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1 **Title**

2

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

4

5 **Short title**

6

7 Memory and cache site preferences

8

9 **Authors' names**

10 Lucinda H. Male¹

11 Tom V. Smulders¹

12

13 ¹ - Newcastle University, Centre for Behaviour and Evolution, Henry Wellcome

14 Building for Neuroecology, Framlington Place, Newcastle upon Tyne, NE2 4HH

15 United Kingdom

16

17 **Corresponding author**

18

19 tom.smulders@ncl.ac.uk

1 **Summary**

2

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

15

16 **Key words**

17

18 Food-hoarding; memory; preferences; learning; persistence; great tit; coal tit

19

1 **Introduction**

2

3 Food hoarding is the handling of food to conserve it for future use (Vander Wall,
4 1990) and many animals use it as a long-term strategy to ensure a food supply at times
5 of shortage, e.g. in the winter. Long-term hoarding is likely to evolve if the hoarder is
6 more likely than other individuals to recover their own caches (Andersson & Krebs,
7 1978). This can be achieved if hoarders employ strategies which enhance their own
8 ability and reduce potential cache pilferers' abilities to find caches. Larder-hoarders
9 store food in a single large cache or a very concentrated area in an animal's home
10 range, whereas scatter-hoarders disperse their caches across their home range. As
11 cache recovery is not a problem for larder-hoarders (because all their food is hoarded
12 in one place), we focus on cache recovery strategies in scatter-hoarding birds, such as
13 corvids and parids.

14

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

27

1 Hoarders could ensure that they recover their own caches by using memory-based
2 retrieval (Cowie et al., 1981; Sherry et al., 1981; Sherry, 1982, 1984a, 1984b;
3 Shettleworth & Krebs, 1982; Shettleworth, 1983). This is certainly a strategy that is
4 used in the short-term in parids (Cowie et al., 1981; Stevens & Krebs, 1986) and for
5 longer periods of time in corvids (Balda, 1980; Balda & Kamil, 1992; Bednekoff et
6 al., 1997). However, some parids are know to hoard food for several weeks or months
7 (Haftorn 1954, 1956b, 1956c) and direct tests of memory in the laboratory (Sherry,
8 1984a; Hitchcock & Sherry, 1990; Healy & Suhonen, 1996; Brodin & Kunz, 1997)
9 show that they can only accurately recall locations of cache sites for up to a maximum
10 of six weeks. So, if parids also have a short-term memory for cache locations in more
11 natural conditions, what other strategies could they use for cache recovery in the long-
12 term?

13

14 Parids could ensure that they recover their own caches by restricting their hoarding
15 and foraging effort to specific sites. The idea that parids enhance long-term retrieval
16 by placing caches in areas where they are likely to forage in the future has been
17 suggested previously (Gibb, 1960; Pravosudov, 1986; Brodin & Kunz, 1997; Brodin,
18 2005). Different species (Alatalo & Carlson, 1987; Suhonen & Alatalo, 1991) and
19 different age classes of individuals (Brodin, 1994a; Lens et al., 1994; Brotons, 2000)
20 have different hoarding preferences (i.e. 'species-specific' and 'age-specific'
21 respectively). It is also feasible that individuals also have certain preferences
22 ('individual-specific') but this has yet to be demonstrated. So do these preferences
23 enhance cache recovery? Brodin and Kunz (1997) showed that long-term cache
24 recovery does depend on site preferences rather than memory. This experiment
25 allowed willow tits (*Poecile montana*) to recover caches after different retention
26 intervals and compared their performance with that of non-caching conspecifics. The

1 importance of site preferences is revealed further by an experiment where willow tits
2 had storage trials followed 24 hours later by separate recovery trials by the same
3 caching bird, another willow tit and a great tit (*Parus major*; Suhonen & Inki, 1992).
4 This study showed that species-specific storage site preferences do enhance foraging
5 efficiency as non-caching willow tits performed better than great tits. Caching willow
6 tits in turn performed better than non-caching willow tits, which was likely to be a
7 result of memory for cache locations. The short retention interval in this experiment
8 makes it impossible to distinguish between individual-specific preferences and
9 memory for cache locations.

10

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

1 **Methods**

2

3 *Subjects*

4

5 We captured 12 coal tits and 10 great tits in Northumberland in September 2004 under
6 English Nature licence number 20042059. The birds were caught by a qualified ringer
7 using mist nets on private land and were transported in cotton holding bags in which
8 they spent a maximum of three hours. The coal tits' ages were determined from the
9 moulting patterns of their greater coverts (Svensson, 1992). Birds born in the
10 Spring/Summer 2004 are referred to as 'juveniles' and birds born in the
11 Spring/Summer 2003 or before are referred to as 'adults'. We used nine coal tits (4
12 juveniles and 5 adults) as one adult and one juvenile did not consistently hoard food
13 or forage and therefore were released, and another adult died. In April 2005, we
14 released all the birds in the same area in which they were caught. All animal
15 experimentation was done according to the ASAB/ABS guidelines and within the law
16 of the United Kingdom. The birds maintained their weight and health during
17 captivity.

18

19 *Conditions*

20

21 We ran the experiment from December 2004 to April 2005. The birds were
22 maintained on a 8.5:15.5 Light:Dark cycle and at a temperature of between 14°C to
23 19°C to ensure the coal tits were in suitable conditions to hoard food (Shettleworth et
24 al., 1995; Clayton & Cristol, 1996). During the experiments, the birds were housed
25 individually in cages which measured 85.0cm by 45.5cm by 95.0cm (width by depth
26 by height) and were located in a room adjacent to the experimental aviary. Water was

1 available *ad libitum*. The coal tits were fed on a daily diet of four split peanuts, two
2 sunflower seeds, three pine nuts, two wax worms, four mealworms and one scoop of
3 EMP/Universal bird mix. The great tits were fed the same daily diet but had whole
4 peanuts, six sunflower seeds and no pine nuts. The coal tits and great tits were
5 deprived of food for one hour and one and a half hours respectively before each
6 storage, retrieval or foraging session. This is consistent with previous studies using
7 species of differing sizes (Suhonen & Inki, 1992).

8

9 *Aviary*

10

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

15

16 Storage sites were available in large tree branches (8 to 13 per branch), placed upright
17 in concrete blocks (Sherry, 1984a; Hitchcock & Sherry, 1990), and in 53 wooden
18 blocks suspended in three concentric rings from the ceiling of the aviary (see also
19 Male & Smulders, 2007). Each storage site consisted of a hole of 0.5 cm in diameter
20 and 1.0 cm in depth (Shettleworth & Krebs, 1982; Sherry, 1984a; Hitchcock &
21 Sherry, 1990; Hitchcock & Sherry, 1995; Healy & Suhonen, 1996), with a 5 cm-long
22 perch below it (Sherry, 1984a). The holes were obscured with lengths of thick
23 string/cord which allowed the bird access but restricted its view of the hole. There was
24 coloured tape below each storage site for identification purposes. Spruce branches
25 were randomly secured on nine of the wooden blocks to act as visual cues. In
26 addition, other landmarks included coloured pieces of cardboard which were

1 positioned on the aviary walls and various objects which were suspended from the
2 ceiling. The birds were tested in two different aviary layouts, which consisted of
3 three trees in different positions, different locations for the spruce branches and
4 different types of cardboard and objects. These made the two aviary layouts as distinct
5 as possible.

6

7 *Training*

8

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

16

17 *Procedure*

18

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

1

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

16

17 Our previous experiments with great tits (Male & Smulders: unpublished results)
18 suggested that they preferentially forage in sites where food was located previously.
19 The six-week retention interval was an important test to reveal species vs. individual-
20 specific preferences. To prevent previous experience with coal tits' caches affecting
21 the foraging efficiency of the great tits when foraging on the cache distribution from
22 the six week retention interval trial, the pilfering coal tits and great tits foraged for the
23 caches generated by the caching coal tits in descending order of retention intervals.
24 This means that, for the pilfering coal tits and great tits only, trials 1 to 6 are the trials
25 on which they foraged on the distributions generated by the caching coal tits during
26 the 6-week, 4-week, 2-week, 1-week, 3-day and 1-day retention interval trials

1 respectively. If any pilfering coal tit hoarded food during the foraging session, it was
2 given an additional session to retrieve this food. This was to minimize the risk that the
3 memory of hoarded food would disrupt future foraging sessions.

4

5 *Analysis*

6

7 Actual number of correct looks

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

12

13 Expected number of correct looks

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

19

$$20 \quad P(X = x) = \frac{\binom{M}{x} \binom{N - M}{n - x}}{\binom{N}{n}}$$

21

22 with x = number of correct looks; n = number of looks; M = possible number of
23 correct looks (the number of nuts hoarded); and N = number of storage sites. All the
24 possible numbers of correct looks (0 to N) were then averaged with a weighted
25 average using the above-calculated probability as the weighting factor. The expected
26 number of correct looks was then divided by the maximum possible number of correct

1 looks to obtain an expected proportion of correct looks. For analysis purposes, this
2 proportion was then arcsine-square root transformed.

3

4 Statistics

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

19

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

- 1 tits or pilfering coal tits in the sites in each of these CPCs for the first 30 looks in a
- 2 foraging session.
- 3

1 **Results**

2

3 *Analysis by trial*

4

5 The pilfering great tits' and pilfering coal tits' foraging performance is presented first.

6 All birds performed better than chance (RM ANOVA: $F_{1,12}=28.612$, $p<0.001$) and there

7 was a significant interaction between species and trial (RM ANOVA: $F_{5,60}=2.843$,

8 $p=0.023$). As there was also a significant 3-way interaction between actual data vs.

9 chance, trial and species (RM ANOVA: $F_{5,60}=2.763$, $p=0.026$), we analysed each

10 species separately. This analysis excluded two pilfering great tits and three pilfering

11 coal tits as they did not forage in all trials.

12

13 Pilfering great tits

14 By the 30th look, the pilfering great tits had made an average of 14% more correct

15 looks than expected by chance (RM ANOVA: $F_{1,7}=7.157$, $p=0.032$). There was a

16 significant interaction between trial and data type (actual data vs. chance) (RM

17 ANOVA: $F_{5,35}=3.713$, $p=0.008$). A higher percentage of correct looks were made in

18 later trials, going from 43% in trial 1 to 65% in trial 6 (linear contrast: $F_{1,7}=8.621$,

19 $p=0.022$), with performance in the last 3 trials significantly higher than chance level

20 ($F_{1,7}=23.067$, $p=0.002$; Figure 1a). The pilfering great tits developed preferred

21 foraging sites as trials increased and these preferred foraging sites corresponded with

22 the coal tits preferred storage sites (Figure 1b).

23

24 All 10 great tits foraged in the final trial. For the first 30 looks, the number of times

25 each great tit looked in a CPC 4 or 5 site (those most preferred by the coal tits for

26 hoarding; see Methods) was compared with the number of times they looked in the

1 nearest CPC 1 or 2 site (those least preferred by coal tits for hoarding). If the pilfering
2 great tits learned the exact sites where food was located, there should be more looks in
3 the CPC 4 or 5 sites. On the other hand, if the pilfering great tits learned the general
4 areas where food was more likely to be located, there should be no differences in the
5 number of looks between the CPC 4 or 5 sites and the nearest CPC 1 or 2 sites. For
6 six of the birds, there was no difference between the number of times they looked in a
7 CPC 4 or 5 site compared to the number of times they looked in the nearest CPC 1 or
8 2 site (χ^2 ranging from 0.154 to 3.769, p ranging from 0.052 to 0.695). The other four
9 birds made significantly more looks in the CPC 4 or 5 sites compared to the nearest
10 CPC 1 or 2 sites (χ^2 ranging from 6.368 to 14.000, p from <0.001 to 0.012).

11

12 Pilfering coal tits

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

23

1 *Analysis by retention interval*

2

3 This analysis only included caching coal tits, pilfering coal tits and the performance
4 expected by chance because we found a change in foraging efficiency over time for
5 the pilfering great tits. Both caching and pilfering coal tits performed better than
6 chance, finding on average 67% and 50% of the items, compared to 35% expected by
7 chance (RM ANOVA: $F_{2,16}=41.242, p<0.001$). The proportion of correct looks by
8 caching coal tits, but not by pilfering coal tits, decreased as the retention interval
9 increased (RM ANOVA interaction between data type and retention interval:
10 $F_{10,80}=2.088, p=0.035$). We analysed this interaction further in two different ways.
11 Firstly, we analysed the performance of caching coal tits and pilfering coal tits
12 separately. Consistent with the previous section, foraging success of the pilfering coal
13 tits did not change with retention interval ($F_{5,40}=0.764, p=0.581$). Caching coal tits'
14 retrieval performance decreased over time ($F_{5,40}=3.456, p=0.011$; Figure 3), with
15 retrieval after 1 day significantly better than all other intervals and retrieval after 6
16 weeks worse than all other intervals except 1 week and 4 weeks. The intermediate
17 delays did not differ significantly from each other. Secondly, we analysed the data by
18 retention interval. Caching coal tits performed significantly better than pilfering coal
19 tits after 1 day, 3 days and 4 weeks (1 day: $F_{1,8}=45.507, p<0.001$; 3 days: $F_{1,8}=10.712,$
20 $p=0.006$; 4 weeks: $F_{1,8}=4.981, p=0.028$; all tests one-tailed), but not after the other
21 retention intervals (1 week: $F_{1,8}=2.952, p=0.062$; 2 weeks: $F_{1,8}=3.048, p=0.060$; 6
22 weeks: $F_{1,8}=0.219, p=0.326$; all tests one-tailed; Figure 3).

23

24

1 **Discussion**

2

3 *Memory, preferences and learning*

4

5 Caching coal tits used memory to retrieve their caches at short retention intervals as,
6 after 1 day, 3 days and 4 weeks, they were statistically more accurate than pilfering
7 coal tits, and after 1 day, 3 days and 2 weeks they were significantly more accurate
8 than after 6 weeks. The accuracy in cache retrieval declined as retention intervals
9 increased in length. Like Hitchcock and Sherry (1990) and Brodin and Kunz (1997),
10 we attribute this to a decline in memory for cache locations. There was no significant
11 difference between the retrieval accuracy of the caching coal tits and the foraging
12 efficiency of the pilfering coal tits after 1 week, 2 weeks and 6 weeks. Whereas after
13 6 weeks, the caching coal tits clearly do not outperform the pilfering coal tits (in fact,
14 their average performance is slightly below that of the pilferers), the performance
15 after 1 and 2 weeks borders on significant and the non-significance of the results is
16 likely due to variability in the data and a lack of power to consistently detect the
17 effect.

18

19 The pilfering coal tits' foraging efficiency was generally above that expected by
20 chance and, even after 6 weeks, when the caching coal tits' memory had completely
21 lapsed, their retrieval accuracy was still above that expected by chance. At that time,
22 there was no difference in the retrieval accuracy of the caching coal tits and foraging
23 efficiency of the pilfering coal tits, indicating that all the birds were using site
24 preferences to enhance retrieval accuracy or foraging efficiency and that individual-
25 specific hoarding preferences were not used. These results on coal tits are consistent
26 with those obtained with willow tits (Brodin & Kunz, 1997). However, our study also

1 had a comparison with great tits which was not used by Brodin and Kunz (1997). This
2 comparison shows that the great tits did not forage more efficiently than chance when
3 first presented with the coal tits' caches. This indicates that there were species-
4 specific storage sites preferences which enhanced the retrieval accuracy and the
5 foraging efficiency of the coal tits in the laboratory.

6

7 Previous studies (Hitchcock & Sherry, 1990; Suhonen & Inki, 1992; Brodin & Kunz,
8 1997) have attributed enhanced recovery by caching birds after long retention
9 intervals and by non-caching birds in general to storage site preferences. Our study
10 shows that the caching coal tits had storage site preferences in the laboratory and that
11 the foraging site preferences of the pilfering coal tits, but not the pilfering great tits in
12 trial 1, corresponded with these storage site preferences. This provides evidence that
13 species-specific storage and foraging site preferences enhance cache recovery. As
14 pilfering juveniles always foraged for conspecific juveniles' caches and, similarly,
15 pilfering adults always foraged for conspecific adults' caches, a comprehensive test of
16 'age-specific' preferences could not be conducted. We found no evidence for
17 individual-specific preferences, as after 6 weeks, there was absolutely no difference in
18 foraging success between the caching and the pilfering coal tits. Brodin & Kunz
19 (1997) investigated what the success rate of a "pilfering" willow tit would have been
20 if it had been foraging on its own caches, and concluded that it would have been
21 slightly better than when foraging on other willow tits' caches. We did not do such a
22 detailed analysis of the individual birds' looks, so this subtle level of individual
23 differences could still exist.

24

25 Interestingly, the pilfering great tits' foraging efficiency was better in later trials. This
26 is because the pilfering great tits learned the coal tits' preferred storage sites and

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

13

14 *Implications for food hoarding*

15

16 This study shows that a coal tit’s memory lasts less than 6 weeks in the laboratory.
17 This is consistent with other studies on parids, which have found memory durations
18 between 1 and 4 weeks (Hitchcock & Sherry, 1990; Healy & Suhonen, 1996; Brodin
19 & Kunz, 1997). And just like for marsh tits, memory duration for coal tits (a
20 presumed short-term hoarder only; Haftorn (1956a, b, c) as cited by Healy & Suhonen
21 (1996)) is not any shorter than that for presumed long-term hoarders such as black-
22 capped chickadees and willow tits. These laboratory data are supported by Brodin’s
23 (1994b) field experiment with willow tits which showed that naturally hoarded items
24 disappeared faster than from re-baited caches but only at retention intervals of less
25 than 6 weeks. However, some parids are known to recover caches well past 6 weeks.
26 A high proportion of the stomach contents of wild, winter-caught crested and willow

1 tits is made up of hoarded food (Haftorn, 1954; Haftorn, 1956b). Our study supports
2 the hypothesis (see also Brodin & Clark, 1997; Brodin, 2005) that this may be
3 attributable to storage site preferences which appear to enhance long-term recovery.
4 In conclusion, it seems likely that coal tits use storage site preferences to enhance
5 long-term cache recovery and memory for cache locations to enhance short-term
6 cache recovery.

7

8 Our study provides evidence for species-specific preferences for storage sites which is
9 consistent with previous studies (Gibb, 1960; Pravosudov, 1986; Alatalo & Carlson,
10 1987; Suhonen & Alatalo, 1991; Suhonen & Inki, 1992; Brodin, 1994a; Lens et al.,
11 1994; Brodin & Kunz, 1997; Brotons, 2000), but not for individual-specific
12 preferences (but see Brodin & Kunz, 1997). Since these preferences are consistent (or
13 at least strongly overlapping) across the species, intraspecific pilferage is likely.

14 Indeed, various field studies have indicated that conspecific flock mates do pilfer
15 caches (Brodin & Ekman, 1994). Even though individual preferences (or caching
16 niches) make the evolution of hoarding more likely (Smulders, 1998), the selection
17 pressure to assure a large niche or preference separation among individuals of the
18 same species is probably not very strong, because reciprocal pilfering can be
19 evolutionarily stable (Smulders, 1998; Vander Wall & Jenkins, 2003). This idea has
20 also been suggested previously in a field study which regarded hoarded food as
21 ‘communal property’ by the members of a flock of boreal chickadees (Haftorn, 1974).

22 However, individual preferences may not have been observed in our experiments
23 because of insufficient numbers of different types of storage sites and because birds
24 never hoarded together.

25

1 Some pilfering great tits learned the exact locations that caches were likely to be in.
2 In the field, this would be unlikely to result in higher cache loss for coal tits because
3 they always hoard in different sites (Haftorn, 1956c). On the other hand, our data
4 suggest that some great tits were able to learn rules about typical cache sites. If they
5 can do this in the field also, this may have major implications for coal tits' hoarding
6 strategies because coal tits are known to hoard in specific types of storage sites
7 (Haftorn, 1956c). In the field, there are thousands of potential cache sites in a bird's
8 home range, which may reduce this possibility. On the other hand, great tits and coal
9 tits often forage in mixed flocks (Ekman, 1989; Hogstad, 1989; Kimberly &
10 Morrison, 1990; Suhonen, 1993; Dolby & Grubb Jr, 1998), so the exposure of great
11 tits to coal tit caches might be high, which may facilitate this learning. If it is possible
12 in natural conditions, it would increase cache loss for the coal tits as the great tits'
13 pilfering efficiency would be enhanced. To prevent this, coal tits may have evolved to
14 use sites which are inaccessible to potential pilferers. For example, coal tits regularly
15 hoard at the extremities of spruce trees using the thinnest needled branches and
16 terminal bud capsules (Haftorn, 1956c) which are probably inaccessible for the larger
17 great tits (great tits are 14cm long and weigh 16-21g; coal tits are 11.5cm long and
18 weigh 8-10g). Indeed, Gibb (1960) noted that great tits are ill-adapted to life in pine
19 plantations, whereas coal tits prefer this habitat. This may be a strategy used by other
20 parid species as well: black-capped chickadees also use cache sites that are somewhat
21 inaccessible to other species (Petit et al., 1989).

22

23 *Conclusion*

24

25 Consistent with previous studies in related species, we show that coal tits can
26 remember cache locations for up to 4 weeks, and can continue to retrieve caches at

1 rates higher than chance for longer intervals using species-specific site preferences.
2 Great tits do not share these site preferences initially, but can learn them through
3 repeated exposure to coal tit caches. In the field, the latter effect may have led to the
4 evolution of coal tit preferences for sites that are inaccessible to great tits.

5

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7

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13

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11

3 **Figure Captions**

4

5 Figure 1 a. Foraging success of the pilfering great tits over the 6 trials (mean \pm SEM).

6 Performance in the last three trials is significantly better than chance. b. Great tit

7 foraging preference scores for each of the coal tits' Cache Preference Categories

8 (CPCs). CPC1 contains the cache sites in which coal tits are least likely to hoard and

9 CPC5 the ones in which they are most likely to hoard. Great tits' preference for

10 foraging in sites in which coal tits are more likely to hoard goes up with experience.

11 Preference scores are calculated as the ratio between the proportion of the first 30

12 looks aimed at sites within that CPC and the proportion of all sites that are contained

13 within that CPC.

14

15 Figure 2 a. Foraging success of the pilfering coal tits over the 6 trials (mean \pm SEM).

16 Performance in all trials is significantly better than chance. b. Pilfering coal tits'

17 foraging preference scores for each of the Cache Preference Categories (CPCs).

18 CPC1 contains the cache sites in which coal tits are least likely to hoard and CPC5 the

19 ones in which they are most likely to hoard. Coal tits prefer to forage in sites in which

20 all coal tits are more likely to hoard. Preference scores are calculated as the ratio

21 between the proportion of the first 30 looks aimed at sites within that CPC and the

22 proportion of all sites that are contained within that CPC.

23

24 Figure 3: Retrieval success of the caching coal tits goes down with retention interval,

25 while foraging success of the pilfering coal tits stays the same. All proportions are

26 expressed as mean \pm SEM. In both situations, birds perform better than chance.

27 Asterisks indicate differences between caching coal tit and pilfering coal tit

28 performance (* $p < 0.10$; ** $p < 0.05$; *** $p < 0.01$; one-tailed tests).

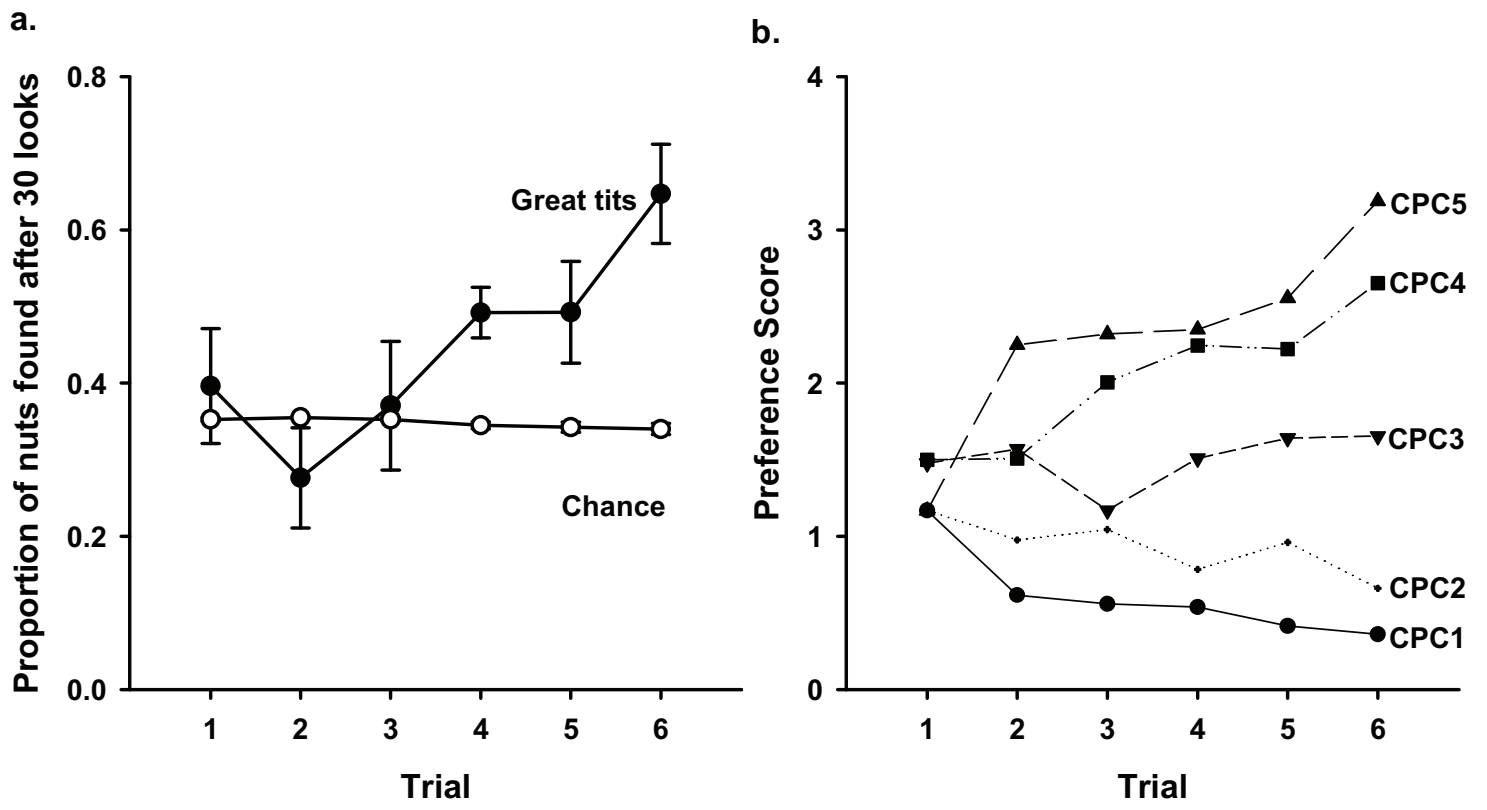
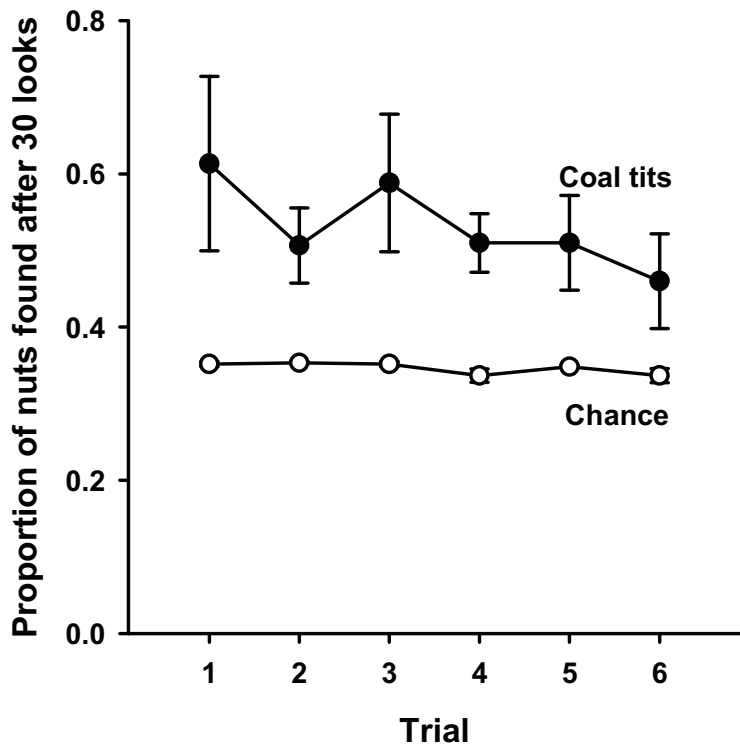


Figure 1

a.



b.

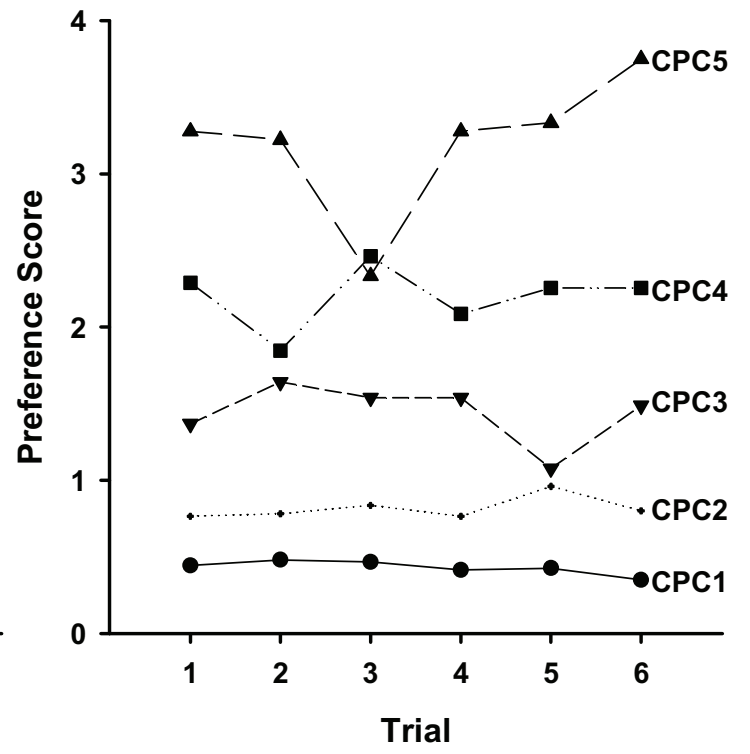


Figure 2

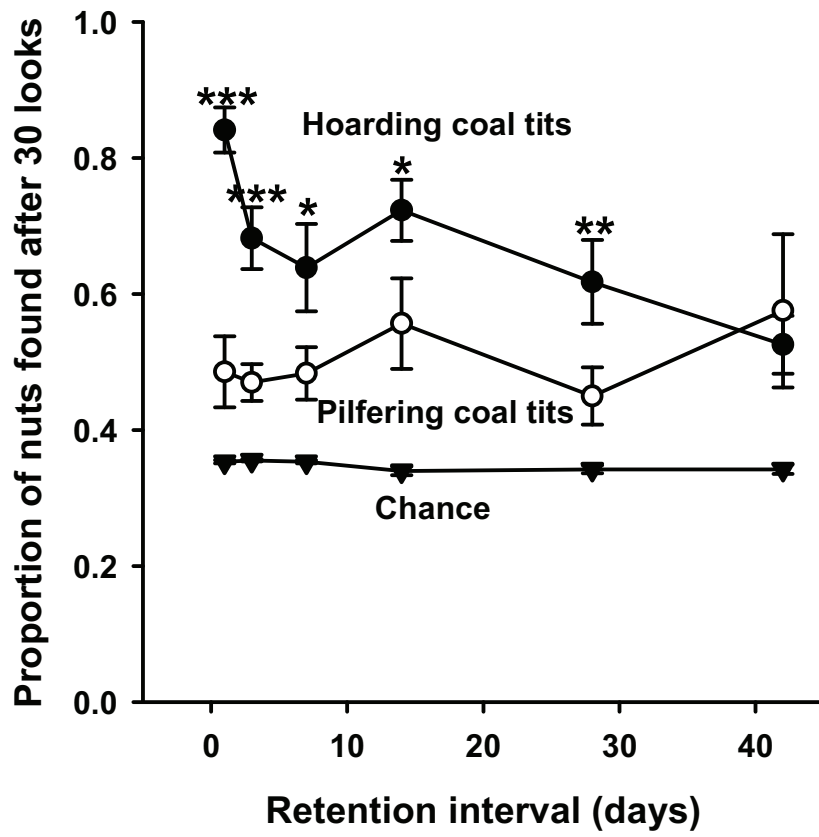


Figure 3