

Memory decay and cache site preferences in hoarding coal tits — a laboratory study

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Summary

Many animals use hoarding as a long-term strategy to ensure a food supply at times of shortage. This study explores the respective roles of memory and site preferences in cache recovery by coal tits (*Periparus ater*). We compared the retrieval accuracy or foraging efficiency of the cacher itself ('caching coal tit'), a naive conspecific ('pilfering coal tit') and a non-hoarding heterospecific ('pilfering great tit'; *Parus major*) after six different retention intervals. Our experiment shows that the persistence of the coal tits' memory is up to 4 weeks in the laboratory. Species specific storage and foraging site preferences enhance cache recovery after longer intervals. We find no evidence for individual-specific preferences. Pilfering great tits are capable of learning the coal tits' hoarding preferences. This ability may affect coal tits' hoarding behaviour in more natural conditions as they frequently forage in mixed flocks with great tits.

Keywords: food-hoarding, memory, preferences, learning, persistence, great tit, coal tit.

Introduction

Food hoarding is the handling of food to conserve it for future use (Vander Wall, 1990) and many animals use it as a long-term strategy to ensure a food supply at times of shortage, e.g., in the winter. Long-term hoarding is likely to evolve if the hoarder is more likely than other individuals to recover their own caches (Andersson & Krebs, 1978). This can be achieved if hoarders employ strategies which enhance their own ability and reduce potential cache pilferers' abilities to find caches. Larder-hoarders store food in a single large

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cache or a very concentrated area in an animal's home range, whereas scatter-hoarders disperse their caches across their home range. As cache recovery is not a problem for larder-hoarders (because all their food is hoarded in one place), we focus on cache recovery strategies in scatter-hoarding birds, such as corvids and parids.

The simplest strategy that could be used to recover caches would be to search randomly but it is hard to envisage how this would enhance cache recovery. Indeed, various studies with corvids (Balda, 1980; Tomback, 1980; Vander Wall, 1982; Bunch & Tomback, 1986) demonstrate that hoarding birds do not search randomly. Olfactory cues could be used to pinpoint a cache's location. Although some corvids can detect caches through olfaction (Buitron & Nuechterlein, 1985; Harriman & Berger, 1986), they do not use this cue to enhance cache recovery (Bossema, 1979; Bunch & Tomback, 1986; Bennett, 1993). Similarly, many of the studies with parids (Sherry et al., 1981; Shettleworth & Krebs, 1982; Shettleworth, 1983; Sherry, 1984a) show that direct cues from the caches are not used during retrieval as caches were removed or moved before the recovery phase and the birds still returned to the original location.

Hoarders could ensure that they recover their own caches by using memory-based retrieval (Cowie et al., 1981; Sherry et al., 1981; Sherry, 1982, 1984a, b; Shettleworth & Krebs, 1982; Shettleworth, 1983). This is certainly a strategy that is used in the short-term in parids (Cowie et al., 1981; Stevens & Krebs, 1986) and for longer periods of time in corvids (Balda, 1980; Balda & Kamil, 1992; Bednekoff et al., 1997). However, some parids are known to hoard food for several weeks or months (Haftorn, 1954, 1956b, c) and direct tests of memory in the laboratory (Sherry, 1984a; Hitchcock & Sherry, 1990; Healy & Suhonen, 1996; Brodin & Kunz, 1997) show that they can only accurately recall locations of cache sites for up to a maximum of six weeks. So, if parids also have a short-term memory for cache locations in more natural conditions, what other strategies could they use for cache recovery in the long term?

Parids could ensure that they recover their own caches by restricting their hoarding and foraging effort to specific sites. The idea that parids enhance long-term retrieval by placing caches in areas where they are likely to forage in the future has been suggested previously (Gibb, 1960; Pravosudov, 1986; Brodin & Kunz, 1997; Brodin, 2005). Different species (Alatalo & Carlson, 1987; Suhonen & Alatalo, 1991) and different age classes of individuals (Brodin, 1994a; Lens et al., 1994; Brotons, 2000) have different hoarding

preferences (i.e., 'species-specific' and 'age-specific' respectively). It is also feasible that individuals also have certain preferences ('individual-specific') but this has yet to be demonstrated. So do these preferences enhance cache recovery? Brodin & Kunz (1997) showed that long-term cache recovery does depend on site preferences rather than memory. This experiment allowed willow tits (*Poecile montana*) to recover caches after different retention intervals and compared their performance with that of non-caching conspecifics. The importance of site preferences is revealed further by an experiment where willow tits had storage trials followed 24 hours later by separate recovery trials by the same caching bird, another willow tit and a great tit (*Parus major*; Suhonen & Inki, 1992). This study showed that species-specific storage site preferences do enhance foraging efficiency as non-caching willow tits performed better than great tits. Caching willow tits in turn performed better than non-caching willow tits, which was likely to be a result of memory for cache locations. The short retention interval in this experiment makes it impossible to distinguish between individual-specific preferences and memory for cache locations.

To consolidate our understanding of the respective roles of site preferences and memory in cache recovery our study combines Suhonen & Inki's (1992) and Brodin & Kunz's (1997) experimental designs. We present the cache recovery accuracy of ('caching') coal tits (*Periparus ater*) after 1 day, 3 days, 1 week, 2 weeks, 4 weeks and 6 weeks. We also present the foraging efficiency of conspecific ('pilfering') coal tits and heterospecific ('pilfering') great tits which forage on the caches made by the caching coal tits. Comparing caching coal tits to pilfering coal tits allows us to discriminate memory-based retrieval (or individual preferences) from species-specific site preferences. If individual advantages of cachers over pilferers decrease over time, this suggests the use of memory, as opposed to individual-specific preferences. Because great tits forage on a number of different coal tits' caches, we can also test whether heterospecific pilferers can learn a caching species' site preferences.

Methods

Subjects

We captured 12 coal tits and 10 great tits in Northumberland in September 2004 under English Nature licence number 20042059. 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 three hours. The coal tits' ages were determined from the moulting 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 nine coal tits (4 juveniles and 5 adults) as one adult and one juvenile did not consistently hoard food or forage and therefore were released, and another adult died. In April 2005, we released all the birds in the same area in which they were caught. All animal experimentation was done according to the ASAB/ABS guidelines and within the law of the United Kingdom. The birds maintained their weight and health during captivity.

Conditions

We ran the experiment from December 2004 to April 2005. The birds were maintained on a 8.5:15.5 light:dark cycle and at a temperature of between 14°C to 19°C to ensure the coal tits were in suitable conditions to hoard food (Shettleworth et al., 1995; Clayton & Cristol, 1996). During the experiments, the birds were housed individually in cages which measured 85.0 × 45.5 × 95.0 cm (width × depth × height) and were located in a room adjacent to the experimental aviary. Water was available *ad libitum*. The coal tits were fed on a daily diet of four split peanuts, two sunflower seeds, three pine nuts, two wax worms, four mealworms and one scoop of EMP/Universal bird mix. The great tits were fed the same daily diet but had whole peanuts, six sunflower seeds and no pine nuts. The coal tits and great tits were deprived of food for one hour and one and a half hours respectively before each storage, retrieval or foraging session. This is consistent with previous studies using species of differing sizes (Suhonen & Inki, 1992).

Aviary

We tested the birds in an experimental aviary measuring 216 × 350 × 235 cm (width × depth × height) whilst viewing through a one-way observation window from an observation room. Water was available on a platform in the centre of the experimental aviary.

Storage sites were available in large tree branches (8 to 13 per branch), placed upright in concrete blocks (Sherry, 1984a; Hitchcock & Sherry, 1990),

and in 53 wooden blocks suspended in three concentric rings from the ceiling of the aviary (see also Male & Smulders, 2007). Each storage site consisted of a hole of 0.5 cm in diameter and 1.0 cm in depth (Shettleworth & Krebs, 1982; Sherry, 1984a; Hitchcock & Sherry, 1990, 1995; Healy & Suhonen, 1996), with a 5-cm-long perch below it (Sherry, 1984a). The holes were obscured with lengths of thick string/cord which allowed the bird access but restricted its view of the hole. There was coloured tape below each storage site for identification purposes. Spruce branches were randomly secured on nine of the wooden blocks to act as visual cues. In addition, other landmarks included coloured pieces of cardboard which were positioned on the aviary walls and various objects which were suspended from the ceiling. The birds were tested in two different aviary layouts, which consisted of three trees in different positions, different locations for the spruce branches and different types of cardboard and objects. These made the two aviary layouts as distinct as possible.

Training

The birds were trained to leave the home cage when it was covered with a black-out cloth and when the experimental aviary was lit, and to return when the aviary lights were extinguished. This procedure has been used in many experiments before and eliminates handling stress (Clayton & Krebs, 1994; Shiflett et al., 2003). The birds were habituated to the experimental aviary by allowing them to forage and eat whilst in the room. They received daily training sessions for a two-week period until they were readily flying from the housing cage to the experimental aviary and back again.

Procedure

Each coal tit was given six 30-min storage sessions in the aviary and retrieved these caches in a 45-min retrieval session after six different retention intervals: 1 day, 3 days, 1 week, 2 weeks, 4 weeks and 6 weeks. These are referred to as the 'caching coal tits'. We separated the coal tits into two sub-groups (A and B) of approximately the same number of adults and juveniles. Group A birds hoarded food in aviary layout 1 and Group B birds hoarded in aviary layout 2. The order of the retention intervals tested was randomized and differed between the two groups of caching coal tits (but was the same for all the birds within each group).

Other coal tits ('pilfering coal tits') and great tits ('pilfering great tits') also foraged on the caches made by the caching coal tits. These foraging sessions occurred after all the storage sessions and retrieval sessions by the caching coal tits had been completed. Different pilfering great tits foraged for the six cache distributions made by a given coal tit. Once the coal tits had retrieved all of their own caches after the different retention intervals, they served as 'pilfering coal tits' and foraged for other coal tits' caches. Group A foraged for Group B's caches and Group B for Group A's caches. The coal tits, therefore, foraged for conspecific coal tits' caches in a different aviary layout to where they had hoarded food previously. This was to minimize the possibility that any remaining memories for cache locations would interfere with the foraging of the pilfering coal tits. Our previous work suggests that the foraging motivation differs between adults and juveniles (Male & Smulders, unpubl. results) so adult coal tits foraged for other adult coal tits' caches and juvenile coal tits foraged for other juvenile coal tits' caches.

Our previous experiments with great tits (Male & Smulders, unpubl. results) suggested that they preferentially forage in sites where food was located previously. The six-week retention interval was an important test to reveal species vs. individual specific preferences. To prevent previous experience with coal tits' caches affecting the foraging efficiency of the great tits when foraging on the cache distribution from the six week retention interval trial, the pilfering coal tits and great tits foraged for the caches generated by the caching coal tits in descending order of retention intervals. This means that, for the pilfering coal tits and great tits only, trials 1 to 6 are the trials on which they foraged on the distributions generated by the caching coal tits during the 6-week, 4-week, 2-week, 1-week, 3-day and 1-day retention interval trials respectively. If any pilfering coal tit hoarded food during the foraging session, it was given an additional session to retrieve this food. This was to minimize the risk that the memory of hoarded food would disrupt future foraging sessions.

Analysis

Actual number of correct looks

We analysed the cumulative proportion of correct looks in the first 30 looks. This was calculated as the number of correct looks in the first 30 looks divided by the total possible number of hoards to be found. For analysis purposes, these proportions were arcsine-square root transformed.

Expected number of correct looks

As in Balda & Kamil (1992), a hypergeometric distribution was used to calculate the expected proportion of corrects looks by the 30th look because there was sampling without replacement from a finite population. We used the hypergeometric distribution to calculate the probability of any given number of correct looks being made by look 30 as follows:

$$P(X = x) = \frac{\binom{M}{x} \binom{N - M}{n - x}}{\binom{N}{n}}$$

where x = number of correct looks; n = number of looks; M = possible number of correct looks (the number of nuts hoarded); and N = number of storage sites. All the possible numbers of correct looks (0 to N) were then averaged with a weighted average using the above-calculated probability as the weighting factor. The expected number of correct looks was then divided by the maximum possible number of correct looks to obtain an expected proportion of correct looks. For analysis purposes, this proportion was then arcsine-square root transformed.

Statistics

We used Repeated Measures (RM) ANOVAs in SPSS for Windows Version 11.0.0 to analyse the data in conjunction with Dytham (2003). Results were considered significant if $p < 0.05$. Our analysis by trial used RM ANOVAs to examine pilfering great tit and pilfering coal tit data with the foraging bird as the unit of analysis and species as the between-bird variable. The within-bird variables were trial (1 to 6) and data type (actual data vs. expected by chance). Our analysis by retention interval used RM ANOVAs with caching coal tit as the unit of analysis. The within-subject variables were retention interval (1 day to 6 weeks) and data type (caching coal tit, pilfering coal tit or expected by chance). We excluded the pilfering great tits from the analysis by retention interval because we found a learning effect in the analysis by trial. For post-hoc comparisons, we used one-tailed tests, as the predictions were always one-directional: caching coal tits should outperform pilfering coal tits; and short retention intervals should yield better performance than longer retention intervals (Hitchcock & Sherry, 1990; Brodin & Kunz, 1997).

To investigate whether great tits learned the exact sites where food was likely to be located (such as, ‘food is always located in Ring 1: Storage site 5’) or general rules about coal tit caching preferences (such as, ‘forage in the left front corner of the room’), the storage sites were divided into five Caching Preference Categories (CPCs), by how many times the caching coal tits (as a group) used the site for hoarding (CPC1: 0-2 times, CPC2: 3-5 times, CPC3: 6-8 times, CPC4: 9-11 times and CPC5: over 11 times). We counted the number of looks made by the pilfering great tits or pilfering coal tits in the sites in each of these CPCs for the first 30 looks in a foraging session.

Results

Analysis by trial

The pilfering great tits’ and pilfering coal tits’ foraging performance is presented first. All birds performed better than chance (RM ANOVA: $F_{1,12} = 28.612$, $p < 0.001$) and there was a significant interaction between species and trial (RM ANOVA: $F_{5,60} = 2.843$, $p = 0.023$). As there was also a significant 3-way interaction between actual data vs. chance, trial and species (RM ANOVA: $F_{5,60} = 2.763$, $p = 0.026$), we analysed each species separately. This analysis excluded two pilfering great tits and three pilfering coal tits as they did not forage in all trials.

Pilfering great tits

By the 30th look, the pilfering great tits had made an average of 14% more correct looks than expected by chance (RM ANOVA: $F_{1,7} = 7.157$, $p = 0.032$). There was a significant interaction between trial and data type (actual data vs. chance) (RM ANOVA: $F_{5,35} = 3.713$, $p = 0.008$). A higher percentage of correct looks were made in later trials, going from 43% in trial 1 to 65% in trial 6 (linear contrast: $F_{1,7} = 8.621$, $p = 0.022$), with performance in the last 3 trials significantly higher than chance level ($F_{1,7} = 23.067$, $p = 0.002$; Figure 1a). The pilfering great tits developed preferred foraging sites as trials increased and these preferred foraging sites corresponded with the coal tits’ preferred storage sites (Figure 1b).

All 10 great tits foraged in the final trial. For the first 30 looks, the number of times each great tit looked in a CPC 4 or 5 site (those most preferred by the coal tits for hoarding; see Methods) was compared with the number of

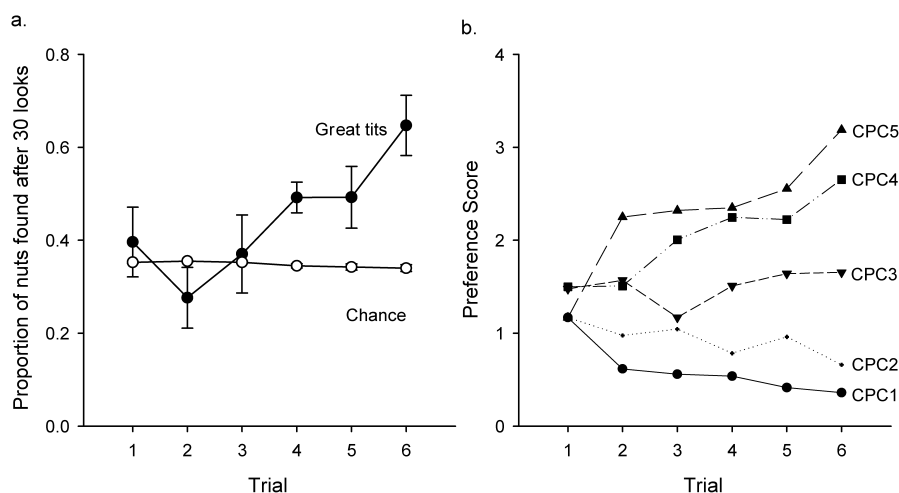


Figure 1. (a) Foraging success of the pilfering great tits over the 6 trials (mean \pm SEM). Performance in the last three trials is significantly better than chance. (b) Great tit foraging preference scores for each of the coal tits' Cache Preference Categories (CPCs). CPC1 contains the cache sites in which coal tits are least likely to hoard and CPC5 the ones in which they are most likely to hoard. Great tits' preference for foraging in sites in which coal tits are more likely to hoard goes up with experience. Preference scores are calculated as the ratio between the proportion of the first 30 looks aimed at sites within that CPC and the proportion of all sites that are contained within that CPC.

times they looked in the nearest CPC 1 or 2 site (those least preferred by coal tits for hoarding). If the pilfering great tits learned the exact sites where food was located, there should be more looks in the CPC 4 or 5 sites. On the other hand, if the pilfering great tits learned the general areas where food was more likely to be located, there should be no difference in the number of looks between the CPC 4 or 5 sites and the nearest CPC 1 or 2 sites. For six of the birds, there was no difference between the number of times they looked in a CPC 4 or 5 site compared to the number of times they looked in the nearest CPC 1 or 2 site (χ^2 ranging from 0.154 to 3.769, p ranging from 0.052 to 0.695). The other four birds made significantly more looks in the CPC 4 or 5 sites compared to the nearest CPC 1 or 2 sites (χ^2 ranging from 6.368 to 14.000, p from <0.001 to 0.012).

Pilfering coal tits

As the coal tits foraged on conspecifics' caches of the same age group and there were unequal numbers of juveniles and adults in the two groups, the

pilfering coal tits foraged on different numbers of cache distributions. In an analysis of the six birds that had experience in six trials each, they found more items (on average 53% of items) than the 35% expected by chance (RM ANOVA: $F_{1,5} = 20.502$, $p = 0.006$). There was no effect of trial on the proportion of correct looks (RM ANOVA: $F_{5,25} = 0.957$, $p = 0.462$; Figure 2a), nor was there a significant interaction between actual data vs. chance and trial number (RM ANOVA: $F_{5,25} = 0.697$, $p = 0.631$). The coal tits' preference for certain sites was clear from the first trial and corresponded with the preferred storage sites (Figure 2b).

Analysis by retention interval

This analysis only included caching coal tits, pilfering coal tits and the performance expected by chance because we found a change in foraging efficiency over time for the pilfering great tits. Both caching and pilfering coal tits performed better than chance, finding on average 67% and 50% of the items, compared to 35% expected by chance (RM ANOVA: $F_{2,16} = 41.242$, $p < 0.001$). The proportion of correct looks by caching coal tits, but not by pilfering coal tits, decreased as the retention interval increased (RM ANOVA interaction between data type and retention interval: $F_{10,80} = 2.088$, $p = 0.035$). We analysed this interaction further in two different ways. Firstly, we analysed the performance of caching coal tits and pilfering coal tits separately. Consistent with the previous section, foraging success of the pilfering coal tits did not change with retention interval ($F_{5,40} = 0.764$, $p = 0.581$). Caching coal tits' retrieval performance decreased over time ($F_{5,40} = 3.456$, $p = 0.011$; Figure 3), with retrieval after 1 day significantly better than all other intervals and retrieval after 6 weeks worse than all other intervals except 1 week and 4 weeks. The intermediate delays did not differ significantly from each other. Secondly, we analysed the data by retention interval. Caching coal tits performed significantly better than pilfering coal tits after 1 day, 3 days and 4 weeks (1 day: $F_{1,8} = 45.507$, $p < 0.001$; 3 days: $F_{1,8} = 10.712$, $p = 0.006$; 4 weeks: $F_{1,8} = 4.981$, $p = 0.028$; all tests one-tailed), but not after the other retention intervals (1 week: $F_{1,8} = 2.952$, $p = 0.062$; 2 weeks: $F_{1,8} = 3.048$, $p = 0.060$; 6 weeks: $F_{1,8} = 0.219$, $p = 0.326$; all tests one-tailed; Figure 3).

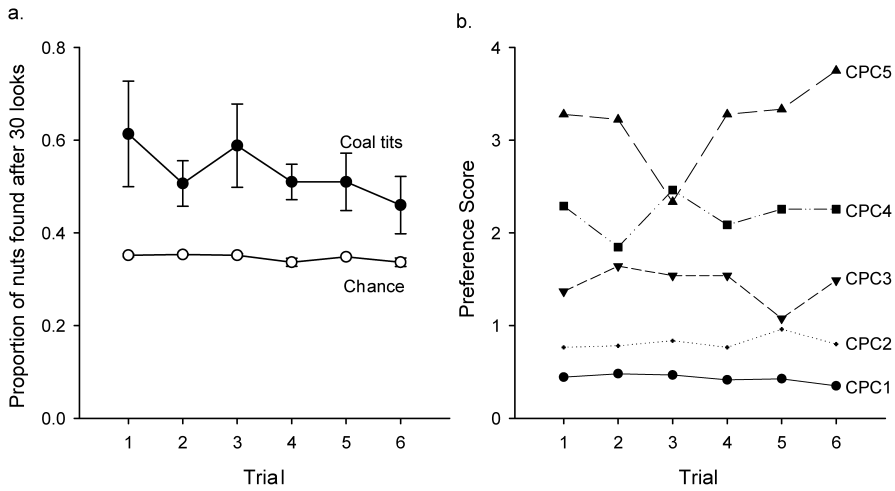


Figure 2. (a) Foraging success of the pilfering coal tits over the 6 trials (mean \pm SEM). Performance in all trials is significantly better than chance. (b) Pilfering coal tits' foraging preference scores for each of the Cache Preference Categories (CPCs). CPC1 contains the cache sites in which coal tits are least likely to hoard and CPC5 the ones in which they are most likely to hoard. Coal tits prefer to forage in sites in which all coal tits are more likely to hoard. Preference scores are calculated as the ratio between the proportion of the first 30 looks aimed at sites within that CPC and the proportion of all sites that are contained within that CPC.

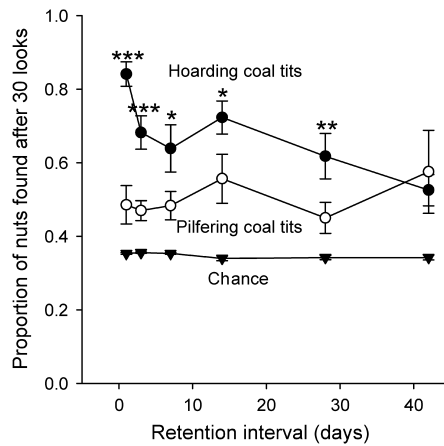


Figure 3. Retrieval success of the caching coal tits goes down with retention interval, while foraging success of the pilfering coal tits stays the same. All proportions are expressed as mean \pm SEM. In both situations, birds perform better than chance. Asterisks indicate differences between caching coal tit and pilfering coal tit performance (* $p < 0.10$; ** $p < 0.05$; *** $p < 0.01$; one-tailed tests).

Discussion

Memory, preferences and learning

Caching coal tits used memory to retrieve their caches at short retention intervals as, after 1 day, 3 days and 4 weeks, they were statistically more accurate than pilfering coal tits, and after 1 day, 3 days and 2 weeks they were significantly more accurate than after 6 weeks. The accuracy in cache retrieval declined as retention intervals increased in length. Like Hitchcock & Sherry (1990) and Brodin & Kunz (1997), we attribute this to a decline in memory for cache locations. There was no significant difference between the retrieval accuracy of the caching coal tits and the foraging efficiency of the pilfering coal tits after 1 week, 2 weeks and 6 weeks. Whereas after 6 weeks, the caching coal tits clearly do not outperform the pilfering coal tits (in fact, their average performance is slightly below that of the pilferers), the performance after 1 and 2 weeks borders on significant and the non-significance of the results is likely due to variability in the data and a lack of power to consistently detect the effect.

The pilfering coal tits' foraging efficiency was generally above that expected by chance and, even after 6 weeks, when the caching coal tits' memory had completely lapsed, their retrieval accuracy was still above that expected by chance. At that time, there was no difference in the retrieval accuracy of the caching coal tits and foraging efficiency of the pilfering coal tits, indicating that all the birds were using site preferences to enhance retrieval accuracy or foraging efficiency and that individual-specific hoarding preferences were not used. These results on coal tits are consistent with those obtained with willow tits (Brodin & Kunz, 1997). However, our study also had a comparison with great tits which was not used by Brodin & Kunz (1997). This comparison shows that the great tits did not forage more efficiently than chance when first presented with the coal tits' caches. This indicates that there were species specific storage sites preferences which enhanced the retrieval accuracy and the foraging efficiency of the coal tits in the laboratory.

Previous studies (Hitchcock & Sherry, 1990; Suhonen & Inki, 1992; Brodin & Kunz, 1997) have attributed enhanced recovery by caching birds after long retention intervals and by non-caching birds in general to storage site preferences. Our study shows that the caching coal tits had storage site

preferences in the laboratory and that the foraging site preferences of the pilfering coal tits, but not the pilfering great tits in trial 1, corresponded with these storage site preferences. This provides evidence that species-specific storage and foraging site preferences enhance cache recovery. As pilfering juveniles always foraged for conspecific juveniles' caches and, similarly, pilfering adults always foraged for conspecific adults' caches, a comprehensive test of 'age-specific' preferences could not be conducted. We found no evidence for individual-specific preferences, as after 6 weeks, there was absolutely no difference in foraging success between the caching and the pilfering coal tits. Brodin & Kunz (1997) investigated what the success rate of a 'pilfering' willow tit would have been if it had been foraging on its own caches, and concluded that it would have been slightly better than when foraging on other willow tits' caches. We did not do such a detailed analysis of the individual birds' looks, so this subtle level of individual differences could still exist.

Interestingly, the pilfering great tits' foraging efficiency was better in later trials. This is because the pilfering great tits learned the coal tits' preferred storage sites and preferentially foraged in these sites. Our data suggest that some pilfering great tits remembered the exact sites where food was likely to be located (such as, 'food is always located in Ring 1: Storage site 5') but others learned a rule with respect to the area where food was located (such as, 'forage in certain areas of the ring layout' or 'forage in high sites'). These different outcomes among individuals probably existed because the birds experienced the caches in different ways whilst learning. For example, each bird did not experience the same series of cache distributions across trials and each bird probably visited the storage sites in different sequences within a trial. Additional experiments are necessary to investigate these learning mechanisms further. In contrast to the pilfering great tits, the pilfering coal tits' foraging efficiency did not increase in later trials. This is because the coal tits always foraged in their preferred cache locations.

Implications for food hoarding

This study shows that a coal tit's memory lasts less than 6 weeks in the laboratory. This is consistent with other studies on parids, which have found memory durations between 1 and 4 weeks (Hitchcock & Sherry, 1990; Healy & Suhonen, 1996; Brodin & Kunz, 1997). And just like for marsh tits,

memory duration for coal tits (a presumed short-term hoarder only; Haftorn (1956a, b, c) as cited by Healy & Suhonen (1996)) is not any shorter than that for presumed long-term hoarders such as black-capped chickadees and willow tits. These laboratory data are supported by Brodin's (1994b) field experiment with willow tits which showed that naturally hoarded items disappeared faster than from re-baited caches but only at retention intervals of less than 6 weeks. However, some parids are known to recover caches well past 6 weeks. A high proportion of the stomach contents of wild, winter-caught crested and willow tits is made up of hoarded food (Haftorn, 1954, 1956b). Our study supports the hypothesis (see also Brodin & Clark, 1997; Brodin, 2005) that this may be attributable to storage site preferences which appear to enhance long-term recovery. In conclusion, it seems likely that coal tits use storage site preferences to enhance long-term cache recovery and memory for cache locations to enhance short-term cache recovery.

Our study provides evidence for species-specific preferences for storage sites which is consistent with previous studies (Gibb, 1960; Pravosudov, 1986; Alatalo & Carlson, 1987; Suhonen & Alatalo, 1991; Suhonen & Inki, 1992; Brodin, 1994a; Lens et al., 1994; Brodin & Kunz, 1997; Brotons, 2000), but not for individual-specific preferences (but see Brodin & Kunz, 1997). Since these preferences are consistent (or at least strongly overlapping) across the species, intraspecific pilferage is likely. Indeed, various field studies have indicated that conspecific flock mates do pilfer caches (Brodin & Ekman, 1994). Even though individual preferences (or caching niches) make the evolution of hoarding more likely (Smulders, 1998), the selection pressure to assure a large niche or preference separation among individuals of the same species is probably not very strong, because reciprocal pilfering can be evolutionarily stable (Smulders, 1998; Vander Wall & Jenkins, 2003). This idea has also been suggested previously in a field study which regarded hoarded food as 'communal property' by the members of a flock of boreal chickadees (Haftorn, 1974). However, individual preferences may not have been observed in our experiments because of insufficient numbers of different types of storage sites and because birds never hoarded together.

Some pilfering great tits learned the exact locations that caches were likely to be in. In the field, this would be unlikely to result in higher cache loss for coal tits because they always hoard in different sites (Haftorn, 1956c). On the other hand, our data suggest that some great tits were able to learn rules about typical cache sites. If they can do this in the field also, this may have major

implications for coal tits' hoarding strategies because coal tits are known to hoard in specific types of storage sites (Haftorn, 1956c). In the field, there are thousands of potential cache sites in a bird's home range, which may reduce this possibility. On the other hand, great tits and coal tits often forage in mixed flocks (Ekman, 1989; Hogstad, 1989; Kimberly & Morrison, 1990; Suhonen, 1993; Dolby & Grubb Jr, 1998), so the exposure of great tits to coal tit caches might be high, which may facilitate this learning. If it is possible in natural conditions, it would increase cache loss for the coal tits as the great tits' pilfering efficiency would be enhanced. To prevent this, coal tits may have evolved to use sites which are inaccessible to potential pilferers. For example, coal tits regularly hoard at the extremities of spruce trees using the thinnest needled branches and terminal bud capsules (Haftorn, 1956c) which are probably inaccessible for the larger great tits (great tits are 14 cm long and weigh 16-21 g; coal tits are 11.5 cm long and weigh 8-10 g). Indeed, Gibb (1960) noted that great tits are ill-adapted to life in pine plantations, whereas coal tits prefer this habitat. This may be a strategy used by other parid species as well: black-capped chickadees also use cache sites that are somewhat inaccessible to other species (Petit et al., 1989).

Conclusion

Consistent with previous studies in related species, we show that coal tits can remember cache locations for up to 4 weeks, and can continue to retrieve caches at rates higher than chance for longer intervals using species-specific site preferences. Great tits do not share these site preferences initially, but can learn them through repeated exposure to coal tit caches. In the field, the latter effect may have led to the evolution of coal tit preferences for sites that are inaccessible to great tits.

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