EVIDENCE AGAINST OBSERVATIONAL LEARNING IN STORAGE AND RECOVERY OF SEEDS BY BLACK-CAPPED CHICKADEES

MYRON CHARLES BAKER, ERIC STONE, ANN EILEEN MILLER BAKER,
ROBERT J. SHELDEN, PATRICIA SKILLICORN,
AND MARK D. MANTYCH
Department of Biology, Colorado State University, Fort Collins, Colorado 80523 USA

ABSTRACT.—Recovery of cached sunflower seeds by Black-capped Chickadees (*Parus atricapillus*) was observed in four laboratory experiments. Results of the first experiment were consistent with the hypothesis that chickadees use spatial memory to recover seeds cached 24 h earlier. The second experiment demonstrated that individuals have a high recovery rate for their own caches and a low recovery rate for caches made by another. The third and fourth experiments demonstrated that one chickadee observing another caching seeds provided no recovery benefit to the observer in comparison to its performance when recovering seeds hidden in its absence. This result held for 2-h and for 6-min delays between observation and attempted recovery. We believe that spatial memory is used by chickadees, that the individual carrying out the caching has a large recovery advantage over a conspecific that searches the same patch, and that the perceptual and motor experience involved in the act of traveling to a cache location may be necessary for the establishment of spatial memory.

Received 6 October 1987, accepted 14 March 1988.

SEVERAL species of birds employ memory to recover food items cached previously (Tomback 1980, Cowie et al. 1981, Sherry et al. 1981, Kamil and Balda 1985). Research on cache recovery has documented both the existence of spatial memory and its accuracy in different species. Investigators have explored properties of memory such as decay, the role of local visual or odor cues in recovery, the sequence of recovery acts in relationship to storage acts, and the revisitation of cache sites from which the forager already recovered the food items (Bossema 1979, Shettleworth and Krebs 1982, Sherry et al. 1981, Vander Wall 1982, Sherry 1984a, Balda et al. 1986, Bunch and Tomback 1986).

Less experimentation has been conducted on the social aspects of food storage and recovery of the cached items. Several food-caching birds, such as the Black-capped Chickadee (*Parus atricapillus*), cache and recover while members of a social flock. This context raises the possibility that other flock members may benefit to the detriment of the individual that cached the food (Andersson and Krebs 1978). Benefits could be gained if one bird searched randomly the local patch of environment used by the cacher and found the stored food; if the searcher had cache-site preferences identical to those of the cacher and found stored food by non-random searching; or, if a bird observed the cacher, remembered the cache locations, and subsequently recovered stored items. Cache loss appears to be high in some cases, e.g. Marsh Tits (*Parus palustris*) (Sherry et al. 1982), but little is known about causes of losses (Vander Wall and Smith 1987).

Kinship within chickadee flocks is low, which suggests no important component of kin-correlated behavior in the caching/flock system throughout most of the flocking season. A few sibling or parent-offspring combinations are present in some flocks into the late summer (Weise and Meyer 1979). Food caching presumably is advantageous to individual chickadees caching food (Sherry 1985) even though the social context within which caching occurs might encourage substantial loss of caches to unrelated individuals. We developed three hypotheses to examine this assumption.

The first hypothesis was that Black-capped Chickadees remember where they cache food items. Although this was established previously

(Sherry 1984a), it was important to confirm it in our experimental setting. The second hypothesis was that the cacher has a better recovery performance than another individual searching the same patch. It was necessary to test this experimentally because conspecifics may have highly convergent preferences for caching sites. If so, another individual would do as well as the cacher in recovering the caches. The third hypothesis concerned the possibility of one bird learning of the food caches made by another. We hypothesized that an observer watching a conspecific cache food cannot remember the locations of stored items. The development of a spatial memory may depend upon performing the motor activities of traveling to a caching location together with the perceptual processes attending that activity. Disproof of the third hypothesis would raise the possibility of "cheater" phenotypes (Andersson and Krebs 1978).

General Methods

Black-capped Chickadees were captured in riparian woodland at 2 sites 100 m apart along the Poudre River east of Fort Collins, Colorado, in November 1986. Birds were housed individually at room temperature in wire cages (46 cm long × 28 cm high × 23 cm deep) under a light regime of 8L:16D. They were provided continuously with sunflower seeds and water and with mealworm larvae 4 or more times per week.

To prepare these birds for the test situation, we placed a 12-cm-tall × 3-cm-diameter branch in each cage. The branch had a 1-cm-diameter perch located 4 cm below a 5-mm hole. Birds were regularly given sunflower seeds in the hole of their branch and thus were trained to recover food items from sites similar to those in our test situation. The birds spontaneously cached sunflower seeds and mealworms in these holes.

The test aviary was an indoor enclosure (3 m long × 2 m wide × 2 m high) with a screen roof and walls covered with black cloth. We observed all tests through one-way glass from a booth at one end of the enclosure. Fifty holes were drilled into the trunks and branches of three aspen trees to provide caching sites. Caching sites had perches about 4 cm below each hole. Caching holes were sufficiently deep and were positioned so that cached seeds in each hole were not in view of a searching bird unless it visited that site and inspected it visually. Furthermore, the color of sunflower kernels was similar to that of the wood inside the holes. We provided the cachers with hulled sunflower seeds in a bowl at one end of the aviary. The bowl was fitted with a lid that could be opened and closed from the observation booth.

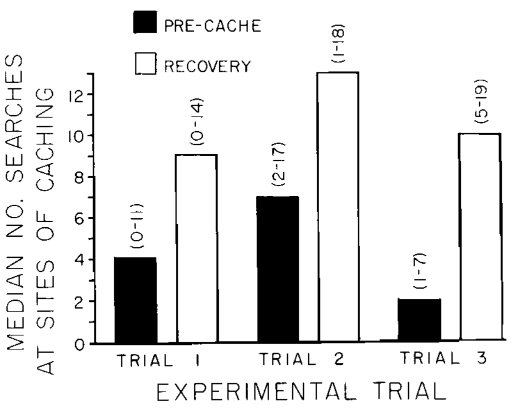

Fig. 1. Median (range in parentheses) number of searches of sites before (pre-cache) and after (recovery) storing seeds in the sites, performed by Black-capped Chickadees in three trials (n = 9, 9, 8).

Experiment One

Methods

To examine the ability of individuals to recover their own caches, we allowed each bird to cache seeds (maximum 15) for 15 min and search for its caches 24 h later. The method was similar to that of Sherry (1984b). Birds were deprived of food for 2 h prior to testing. During a 15-min pre-cache period, a bird was allowed to search the aviary and we recorded all sites the bird visited and searched. Searching was primarily by visual inspection of the holes, but a bird sometimes probed a hole. Immediately following the pre-cache period the bird was allowed access to seeds for 15 min, and we recorded the number of seeds eaten and the cache sites used for storage. Each bird was tested 24 h later following 2 h of food deprivation. During this "recovery" session, no seeds were present and we recorded the holes searched. Each bird served as its own control in three trials of this matched-pairs design ($n = 9$ for the first two trials; $n = 8$ for the third).

Results

If a bird formed a site memory by making a cache there, then it should be more likely to search that site during the recovery period than during the pre-cache period (Sherry 1984b). All subjects (Fig. 1) exhibited a preference for searching cache sites during the recovery period in comparison to searching of those same sites during the pre-cache period (trial 1: $n = 9$, $T = 5.5$, $P < 0.05$; trial 2: $n = 9$, $T = 2.5$, $P < 0.02$; trial 3: $n = 8$, $T = 0$, $P < 0.01$; two-tailed

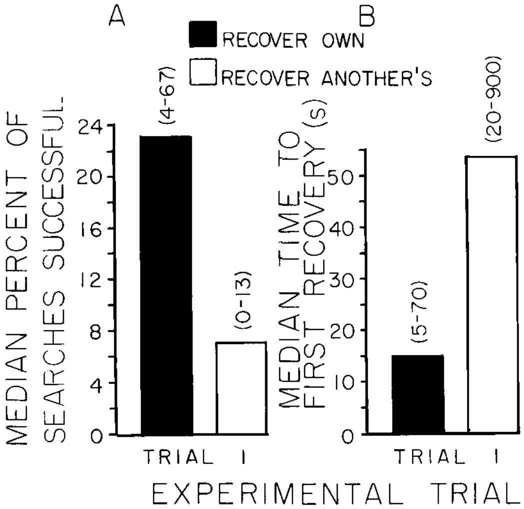

Fig. 2. Recovery performance of subjects searching for seeds cached by themselves or by another individual. Median (range in parentheses) percent of searches that were successful (A), and time required to find the first seed (B) by Black-capped Chickadees in one trial ($n = 8$).

Wilcoxon matched-pairs signed-ranks test, Siegel 1956).

During the pre-cache period, birds averaged 26 searches of potential cache sites. During the caching period, a bird usually ate a few seeds ($\bar{x} = 2.9$) before caching ($\bar{x}$ cached = 7.6). During the recovery period, birds averaged 23 searches of potential cache sites. No bird in experiment 1 exhibited a frequency of cache-site use different from that expected under a Poisson random distribution of caching sites (all Ps > 0.05, NS, goodness-of-fit G-test; Sokal and Rohlf 1969). Consequently, one cannot attribute enhanced searching of specific sites to individual cache-site preferences (Shettleworth and Krebs 1982).

EXPERIMENT TWO

METHODS

We examined the recovery performance of eight birds under each of two conditions to determine the relative success of a searcher in recovering its own caches compared to recovering caches made by another bird. Following overnight deprivation, each subject cached three seeds. Two h later each individual was allowed to recover its caches. Following overnight deprivation, each bird was tested the next day, this time on its ability to find three seeds cached by another bird. We recorded both the sequence of holes searched by the subject and the time required to find the first seed on each trial in this matched-pairs design.

RESULTS

The number of seeds obtained per site searched was greater for a bird hunting for its own caches than when hunting for caches made by another individual (Fig. 2A: $n = 8$, $T = 0$, $P = 0.01$, two-tailed Wilcoxon test). The time to the first recovery of a seed was shorter when a bird hunted for seeds it cached than when it searched for seeds cached by another individual (Fig. 2B: $T = 0$, $P = 0.01$, two-tailed Wilcoxon test).

Serial position analysis.—From data in experiments 1 and 2, we examined the relationship between the order in which seeds were cached and the order in which they were recovered. We used the statistical design of Cowie et al. (1981). Each bird in each trial produced a sequence of numbers (from 1 to n) which represented the serial order in which n seeds were cached. The question is whether a bird recovers low sequence numbers (early caches) first and then higher sequence numbers (later caches), or follows the opposite pattern of recovery. To obtain the largest possible number of individuals for each of the four tests, we required a bird to recover a minimum of two seeds. In none of the four tests were seeds consistently recovered in either the same or reverse order in which they were cached (experiment 1: trial 1, $n = 8$, $T = 13.5$; trial 2, $n = 7$, $T = 10$; trial 3, $n = 8$, $T = 12$; experiment 2: $n = 7$, $T = 12$; all Ps > 0.05, NS, Wilcoxon matched-pairs signed-ranks test, two-tailed; Siegel 1956).

EXPERIMENTS THREE AND FOUR

METHODS

The possibility of observational learning was tested in two experiments that differed in the time between the demonstration of caching by one bird and an observer bird's attempts to recover seeds. The delay was two h in experiment 3 and about 6 min in experiment 4. We deprived an observer and demonstrator overnight, placed the observer in a cage near the food dish, and allowed the demonstrator to cache three seeds. Two h (experiment 3) or about 6 min (experiment 4) later, the observer was allowed to search for the caches. Twenty-four h later, again after overnight deprivation, each observer was allowed to re-

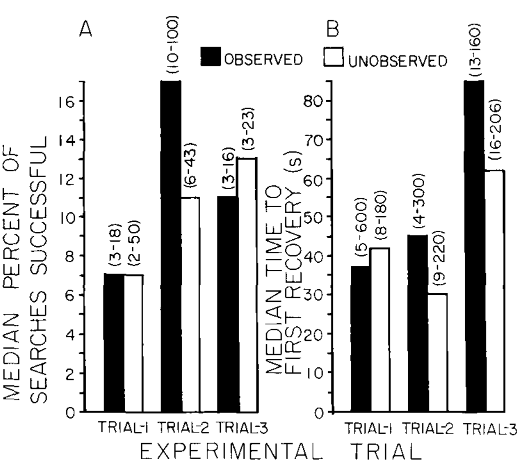

Fig. 3. Recovery performance of observer birds 2 h after watching demonstrator birds cache seeds, compared to the performance of birds searching for caches made randomly by the experimenter. Median (range in parentheses) percent of searches that were successful (A), and the time required to find the first seed (B), by Black-capped Chickadees in three trials (n = 8, 8, 8).

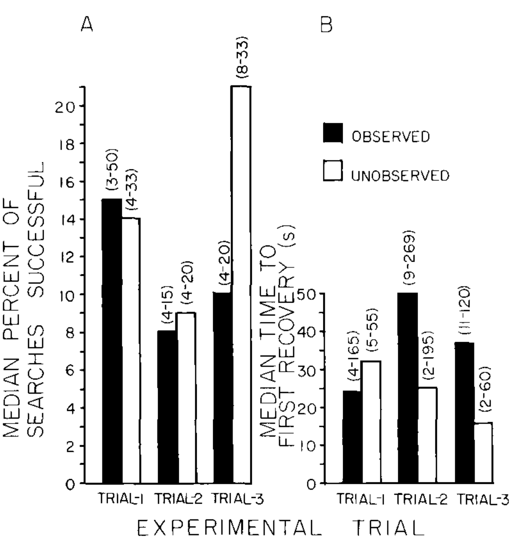

Fig. 4. Comparison of recovery performance of observer birds 6 min (range 5–12) after watching demonstrator birds cache seeds with the performance of birds searching for caches made randomly by the experimenter. Median (range in parentheses) percent of searches that were successful (A), and the time required to find the first seed (B), by Black-capped Chickadees in three trials (n = 8, 7, 7).

cover three seeds randomly placed in cache sites by an experimenter. Thus, in each experiment each bird was tested for recovery of three observed and three unobserved caches. We carried out 3 trials in experiment 3 ($n = 8$ birds in each trial) and 3 in experiment 4 ($n = 8$ birds in the first trial and $n = 7$ in the second and third). We recorded the sequence of holes searched by the observer and the time to recovery of the first seed in each trial.

RESULTS

The results of experiment 3 (2 h delay) indicated that there was no benefit from watching a demonstrator. The number of seeds found per site searched was no different for observed and unobserved caches in any of 3 trials (Fig. 3A: trial 1, $n = 8$, $T = 17$; trial 2, $n = 8$, $T = 12$; trial 3, $n = 8$, $T = 11$; all $Ps > 0.05$, two-tailed Wilcoxon test). Parallel results were obtained from a second measure of recovery performance, the time to recovery of the first seed. In all 3 trials there was no difference in recovery performance in comparing observed and unobserved caches (Fig. 3B: trial 1, $T = 14.5$; trial 2, $T = 8$; trial 3, $T = 13$; all $Ps > 0.05$, two-tailed Wilcoxon test).

In experiment 4 (median delay 6 min, range 5-12) the number of seeds found per site-searched for observed vs. unobserved caches was no different for two of the three trials (Fig. 4A: trial 1, $n = 8$, $T = 12$; trial 2, $n = 7$, $T = 12$; both $Ps > 0.05$, two-tailed Wilcoxon test). In the third trial, birds recovered more seeds per site-searched for unobserved than for observed caches ($n = 7$, $T = 0$, two-tailed Wilcoxon test). This was opposite the expectation if observational learning occurred. In the second measure of recovery performance, two trials indicated no difference in the time to recovery of the first seed for birds searching for observed vs. unobserved caches (Fig. 4B: trial 1, $T = 15$; trial 2, $T = 9.5$; both $Ps > 0.05$, two-tailed Wilcoxon test). In trial 3 the birds performed somewhat better if they had not observed the demonstrator, although the difference was barely significant ($T = 3.5$, $P = 0.05$, two-tailed Wilcoxon test).

DISCUSSION

Black-capped Chickadees use memory to recover caches of seed made the previous day (experiment 1 and Sherry 1984b). The birds had a strong bias to search at sites where they had cached seeds 24 h earlier. This bias was not a preference for particular caching sites. All birds used potential cache sites with a frequency no different from that predicted by the Poisson random distribution. Confounding effects of cache-site preferences have been reported in other species (Vander Wall 1982, Shettleworth and Krebs 1982, Bunch and Tomback 1986).

Black-capped Chickadees have better recovery performance when searching for seeds they cached than when searching for seed cached by a conspecific (experiment 2). We think that this performance differential would be greater in natural habitats than in the laboratory, because potential cache sites are far more numerous in the field. In the natural setting, the opportunity for a bird to find by chance the caches of another bird probably would be greatly reduced. An exception may occur when two birds make caches fairly close together (Cowie et al. 1981). Bunch and Tomback (1986) used a 24-h delay in an experiment in which Gray Jays (*Perisoreus canadensis*) searched for food boli cached in cones in the laboratory. The Gray Jays exhibited a higher recovery performance when searching for their own caches than when searching for those caches made by another individual.

We found no evidence that seeds were recovered in either the same order or reverse order of storage. Sherry (1984a) argued that because older caches have a higher chance of loss to other predators, reverse-order recovery (recency effect) would give the highest yield per unit time spent foraging. Shettleworth and Krebs (1982) described this reverse-order pattern of cache recovery by Marsh Tits in a laboratory study. In a field study of Marsh Tits (Cowie et al. 1981), seeds were recovered in the same order (primacy effect) as that in which they were cached. The most frequent finding has been of no significant serial position effect (Balda 1980; Sherry et al. 1982; Sherry 1982, 1984b).

Chickadees did not remember caching locations they had observed another individual use (experiments 3 and 4). Our subjective impressions were that the observer bird saw the demonstrator making the caches. Further, previous studies of chickadees foraging (Baker pers. obs.) indicated that individuals were responsive to each other when foraging, exhibiting "local enhancement" (Thorpe 1956) and rapid recruitment to a newly discovered food source (Krebs et al. 1972). Social learning in chickadees has been demonstrated previously (Sherry and Galef 1984). Individual chickadees were attentive to the foraging behavior of conspecifics in a laboratory setting. Thus, we are reasonably confident that chickadees observed the caching activities of the demonstrators, although this is difficult to prove.

In a similar experiment, Bunch and Tomback (1986) were unable to find an advantage to observer Gray Jays attempting to recover the caches of the demonstrator birds. Recovery of a seed by an observer that watches another individual making a cache can occur in Clark's Nutcracker (Vander Wall 1982). The current thinking suggests that a phenotype that exhibits a cheat-only strategy for obtaining cached food by observing honest cachers has not been successfully established. The results are probably too preliminary to argue strongly for or against the possibility of mixed strategies of some amount of cheating by food-caching birds. We would be surprised if some chickadees did not sometimes steal the caches of others after observing them being put into place, as noted in Crested Tits, *Parus c. cristatus* (Haftorn 1954).

Different experimental approaches might give results consistent with observational learning of cache locations. All the individuals we studied were familiar with the potential cache locations. They cached and searched in them several times prior to the onset of experiments 3 and 4. In a natural situation, environmental complexity makes it probable that a chickadee never re-uses the exact same cache sites (Shettleworth and Krebs 1982). Thus, it might be that the experimental birds recovered seeds that they did not observe being cached at a level artificially higher than they would achieve in natural habitats. The effect would be to diminish and perhaps eliminate any difference in recovery performance under the two experimental conditions (observed vs. unobserved caches). It also may be that if cheating occurred in the wild it was the result of a cheater observing an act of caching and stealing the seed as soon as it was stored. This behavior would not require as complex a memory process as our experimental design imposed and might more realistically reflect cheating as it occurs under field conditions.

We reason that the development of a spatial memory for a set of food caches does not occur in an observer located at a fixed site during the caching activity of a conspecific demonstrator. Instead, traveling to a particular cache site, placing a seed, and memorization of spatial arrangements and points of reference relative to the cache site may all be involved in distinguishing the experience of the caching individual from that of an observer. The act of placing the seed at the site is not an essential component of the process of forming a spatial memory (Shettleworth and Krebs 1986).

ACKNOWLEDGMENTS

We thank Tammie Nakamura for helping formulate and initiate this study, Carol Guyon for assistance in capturing the birds, and participants at the Winter Animal Behavior Conference IX for suggestions on improving the experiments. Jeff Galef, Dave Sherry, Diana Tomback, and Stephen Vander Wall provided many helpful suggestions on the manuscript. Heather Bartman and Tom Wilson donated the aspen trees. The birds were obtained under Federal Fish and Wildlife permit PRT-694924 and Colorado Division of Wildlife permit 86-0035.

LITERATURE CITED

ANDERSSON, M., & J. R. KREBS. 1978. On the evolution of hoarding behaviour. Anim. Behav. 26: 707-711.

BALDA, R. P. 1980. Recovery of cached seeds by a captive *Nucifraga caryocactes.* Z. Tierpsychol. 52: 331-346.

———, A. C. KAMIL, & K. GRIM. 1986. Revisits to emptied cache sites by Clark's nutcrackers (*Nucifraga colombiana*). Anim. Behav. 34: 1289-1298.

BOSSEMA, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70: 1-117.

BUNCH, K. G., & D. F. TOMBACK. 1986. Bolus recovery by gray jays: an experimental analysis. Anim. Behav. 34: 754-762.

COWIE, R. J., J. R. KREBS, & D. F. SHERRY. 1981. Food storing by marsh tits. Anim. Behav. 29: 1252-1259.

HAFTORN, S. 1954. Contributions to the food biology of tits especially about storing of surplus food, part I. The Crested Tit (*Parus c. cristatus* L.). Det Kongelige Norske Videnskabers Selskabs Skrifter 4: 1-122.

KAMIL, A. C., & R. P. BALDA. 1985. Cache recovery and spatial memory in Clark's Nutcracker (*Nucifraga columbiana*). J. Exp. Psychol.: Anim. Behav. Processes 11: 95-111.

KREBS, J. R., M. H. MACROBERTS, & J. M. CULLEN. 1972. Flocking and feeding in the Great Tit *Parus major*—an experimental study. Ibis 114: 507-530.

SHERRY, D. F. 1982. Food storage, memory, and marsh tits. Anim. Behav. 30: 631-633.

———. 1984a. What food storing birds remember. Can. J. Psychol. 38: 304-321.

———. 1984b. Food storage by black-capped chickadees: memory for the location and contents of caches. Anim. Behav. 32: 451-464.

———. 1985. Food storage by birds and mammals. Pp. 153-188 *in* Advances in the study of behavior (J. S. Rosenblatt, C. Beer, M-C. Busnel, and P. J. B. Slater, Eds.). New York, Academic Press.

———, M. AVERY, & A. STEVENS. 1982. The spacing of stored food by marsh tits. Z. Tierpsychol. 58: 153-162.

———, & B. G. GALEF JR. 1984. Cultural transmission without imitation: milk bottle opening by birds. Anim. Behav. 32: 937-938.

———, J. R. KREBS, & R. J. COWIE. 1981. Memory for the location of stored food in marsh tits. Anim. Behav. 29: 1260-1266.

SHETTLEWORTH, S. J., & J. R. KREBS. 1982. How marsh tits find their hoards: the roles of site preference and spatial memory. J. Exp. Psychol.: Anim. Behav. Processes 8: 354-375.

———, & ———. 1986. Stored and encountered seeds: a comparison of two spatial memory tasks in marsh tits and chickadees. J. Exp. Psychol.: Anim. Behav. Processes 12: 248-257.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, Freeman.

THORPE, W. H. 1956. Learning and instinct in animals. London, Methuen.

TOMBACK, D. F. 1980. How nutcrackers find their seed stores. Condor 82: 10-19.

VANDER WALL, S. B. 1982. An experimental analysis of cache recovery in Clark's nutcracker. Anim. Behav. 30: 84-94.

———, & K. G. SMITH. 1987. Cache-protecting behavior of food-hoarding animals. Pp. 611-644 *in* Foraging behavior (A. C. Kamil, J. R. Krebs, and H. R. Pulliam, Eds.). New York, Plenum.

WEISE, C. M., & J. R. MEYER. 1979. Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. Auk 96: 40-55.