should memory be used?*

For food-storing to evolve, hoarders must be more likely to recover stores than 'cheaters' who do not invest time and energy in storing (Andersson & Krebs 1978). This is not to say, however, that the hoarder needs to recover every one of its caches. Formal models might profitably be used to explore what incidence of cheating and cache loss is tolerable under various conditions.

To say that a hoarder must be able to recover more stores than a conspecific that does not hoard is not to say that it must remember every single individual storage site, nor even that it need use memory at all. An individual's chances of recovering its own stores can be enhanced relative to the chances of others, by mechanisms such as individual-specific site preferences or species-specific site preferences aided by memory for general areas where storing was done. With the exception of Lohrl (1950), most early observers of storing thought it unlikely that birds remember individual storage sites, and indeed, arguments like those of Haftorn (1956) for other mechanisms are quite compelling.

The three species Haftorn observed, the coal tit, crested tit (*P. cristatus*), and willow tit (*P. montanus*), preferred different heights and parts of spruce and pine trees for storage (see also Bardin (1975); Petit *et al.* (1989); Pravosudov (1985)). The small coal tit was found most hanging upside down at the ends of spruce branches, poking items in among the needles. Willow tits stored most on tree trunks and on top of the thickest branches. Crested tits nearly always stored on the undersides of branches. Three quarters of their stores were in small patches of lichen, and 51 % were at the junctions of small branches or twigs. Moreover in 81 % of the stores half or more of the item was visible. These birds spend most of the daylight hours in winter busily examining twigs and branches, covering very large areas of the forest. Pravosudov (1983) estimated that in the region of Murmansk, on the Arctic Circle, Siberian tits (*P. cinctus*) visit 12.7 ± 1.1 trees and willow tits 10.3 ± 4.0 trees per 10 min and that they find 2700 and 2100 food items per winter day, respectively (Pravosudov 1985). It is easy to see how a high level of activity in species-specific storing areas, combined with mem-

ory for the general location of stores, could lead to considerable recovery success in birds like these.

The marsh tits studied near Oxford (Cowie *et al.* 1981; Stevens & Krebs 1986) present a different picture. They store in a wider variety of different substrates for a shorter time and space their stores much more than the Scandinavian and Siberian tits, which seem to cram their preferred areas with items taken from elsewhere in the trees. Thus the problem the marsh tits face might lend itself more easily to solution by memory for the individual sites. The same could be said for Clark's nutcracker, for different reasons. The cost of digging at random, especially through snow cover, in an area where items are stored is probably too great to make random search profitable.

(b) *Evidence that memory is used in the field*

The evidence that either tits or corvids use memory to recover caches in the field is largely circumstantial. Examinations of stomach contents or observations of tits eating items like seeds of low-growing plants long buried in snow (see, for example, Haftorn (1956)) establish that stored food is being eaten, but not necessarily by the bird that stored it, still less that the bird used memory of any kind to find it. Observations of corvids digging straight through snow and uncovering a cache without trial and error (see, for example, Swanberg (1951); Tomback (1980)) are more compelling, especially when combined with evidence from the laboratory that these birds cannot smell out buried caches (Vander Wall 1982).

The experimental evidence for memory use by corvids in field conditions comes from a study by James and Verbeek (1985) in which a northwestern crow took clams from a feeder to a nearby field. It recovered 99 % of these, apparently probing accurately for each one. It never revisited the cache sites which it had already emptied, unlike the case with nutcrackers in the laboratory (Balda *et al.* 1986).

Studies of marsh tits near Oxford provide the most extensive and direct evidence for memory use in the field by any storing species. In these field experiments, marsh tits were allowed to store radioactively labelled seeds which could then be located by the experimenters, marked, and their fate tracked through periodic inspections. Cowie *et al.* (1981) placed control seeds in similar sites either 10 cm or 100 cm away from the storage sites and found that the stored seeds disappeared sooner than the controls. This could only happen, they argued, if the birds returned accurately to their own stores. If the marsh tits had been searching at random in a general area, nearby control and stored seeds would be expected to disappear at the same rate.

More direct evidence that stored seeds are taken by the bird that stored them was obtained by banding marsh tits with small magnets and placing a magnet detector connected to a clock beside each stored seed (Stevens & Krebs 1986). Within the three days following storage, the birds visited 32 of 135 storage sites and none of 60 control sites. The majority of visits were within the first 12 h of daylight after storage, when the birds' success rate was 90.9 %. Thereafter, so

many seeds had been pilfered by rodents and other birds that the success rate dropped to 20%. By the end of three days, nearly all the remaining stores were gone, and the storing individuals' frequency of visiting had dropped to low levels.

(c) *What is being remembered in the field and how?*

Lohrl (1950) raised the question whether birds recall storage sites and set out to them when they are out of sight or simply recognize those they encounter in the course of normal foraging. We still do not know the answer to this question for tits in the field, nor have any attempts been made to discover the answer in the laboratory. Clark's nutcrackers and Northwestern crows, however, store in special areas, away from where they harvest the food to be stored. Thus their memory may be organized hierarchically: they first recall an area where food is stored and set out for it from some distance away. Once in that area they could either recognize or recall individual cache sites from nearby landmarks. (Vander Wall 1982).

If descriptions of storing in the wild do not always make clear how memory is used, if at all, they do nevertheless indicate something of what memory for cache sites would have to be like. For individual sites to be remembered, whatever cues are used must be encoded on the basis of a single brief visit to each site. Tits, for example, may spend only a few seconds storing each item. Pravosudov (1983) reports that Siberian tits may spend as little as 12 s to find and store an item. This may include unsuccessfully trying more than one potential storage site. Crested tits spend 30–50 s per item (Haftorn 1954; see also Bardin (1975)). The available evidence (Cowie *et al.* 1981) also shows that storage sites are not reused, so each site to be remembered must be different. Information about this large number of unique, yet similar, sites has to be retained for days or months.

Unlike remembering individual sites, remembering the general area where items are stored, like a tree or a part of the forest, is a multi-trial problem: a bird makes many storing trips to an area, perhaps because it has found a bonanza of ripe cones nearby, but it only visits each individual storage site once. Thus it should be more likely to remember the general area than the individual sites within it. This argument applies particularly to the northern tit species, which seem to hide many items in similar sites relatively close both to each other and to where they are found (Haftorn 1956; Pravosudov 1985). Marsh tits near Oxford, on the other hand, space items an average of seven metres apart and at any given time one individual may use a variety of different types of sites (Cowe *et al.* 1981). As these birds also probably do not accumulate the thousands of stored items estimated for more northerly tits nor keep their stores for so long, they are in a better position to remember individual sites.

3. MEMORY FOR FOOD STORED IN THE LABORATORY
(a) *Two examples*

A study by Shettleworth & Krebs (1982) using marsh tits shows some features of laboratory tests of memory for stored food in parids. The birds were tested individually in a large aviary furnished with tree branches. These provided 97 storage sites in the form of holes drilled at 8–12 inch† intervals, each one the right size to hold a single hemp seed. So that birds could not see the seeds from a distance a small flap of black cloth hung down over each hole. This also meant that 'looks' for seeds could be scored by recording when the bird lifted the cloths.

Marsh tits had a series of daily trials in which they were allowed to store 12 hemp seeds. Phase two of each trial, the recovery or test phase, consisted of allowing the hungry bird back into the aviary two hours after storing. Seeds were in the places where they had been stored in the first phase. The locations of holes the bird inspected were recorded. Performance was very accurate, especially at the beginning of each trial. Random search would have required inspecting about eight holes to find each seed but on average the birds took not much more than one look per seed at the beginning of trials.

At the end of the experiment the birds had a few trials in which the seeds they stored were moved to different sites between the two phases of the trial to control for the possibility that they were using cues emanating from the seeds themselves. They continued to visit the sites they had used for storage and encountered the relocated seeds at a rate a little above chance. The rate was above chance because most birds did not ever use, or even visit, all the potential storage sites. The distribution of seeds in the control trials took this into account by using only sites that the individual being tested had used for storage on earlier trials in the experiment.

Other ways of assessing memory and controlling for cues from the seeds have been used in other experiments. Perhaps the cleverest is the demonstration by Sherry *et al.* (1981) that when a marsh tit stored seeds with one eye covered it was unsuccessful at finding the seeds when the other eye was covered. This is attributable to the lack of interocular transfer of visual information in these birds.

A second experiment by Shettleworth & Krebs (1982) was a fairly direct demonstration that the birds do not achieve accurate performance merely by visiting the same preferred places every time they go into the aviary. Rather, memory of where seeds are guides their behaviour in a flexible way. Instead of recovering seeds, the marsh tits were allowed to store more seeds after the 2 h retention interval. Now if the birds remembered where they had stored seeds in the first phase of the trial they should visit different sites in the second phase rather than going back to the same sites as they would when recovering seeds. This is what happened.

† 1 inch = 2.54 cm.

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In the first laboratory studies of cache recovery in corvids, Clark's nutcrackers (Vander Wall 1982) and a Eurasian nutcracker (*Nucifraga caryocactes*) (Balda 1980) were allowed to bury seeds anywhere in the floor of the experimental aviaries. Although a high proportion of recovery attempts were successful in these studies, and the birds were evidently not using smell or other local cues to relocate caches (Vander Wall 1982), the fact that they were entirely free to choose storage sites left open the possibility that individual preferences guided their behaviour. The method used by Kamil & Balda (1985, 1990 a) allows the experimenter to 'present' the 'items' to be remembered, in much the same way as is done in conventional tests of memory, as well as to quantify search for caches more readily. The birds' caching is restricted to many (90 or more) of sand-filled cups set into the floor of an aviary. By tightly capping some of the holes during caching, the experimenters can 'instruct' the birds to store in a preselected subset of sites. After a retention interval of 10–15 d, accuracy at the beginning of recovery in the first reported study of Kamil & Balda (1985) averaged about 55 %, compared with less than 20 % expected by chance. This same general method has been used to test pinyon jays and scrub jays in the laboratory (Balda & Kamil 1989). Gray jays (*Perisoreus canadansis*), a corvid that stores food boli in trees over the winter, have been tested with a method more like that used with parids and also have been shown to use memory for cache sites (Bunch & Tomback 1986).

Nutcrackers' accuracy, like that of marsh tits (Shettleworth & Krebs 1982) falls off as recovery proceeds. In the case of nutcrackers, successive tests with a different 25 % of the holes uncapped each time indicate that the decline in accuracy reflects that some holes are simply remembered better than others. If they are allowed free choice of where to search the birds recover seeds from the best-remembered sites first and most accurately (Kamil & Balda 1990 a).

With the fact that tits and corvids can use memory to recover stored food in the laboratory firmly established, several investigators have gone on to analyse various characteristics of that memory such as the retention interval over which it is sustained, the cues used to relocate storage sites, and the features of stored items remembered. Table 1 summarizes the results of these studies. In addition to remembering where it put items in the first place, the bird recovering stored food needs a mechanism to prevent it constantly revisiting storage sites which it has already emptied. Memory for sites already searched has also been examined in both tits and corvids.

(b) Some limitations of laboratory studies of food-storing

Although the studies summarized in table 1 show that food-storing birds remember a number of subtle features of storing episodes, all the studies on captive birds to date have some limitations. They focus exclusively on memory for individual sites and say nothing about other memories that may play a role in the field. Birds have no opportunity to show whether they remember anything about the general area where they stored nor whether they are able to recall it and navigate to it from a distance. Instead, tits and corvids have routinely been tested in aviaries that are very small compared to the areas they cover in the field. They are within sight of, and potentially can recognize, most or all of the possible storage sites at any one time.

Not only have laboratory studies to date focused on individual site memory, they have done so under conditions where it is arguably less good than it might be in the field. Most important, all the sites look fairly similar and are relatively close together. This would be expected to make them less easy to discriminate than natural storage sites. Compare, for example, the seven metre inter-item distance and the variety of site types found by Cowie *et al.* (1981) for marsh tits in the field to the 3 m × 4 m aviary and single site type used by Sherry *et al.* (1981) and by Shettleworth & Krebs (1982) to test marsh tits in the laboratory. Moreover, whenever birds have multiple trials in the same aviary, they are forced to re-use sites, something that has not been found in the field (Cowie *et al.* 1981; Stevens & Krebs 1986). Interference between memories from repeated trials may reduce performance in a way that would not occur if different sites were available on each trial (see §5 in Brodbeck (1989)). Some studies (see, for example, Sherry *et al.* (1981); Sherry (1984 a); Shettleworth & Krebs (1986)) have attempted to eliminate this problem by rearranging the aviary for each trial but this practice could also reduce performance by putting local cues (from the fixed set of trees, beds of moss, etc.) into conflict with global cues, or by making it difficult for the birds to form a cognitive map of the aviary into which they can fit information about the current status of sites, if this is important in successful recovery.

Although possibly making sites more difficult to discriminate from each other than they are in the field, laboratory studies of storing tax the birds less in other ways. In particular, the numbers of stored items have typically been much smaller and, at least for some of the species tested, the interval between storing and recovery much shorter than typical in the field. Thus on balance it is unclear exactly how accuracy of recovery in the field would be expected to compare quantitatively to that in the laboratory.

The importance of the foregoing comparisons is that while several food-storing tits and corvids undoubtedly have excellent memory for individual storage sites, laboratory tests of their memory have not yet tapped other aspects of memory that may be important in finding stored food. This needs to be kept in mind when comparing species to one another (see §4 and Krebs, this symposium). It could well be that the major species differences occur in aspects of memory such as long retention of a very large number of items (Sherry 1990 a) or organization of large-scale spatial information, that have not yet been tested in the laboratory.

Table 1. *laboratory studies of memory for stored food in tits and corvids*

topic	finding	species	reference
retention interval	no decline from 2–3 to 24–26 h	marsh tit, chickadee	Sherry *et al.* (1981) Shettleworth *et al.* (1990)
	no difference in recovery of stores 24 and 48 h old	chickadee	Sherry (1984*a*)
	decline in recovery at 28 days, but still above controls	chickadee	Hitchcock & Sherry (1990)
	above chance after 6 months	nutcracker	Kamil & Balda (1990*b*)
revisits to emptied sites	avoid revisits within a bout of recovery	marsh tit, chickadee	Shettleworth & Krebs (1982) Sherry & Vaccarino (1989)
	avoid sites emptied 21–24 h ago	marsh tit, chickadee	Sherry (1982), Sherry (1984*a*)
	avoid revisiting sites found to be emptied by experimenter	chickadee	Sherry (1984*a*)
	revisit emptied sites more than chance	nutcracker	Balda *et al.* (1986)
cues used	use large landmarks but not local cues	chickadee	Sherry (1990*b*)
	follow relocated landmarks	nutcracker	Vander Wall (1982)
	use sun compass	scrub jay	Wiltschko & Balda (1989)
features of stores remembered	return preferentially to sites of preferred items	chickadee	Sherry (1984*a*)
	switch storage away from 'predated' to 'safe' site types	marsh tit	Stevens (1984)
	do not remember sites where others seen caching	chickadee	Baker *et al.* (1988)
other	some sites remembered better and recovered first	nutcracker	Kamil & Balda (1990*a*)
	increased cost of searching increases accuracy	nutcracker	Kamil & Balda (1990*b*)
	no consistent serial position effect	nutcracker, marsh tit, chickadee	Kamil & Balda (1990*b*) Sherry (1984*b* (reviews))

All references to 'chickadee' refer to black-capped chickadees. All references to 'nutcracker' refer to Clark's nutcrackers.

4. DO FOOD-STORING BIRDS HAVE AN ADAPTIVE SPECIALIZATION OF MEMORY?

(a) *What are adaptive specializations?*

Rozin & Kalat (1971) introduced the notion that some kinds or aspects of learning and memory might be adaptively specialized for tasks that the species possessing them confront in natural conditions. Adaptive specializations are quantitative or (as is more usually implied) qualitative differences in the properties of learning or memory that parallel differences in functional requirements for that memory. A familiar example from associative learning is conditioned taste aversion. Although it appears to have the same properties as other forms of associative learning, the delay between conditioned stimulus (cs) and unconditioned stimulus (us) that can be sustained is much greater than in, say, fear conditioning (Rescorla 1988). This quantitative difference parallels a difference in requirements for learning about food, where consequences of ingestion may be delayed, as compared to learning about the consequences of signals for immediate danger.

In their further development of the idea of adaptive specialization, Sherry & Schacter (1987) pointed out that separate learning or memory systems having different rules of operation might be expected to evolve when a species must solve learning or memory problems that have functionally incompatible requirements. They cite, for example, the apparently very different requirements of song learning and food-storing. In song learning (at least in some species; see Marler, this symposium), a highly specific class of inputs is encoded permanently on the basis of more or less passive exposure during a restricted period early in life, while in food-storing the bird must remember an ever-changing set of information throughout its adult life. However, as Sherry & Schacter point out, it is not clear that the memory used in recovering stored food need have qualitatively different characteristics from the memory necessary in normal foraging or, indeed, in remembering the locations of rivals, territorial boundaries, mates, or other resources (see also Sherry (1987)).

Nevertheless, remembering locations of stored food does appear to require that more items be remembered for longer and perhaps with greater accuracy than is otherwise necessary in foraging. After all, the whole point of storing food is to place it somewhere inaccessible to predators who might otherwise remove it before the storer can return to eat it. Storing food is not worthwhile unless it makes remembering the location of that food more valuable than remembering its original location or the locations of similar items. This sort of argument suggests that food-storing

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memory should be adaptively specialized in a quantitative manner, to retain a lot of accurate information for a long time. For example, the long sharp beaks and strong flight muscles of nutcrackers (quantitative morphological specializations) might be accompanied by improvement in some aspect(s) of memory needed to recover caches. All would be specializations for food-storing.

(b) *How might food-storing memory be adaptively specialized?*

Saying that food-storers need good spatial memory is not very helpful by itself, as studies reported elsewhere in this symposium (see, for example, Horn; Mishkin; Weiskrantz) show that memory has a number of dissociable components. Considering the requirements of recovering stored food in the field, reviewed in §1, suggests a number of specific ways in which memory for storage sites might be adaptively specialized. First of all, to remember individual sites the birds must be good at making one-trial associations between unique spatial or configural cues of some kind with food (or, in the case of remembering where stored items have been recovered, the lack of it) (Shettleworth 1985). Forgetting is in effect the loss of discrimination between items. That is to say, discriminating potential storage sites that actually hold food from those that do not is an essential part of long-term retention, resistance to interference, and accurate memory for large numbers of sites. Food-storers may encode information about food locations (whatever that information is, for a particular species) in great detail. Perhaps they have more of the sort of neural units assumed in element theories of memory (see, for example, McLaren *et al.* (1989)) devoted to processing this sort of information.

Of course it may not be memory for individual sites that is specialized in food-storers but rather some of the other aspects of memory that have not yet been analysed experimentally in these species. For example, birds like nutcrackers might be especially good at organizing or using the large-scale spatial information needed to navigate to general areas where food is cached. The analysis of how this sort of spatial information is stored and used is well developed for other species (see, for example, Bingman (1989); Cartwright & Collett (1987); Thinus-Blanc (1988)) and the same ideas might profitably be applied to food-storing. For example, it is more efficient to store large amounts of spatial information in a Cartesian grid, an analogue to a true map, than as sets of navigational vectors (Thinus-Blanc 1988). Food-storers might have a spatial memory that differs qualitatively from that of non-storers in this respect.

(c) *How can adaptive specializations be identified?*

If some aspect or aspects of memory in food-storers are specialized for recovering stored food, there are two forms which this specialization might take. Memory for caches could be a separate memory system within caching species, a memory system that differs in some qualitative way from the memory used in normal

foraging or in solving other spatial problems. Alternatively, memory for food locations in general might be better in some quantitative way in storing species than in other animals. The first possibility can be addressed by comparing memory for stored food and food not stored within a storing species. The second by comparing various aspects of memory across species that depend on storing to different degrees. Results of experiments taking the second approach are discussed by Krebs (this symposium). Such experiments are encouraged by the results of the first approach, which indicates that, at least in tits, memory for stored food is no different from memory for food encountered by the bird under similar circumstances. This work is reviewed in the next section.

5. PERFORMANCE OF FOOD-STORING BIRDS ON OTHER TESTS OF MEMORY
(a) *Stored versus encountered seeds*

To properly compare memory for locations of stored food and food not stored within a storing species it is necessary to use a task like storing in every respect except that of requiring the bird to store (Shettleworth 1985, 1990). We can then ask; does storing food give its location a special status in memory or is it the favourable procedural aspects of storing, such as visiting spatially separated sites and seeing the food in them, that makes memory for stored items so good? This has been done with tits in two ways: (i) by allowing birds to encounter items placed in potential storage sites by the experimenter while they were trying to store food themselves, and (ii) by testing birds on 'window-shopping' (Shettleworth & Krebs 1986; Shettleworth *et al.* 1990).

In window-shopping a bird first visits a number of sites and sees food in some of them behind a small window. Then, in phase two of each trial, after a retention interval, the windows are opened and the bird is allowed to return and eat food in the sites where it saw food in phase one. Food-storing tits can recover seeds they have seen behind windows at well above chance with relatively little training. However, recovery of window-shopped seeds is less good than recovery of stored seeds, even though recovery of stored seeds and seeds encountered without windows while storing does not differ. The clearest demonstration of this is an experiment (Shettleworth *et al.* 1990) in which black-capped chickadees (*Parus atricapillus*) experienced a series of three types of trials. They stored five seeds in each trial and while doing so they either encountered seeds without windows, saw seeds behind windows, or encountered sites blocked off with a paper sticker. After a 90-minute retention interval, stored seeds and seeds encountered without windows while storing were recovered equally well, but seeds seen behind windows were recovered less well than seeds stored in the same episode. Nevertheless, the birds were more likely to return to the window-shopping sites than to holes merely covered with a paper sticker. Chickadees and coal tits have also been trained to window-shop when they are not storing food (Shettleworth & Krebs 1986; Shettleworth *et al.* 1990).

Comparisons of performance in separate window-shopping and storing trials supports the same conclusion: having a window in front of encountered seeds degrades performance for several possible reasons (Shettleworth *et al.* 1990).

The main result from this series of experiments, then, is that the locations of seeds encountered while storing can be remembered as well as seeds stored by the bird. The next question is whether the birds treat stored and encountered seeds in the same way under all conditions. Although the evidence cited in table 1 shows that food-storing tits can remember a number of details of a storing episode, do they nevertheless encode stored and encountered seeds in the same way? On both functional and causal grounds one might expect some discrimination between these two classes of items. Seeds stored by the bird ought to be safer and therefore remembered better than seeds just found lying around or stored by another bird. Moreover, birds appear to spend longer at storage sites, poking the seed into place, than at sites where they simply see seeds. This might be expected to favour memory for the stored items.

The most direct way to ask if birds discriminate stored and encountered seeds is to make it worth their while to do so, for example, by removing encountered seeds before recovery while allowing stored seeds to be recovered. Such experiments are under way. We have also tested the notion that encountered seeds ought eventually to be remembered less well than stored seeds by comparing recovery of the two types of items after 2 h and 26 h retention intervals (see Shettleworth *et al.* (1990), experiment 3). There was no significant decrement in recovery of either type of item after 26 h.

It is always possible that some further test will reveal differences in memory for locations of stored and encountered seeds, but the results so far are consistent with the conclusion that memory for the two types of item is supported by the same memory system. They therefore encourage the sort of research programme described more fully by Krebs (this symposium) in which tests of memory not involving food-storing are used to compare species that depend on stored food to different degrees and to analyse how their memories differ. Some of these experiments have used window-shopping, as it is the task with requirements most like those of food-storing, while others have required the birds to do only some of the things food-storers must do to recover food successfully.

(b) One-trial associative memory and interference

If locations of stored food are encoded and remembered in the same way as locations of food not stored by the bird, we can use the sorts of memory tests that have been used with other species to dissect the memory important for food-storing into its components. One example of this approach is a study by Brodbeck (1989) of one-trial associative memory in black-capped chickadees. In the field, locations of stored items are always different from each other in spatial location and details of appearance. Food-storing birds should be very good at remembering such

sites on the basis of a single brief visit to each one. Brodbeck attempted to capture this aspect of food-storing in a task in which a chickadee flew into an aviary in phase one of each trial and found three differently decorated feeders, one of which had a peanut wedged into it. The bird was allowed to peck the peanut for 30 s, after which it was sent out of the aviary for a retention interval. On its return five minutes later, the holes in all three feeders were covered with sticky paper. The bird could tear the paper off the baited feeder and finish the peanut. For the experimental group, 55 different feeders were used, and each one could appear in any of 78 locations on three walls of the aviary. Three different feeders and three different locations were used on each trial. The controls had the same three feeders in the same locations on every trial; only the location of the peanut changed.

As would be expected from demonstrations that other species perform better with trial-unique stimuli than with repeated ones (see, for example, Mishkin & Delacour (1975); Wright *et al.* (1988)), the chickadees with new feeders and locations on every trial performed much better than the controls. By the third block of five trials their performance was well below the chance level of two looks to find the peanut; the birds with non-unique stimuli performed at chance for the 40 trials that the experiment continued. In a second experiment, performance was similar at a 30-min retention interval to what it had been with five minutes but it was close to chance after 24 h. This appears to contradict the finding of Shettleworth *et al.* (1990) that memory for both stored and encountered seeds is as good after 26 h as after two, but judgement should be reserved on this issue until storing is tested in the same demanding set-up used by Brodbeck.

Thus, as predicted, chickadees are very good at remembering unique locations of food after a single brief visit (where 'locations' differ in both spatial and local cues; we do not yet know which is more important). The birds acquired this performance more rapidly than other animals have acquired comparable delayed matching tasks. For example, the pigeons trained by Wright *et al.* (1988) required hundreds of trials to acquire delayed matching of trial-unique video displays. Rats performed significantly above chance from the beginning of training on nonmatching with trial-unique objects, but their performance declined after a delay of only two minutes (Rothblat & Hayes 1987). One reason for the chickadees' superior performance could be that spatial locations in a 3 m × 4 m room are very discriminable from one another for them; also, unlike the pigeons and rats, they only had one or two trials a day. However another reason for their superiority could be species differences in memory (see Krebs, this symposium).

The results from the non-unique group indicate that other experiments with repeated trials of storing or window-shopping in the same sites have probably not revealed the birds' best performance. It is interesting to note, however, that other tits given a task similar to Brodbeck's non-unique task, but with seven repeated sites instead of three, do perform better than chance,

even after 24 h (Krebs *et al.* 1990; Healy & Krebs 1990). The results of these and other memory tasks are discussed further by Krebs (this symposium).

6. CONCLUSIONS

The research described in this paper shows that at least some species of food-storing parids and corvids use memory for individual storage sites to recover items they have stored days or weeks previously. It also establishes some of the properties of memory for stored food (table 1) and indicates that, at least in parids, memory for stored food is not subserved by a qualitatively specialized memory system. Thus if food-storers have an adaptive specialization of memory it should be as evident in memory for food encountered by the bird as in memory for stored food, at least if memory for individual items is tested.

Although much has been learned in the last decade about spatial memory in food-storing tits and corvids, there is still a very large gap between a Siberian tit or a Clark's nutcracker storing thousands of seeds all over the forest for the winter and a chickadee asked to remember the location of a single peanut in an aviary for half an hour. Some of the differences are of the kind that is inevitable when a phenomenon observed in the field is brought into the laboratory. Yet as research on food-storing moves into a phase where tits and corvids are being tested on radial mazes and operant delayed matching tasks (Krebs, this symposium), it might be as well to bear in mind how little we know about the ways in which memory is actually used by these birds to recover their stores in the field. Experiments analysing memory for individual sites into its components should perhaps be accompanied by attempts to study issues like how, if at all, memory for the general areas of hoards enters into successful recovery, how this memory might be organized and how recovery of stored food is integrated with normal foraging.

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