

# Memory for food caches: not just for retrieval

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Many animals use hoarding as a long-term strategy to ensure a food supply at times of shortage. Hoarders employ strategies that enhance their ability to relocate caches such as remembering where caches are located. Long-term scatterhoarders, whose caches have potentially high pilferage rates, should also hoard in a way to reduce potential cache pilferers' ability to find caches. Previous studies have demonstrated that this could be achieved by hyperdispersing caches to reduce the foraging efficiency of pilferers. This study investigates whether coal tits (*Parus ater*) indeed place their caches away from existing ones. In our experiment, birds hoarded food in 3 conditions: when caches from a previous storage session were still present, when caches from a previous storage session were not present anymore because the bird had retrieved them, and when caches from a previous storage session had been removed by the experimenter. We show that coal tits hoard away from existing caches and that they do not use cues from extant caches to do this. This evidence is consistent with the use of memory for the locations of previous caches when deciding where to place new caches. This finding has important implications for our understanding of the selective pressures that have shaped spatial memory in food-hoarding birds. *Key words:* cache dispersal, coal tits, cognitive ecology, food-hoarding birds, *Parus ater*. [*Behav Ecol*]

Hoarding food to help ensure a food supply at times of shortage is a strategy employed by many animals. Scatterhoarding birds distribute their caches across a wide area, usually only hoarding 1 or 2 items in any given cache site (Vander Wall 1990). The challenge of cache retrieval has been discussed in great detail in the literature, and the strategies used include caching in species- and age/social group-specific niches (Brodin 1994b; Lens et al. 1994; Brodin and Clark 1997; Smulders 1998) and detailed memory for the exact cache locations (Cowie et al. 1981; Sherry et al. 1981; Stevens and Krebs 1986; Baker et al. 1988; Balda and Kamil 1989; Brodin 1994a; Healy and Suhonen 1996). However, retrieval strategies are useless if the caches have been pilfered when the hoarder returns. Therefore, it is also crucial for these birds to adopt hoarding strategies that minimize cache loss to other animals (typically heterospecifics, but potentially also conspecifics).

Some strategies to minimize cache loss are straightforward, such as caching mainly nonperishable items (Vander Wall 1990). Scatterhoarding itself also prevents major cache loss by literally spreading the risk of cache loss over many locations. Work conducted in the 1980s showed that marsh tits distribute their caches at an optimal average nearest neighbor distance (Sherry et al. 1982). Subsequent work has suggested that hyperdispersed caches (a distribution in which the presence of one cache would decrease the probability of finding another cache nearby; Dale 1999) may be a strategy used by hoarders to reduce cache loss (Male and Smulders forthcoming). Indeed, previous work (Shettleworth and Krebs 1982; Waite and Reeves 1994) indicates that birds do take extant caches into account when hoarding new ones. However, the mechanism by which they do this has not yet been studied. One way to generate hyperdispersed distributions of caches would be to remember where previous caches have been hoarded in order to hoard subsequent caches at reasonable distances away from them (Waite and Reeves 1994; Smulders

and Dhondt 1997; Smulders 1998). Alternatively, it is possible that hyperdispersed cache distributions are generated by using the visual cues from the caches, especially as parids are known often to leave caches partially exposed (e.g., Haftorn 1954, 1956a, 1956b; Petit et al. 1989). Our experiment was designed to distinguish between these 2 possibilities by manipulating whether or not previous caches were present. It was predicted that the birds would alter their distributions when they remembered where caches still remained.

## METHODS

### Subjects

Twelve coal tits were captured in Northumberland in September 2004 under an English Nature license. The birds were caught by a qualified ringer using mist nets on private land and were transported in cotton holding bags in which they spent a maximum of 3 h. The birds' ages were determined from the molting patterns of their greater coverts (Svensson 1992). Birds born in the Spring/Summer 2004 are referred to as "juveniles," and birds born in the Spring/Summer 2003 or before are referred to as "adults." We used 5 adults and 2 juveniles. The birds were released in April 2005 in the same area in which they were caught. The birds maintained their weight and health during captivity.

### Housing conditions

The experiment was run in March and April 2005. The birds were maintained on a 8.5:15.5 h light:dark cycle and at a temperature of between 14 and 19 °C to ensure they were in suitable conditions to hoard food (Shettleworth et al. 1995; Clayton and Cristol 1996). During the experiments, the birds were housed individually in cages that measured 85.0 × 45.5 × 95.0 cm (width × depth × height) and were located in a room adjacent to the experimental aviary. They were positioned so that the birds always had visual contact with other conspecifics. Each cage had at least 4 perches and a sliding tray that was cleaned daily. Birds were caught through a hatch in the side of the cage for regular health checks. Water was available ad libitum in a bowl, which was large enough for bathing, and in a dispenser on the side of the cage. The birds were fed on

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a daily diet of 4 split peanuts, 2 sunflower seeds, 3 pine nuts, 2 wax moths, 4 mealworms, and one scoop of EMP/Universal bird mix. They were deprived of food for 45 min before each storage or retrieval session.

### Aviary

The birds were tested in an experimental aviary measuring  $216.3 \times 349.5 \times 234.9$  cm (width  $\times$  depth  $\times$  height) and were viewed through a 1-way observation window from an observation room. Water and pieces of peanut or water only were available on a platform in the center of the experimental aviary in storage or retrieval sessions, respectively. A preliminary experiment (data not shown) showed that the birds preferred to hoard in high sites. It is possible that hoarding in preferred locations may overrule the hyperdispersing of caches, as different priorities in decision making related to hoarding have been seen in other studies (Bossera 1979). In an attempt to prevent this, we increased the number of high sites in the experimental aviary by suspending 53 wooden blocks on 3 concentric rings that were fixed to the ceiling of the aviary (Figure 1). There were 11 blocks on the inner ring (Ring 1), 18 on the middle ring (Ring 2), and 24 on the outer ring (Ring 3). The distance between rings and between blocks within a ring was approximately 28 cm. Storage sites consisted of holes (0.5 cm in diameter and 1.0 cm in depth) drilled in the blocks. A perch 5 cm in length was positioned below each hole. Each hole was obscured with lengths of thick string/cord that allowed the bird access but restricted its view of the hole (Figure 1, inset). The food platform was always located in the center of the 3 concentric rings. Colored pieces of cardboard were also randomly positioned on the walls in the aviary in each new trial to ensure that the birds treated each trial separately. These also act as spatial cues, which may help the birds remember cache locations (Balda and Kamil 1992; Brodbeck 1994; Herz et al. 1994).

### Procedure

Each bird was allowed to hoard a number of peanut fragments from the food platform in the experimental aviary in the first storage session (SS1). After this initial phase, there were 3 experimental conditions:

#### *Condition 1—SS1 caches retrieved (Retrieved)*

The bird was allowed to retrieve all its caches 3.5 h after SS1 in a retrieval session. The bird was then allowed to hoard again in the same aviary layout the following day in the second storage session (SS2). Caches made in SS2 were retrieved in another retrieval session 3.5 h after SS2.

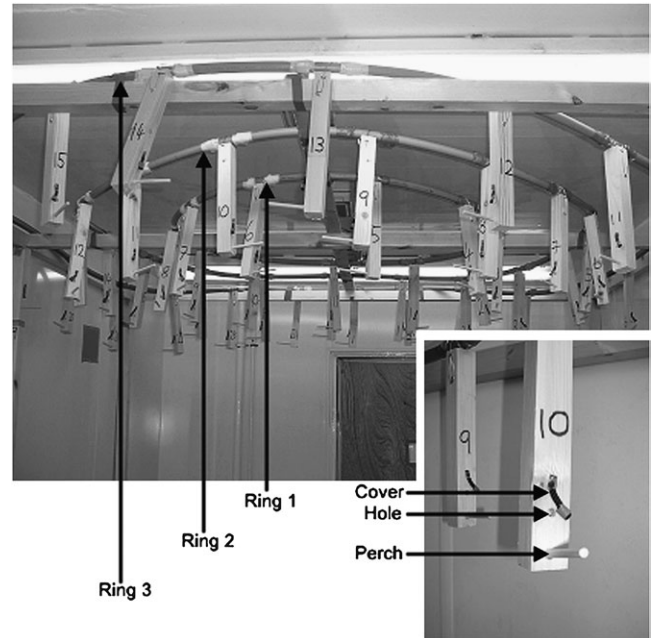
#### *Condition 2—SS1 caches present (Present)*

The bird was not allowed to retrieve caches after SS1. It was allowed to hoard again in the same aviary layout the following day in SS2. Caches made in both SS1 and SS2 were retrieved in a retrieval session 3.5 h after SS2.

#### *Condition 3—SS1 caches removed (Removed)*

The bird was not allowed to retrieve caches after SS1. Instead, the cached nuts were removed by the experimenter. The bird was then allowed to hoard again in the same aviary layout the following day in SS2. Caches made in both SS1 and SS2 were then replaced in the correct locations by the experimenter and retrieved by the bird in a retrieval session 3.5 h after SS2.

All storage and retrieval sessions lasted 30 min. The design was within subject, and each bird was exposed to each of the 3 conditions. The adult birds were exposed to each condition



**Figure 1**

Photographs of the aviary ring layout from the side. Blocks are suspended on 3 rings from the ceiling. All blocks are at the same height, and the 3 rings are concentric around the food platform. Each block contains one storage site above a perch and covered by a piece of string (inset).

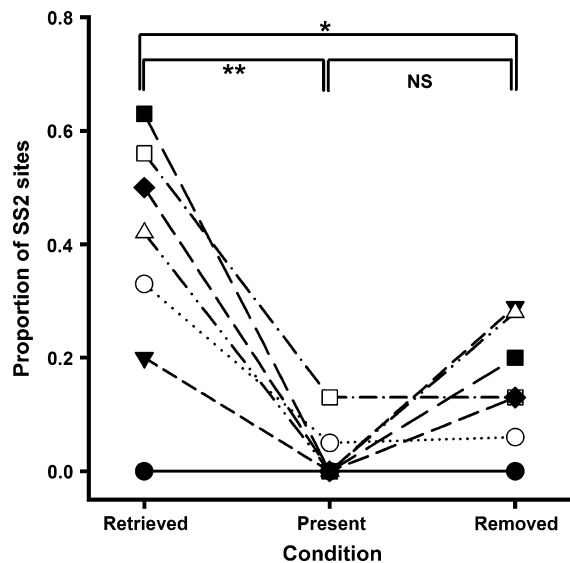
twice; the 2 juveniles were run in each condition only once. Different birds started with different conditions, and the order of conditions was allocated randomly to each bird. The birds were always given the opportunity to retrieve any caches made as they may be sensitive to pilfering (Lucas and Zielinski 1998). We recorded the behavior of the birds during the storage and retrieval sessions.

### Analysis

In general, we used repeated measures analyses of variance to analyze the data with bird as the unit of analysis. All data were normally distributed unless stated otherwise. Results were considered significant if  $P < 0.05$ . The dependent variables in the different analyses included the distance from a SS2 site to the nearest site used in SS1, the number of nuts hoarded in SS2 in the same sites used in SS1, and the number of nuts hoarded in SS2. The within-bird variable was condition (Retrieved, Present, and Removed). Age was a between-bird variable.

In the analysis of the mean distance of each SS2 site to the nearest SS1 site, those SS1 sites that the bird had already discovered to be empty in the Removed condition were not counted. As such, all SS1 sites that were hoarded in or looked in before a given SS2 nut was hoarded were excluded when calculating the distance of an SS2 cache to its nearest SS1 cache. This was to compensate for the birds inadvertently discovering that their caches from SS1 were missing as our preliminary experiment suggested that this may occur in SS2. For one bird, this meant there were no useful data remaining, so this analysis is based on 6 birds only.

Even birds that were run twice in the same condition did not always provide useful data for both trials, as they sometimes hoarded only one nut. For birds that had 2 useful data sets for a particular condition, the data were averaged across the 2 trials for that condition.



**Figure 2**

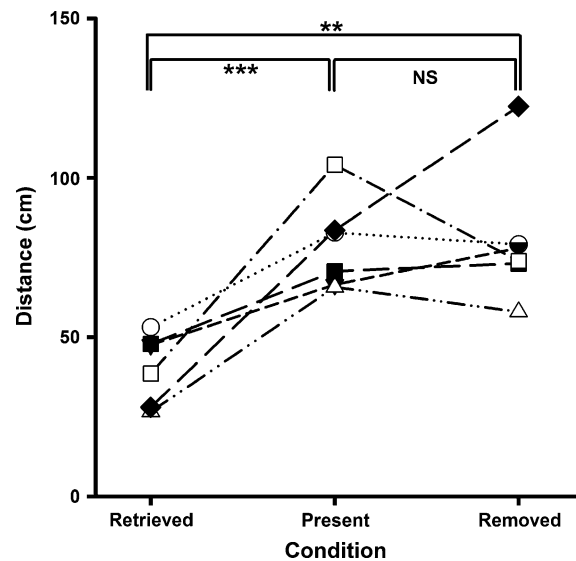
The proportion of the number of SS2 sites that had previously been used in SS1 is higher in the Retrieved condition than in the Present or Removed conditions. There was no difference between the latter 2 conditions. Each set of connected symbols represents data from a different bird. (\* $P < 0.05$ ; \*\* $P < 0.01$ ; repeated measures analysis of variance).

## RESULTS

There were differences across conditions in the mean distance from each SS2 site to the nearest SS1 site ( $F_{2,18} = 42.1$ ,  $P < 0.001$ ). The distance was an average of 54 cm closer when caches had been retrieved compared with when they were still present ( $F_{1,12} = 188.4$ ,  $P < 0.001$ ) or when they had been removed by the experimenter ( $F_{1,12} = 53.5$ ,  $P = 0.002$ ). There was no difference between Present and Removed ( $F_{1,12} = 0.2$ ,  $P = 0.686$ ) and no difference between the age groups ( $F_{1,18} = 2.8$ ,  $P = 0.168$ ).

There were also differences across conditions in the proportion of nuts hoarded in SS2 in sites previously used in SS1 ( $F_{2,21} = 13.6$ ,  $P = 0.001$ ; Figure 2). In SS2, a higher proportion of nuts were hoarded in SS1 sites when SS1 caches had been retrieved (an average of 0.38) compared with when SS1 caches were still present (an average of 0.03) ( $F_{1,14} = 18.7$ ,  $P = 0.008$ ) or when they had been removed by the experimenter (an average of 0.16) ( $F_{1,14} = 12.0$ ,  $P = 0.018$ ). There was no difference between the Present and Removed conditions ( $F_{1,14} = 3.9$ ,  $P = 0.107$ ). To determine whether the differences in distances from each SS2 site to nearest SS1 site were solely due to more SS1 sites being reused (i.e., 0 cm distances), the analysis was repeated excluding all SS2 sites used in SS1. Again, there were differences across conditions in the mean distance from the SS2 site to the nearest SS1 site ( $F_{2,18} = 18.8$ ,  $P = 0.001$ ; Figure 3) but again no differences across age groups ( $F_{1,18} = 18.8$ ,  $P = 0.143$ ). The mean distance of SS2 sites to the nearest SS1 sites was an average of 40 cm closer when SS1 caches had been retrieved compared with when they were still present ( $F_{1,12} = 145.0$ ,  $P < 0.001$ ) and when they had been removed by the experimenter ( $F_{1,12} = 26.0$ ,  $P = 0.007$ ). There was no difference between the Present and Removed conditions ( $F_{1,12} = 0.1$ ,  $P = 0.833$ ).

There was a difference across conditions in the number of nuts hoarded in SS2 ( $F_{2,21} = 9.9$ ,  $P = 0.004$ ). A higher number of nuts (an average of 3 extra nuts) were hoarded when SS1 caches had been removed by the experimenter than when SS1 caches were still present ( $F_{1,14} = 29.3$ ,  $P = 0.003$ ) or when



**Figure 3**

The mean distance from each SS2 site to the nearest SS1 site is lower in the Retrieved condition than in the Present or Removed conditions. There was no difference between the latter 2 conditions. The data exclude the sites used in both SS1 and SS2 (i.e., 0 cm distances). Each set of connected symbols represents data from a different bird. (\*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; repeated measures analysis of variance).

SS1 caches had been retrieved ( $F_{1,14} = 11.1$ ,  $P = 0.021$ ). There were no differences between the Retrieved and Present conditions ( $F_{1,14} = 0.9$ ,  $P = 0.380$ ). The juveniles also hoarded an average of 7 more nuts than the adults ( $F_{1,21} = 7.5$ ,  $P = 0.040$ ).

## DISCUSSION

Coal tits attempted to disperse their caches away from previous caches and did not use cues from the existing nuts to do so. This evidence is consistent with the use of memory for the existing caches during hoarding. This follows from the observation that caches were further from previous caches and fewer nuts were hoarded in the sites used previously when caches were still present from a previous hoarding session (Present) and when the birds “believed” the caches were still present but they had been removed by the experimenter (Removed) compared with when the birds had retrieved the caches (Retrieved).

This study suggests that coal tits attempt to approximate a more hyperdispersed distribution. This is also supported by previous work (Shettleworth and Krebs 1982; Waite and Reeves 1994). However, these studies did not distinguish between memory and cues from the extant caches. Our results are consistent with the idea that memory at least plays an important role in this process. Remembering all the existing caches while creating new ones would require a large memory capacity. Such an enhanced spatial memory may be costly in terms of its physiological and developmental requirements and, therefore, can only be adaptive if it gives the hoarder advantages over other hoarders without this specialization. As our previous results (Male and Smulders forthcoming) clearly show large survival advantages for more hyperdispersed cache distributions, we think it is likely that such an advantage does exist. We are currently investigating under exactly which ecological conditions such a strategy would be advantageous. The evolution of an enhanced spatial memory

for use in cache dispersion may also have been made easier by the fact that food-hoarding birds had already evolved an enhanced spatial memory for the retrieval of caches, at least over a period of weeks (in tits; Hitchcock and Sherry 1990; Healy and Suhonen 1996; Brodin and Kunz 1997). It is not hard to imagine that such a “preadaptation” could have been beneficial in the evolution of a memory-based cache-dispersion strategy.

Of course, parids are not the only animals known to use memory for cache locations for retrieval. Others, such as corvids (e.g., Balda and Kamil 1989) and rodents (e.g., Jacobs and Liman 1991; Jacobs 1992), do as well. Some have also been noted to attempt to hyperdisperses their caches, such as gray jays (Waite and Reeves 1994), kangaroo rats (Jenkins and Peters 1992; Leaver and Daly 1998), and chipmunks (Vander Wall 1995). Several of these may also have used memory to achieve these cache-dispersion strategies, although other mechanisms are also possible under different ecological conditions. Further investigation into these other species is necessary to appreciate the extent of this phenomenon.

Some of the birds also appeared to notice the removal of at least some of their caches in the Removed treatment, as they hoarded more nuts in Removed compared with Present and Retrieved. This may have been the birds’ response to cache loss as higher hoarding rates have been reported when seeds are pilfered compared with when they are not (Lucas and Zielinski 1998). However, there is no evidence that those birds that noticed that some of their caches were missing dispersed future caches away from these pilfered sites to avoid further cache loss (analysis not shown). As explained in Methods, the fact that some cache loss might have been detected in the Removed condition did not affect our main results, as we took this into account in the analysis.

In conclusion, this study shows that scatter-hoarding tits take the location of existing caches into account when placing new ones. Our data are consistent with the use of memory during this process. These insights are crucial in obtaining a complete understanding of the food-hoarding system and the adaptive demands it places on both cognitive and neural substrates.

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