

Effects of demanding foraging conditions on cache retrieval accuracy in food-caching mountain chickadees (*Poecile gambeli*)

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Birds rely, at least in part, on spatial memory for recovering previously hidden caches but accurate cache recovery may be more critical for birds that forage in harsh conditions where the food supply is limited and unpredictable. Failure to find caches in these conditions may potentially result in death from starvation. In order to test this hypothesis we compared the cache recovery behaviour of 24 wild-caught mountain chickadees (*Poecile gambeli*), half of which were maintained on a limited and unpredictable food supply while the rest were maintained on an *ad libitum* food supply for 60 days. We then tested their cache retrieval accuracy by allowing birds from both groups to cache seeds in the experimental room and recover them 5 hours later. Our results showed that birds maintained on a limited and unpredictable food supply made significantly fewer visits to non-cache sites when recovering their caches compared to birds maintained on *ad libitum* food. We found the same difference in performance in two versions of a one-trial associative learning task in which the birds had to rely on memory to find previously encountered hidden food. In a non-spatial memory version of the task, in which the baited feeder was clearly marked, there were no significant differences between the two groups. We therefore concluded that the two groups differed in their efficiency at cache retrieval. We suggest that this difference is more likely to be attributable to a difference in memory (encoding or recall) than to a difference in their motivation to search for hidden food, although the possibility of some motivational differences still exists. Overall, our results suggest that demanding foraging conditions favour more accurate cache retrieval in food-caching birds.

Keywords: food caching; cache retrieval accuracy; spatial memory; unpredictable food; mountain chickadee

1. INTRODUCTION

Some species of birds and mammals are known to cache food for later use (see Vander Wall 1990). Chickadees and titmice cache enormous amounts of food every year, mostly between August and November (Haftorn 1956; Pravosudov 1985). Based on field observations, it has been estimated that an individual tit may make more than 50 000 independent scatter hoards annually and, in some years, more than 500 000 caches (Haftorn 1956; Pravosudov 1985; Brodin 1994). Unpredictability of food supply and photoperiod have been suggested as possible causes of food caching in birds (e.g. McNamara *et al.* 1990; Pravosudov & Grubb 1997).

Laboratory studies have shown that parids rely on spatial memory for cache retrieval (e.g. Shettleworth & Krebs 1982; Hitchcock & Sherry 1990) and can remember the spatial locations of caches for relatively long periods of time (Hitchcock & Sherry 1990; Healy & Suhonen 1996). In a series of studies, Shettleworth & Krebs (1986) and Shettleworth *et al.* (1990) showed that, although parids are better at recovering food that they have cached themselves, they readily perform one-trial associative memory tasks and retrieve the encountered food more accurately than chance. Subsequent experiments have also shown that food-caching birds can perform significantly better than their non-caching

relatives on one-trial associative spatial memory tasks (reviewed by Shettleworth 1995).

Food-caching birds have an enlarged hippocampal formation compared to birds that do not cache (Krebs *et al.* 1989; Sherry *et al.* 1989). Furthermore, species that cache intensively have larger hippocampal volumes than do species that cache less intensively within a family (Sherry & Vaccarino 1989; Healy & Krebs 1992; Hampton *et al.* 1995; Basil *et al.* 1996). All these findings have led to the idea that the hippocampal enlargement of food-caching birds has evolved in response to the increased cognitive demands that may accompany scatter hoarding (Krebs 1990; Clayton & Krebs 1995; Krebs *et al.* 1996).

We approached the question of cache recovery from an ecological perspective.

Both photoperiod (e.g. Krebs *et al.* 1995; Shettleworth *et al.* 1995) and unpredictability of food (e.g. Pravosudov & Grubb 1997) can trigger an increase in food-caching behaviour, but little is known about how they affect the efficiency of cache retrieval. Changes in cache retrieval accuracy may sometimes change with photoperiod (Clayton & Cristol 1996) but it is not clear whether this is due to a direct effect of photoperiod or a consequence of the fact that, when birds are housed on short days but deprived of food for an equal length of time to those housed on long days, then they are necessarily more energetically stressed because there are fewer hours in the day in which they can feed. We hypothesized that the evolutionary pressure on cache retrieval efficiency may vary during the year because of ecological differences in energy demands. Food caches represent an important

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energy source, one that complements body fat and significantly decreases the probability of death from starvation (Pravosudov & Grubb 1997). If a bird is inefficient at finding its caches during late summer when food is plentiful and it is easy for a bird to maintain its energy balance, then such a lapse should not have a strong effect on its survival. However, during the winter, when food is unpredictable and an energetic balance is hard to meet, it could die if it does not retrieve sufficient caches or expends unnecessary energy attempting to relocate them.

The aim of this study was to test the hypothesis that birds should be more efficient at finding their hidden food caches when food is limited and unpredictable than when food is not limited. Since food-storing parids rely, at least in part, on memory for accurate cache retrieval (Shettleworth 1995) it seems likely that any change in cache retrieval efficiency may be mediated by changes in spatial memory. We used the mountain chickadee (*Poecile gambeli*) for our study because it actively caches food during autumn and winter (Haftorn 1974; V. Pravosudov, personal observations) and it lives at high elevations with significant snow cover and fairly unpredictable weather patterns over the winter. In these conditions, mountain chickadees are likely to encounter demanding foraging conditions.

2. METHODS

The subjects were 24 wild-caught mountain chickadees that were caught during November 1999 near the Sage Hen Field Reserve of Tahoe National Forest in northern California using mistnets near the feeders. After capture, all birds were transported to the laboratory and individually placed in wire-mesh cages (60 cm × 42 cm × 60 cm). We randomly assigned birds into two groups after one week in captivity, with 12 birds in each group. All birds were maintained under a 8L:16D cycle at a constant 20 °C temperature. Birds were fed with a mixture of shelled sunflower seeds, crushed peanuts and mealworms and given *ad libitum* water. One group was maintained on *ad libitum* food and the other group was given a limited and unpredictable food schedule. In the limited and unpredictable food schedule all birds were given three or four 20 min intervals of unlimited access to food per day, resulting in either 60 or 80 min of access to food per day. Each day, we randomly determined whether birds received three or four 20 min feeding intervals. We also randomly spread these intervals throughout the day except that we did not allow any two feeding intervals to be contiguous. Food was manually delivered into cages in plastic feeders.

After all birds had been maintained on their feeding schedules for 60 days, we tested their spatial memory performance in a cache recovery task and subsequently in three versions of a one-trial associative learning task. Prior to these behavioural tests, all birds were individually acquainted with the experimental room for 2 h each. There were no differences between the two treatment groups in either body size (wing length) (ANOVA, $F_{1,20} = 0.32$ and $p = 0.59$) or body mass (ANOVA, $F_{1,20} = 0.003$ and $p = 0.96$) at the beginning of the experiments. Over the course of the experiment, food-restricted birds increased their mass significantly by 4.6% (paired *t*-test, d.f. = 10, $t = -4.25$ and $p = 0.002$), whereas birds in the *ad libitum* food group did not change their body mass significantly (paired *t*-test, d.f. = 11, $t = -1.59$ and $p = 0.14$).

(a) *Experimental room*

All birds were individually tested in the room (325 cm × 218 cm × 312 cm) and observed through a one-way Plexiglas window. The room contained 144 caching sites. There were two trees with ten caching holes in each tree, 24 caching blocks, which were hung from a wire mesh screen attached to the two opposite walls of the room (12 blocks on each wall), and ten boards each containing ten rubber pockets (five boards on each wall). Each caching block consisted of a wooden block (8 cm × 14 cm × 3.5 cm). There was a hole in the centre of the block. The holes in both the trees and wooden blocks were 0.5 cm in diameter and 0.5 cm deep. Each hole could be covered by a knot at the end of a short string attached above the hole in order to prevent the birds from seeing the content of the hole (Clayton 1994). A wooden perch was located below each hole. The rubber pockets on the board were 3 cm deep and, in order to inspect the content of each rubber pocket, a bird had to probe it with its bill because the seed at the bottom of the pocket was not visible. The birds readily landed on boards with rubber pockets and cached food there or inspected them for food. Different types of caching sites made the testing environment richer and more naturalistic because in the wild there are always many different types of caching substrates.

The birds were allowed to fly in and out of the experimental room by manipulating the lights and opening the flaps connecting the home cages with the room. At the start of a trial the lights were turned off in the home cage and turned on in the experimental room because birds fly from the dark to the light. At the end of the trial, the lights were reversed and the bird would fly into the home cage. By using this procedure, we avoided stress induced by handling birds.

(b) *Cache recovery task*

The cache recovery task consisted of two phases separated by a retention interval of 5 h. Birds were deprived of food 1 h before night roost and 1 h prior to phase 1, in which birds were allowed to eat and individually cache food for 20 min in the experimental room with 144 available caching sites. During phase 1 an unlimited amount of sunflower seeds was provided in a bowl. After phase 1, birds were returned to their home cages and maintained on their experimental feeding schedules (limited and unpredictable versus *ad libitum* food) and then deprived of food 2 h prior to phase 2. During phase 2, birds were allowed in the experimental room for 10 min and the only food available to the bird was that which it had cached during phase 1. During phase 2, all caching holes were covered with a string knot so that the contents of caching sites were not visible. In order to retrieve a cache, a bird had to pull the string away from the hole in the trees and wooden blocks (which all birds readily did) or to probe into a rubber pocket (which all birds also readily did).

During the storage phase, we recorded the number of cache sites and seeds cached. During the recovery phase, we recorded the number of caches each bird recovered and the number of looks to find each seed. A bird was recorded as having had a look when it pulled at the string covering one of the potential cache sites or when it probed a rubber pocket with its bill.

Each bird was individually tested in a cache recovery task every fourth day for three trials from 24 February to 11 March 2000. We used individual birds' means from all three trials for statistical analyses.

(c) One-trial associative learning task

After the cache recovery trials were completed, we also tested each bird individually in a one-trial associative learning task. In this task, birds were trained to search for food in phase 2 in sites in which they have found food previously during phase 1 of a trial (see Clayton & Krebs 1994; Clayton 1995). Birds were tested on a one-trial associative learning task for two reasons. This task can test memory that does not depend on caching behaviour. Furthermore, in a cache recovery task birds may differ in the number of caches they make and in the number of food items they take from the feeder, whereas in the one-trial associative learning task all birds have exactly the same experience.

We used three versions of the one-trial associative learning task and, in all versions, only one site was baited with food. In version 1 (12–13 March 2000) birds had 144 sites available to them exactly as in the cache recovery task, including the same number of sites in trees, wooden blocks and rubber pockets. In version 2 (14–15 March 2000) we limited the sites available to 12 wooden blocks. The birds had to rely on memory in both task versions in order to return accurately to the site that contained food. We also tested birds in a third version (18–19 March 2000) in order to examine the effect of motivation on performance. We used 12 sites as in version 2, but this time the baited site was colour marked so that the birds did not have to rely on spatial memory in order to remember which feeder contained the hidden food in phase 2. If birds differ in their motivation to search for food they should have differed in performance on all three versions of the task. With 12 sites versus 144 sites there should have been less searching for food because there were fewer sites. With the colour-marked feeding site, birds would not have had to search for food and, instead, they should have just searched for the marked site. If the two treatment groups differed in memory but not motivation, then they should have differed in performance in versions 1 and 2 but not 3.

Each trial consisted of two phases separated by a retention interval of 40 min. In phase 1, each bird searched for a visible piece of peanut, half of which was always extending from the feeding hole. Each bird was allowed to eat a small part of the peanut for 30 s, after which the lights in the experimental room were turned off and the bird returned to its home cage. Birds were deprived of food 1 h before night roost and 1 h prior to phase 1. Birds also had no food between phase 1 and phase 2. In phase 2, all caching sites were covered with a knot at the end of the string. If the bird remembered precisely where it had encountered the food, it should have gone directly to the site from which it had partially consumed the peanut in phase 1 (Healy & Krebs 1992; Clayton & Krebs 1994).

We recorded the number of looks made during phases 1 and 2 of each trial for each bird. In phase 1, we recorded a look when a bird landed on a perch near the open site and either closely inspected it or probed it with its bill.

3. RESULTS**(a) Cache retrieval task**

All 12 birds cached food in the limited and unpredictable food treatment in the cache retrieval task, but only nine birds cached food in the *ad libitum* food treatment. There were no significant differences between the two groups in the proportional use of each of the three available caching site types (pockets, blocks and tree sites) (Mann–Whitney *U*-test, $n_1=12$, $n_2=9$, $-0.45 < z < 0.07$ and $p > 0.64$). There were no statistically significant

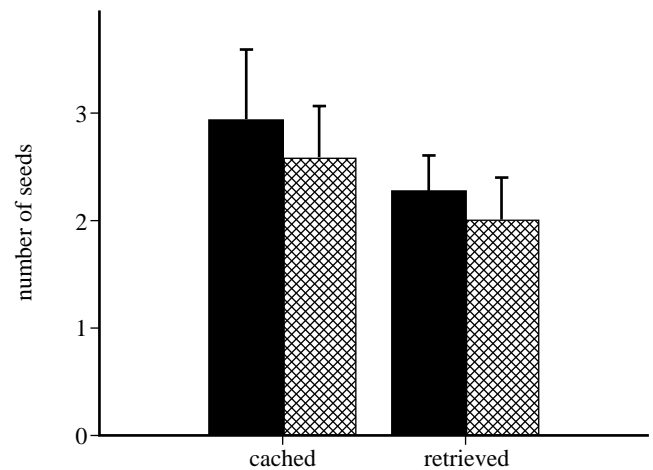


Figure 1. Mean and standard error of the number of caches made in phase 1 and the number of caches retrieved during phase 2 of the cache recovery task. Solid bars represent the limited and unpredictable food schedule and hatched bars represent the *ad libitum* food schedule.

differences between groups in the number of caches made by the birds during phase 1 (Mann–Whitney *U*-test, $n_1=12$, $n_2=9$, $z = -0.22$ and $p = 0.828$) (figure 1) or in the number of caches retrieved during phase 2 (Mann–Whitney *U*-test, $n_1=12$, $n_2=9$, $z = 0.62$ and $p = 0.537$) (figure 1). Birds in both groups performed significantly better than would be expected from random searching (Wilcoxon test, $z > 2.65$ and $p < 0.01$). Birds in the limited and unpredictable food schedule made significantly fewer looks when relocating their caches in phase 2 compared with birds maintained on the *ad libitum* food schedule (Mann–Whitney *U*-test, $n_1=12$, $n_2=9$, $z = -3.22$ and $p = 0.001$) (figure 2). Birds in both groups revisited the same sites extremely rarely during phase 2 (0.07 ± 0.05 times in the unpredictable food treatment and 0.17 ± 0.09 times in the *ad libitum* food treatment) (Mann–Whitney *U*-test, $n_1=n_2=12$, $z = -0.66$ and $p = 0.51$).

(b) One-trial associative learning task

There were no differences between the groups in the number of looks to find a site with a visible peanut during phase 1 of version 1 (144 sites) (unpredictable food, 1.92 ± 0.36 looks and *ad libitum* food, 2.33 ± 0.82 looks) (Mann–Whitney *U*-test, $z = 0.43$, $n_1=n_2=12$ and $p = 0.66$). Only one bird from the *ad libitum* food schedule in version 2 (12 sites) found a visible peanut on the second look, whereas all other birds from both groups found a peanut on the first look. All birds found the visible peanut on the first look during phase 1 of version 3 (colour-marked site).

Birds in both groups performed significantly better than would be expected from random searching in phase 2 of versions 1 and 2 (Wilcoxon test, $z > 1.95$ and $p < 0.05$). However, birds on the limited and unpredictable food schedule made significantly fewer looks in order to find the seed in phase 2 than birds on the *ad libitum* food schedule (Mann–Whitney *U*-test, version 1 with 144 sites $n_1=11$, $n_2=10$, $z = -2.23$ and $p = 0.025$ and version 2 with 12 sites $n_1=11$, $n_2=9$, $z = -3.15$ and $p < 0.001$) (figure 3). However, there were no significant differences between the two groups during phase 2 of version 3

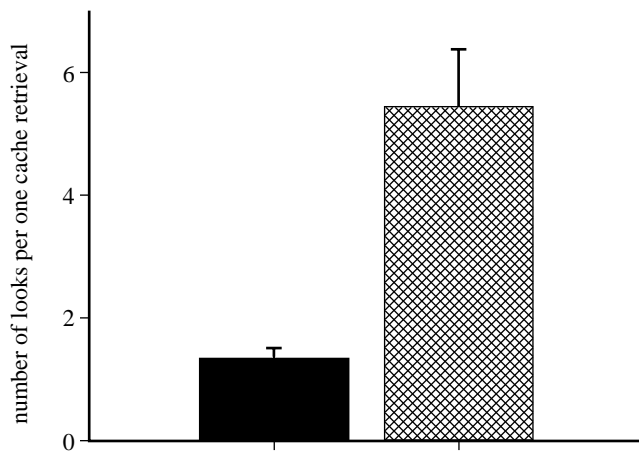


Figure 2. Mean and standard error of the number of sites visited in phase 2 of the cache recovery task per one successful cache retrieval. The solid bar represents the limited and unpredictable food schedule and the hatched bar represents the *ad libitum* food schedule.

(colour-marked site containing food) (Mann–Whitney *U*-test, $n_1=11$, $n_2=10$, $z=1.34$ and $p=0.181$) (figure 3).

4. DISCUSSION

The birds' performances in both the cache recovery task and the two versions of the one-trial associative learning task showed that birds maintained on limited and unpredictable food made fewer looks in order to find the hidden food than birds maintained on *ad libitum* food. These results suggest that birds maintained on a limited and unpredictable food supply are more accurate at cache retrieval than those maintained on an *ad libitum* food supply. There are a number of reasons why the treatment groups may have differed. The birds maintained on limited and unpredictable food may have been more motivated to search for food during both caching and recovery or they may have had a more accurate memory of the locations of their caches. Furthermore, a difference in memory accuracy may have arisen because birds on the limited and unpredictable food supply may have paid more attention to the cache sites during caching and, therefore, encoded the information more accurately and/or because they may have shown enhanced recall for where they had hidden their caches. The results of our experiments do not distinguish between differences in attention and differences in memory recall.

It is possible that the two treatment groups differed in their motivation for caching and recovering food. It is well-known that caching is under motivational control of the feeding system (see the review by Pravosudov & Grubb 1997). However, the motivation to cache is not directly dependent on hunger levels: if it were, then birds would be unlikely to cache during periods of food surplus when they are likely to be sated. Furthermore, recent work on food-storing scrub-jays has shown that both the feeding system and an independent caching system control caching behaviour (Clayton & Dickinson 1999). Thus, if the feeding schedule had caused motivational differences, then one would expect there to have been differences between treatments in the amount of food

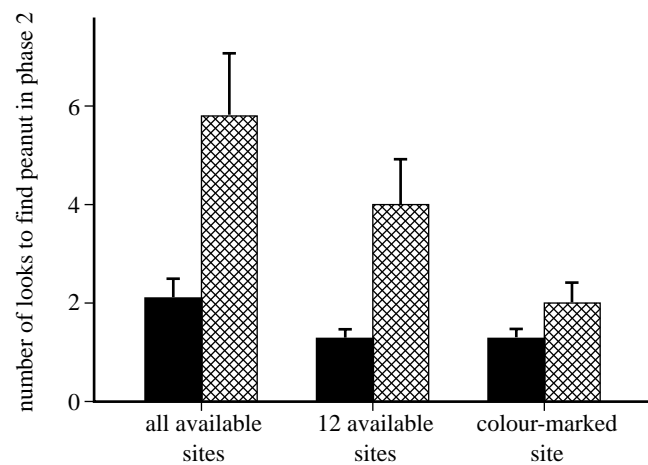


Figure 3. Mean and standard error of the number of sites visited in phase 2 of a one-trial associative learning task before finding a site in which food was previously found during phase 1. Solid bars represent the limited and unpredictable food schedule and hatched bars represent the *ad libitum* food schedule. Data are presented for three versions of the task: version 1 with all 144 sites available, version 2 with only 12 sites available and version 3 with 12 sites available but with the site containing a peanut colour marked.

cached. Although there were no significant differences in caching intensity, it is interesting to note that all 12 birds in the limited and unpredictable group cached food whereas only nine out of the 12 birds in the *ad libitum* group cached food during the food-storing trials.

Both groups performed significantly better than would be expected by random searching in all the tasks, suggesting that birds in both treatment groups were motivated to perform the task and to search for food. Nonetheless, it is possible that the birds on limited and unpredictable food were more motivated to find food than those maintained on an unlimited food supply. However, there were no differences between the two groups in the number of looks to find a visible peanut in phase 1 of the one-trial associative learning task, which suggests that motivational differences between the two groups in searching for food were minimal. Furthermore, when birds in both groups were tested for motivation levels in version 3 of the one-trial associative learning task in which a site containing food was colour marked, the differences between the groups disappeared. This result might therefore suggest that both groups had similar levels of motivation for searching for food. The problem is that the birds in the *ad libitum* food schedule performed well on all tasks, so it is possible that there was a floor effect and that the test was not sensitive enough to detect possible differences in motivation. Although the possibility of motivational differences between the two groups cannot be completely discarded, it seems more likely that the two groups differed mostly in memory, not motivation.

To the authors' knowledge, this is the first study to suggest that energetically demanding conditions may trigger better spatial memory performance in food-caching birds. While some studies have reported an increase in hippocampal size and an increase in neurogenesis in free-ranging parids during peak caching activity (Barnea & Nottebohm 1994; Smulders *et al.*

1995), there are no data available on whether food-caching birds are more accurate in retrieving their caches during that time. It is also unknown whether any seasonal changes are directly related to changes in food-caching behaviour or whether they arise as a consequence of other factors such as changes in energetic demands and territory use. Our study demonstrates that cache retrieval accuracy may change even in the absence of changes in caching activity. In other words, caching experience *per se* did not have to have been involved in causing the changes in cache retrieval accuracy or changes in performance in the one-trial associative memory tasks.

Grubb & Pravosudov (1994) suggested that caching may be a two-stage process in parids: most of the long-term caches are created during the autumn when food is abundant (Haftorn 1956; Pravosudov 1985) and, in the winter, when food is limited and unpredictable, very few new caches are made but the birds may recache previous caches (Grubb & Pravosudov 1994). Most of the caches are not recovered until the winter when cache recovery is critical for supplementing afternoon feeding, which is when accumulating a sufficient amount of energy reserves determines whether a bird survives the night and when environmental conditions make normal foraging very difficult (Pravosudov & Grubb 1997). Our experiments demonstrated that birds maintained on limited and unpredictable food showed more accurate performance on memory tasks than those maintained on unlimited food. This suggests that birds might have more accurate recall during the winter when food is limited and unpredictable.

It is a common practice in experiments testing memory for food caches to deprive birds before the test for 2 h or more and often overnight (e.g. Clayton 1994). The results of our experiment suggest that birds show more accurate cache retrieval and perform better on these memory tasks when they are maintained on a temporally unpredictable and limited food schedule. It is worth noting that the birds maintained on an unpredictable and unlimited food schedule made fewer looks in order to find the hidden seed in phase 2 than is typically found in these one-trial associative memory tasks across a variety of different species of food-storing parids. It is therefore possible that previous studies of cache retrieval have underestimated the performance of these birds. The use of this unpredictable and limited feeding schedule may help in determining the cognitive capacities of the birds in future experiments.

Food restrictions similar to our limited and unpredictable food schedule are generally thought to produce stress in animals, which, in turn, is suggested to impair animals' cognitive abilities including memory (McEwen & Sapolsky 1995; Sapolsky 1996). In contrast, our experiment demonstrated that long-term food limitation could result in enhanced cache retrieval accuracy in mountain chickadees. More studies are needed in order to understand the relationship between stress and memory better and the extent to which this relationship depends directly on energetic demands, as well as the relationship between motivation and memory. It is also unknown whether energetically demanding conditions such as limited and unpredictable food can trigger changes in the hippocampal formation. In order to understand the evolution

of memory and its underlying neurological mechanisms better we need to search for ultimate and proximate mechanisms of changes in both memory and the brain.

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