

THE EFFECTS OF CONSPECIFICS ON FOOD CACHING BY BLACK-CAPPED CHICKADEES¹

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Abstract. We examined food-caching behavior of captive Black-capped Chickadees (*Parus atricapillus*) to determine if conspecific density and relative social status influenced caching behavior. Individuals cached significantly fewer seeds and initiated caching later in the trial when conspecific densities were high than when alone or in the presence of a single conspecific. Social rank was not related to the observed variation in seed caching. The results suggest that conspecifics might be perceived as a source of potential cache loss by individuals but only when several are present.

Key words: Food caching; conspecific density; flock; *Parus atricapillus*; Black-capped Chickadees.

INTRODUCTION

Black-capped Chickadees (*Parus atricapillus*) regularly store food items and recover them during periods of food scarcity (Odum 1942; Glase 1973; Sherry 1984a, 1984b, 1985; Shettleworth and Krebs 1986). They often travel in social flocks in late fall and winter which raises some important questions concerning the costs and benefits of food storage among highly, or at least seasonally, social species. As the number of conspecifics sharing an area increases so too would the likelihood that members of the same flock would encounter one another's food caches.

Chickadees may cache fewer seeds in the presence of conspecifics than they would if they were alone because of a perceived threat of cache loss. A hypothesis such as this was proposed for Northwestern Crows (*Corvus caurinus*) by James and Verbeek (1983). They proposed that crows which would not cache in the presence of conspecifics perceived a threat of cache pirating by other crows.

The opposite outcome was demonstrated for deer mice (*Peromyscus* sp.) by Sanchez and Reichman (1987). In their experiments the presence of conspecifics led mice to increase the quantity of food that was cached. These authors postulated that the increase in caching in the presence of conspecifics made sense if caches could be actively defended against theft.

It appears from earlier work that chickadees do not readily remember the location of stored food unless they themselves have stored it (Baker et al. 1988), or encountered it in the course of foraging for other food items (Shettleworth and Krebs 1986). Thus, we assumed that if the presence of conspecifics increases the probability of cache loss it is due to them finding or encountering each other's food caches simply by chance.

A further hypothesis involves the spatial distribution of food caches. Clarkson et al. (1986) citing evidence from Black-billed Magpies (*Pica pica*) proposed that caches should be distributed more widely where conspecific density was higher. It is uncertain whether chickadees defend their caches against conspecifics and yet cache loss may be prevented by distributing caches either less widely so as to defend them against theft, or more widely so as to prevent the loss of all caches in an individual's home range.

We performed a series of experiments to ascertain whether the act of food caching was altered by changes in conspecific density. Our hypothesis was that if chickadees perceived conspecifics as potential sources of cache loss they would decrease the number of caches made or alter their food-storing activities in one of several ways that could be interpreted as attempts to minimize cache losses.

GENERAL METHODS

Black-capped Chickadees were obtained in early spring (February–March) from an area of riparian habitat near Fort Collins, Colorado. Twenty chickadees were used in all, 13 birds in experi-

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ment 1 and seven in experiment 2. All birds were given a unique combination of colored plastic leg bands. Age and sex could not be determined accurately. The birds were housed individually at room temperature in wire cages (46 × 28 × 23 cm) under a light cycle of 8L:16D. They were maintained on a diet of sunflower seeds, mealworms (*Tenebrio* sp.), poultry supplement, and provided with water and grit.

The experimental aviary (3 m long, 2 m wide, 2 m high) contained 50 cache sites, which were holes drilled into the trunk and branches of three aspen trees. At one end of the aviary, a platform 60 cm off the floor held a feeding dish which could be opened or closed from within an observation booth. Walls of the aviary were covered with black cloth. All cache sites were numbered with plastic tags. Those cache sites which did not have a natural perch were fitted with a wooden dowel approximately 4 cm below the site so that all cache sites were readily accessible to chickadees.

The aviary, though small compared to the environment in which a chickadee might naturally be caching, had advantages over a field-based study. First, it allowed observations of behaviors that occur when food is obtained (i.e., social interactions with other birds) and when food is cached. "False caches" and "recaches" occurred quite regularly. A false cache occurs when a bird places a seed in a cache site and immediately removes it, subsequently caching it elsewhere. Recaches occur when a bird recovers a previously cached seed and caches it in another location. The possibility exists that false caches and recaches are strategies for protecting caches from theft by another bird if the thief could learn the location of caches by observing the cacher. Though we have shown this to be unlikely (Baker et al. 1988) we investigated the possibility that cachers use false caches and recaches as deceptive caching strategies when in the presence of conspecifics.

Secondly, environmental factors such as weather, temperature, and the physiological condition (e.g., hunger levels) of the animals could be controlled. Though the distances between caches were recorded they are not included in our analysis because the small size of the aviary was considered to impede on the dispersion of caches that might have occurred under more natural circumstances. Otherwise it was assumed that the aviary did not affect caching in other

ways or, if it did, it did so equally under all treatments and would not affect the conclusions.

Prior to testing, the birds were trained in the aviary in three to nine 30-min sessions, during which they were permitted to cache an unlimited number of hulled sunflower seeds. Each bird was considered ready for the experiment when it had cached at least three seeds during two successive training sessions. To prevent loss of motivation to cache seeds, the birds were also allowed to recover their caches approximately 2 hr after caching.

EXPERIMENT 1 METHODS

To examine the effects of conspecifics on caching behavior, 10 of the 13 chickadees were allowed to cache an unlimited number of hulled sunflower seeds for 15 min under three treatment conditions: (1) alone, (2) in the presence of one conspecific, and (3) in the presence of three conspecifics. A trial consisted of the completion of all three treatments by every bird used in the experiment. Experiment 1 consisted of two trials with the order of treatments given as 1, 2, 1, 3, 1, 2, 1, 3. In this way, treatment 1 acted as a control for any changes in the bird's response over time which might have resulted from familiarization to the aviary or loss of motivation to cache seeds. There were no significant differences in the number of seeds cached between any of the four tests (two trials) of treatment 1 ($F = 0.378$, $df = 3, 24$, $P > 0.10$, two-way ANOVA). Therefore each trial represented repeated measurements on the same birds yielding the following results: 10 birds × eight treatments (four × treatment 1, two × treatment 2, and two × treatment 3) for a sample of 80 individual tests. Three birds became ill or died during the course of the experiments leaving three tests less in treatment 1, and three less in treatment 3 for a total of 74 tests.

The maximum number any bird cached during the 15-min test was 17 seeds. To prevent observers from interfering with the activities of the cachers, observers were placed inside the aviary in their cages. Observers were familiar conspecifics that had been housed with the cachers, yet kept in individual cages in an animal care facility. The same observers were used in all tests in treatments 2 and 3. Once the cacher entered the aviary it was in continuous visual and auditory contact with the observer.

At 16:00 on the day prior to testing all food

TABLE 1. Variables examined and mean values (\pm SE) in each treatment of experiment 1.

Variables	Treatments			χ^2 (df = 2)	P
	1	2	3		
Seeds cached	4.90 \pm 0.56	4.60 \pm 0.76	2.24 \pm 0.82	13.35	0.005
Seeds eaten	3.00 \pm 0.31	3.80 \pm 0.42	2.12 \pm 0.46	10.11	0.01
Sites searched	27.86 \pm 2.50	28.40 \pm 3.40	29.71 \pm 3.69	4.20	ns
False caches	5.08 \pm 1.13	3.05 \pm 1.53	3.59 \pm 1.66	0.24	ns
Recaches	0.27 \pm 0.10	0.45 \pm 0.13	0.29 \pm 0.14	1.75	ns
Time of first cache (sec)	381.1 \pm 35.0	302.4 \pm 47.6	505.9 \pm 51.6	6.82	0.05
Paired <i>t</i> (df = 9)					
Interactions		4.90 \pm 1.31	8.65 \pm 1.42	-1.766	ns

(but not water) was removed from the cages. The duration of food deprivation remained constant for each bird in all treatments and trials of the experiment. Each test was separated from the one preceding and following it by at least 2 days. All experiments were conducted at 20°C.

To assess any change in caching behavior attributable to the three treatments, we measured the following variables: (1) the number of seeds cached, (2) the number of seeds (or partial seeds) eaten, (3) the number of cache sites searched while caching, (4) the number of false caches (placing a seed in a hole but removing it immediately), (5) the number of recaches (returning to a cache site, removing the seed, and caching it elsewhere), (6) the number of interactions between birds (cacher landing on the platform containing the observer's cage or any part of the cage itself, usually accompanied by vocal and visual displays), and (7) the elapsed time before the first cache.

The data collected on each bird was averaged for each treatment because of the unequal sample sizes created when birds could not finish all three trials. Data were analyzed for significant treatment effects using the Friedman nonparametric ANOVA except for variable 6 (the number of interactions between birds) for which a paired *t*-test was employed (Zar 1984).

To determine if a change in caching behavior was caused by the distraction of having another bird in the aviary with the cacher, rather than a treatment effect (i.e., perceived threat of cache loss), we recorded any change in the number of sites searched while caching. If the effects of treatments 2 and 3 were to distract the cacher, who would thereby make fewer caches, this should also result in fewer cache sites being searched during the test situation. If, however, the cacher

altered its caching behavior, while still searching the same number of cache sites, then this would suggest that the cacher was not distracted by the conspecifics.

EXPERIMENT 1 RESULTS

The subjects cached fewer seeds and initiated caching later in treatment 3 than in the other two treatments. There was a tendency for birds to eat more seeds in the presence of a single observer than they eat when alone or in the presence of several observers. There were no significant differences among treatments for any of the other variables. These results are summarized in Table 1.

EXPERIMENT 2 METHODS

To determine if a cacher behaves differently in the presence of either a dominant or a subordinate observer, an experiment was conducted with the following treatment conditions: (1) cacher alone, (2) with a subordinate observer present, and (3) with a dominant observer present. Five of the seven birds were used in three trials. Each trial consisted of three treatments yielding 45 tests (combined trials). The order of treatments was rotated among the five birds.

Observers in experiment 2 were chosen following a series of dyadic encounters in which all birds were paired with each other in a neutral cage and allowed to compete for a single mealworm. The bird that obtained the mealworm was considered to be dominant. In addition, by observing threat displays and vocalizations it was clear in each dyadic test that one bird of the pair was dominant to the other (Ficken et al. 1987). In this manner it was possible to find the bird that was dominant to all others and the one that

TABLE 2. Variables examined and mean values (\pm SE) in each treatment of experiment 2.

Variables	Treatments			χ^2 (df = 2)	P
	1	2	3		
Seeds cached	2.20 \pm 0.58	2.93 \pm 0.58	1.20 \pm 0.58	2.0	ns
Seeds eaten	1.60 \pm 0.41	2.27 \pm 0.41	1.87 \pm 0.41	1.4	ns
Sites searched	17.27 \pm 2.74	24.00 \pm 2.74	24.60 \pm 2.74	2.0	ns
False caches	1.20 \pm 0.58	2.27 \pm 0.58	1.13 \pm 0.58	3.5	ns
Recaches	0.00 \pm 0.01	0.07 \pm 0.01	0.27 \pm 0.01	4.7	ns
Time of first cache (sec)	547.0 \pm 55.7	416.9 \pm 55.7	449.7 \pm 55.7	2.0	ns
Paired <i>t</i> (df = 4)					
Interactions		5.47 \pm 0.91	3.33 \pm 0.91	1.77	ns

was subordinate. These birds then became the observers for this experiment.

EXPERIMENT 2 RESULTS

There were no significant differences between treatments for any of the variables measured (Table 2). There were no significant differences in the number of seeds cached among any of the groupings of treatment order (1,2,3; 2,3,1; and 3,1,2; $F = 0.595$, $df = 2, 35$, $P > 0.557$) so it was assumed that if any cumulative effect of the treatments on an individual's caching behavior existed it was distributed throughout the three treatments.

DISCUSSION

In this study we have demonstrated that the presence or absence of conspecifics may modify food caching behavior in Black-capped Chickadees. While we did not attempt to determine if our test subjects were known to each other (i.e., flock mates), or if other treatments of conspecific densities would have the expected effect (caching decreases with conspecific densities), we feel that our results are consistent with the hypothesis previously stated; if cache loss was dependent on the density of conspecifics sharing a territory then caching might be expected to decrease with increasing densities.

An alternative hypothesis to the "perceived threat" of cache loss may be that they were merely distracted by the presence of a conspecific observer. Chickadees did not appear to be distracted by the presence of another individual as evidenced by the lack of change in the number of sites searched between treatments in both experiments 1 and 2.

A confounding factor, that of social status, was eliminated as having influenced the behavior of

the cacher. Experiment 2 shows that birds did not respond to a single dominant or subordinate observer any differently than from when they were caching alone. Therefore, the results can be seen as consistent with the hypothesis that chickadees are aware of the density of conspecifics and alter their food-caching behavior to compensate for potential losses.

Both experiments 1 and 2 showed that false caches and recaches are probably not employed as deceptive caching strategies designed to fool conspecifics with regard to the location of an individual's caches. Perhaps these behaviors indicate a bird's assessment of the cache site's desirability.

It is unclear why the birds would have eaten more in treatment 2 of experiment 1 (single observer) than in the other two treatments. Perhaps this resulted from behavioral or social facilitation upon encountering a conspecific after food deprivation. Why this increase did not persist in treatment 3 will require further study.

In summary, conspecific density modifies food caching in Black-capped Chickadees by delaying or decreasing it in the presence of conspecifics. We conclude that conspecifics are perceived as sources of potential cache loss by cachers because they forage in the same area and thus might be expected to encounter one another's caches by chance rather than by observing and remembering the location of another's caches.

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