The effects of cache loss on choice of cache sites in black-capped chickadees

Black-capped chickadees (Parus atricapillus), along with most other birds in the family Paridae, store food. They may store hundreds of items per day, placing one item at each storage site and scattering their storage sites over a wide area. Stored food is recovered hours to days after caching it (Cowie et al., 1981). Both black-capped chickadees and marsh tits (Parus palustris) use memory for the locations of caches to retrieve stored food (for reviews see Sherry, 1989; Shuttleworth, 1990).

Food-storing birds lose a great deal of their stored food to conspecifics, rodents, and other animals (Bardin and Markovets, 1990; Clarkson et al., 1986; James and Verbeek, 1983; Sherry et al., 1982; Tombak, 1980; Waite, 1988). If an animal detects disproportionate loss of caches in some sites, or types of sites, it might be expected to change its choice of cache sites to reduce this loss. Many natural situations exist in which adjustments to caching behavior can reduce cache loss (Källander and Smith, 1990; Vander Wall, 1990). For example, the tops of branches are more vulnerable to snow cover than the undersides, and this may be why boreal chickadees (Parus hudsonicus) tend to cache on the undersides of branches (Haf脱离n, 1974).

Field observations have shown that several parid species overlap less in their choice of cache sites than in their choice of foraging sites, perhaps to reduce pillaging by members of other species (Alatalo and Carlson, 1987; Petit et al., 1989; Suonen and Alatalo, 1991). Animals that learn to avoid caching in relatively high-risk sites should recover more of their stored food than animals that do not adjust the distribution of caches.

Stevens (1984) examined whether choice of cache sites by individual marsh tits changed in response to cache loss. All seeds stored in moss by experimental birds were removed from an indoor avairy before cache recovery was permitted. Three of four experimental birds decreased caching in moss, but no control birds reduced their caching in moss. Because the moss always occupied the same locations in the aviary, it is not clear from this experiment whether the tits learned to avoid caching in specific types of site or learned to avoid caching in particular places in the aviary.

The possibility that food-storing birds learn to avoid caching in sites where caches have been lost is also of interest as a learning phenomenon because of the long delay between the time of caching and the time of attempted cache recovery. Birds could alter their choice of cache sites in response to cache loss in at least two different ways: by a generalized shift in the use of space away from sites where cache loss occurs, or by a specific cessation of caching in certain sites, despite continued use of these sites for other types of activity. Which behavioral change occurs may indicate how chickadees form associations between the choice of cache sites and the loss of stored food.

We conducted three experiments to answer the following questions: Do black-capped chickadees respond to systematic cache loss? Is spatial location, site type, or both used to identify settings in which cache loss occurs? Do birds learn a generalized avoidance of such sites, or is caching behavior affected selectively?

EXPERIMENT 1
We conducted experiment 1 to determine whether chickadees alter their selection of cache sites in response to spatial information and local cue information that predicts cache loss and to determine whether this information affects the selection of sites for other behaviors.
Methods

We maintained nine wild-caught black-capped chickadees individually in 36 × 36 × 61-cm wire-mesh cages on an 11 h:13 h light:dark cycle (light onset 0700 h), between 14°C and 21°C. On experimental days food was removed from cages after dark. Birds were deprived of food a further 2–4.5 h in the morning before each observation session.

The indoor observation aviary measured 2.25 H × 3.0 × 3.7 m and contained four artificial trees, each with 12 small holes (6 mm diam, 6 mm deep) where the birds could cache seeds. We tied a string with a knot at the end to the perch 3–5 cm from each hole so that the knot could be placed to plug the cache hole. We wrapped a red or blue Velcro strip, 2 cm in width, around the branch immediately above each hole. A trap door allowed birds to enter and exit the aviary from their home cage. We made observations through a smoked plexiglas window.

While birds were in the aviary, we continuously recorded their behavior and location in the aviary using an event recorder keyboard. Each time a bird went to a site, only a single behavior was recorded at that site, as described below:

Cache: Bird leaves a seed fragment in a hole.

Eat: Bird eats part or all of a seed fragment, and does not cache before moving to another site. A second occurrence of eat was not recorded at the same site until the bird had moved more than one body length away, then returned and began eating again.

Approach: Bird perches within one body length of a hole, but neither eats nor caches before moving to another site.

Look: Bird removes knot from hole. This could occur only once per hole per session.

We randomly assigned the colored Velcro bands to holes each day, with the constraint that every day each tree and had six bands of each color and that over 6-day blocks of sessions each hole was red on 3 days and blue on 3 days.

To allow birds to habituate to the aviary, we released them individually into the aviary several times for about 2 h to eat, cache, and explore. Birds were then given sessions of caching and recovery. During caching, we placed a bowl of sunflower seed fragments in the center of the aviary on the floor. The holes for caching were not plugged. We observed birds in the aviary until they had cached five seeds, or 20 min had elapsed, whichever came first. Birds then returned to the home cage, where food was available, for 1–4 h. The animals were later deprived of food for 2 h before cache-recovery sessions. During these and all subsequent sessions, we removed seeds cached in locations other than the 48 designated holes in the trees before cache recovery. For cache recovery, all holes were plugged with the string knot to prevent birds from seeing stored seeds. We allowed each subject to return to the aviary and search for the seeds it had stored during the previous caching session. Birds pulled the string to look into a cache hole and obtain the seed inside. We permitted subjects to search for caches for 10 min, or until they had looked in every site in which they had placed a cache. Birds then returned to the home cage where food was available until dark. This habituation phase was continued until all birds were reliably caching five seeds in less than 20 min, which required from four to six sessions for different subjects.

The baseline phase consisted of six daily sessions of caching and recovery and constituted the first block of sessions. Each morning, we released food-deprived birds singly into the aviary and allowed them to eat seed fragments and make up to 10 caches. Recovery sessions followed as during habituation.

Systematic cache loss followed for 24 sessions of caching and recovery. This phase of the experiment proceeded exactly as baseline, except that some of the seeds cached by the birds were removed before recovery. One color of Velcro band (red or blue) and one side of the aviary (the observer's right or left) were designated safe for each bird. We assigned safe colors and sides to birds at random, unless during baseline a bird had shown a site or color preference for caching that exceeded 70%. This occurred in only one case, and was with respect to side of the aviary. For that bird, the side opposite its preferred side was designated safe. Only seeds cached in the safe color and safe side of the aviary were available for the birds to recover. Only 25%, or 12 of the 48 sites in the aviary, were safe for each bird.

We used the first five instances of each behavior during a session for most analyses. Exceptions are mentioned when they appear. We calculated six measures of behavior for each bird in each caching session. Two of these were the proportion of the first five caches made that were in sites of the safe color and the proportion of the first five caches made that were on the safe side of the aviary. While making these caches, birds approached sites and ate seeds. We used approaches and eating that occurred while the bird was making its first five caches to calculate four more measures: the proportion of all approaches that were made to sites of the safe color, or to the safe side, and the proportion of all eating that occurred at sites of the safe color, or safe side. Each score for caching was generated from five observations, whereas scores for approaches and eating were generated from variable numbers of observations, depending on the number of these behaviors that occurred before five caches had been made. Recovery sessions were treated identically, but only the data on the "look" behavior were analyzed. We averaged daily scores across blocks of six sessions, and these six-session averages were used in the analyses below.

Results and discussion

Caching sessions

Figure 1a depicts the proportion of seeds cached in safe sites by color and location. A paired t test comparing caching by color in blocks 1 and 5 was not significant ($t_9 = 1.98, p < .05$). However, there was a significant shift in caching by location between blocks 1 and 5 ($t_9 = 2.34, p < .05$). It was possible for the birds to respond to the color cues only on the safe side of the aviary, but a paired t test comparing caching at the safe color on the two sides of the aviary in block 5 was not significant ($t_9 = 1.42, p < .19$). Thus, birds used location but not local color cues to reduce caching at unsafe sites.

The proportions of approaches to safe sites and
Figure 1
The mean proportions (±SE) of (a) caches, (b) approaches during caching and (c) eating bouts on the safe side of the avairy (location) and on sites of the safe color (color). Block 1 is a 6-day baseline period, followed by four 6-day blocks of experience with cache loss.

Proportion of caches at safe sites for a session, not just the first five. A paired t test comparing the proportion of "looks" made in safe sites to the proportion of caches made in safe sites during block 5 was significant for color (caches = 0.51, looks = 0.63, t = 5.71, p < .01) and location (caches = 0.59, looks = 0.91, t = 7.32, p < .01). That is, birds search in safe sites more than would be expected from the proportion of caches they placed in these sites. A measure of this effect, the "search bias," is the ratio of looks in safe sites to caches in safe sites. Figure 2a depicts search biases for color and location as a function of blocks of sessions. There was no significant change in search bias with respect to color (t = 2.01, p < .08), but the change in bias with respect to location was significant (t = 3.16, p < .01). A t test comparing the search bias for color to that for location in block 5 was also significant (color = 1.26, location = 1.6, t = 3.76, p < .01).

A measure of the birds' recovery accuracy is the ratio of the number of caches found in five looks to the number of caches that one would expect a bird searching sites at random to find in five looks. In this analysis, "number of caches found" was the number of looks that occurred in sites where the bird had cached a seed, even if the seed may have been removed by the experimenter. The number of looks expected by chance was estimated as 5 × (NC/48); where 5 is the number of looks, NC is the number of caches the bird made, and 48 is the total number of cache sites in the avairy. The ratio of number of caches found to number expected by chance is plotted in Figure 2b. A comparison of accuracy in blocks 1 and 5 was not significant (t = 0.79, p = .45). The number of caches found differed significantly from the number expected by chance in both block 1 (found = 1.88, expected = 0.69, t = 5.43, p < .01) and block 5 (found = 2.33, expected = 0.96, t = 7.78, p < .01).

In response to cache loss, chickadees learned to change their choice of spatial location for caches but not their choice of local color cues at cache sites. These results suggest that the marsh tits in Steven's (1984) experiment that stopped caching in moss after seeds were systematically removed may have responded to the location of the moss rather than to the moss itself. Local color cue in the present experiment was a simple stimulus compared to Steven's site type, however. Moss differs from bark along more dimensions than color. It is possible that the richer variety of cues defining site type in Steven's experiment had a greater effect on the choice of cache site than the unidimensional distinction of red versus blue in the present experiment.

Caching behavior changed in the present experiment independently of approaching and eating. The shift in caching was not due to a shift in the birds' willingness to approach or eat at particular sites. Because caching preceded recovery by hours, the behavior of caching can be associated with its consequences, despite a long delay separating the behavior from its outcome.

Another consequence of systematic cache loss was a change in the behavior of birds during cache recovery. Birds learned to search sites of the safe side more than would be expected on the basis of the proportion of caches made in these locations.

Recovery session
During the cache-loss phase of this experiment, birds had the opportunity to learn not only where to cache seeds but also where to look for seeds during recovery. A bird might never learn to change the distribution of its caches but still concentrate its recovery efforts at safe sites in the avairy. For the following analysis of recovery behavior, "safe caches" were taken to be all caches in safe sites for a session, not just the first five. A paired t test comparing the proportion of "looks" made in safe sites to the proportion of caches made in safe sites during block 5 was significant for color (caches = 0.51, looks = 0.63, t = 5.71, p < .01) and location (caches = 0.59, looks = 0.91, t = 7.32, p < .01).
EXPERIMENT 2

The difference in the ability of the birds to use spatial location and local color cues to reduce cache loss in experiment 1 could be due to differences in the case with which birds discriminate between the two types of information. We conducted experiment 2 to determine whether the observed difference in use of these two types of information was due to a difference in the birds' ability to discriminate between spatial and color cues.

Methods

Eight birds used in experiment 1 served as subjects in the present experiment, which we conducted immediately after experiment 1. Birds were deprived as before but were given as many as four sessions in a single day, separated by 1–2 h.

We randomized the placement of color cues before each session, as in experiment 1. For each bird, we placed seeds in sites of the other color, and in the opposite half of the aviary, than had been safe in experiment 1. Thus, 25% of the sites in the aviary contained seeds. We released birds into the aviary and recorded their behavior as in the previous experiment. Each bird was observed for 24 sessions, each lasting either 5 min or until the bird had made five looks, whichever took longer.

Results and discussion

Paired t tests demonstrated improvement between blocks 1 and 5 for both color ($t_5 = 7.70, p < .01$) and location ($t_5 = 11.55, p < .01$; Figure 3). A t test comparing performance with respect to color in block 5 to performance with respect to location in block 5 was significant ($t_5 = 7.56, p < .01$). Scores are below 50% in block 1, reflecting the carry-over effect of experience in experiment 1. The birds discriminated both the colors and locations used in experiment 1, but performance on the location discrimination was superior.

EXPERIMENT 3

In experiment 1 birds changed their selection of cache sites independently of their use of space for other behaviors. The dissociation of these behaviors suggests that chickadees are able to associate the behavior of caching directly and specifically with its consequences, despite the long delay between the two. This conclusion, however, depends on the observed result of no significant change in approaches. Negative results can be obtained for many reasons, including insufficient statistical power to detect a difference. In experiment 3 we therefore reversed null and alternative hypotheses. If the selection of cache sites is independent of approach behavior, it should be possible to produce a change in approach behavior without affecting the selection of cache sites: the reverse of the result obtained in experiment 1.

Results and discussion

Figure 4 shows the proportion of correct looks and caches for the three phases of the experiment. The data for the approach phase are taken from the last 3 days of approach training. The distribution of caches in cache phase 2 did not differ significantly from that observed in cache phase 1 ($t_4 =
Figure 4
The mean proportions (±SE) of looks and caches made on the correct side of the aviary. During cache 1 and cache 2, looks were recorded while birds searched for food placed in sites by the experimenter.

1.19, p < .30, paired t test). Analysis of variance indicated that the proportion of looks did change significantly across the phases of the experiment (F3,11 = 11.0, p < .01). Student-Newman-Keuls Multiple-Range Test showed that looks in cache 1 differed significantly from looks in approach and cache 2, which did not differ from each other. Birds learned to approach holes in one-half of the aviary, but this had no effect on the distribution of caching. A t test comparing the proportion of correct caches to the proportion of correct looks in cache 2 was significant (t6 = 3.77, p < .05).

Despite a change in activity, produced by reinforcing approaches to some sites in the aviary and not others, no change occurred in the distribution of caches. Experiment 1 showed that a change in the distribution of caches occurs in response to cache pilfering, without a change in the distribution of approach to cache sites. The present experiment shows that a change in approach can occur without any effect on the distribution of caching. These two results indicate that caching and approach can vary independently, and that caching can be selectively affected by cache loss, without a generalized change in the distribution of activity.

GENERAL DISCUSSION
Black-capped chickadees are sensitive to the loss of cached food. After experience with systematic cache loss, the birds are able to place caches in a manner that reflects this pattern of cache loss, at least with respect to spatial information. This capability may have important consequences in the wild because cache loss is such a common event (Bardin and Markovets, 1990; Clarkson et al., 1986; James and Verbeek, 1983; Sherry et al., 1982; Tombak, 1980; Waite, 1988). An animal that avoids caching in sites where caches are lost at high rates will be able to successfully recover a larger proportion of caches than an animal that cannot respond to systematic cache loss. The need to return and retrieve food from many individual cache sites has probably led to the selective enhancement of some properties of memory in food-storing birds (Krebs et al., 1989; Sherry et al., 1989; Shettleworth, 1990). The utility of learning about cache loss may produce additional selective pressure for memory in food-storing birds.

That the birds learned about cache loss is notable because several aspects of the experiment make the task difficult. Birds had only 12 safe sites of 48 in which to place 5–10 caches each day. Simultaneous testing of both color cue and spatial information meant that 50% of caches placed correctly with respect to one type of information could be lost nonetheless because they were placed incorrectly with respect to the other type of information. Compared to the natural environment, the laboratory setting in which these animals were tested is relatively barren of landmarks and other sources of information that the birds might use to solve the cache-loss problem in the wild. Increasing the complexity of the testing environment improves memory for the locations of recently encountered food in black-capped chickadees (Crystal and Shettleworth, in press). It is possible that chickadees in the natural environment make more dramatic responses to cache loss than the birds in these experiments. Even small increases in cache recovery success resulting from adaptive placement of caches could be of significance to chickadees that depend on cached food stores in winter.

Both experiments 1 and 3 dissociated learning of an approach response from the process of cache-site selection. These results suggest that the behavior of caching is affected directly by cache loss. The temporal relation between events is critical in both operant and classically conditioned associations. It is unusual for learning to occur when the delay between behavior and reinforcer, or between conditioned and unconditioned stimuli, is more than a few minutes (Domjan, 1983; Rescorla, 1988). The best-known exception to this restriction on the length of the delay between a signal and a subsequent event is the formation of taste aversions. In taste-aversion learning, conditioning is successful even with delays of an hour or more between tasting a novel food and experiencing illness.

At least two learning mechanisms could underlie change in the distribution of caches observed in the present experiments. A long-delay learning account would consider caching to be a discriminated operant (Reynolds, 1968), under the control of stimuli such as location and color cues that distinguish cache sites from each other. The consequence of caching in the presence of a given set of discriminative stimuli is not evident for hours, until the bird attempts to recover its stored seeds. A long-delay learning mechanism is required to associate the operant of caching with its consequences.

An alternative hypothesis assumes that the bird has a set of modifiable cache site criteria, and it uses these criteria to select cache sites. Each time the bird returns to a cache site, the current characteristics of that site are given positive or negative weightings depending on whether the previously cached food is present. In this way, the weights of different cache-site attributes could be altered by experience. When the bird next stores a seed, it uses the newly weighted criteria to select cache sites. The caching bird approaches a site, prepared to cache, and compares that site to its representation of the ideal site. If there is no discrepancy, the bird caches. What is important about this explanation is that it does not require the formation of associations over a long delay. The ideal cache representation is modified at the time of recovery, using information the bird acquires at the time of recovery. In contrast, the long-delay learning account requires that the birds associate the conse-
quences of caching with a memory of the cache site formed at the time of caching.

The independence of cache-site choice from other behaviors is crucial to the utility of caching behavior, regardless of the learning mechanism involved. If birds cached in the same sites in which they foraged for food, caches would be vulnerable to discovery by other animals exploiting the same foraging niche, such as conspecifics. The control of cache site selection by different criteria than selection of sites for foraging allows hoarding animals to evade the foraging strategies of other animals.

The fact that search bias with respect to location in experiment 1 was approximately 1.0 in the first block of sessions, indicating no bias, and that search bias increased over blocks shows that birds learned not only that caching is rewarded only at specific sites but also that cached food is available for recovery only at specific sites.

The difference in the birds use of spatial and color cue information in the selection of cache sites is of interest, given the evidence for the independence of the neural mechanisms serving spatial and cue solutions to food-finding tasks in chickadees (Sherry and Vaccarino, 1989). The apparent difference in the birds' ability to discriminate the two types of information in experiment 2 makes interpretation of the difference in use of the two types of information during caching difficult. Birds could discriminate between locations and between color cues, but they were clearly more successful at discriminating locations, achieving 100% accuracy for locations by block 4, compared to 70%–80% accuracy for color cues (Figure 3). This difference may be more apparent than real, however. Sites on a single tree are much closer together than sites in opposite halves of the avairy. For a bird that had already entered the avairy and begun searching, the cost in travel time of looking in a site of the wrong color was much less than the cost of looking in a site on the wrong side of the avairy. There is evidence that such differences in the cost of errors produce differences in performance on memory tasks (Brown, 1990; Kamil and Balda, 1990). There may have been little cost to looking at sites of the wrong color in experiment 2. While birds were caching seeds, in experiment 1, however, this difference in the cost of errors was not present. This is because birds almost always returned to the seed bowl at the center of the avairy between making one cache and the next. Returning to the center of the avairy makes all sites nearly equidistant. When caching, the cost of going to a site of the wrong color is the same as the cost of going to a hole on the wrong side of the avairy. Thus, the observed difference in the use of spatial location and color cue to choose cache sites in experiment 1 was probably not due to an inability to discriminate between red and blue color cues.

These results demonstrate that chickadees respond to cache loss that occurs systematically in certain spatial locations. Discrete color cues are not used to identify sites where cache loss occurs, even though birds will learn to search for food at sites marked with these cues. This difference in the use of location and color cues suggests that birds do not learn to avoid caching in certain types of sites, such as particular plant species. The change in caching occurs without accompanying changes in the use of sites for other behaviors, indicating that cache loss causes a selective modification of caching behavior rather than a general avoidance of places where cache loss occurs. Responses to cache loss reported for food-storing birds in the field and the cache site preferences of these birds may be the outcome of the kind of learning about cache loss shown in the present experiments to occur in black-capped chickadees.

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