

The effects of requiring different response strategies following caching in Clark's nutcrackers (*Nucifraga columbiana*)

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Clark's nutcrackers use spatial memory to recover stored food in the field and have performed very well in laboratory tests of spatial memory. During the present experiment, two groups of nutcrackers cached seeds every 4 days. Following each cache session, the stay group was tested with seeds in their caches; the shift group found seeds in novel sites. The stay group performed accurately throughout the experiment, but the shift group gave no indication of being able to learn to avoid sites where they had stored seeds. These results suggest that although nutcrackers can learn to shift away from remembered locations during some memory experiments, they cannot learn to shift away from cache sites. This raises interesting questions about the relationship between task characteristics, response strategies, and memory.

Every winter and spring, Clark's nutcrackers (*Nucifraga columbiana*) obtain most of their food by relocating and retrieving pine seeds they have cached the previous fall. Many studies have shown that these birds use spatial memory for individual cache sites to find these stored seeds (see Kamil & Balda, 1990b, for a review). This phenomenon has led to the study of the memory abilities of Clark's nutcrackers in several paradigms in addition to cache recovery. Olson (1991) found that nutcrackers perform extremely well in delayed spatial nonmatching-to-sample, doing significantly better than pigeons or scrub jays. Balda and Kamil (1988) and Olson, Kamil, and Balda (1993) found that nutcrackers perform extremely well in an analogue of the radial arm maze, with performance well above chance after 5- to 7-h retention intervals.

In the radial maze analogue, Olson et al. (1993) tested the effects of different response strategies on acquisition and memory. Olson et al. used a small room with 12

holes drilled in the floor in a circular pattern. Each hole could be filled with sand or capped with a wooden plug. Each trial consisted of two parts. First, the bird was released into the room with 4 holes open, each containing a seed. After the bird removed these seeds, it left the room. Following a retention interval, the bird reentered the room. The 4 holes open during the first stage remained open, along with 4 new holes. Birds in the shift group were tested with seeds in the new holes; birds in the stay group, with seeds in the old holes. The shift group found their seeds somewhat more accurately early in acquisition and were very slightly more accurate than the stay group throughout extensive retention testing, but these differences were not statistically significant. Thus it appears that in radial maze type procedures during which the bird removes seeds from the to-be-remembered site, there are at most only small differences between birds using a stay strategy and birds using a shift strategy.

The results of several studies on the effects of different response strategies suggest that the preferred strategy may depend on the pattern of food distribution and/or depletion experienced during the experiment (e.g., Cole, Hainsworth, Kamil, Mercier, & Wolf, 1982; Herrmann, Bahr, Bremner, & Ellen, 1982; Olson & Maki, 1983; Roitblat, Tham, & Golub, 1982). This suggests that nutcrackers might show different response strategy effects if, instead of removing seeds from holes as in the radial maze procedures, they *placed* seeds in the to-be-remembered sites as they do during caching.

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The purpose of the present study was to determine whether response strategy effects would be found when the bird cached seeds in the to-be-remembered site.

Our goal in designing this experiment was to make the procedures as similar as possible to those of the radial arm maze analogue experiments. However, because the concept being explored required the birds to cache in the to-be-remembered sites, a number of methodological differences were inescapable. In particular, although nutcrackers are hungry at the start of cache sessions, they do not begin to cache until they have eaten many seeds. Because a bird must be hungry before it will attempt to recover seeds, a minimum of 24 h between the cache session and the test session was necessary. In addition, because the design required birds to create caches, it was necessary to provide them with some choice of sites for their caches. The present experiment tested the ability of nutcrackers to learn to either return to (stay) or avoid (shift) sites in which they had cached the previous day, working within these constraints.

METHOD

Subjects

Twelve wild-caught Clark's nutcrackers of unknown sex and age served as subjects in this experiment. Seven of the birds had been in the laboratory for 3–12 years and 5 for 1–2 years. All had served in previous caching experiments, but none of the birds had been exposed to the experimental room used during this experiment. All birds had served in at least one previous experiment, and 1 bird had served in 11 different experiments. The birds were randomly divided into two equal-sized groups, the stay and shift groups, before the experiment began. (Two additional birds, 1 from each group, were dropped from the study because they consistently refused to cache either during pretraining or early in Block 1.)

The birds were maintained in large metal cages and were fed a mixed diet of sunflower seeds, pinyon pine nuts, cracked corn, turkey starter, pigeon pellets, and mealworms. The birds were also provided with a vitamin supplement and oyster shells. During the experiment, the birds only received pine seeds in the experimental room and were deprived of all food for 24 h before each caching or recovery session. They were maintained on a constant 10:14-h light:dark cycle.

Experimental Room

The experiment was conducted in a 3.12 × 3.61 m room with a raised plywood floor. There were two hundred thirty-eight 5.1-cm-diameter holes drilled in the floor, 20.3 cm apart (center to center) and arranged in 14 rows × 17 columns. Each hole contained a tightly fitting paper cup that could be either filled with sand of a uniform texture or capped with a wooden plug. The holes in the center column remained capped throughout this experiment. Both the sand-filled cups and the wooden plugs were approximately level with the plywood floor. Visual stimuli were provided by rocks, boards, cans, and plastic containers placed on the wooden floor and by posters placed on the walls. A large rectangular platform with a slotted top and false bottom was placed in the center of the room. When seeds were presented to the birds for caching, they were placed in the slots at the beginning of the session. When the desired number of caches had been made, a solenoid connected to the false bottom could be activated from the observation area, causing the remaining seeds to fall into an inaccessible container below the platform.

The birds entered and exited the experimental room through a porthole in a wall that connected directly to their cage. The same

wall contained an entrance door for the experimenters and a one-way glass window through which the birds were observed.

Procedure

The experiment was conducted in three stages: pretraining (4 trials), acquisition (26 trials), and preference testing (8 trials).

Pretraining. Each pretraining trial consisted of two sessions, a cache session followed 22–25 h later by a recovery session. There were 2 days off between a recovery session and the next cache session. During each cache session, eight holes were made available, two randomly selected from each quarter of the room, and there were 121 seeds on the feeder. (The large number of seeds was provided because the bird would eat seeds before beginning to cache.) The bird was placed in the room, and the cache session continued until either six caches were made (in six different locations) or the bird was inactive for 5 min. The lights were then turned off, and the bird returned to its home cage. If x caches were made during the cache session, then x holes were opened during the recovery session. If the bird was in the stay group, the x holes were the sites cached in the previous day. If the bird was in the shift group, the x holes were new holes. During the first recovery session, the seed was placed on top of the sand in each of the x open cups. Over the next three pretraining trials, the extent to which the seeds were buried was gradually increased so that during the fourth pretraining session, the seeds were completely buried.

Acquisition. During the first 7 acquisition trials, all conditions were identical to those of the last pretraining trial with one major exception. During the recovery session of each trial, $2x$ holes were available. These consisted of the x holes cached in the previous day plus x additional, new holes. If the bird was in the stay group, there was a seed buried in each of the x cache sites from the day before. If the bird was in the shift group, there was a seed buried in each of the x new holes. Thus, for stay birds, the correct holes (those containing seeds) were the holes in which caches had been placed; for shift birds, the correct holes were the new holes. During the last 19 acquisition trials, all conditions were identical to those of the first 7 acquisition trials except that 24 holes, 6 randomly selected from each quarter of the room, were made available for caching. Throughout acquisition, the criteria for ending the caching phase of each trial were as they had been during pretraining. The recovery phase ended when all seeds had been recovered, when the number of different holes probed equaled the number of caches made plus two (so that errors reduced the number of seeds obtained in the test session), or when the bird was inactive for 5 min, whichever came first.

The holes were selected for each trial as follows: the middle column of 14 holes remained capped and were not used during the experiment, leaving 224 of the 238 holes available. These holes were divided into four quadrants, each containing 56 holes arranged in 7 rows × 8 columns. During the first seven trials, 2 holes were randomly selected within each quadrant for each trial and used as cache sites. Then, during the test session, 1 new hole was selected for each cache site (incorrect hole for the stay group; correct hole for the shift group). This new hole was always within the same quadrant as was the cache site. No hole was used more than once during these seven sessions. The same procedure was used during the remainder of testing, except that 6 holes were selected from each quadrant as cache sites, and no hole was used twice within any three consecutive sessions. Throughout testing, no 2 adjacent holes were used during the same session.

Preference testing. The purpose of the third stage of the experiment was to test for the possible effects of site preferences on the performance of the two groups. During preference testing, only 12 holes were made available during each cache session, and performance was examined under three conditions which differed in the types of holes made available to the birds during caching. During the *accepted condition*, all holes made available to the birds for caching were holes that had previously been accepted by the

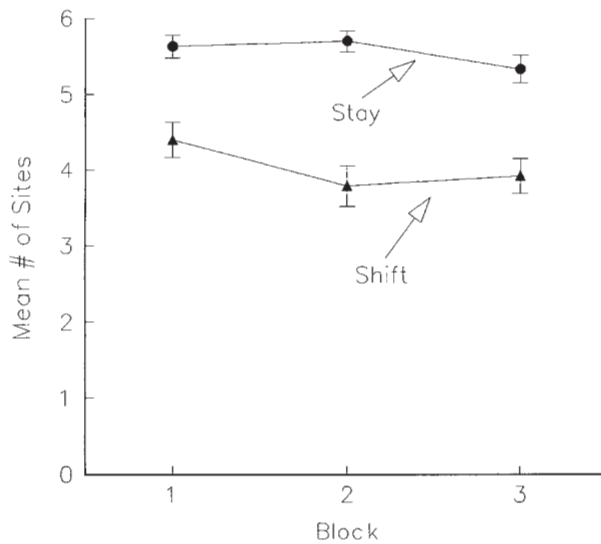


Figure 1. Mean number of sites ($\pm SE$) in which caches were placed for each group during the three blocks of acquisition.

nutcracker as cache sites when offered and were therefore presumably preferred holes. During recovery sessions in the accepted condition, all the new holes opened were holes that had previously been made available during caching but that the bird had not used and therefore were presumably nonpreferred. During the *rejected condition*, the arrangement was reversed. All holes made available for caching were holes that had previously been made available during caching but that the bird had rejected as cache sites. All new holes made available during recovery were holes that had previously been accepted as cache sites. During the *control condition*,

all holes made available for caching and during recovery were holes that had never before been made available for caching and therefore could not be classified as either preferred or nonpreferred. In summary, then, holes that had previously been accepted as cache sites earlier in the experiment were correct during the accepted condition for the stay birds, but incorrect for the shift birds. During the rejected condition, holes that had been avoided as cache sites earlier in the experiment were correct for the stay birds, but incorrect for the shift birds. If site preferences affect choice, performance should be highest when accepted sites are the correct sites during the choice test.

RESULTS

One bird from the stay group died during pretraining. The other 11 birds completed acquisition, although some of them occasionally did not cache. On the average, the birds completed 23.9 of the 26 scheduled cache-test session cycles. In the analyses of behavior, acquisition was divided into three blocks: Block 1 included Sessions 1–7 (8 holes available during caching), Block 2 included Sessions 8–16, and Block 3 included Sessions 17–26. The data were then analyzed with a mixed design analysis of variance (ANOVA), with groups and blocks as factors.

The willingness of the birds to create caches during the experiment was assessed by analyzing the number of caches made. The stay group made significantly more caches than did the shift group [$F(1,9) = 13.35, p < .01$], but neither the blocks effect nor the interaction was significant (Figure 1).

Two measures of the choice accuracy were analyzed, the percentage correct of all choices and the percentage correct during the first N choices (where

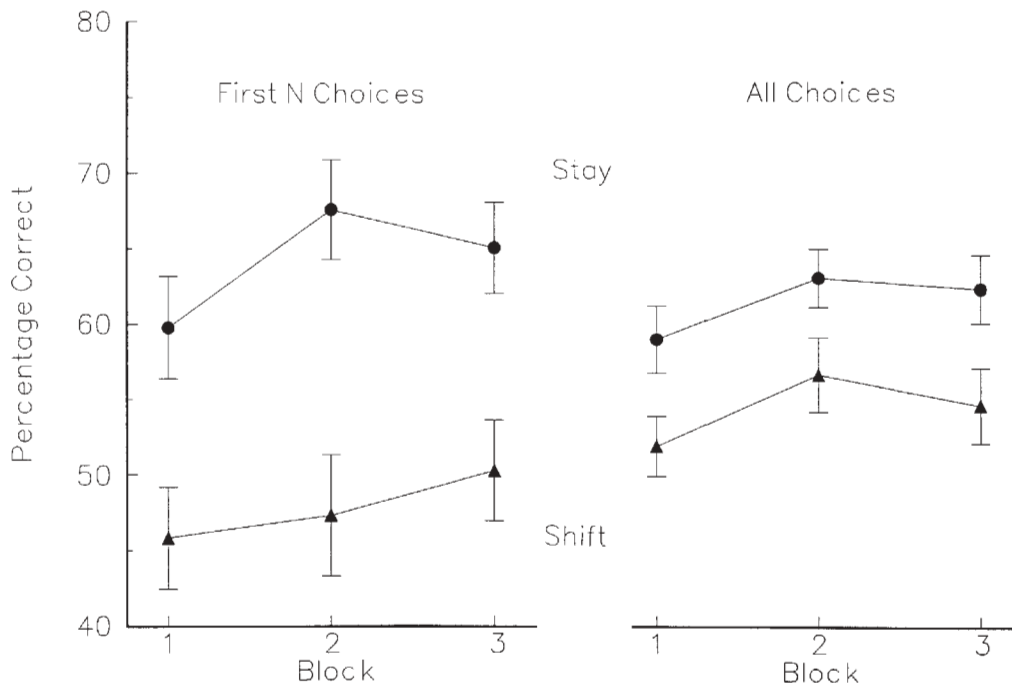


Figure 2. Mean choice accuracy ($\pm SE$) for each group during each block of acquisition. The left panel shows accuracy during the first N choices; the right panel shows accuracy for all choices.

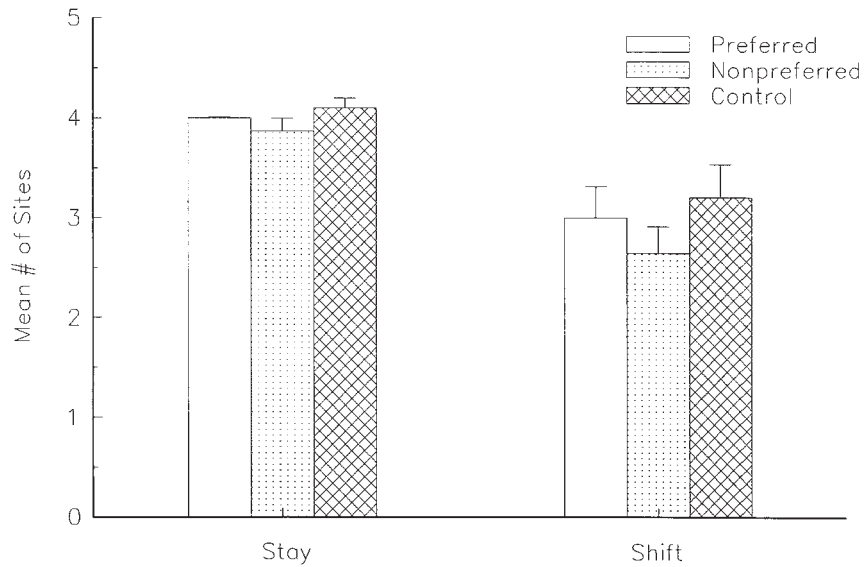


Figure 3. The number of sites ($\pm SE$) in which seeds were placed during preference testing, as a function of group and type of hole presented as potential cache sites.

N = no. caches made up to four). For both these measures, the level of performance expected by chance was 50% (because the number of correct holes always equaled the number of incorrect holes). The analysis of the first N choices was included for two reasons. First, this measure has been used in the analysis of cache recovery in our previous experiments (e.g., Kamil & Balda, 1985, 1990). Second, the stay group

tended to make more caches than the shift group did. If there were any effects of the differential length of recovery sessions on accuracy, these effects would be minimized in the N -choice measure. The stay group performed more accurately throughout the experiment, in terms of both overall percentage correct [$F(1,9) = 9.88, p < .05$] and percentage correct during the first N choices [$F(1,9) = 24.56, p < .001$]. There were no

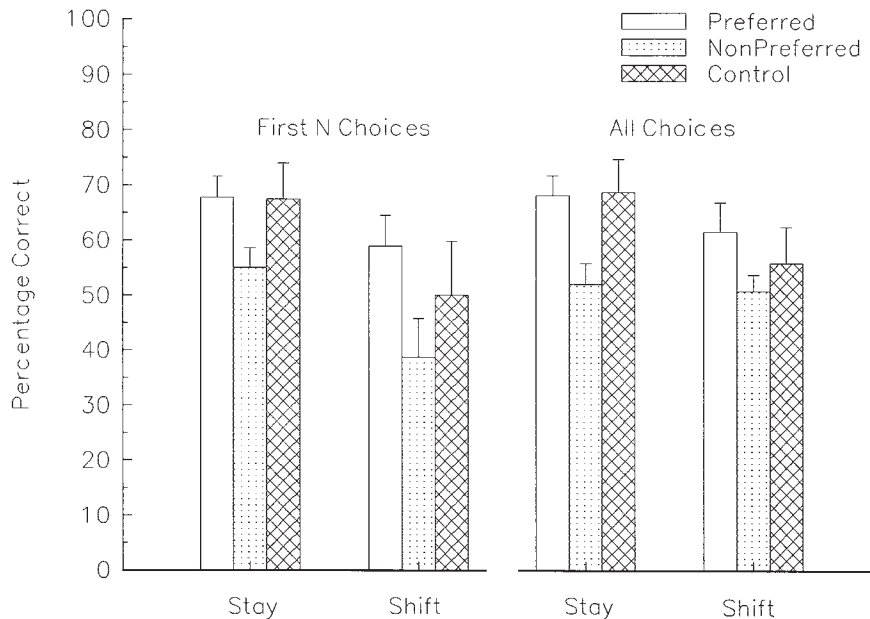


Figure 4. Mean choice accuracy ($\pm SE$) during the first N choices (left panel) and for all choices (right panel) during preference testing, as a function of group and type of hole that was correct.

effects of blocks or group \times blocks interactions in either case (Figure 2).

Analysis of behavior during preference testing was carried out with two-way mixed ANOVAs (1 bird could not be tested during this stage). The nature of the design of preference testing provided two ways of partitioning the test sessions. Sessions could be classified on the basis of the type of holes (accepted, rejected, or control) offered during cache sessions. Alternatively, the partitioning could be made on the basis of the type of holes that were correct during the test sessions. Caching behavior was analyzed for the effects of type of holes available for caching; recovery behavior was analyzed for the effects of type of correct holes during test sessions.

As during the acquisition phase of the experiment, the stay group cached in significantly more holes overall than did the shift group [$F(1,8) = 13.47, p < .01$] (Figure 3). There were no significant differences among the cache site conditions in the number of caches created, nor was there a significant interaction of type of site with group. Throughout preference testing, the stay group also continued to choose holes more accurately than did the shift group, both in the first N choices [$F(1,8) = 6.72, p < .05$] and overall [$F(1,8) = 9.87, p < .05$] (Figure 4). There was also a significant effect of hole type on the accuracy of recovery. When the correct holes were holes that had been rejected when offered as cache sites during acquisition, performance was significantly lower than during either of the other two conditions (accepted or control). This was true for both percentage correct during the first N choices [$F(2,64) = 4.63, p < .05$] and overall [$F(2,64) = 4.90, p < .05$]. The interaction of site type \times group was not significant.

DISCUSSION

Three major aspects of these results need to be considered. First, the shift group gave no indication of any learning to avoid cache sites during acquisition. Not only did this group consistently perform at levels well below those of the stay group, but they never gave any indication of above chance performance. It is, of course, quite possible that with further training, or with different procedures, the nutcrackers could learn to avoid cache sites. These results stand in direct contrast, however, to those obtained with Clark's nutcrackers in studies of the effects of response strategies on learning and memory in either the radial maze or operant tasks. In the radial maze analogue, Olson et al. (1993) found that learning to avoid a visited site was slightly faster than learning to revisit such a site, and that there were no significant differences between the two strategies throughout a long period of acquisition and retention testing. When Basil, Olson, Kamil, and Balda (1994) tested the effects of response strategies on spatial matching versus nonmatching performance in nutcrackers, they found that returning to a site on a television monitor that had been pecked was learned more quickly than avoiding

that location. But as in the radial maze testing, this difference disappeared early in acquisition and was not apparent throughout lengthy retention testing.

Thus, the results of this experiment, when taken together with the previous response strategy work in radial and operant tasks, suggest that response strategies are an important component of performance during "natural" cache recovery situations but not during more abstract tests of spatial memory. These effects of response strategies following caching could be an innate characteristic of nutcrackers. That is, nutcrackers could possess a strong unlearned tendency to return to a cache site which prevented the birds in the shift group from learning the task. However, "naturalness," in and of itself, is a somewhat arbitrary concept, and we do not mean to imply that "naturalness" per se is responsible for the difference in response strategy effects among different paradigms. It seems most likely that some specific feature or set of features of the cache recovery task is responsible for the large difference between stay and shift strategy requirements. One possibility is that after caching, there is food in the to-be-remembered sites, which is not characteristic of the other tasks that have been tested with nutcrackers. This suggests that it might be interesting to test nutcrackers with one of the noncache procedures developed by Shettleworth and Krebs (1986). With these procedures, food remains in the site, either visible behind a window or wedged in place. Therefore, the effects of the presence of food without caching behavior could be assessed. Another possible difference is that cache recovery involves much longer retention intervals than do either operant nonmatching or radial maze procedures.

It is also possible that the response strategy effects found in this experiment could reflect effects of previous caching experience in either the laboratory or the field. Wunderle and Martinez (1987) found that the learning of adult-caught bananaquits, but not that of juveniles hand-raised in the laboratory, was affected by stay versus shift response strategies. Given that all the nutcrackers in this study probably had extensive previous experience with cache recovery before capture and had served as subjects in one or more cache recovery experiment in the laboratory, further experiments with naive, hand-raised birds would be of interest.

Second, the results of preference testing indicate the possible influence of site preferences on performance during the experiment. Site preferences could have affected the performance of the two groups differentially. It could be argued that sites selected as cache sites are preferred over sites that are not selected as cache sites. Then, this preference (which determines selection as a cache site in the first place) would lead to superior performance by the stay group over the shift group, since the stay group is required to return to a preferred set of holes whereas the shift group is required to avoid the presumably preferred sites. The data from the preference testing stage are consistent with this interpretation. When correct holes were those that had been avoided as

cache sites earlier in the experiment, performance was significantly lower than it was either during the control condition or when the correct holes had been accepted as cache sites earlier in the experiment. The virtually identical accuracy observed during the accepted and control conditions by the stay group strongly suggests that this was the case. However, it seems unlikely that site preferences alone could have produced the group difference observed throughout the experiment. In all our previous research with nutcrackers, during cache recovery (Kamil & Balda, 1985), the radial maze analogue (Balda & Kamil, 1988), and operant tasks (Basil et al., 1994), preferences have been present but have never seriously affected choice accuracy. If site preferences were responsible for the difference between the stay and shift groups during the present experiment, it would represent the first instance in which such preferences may have interfered with learning.

Third, there are indications that the cache site memory system of Clark's nutcrackers has some unusual characteristics, especially when the results of the present experiment are considered together with the results of a previous experiment. Kamil and Balda (1990a) forced nutcrackers to use the same holes as cache sites three times in a row. It might be expected that each caching cycle would serve as a trial in which the same information needed to be retained so that memory would improve when the same set of cache sites needed to be remembered over several successive trials. However, recovery accuracy declined across the three trials. During the present experiment, the performance of the stay group was stable throughout the experiment. The conditions of this experiment represent the most intensive scheduling of caching and recovery ever attempted with Clark's nutcrackers. The birds experienced 26 cache-test cycles in 104 days, which might have been expected to produce considerable proactive interference, with a resulting decline in performance. The accurate cache recovery observed in the stay group during the last block of the experiment suggests that the cache site memory of nutcrackers is very resistant to proactive interference. Similar resistance to interference has been found in other tasks, notably the radial maze (e.g., Maki, Brokofsky, & Berg, 1979) and tasks using trial-unique stimuli (e.g., Sands & Wright, 1980). Cache recovery shares features with both of these tasks, since cache site relocation is clearly spatial in nature and cache sites are rarely used more than once during cache recovery. Further research needs to be carried out by applying stan-

dard procedures from the study of memory to the cache recovery memory of the Clark's nutcracker in order to learn more about the characteristics of cache site memory in this species.

REFERENCES

- BALDA, R. P., & KAMIL, A. C. (1988). The spatial memory of Clark's nutcrackers (*Nucifraga columbiana*) in an analogue of the radial arm maze. *Animal Learning & Behavior*, **16**, 116-122.
- BASIL, J., OLSON, D. J., KAMIL, A. C., & BALDA, R. P. (1994). *The effects of matching and nonmatching response strategies, retention interval and memory load on the performance of Clark's nutcrackers*. Manuscript submitted for publication.
- COLE, S., HAINSWORTH, F. R., KAMIL, A. C., MERCIER, T., & WOLF, L. L. (1982). Spatial learning as an adaptation in hummingbirds. *Science*, **217**, 655-657.
- HERRMANN, T., BAHR, E., BREMNER, B., & ELLEN, P. (1982). Problem solving in the rat: Stay vs. shift solutions on the three-table task. *Animal Learning & Behavior*, **10**, 39-45.
- KAMIL, A. C., & BALDA, R. P. (1985). Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes*, **11**, 95-111.
- KAMIL, A. C., & BALDA, R. P. (1990a). Differential memory for cache sites in Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes*, **16**, 162-168.
- KAMIL, A. C., & BALDA, R. P. (1990b). Spatial memory in seed-caching corvids. In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 26, pp. 1-25). New York: Academic Press.
- MAKI, W. S., BROKOFKY, S., & BERG, B. (1979). Spatial memory in rats: Resistance to retroactive interference. *Animal Learning & Behavior*, **7**, 25-30.
- OLSON, D. J. (1991). Species differences in spatial memory among Clark's nutcrackers, scrub jays, and pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, **17**, 363-376.
- OLSON, D. J., KAMIL, A. C., & BALDA, R. P. (1993). The effects of response strategy and retention interval on performance of Clark's nutcrackers in a radial maze analog. *Journal of Experimental Psychology: Animal Behavior Processes*, **19**, 128-148.
- OLSON, D. J., & MAKI, W. S. (1983). Characteristics of spatial memory in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, **9**, 266-280.
- ROITBLAT, H. L., THAM, W., & GOLUB, L. (1982). Performance of *Betta splendens* in a radial arm maze. *Animal Learning & Behavior*, **10**, 108-114.
- SANDS, S. F., & WRIGHT, A. A. (1980). Primate memory: Retention of serial list items by a rhesus monkey. *Science*, **209**, 938-939.
- SHETTLEWORTH, S. J., & KREBS, J. R. (1986). Stored and encountered seeds: A comparison of two spatial memory tasks in marsh tits and chickadees. *Journal of Experimental Psychology: Animal Behavior Processes*, **12**, 248-257.
- WUNDERLE, J. M., JR., & MARTINEZ, J. S. (1987). Spatial learning in the nectarivorous bananaquit: Juveniles vs. adults. *Animal Behavior*, **35**, 652-658.