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The spatial memory of Clark's nutcrackers (*Nucifraga columbiana*) in an analogue of the radial arm maze

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Clark's nutcrackers (*Nucifraga columbiana*) use spatial memory to recover stored food in the field. In the present experiments, an open-field analogue of the radial arm maze was developed and used to test the ability of nutcrackers to remember spatial locations. The nutcrackers showed high levels of retention after 6 h, but were close to chance levels after a 24-h retention interval. These results suggest that nutcrackers may use different spatial memory systems under different conditions. After long retention intervals, nutcrackers performed more accurately than pigeons tested by other experimenters using similar procedures. This raises the possibility of species differences in spatial memory, although much more research will be required to resolve this important issue.

The development of the radial arm maze (Olton & Samuelson, 1976) and the experimental demonstration of the use of memory by food-storing birds (Balda, 1980; Sherry, 1982, 1984; Shettleworth & Krebs, 1982; Vander Wall, 1982) have stimulated renewed interest in the study of animal spatial memory. Data collected in each of these paradigms have shown that animals possess greater abilities to remember locations in space than had previously been appreciated. The purpose of the experiments reported here was to test Clark's nutcrackers (*Nucifraga columbiana*), a species with excellent memory for the location of cached food (Balda, 1980; Balda, Kamil, & Grim, 1986; Kamil & Balda, 1985; Vander Wall, 1982), in an analogue of the radial arm maze (Olton & Samuelson, 1976). Studying nutcrackers' memory in this way facilitates understanding of the contributions of species and methodological effects to the results of different experiments on spatial memory.

Every fall, when the pine cones ripen, Clark's nutcrackers spend most of their time harvesting and storing pine seeds. A single nutcracker will store between 22,000 and 33,000 seeds in about 7,500 separate subterranean caches (Tomback, 1977; Vander Wall & Balda, 1977). These stored seeds provide almost all of the diet of the birds and their young through the winter and spring

(Mewaldt, 1956; Tomback, 1980), and are still being recovered in early summer (Vander Wall & Hutchins, 1983). Laboratory evidence clearly shows that spatial memory plays a crucial role in the recovery of these cached pine seeds (Balda, 1980; Kamil & Balda, 1985; Vander Wall, 1982). The memory used to recover cached seeds is remarkable in two respects, capacity and duration. Under controlled laboratory conditions, nutcrackers easily keep track of up to 30 cache sites, the maximum number that can reasonably be studied in our experimental procedures. They routinely perform at high levels of accuracy after retention intervals of 10-15 days. In a pilot study, we observed accurate cache recovery after 6 months.

Such characteristics of memory differ markedly from those exhibited by rats and pigeons in the radial arm maze. Nutcrackers have been required to remember 25-30 cache sites in a room with 180 potential cache locations, whereas rats, in tests using radial arm mazes, which typically have 8 or 17 arms, have had far fewer demands made on their memorial capabilities, and they have exhibited memory durations of only about 8 h (Beatty & Shavalia, 1980). In the case of pigeons, special training is required to obtain accurate performance in a radial maze, and there is significant forgetting within 5 min (Roberts & Van Veldhuizen, 1985). Spetch and Edwards (1986), using an open-field analogue of the radial arm maze, also found that pigeons had significant memory loss within 5 min.

These differences between radial arm maze and cache recovery results could be due to either species differences or methodological effects, or both. One obvious first step toward understanding these differences would be to test

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nutcrackers in a radial arm maze task. This would provide information for the first time on radial maze performance of a species known to possess excellent spatial memory in a natural setting. In Experiment 1, we developed and tested an open-field procedure designed to be directly analogous to the radial arm maze. In Experiment 2, we used this procedure to test the duration of nutcrackers' memory.

EXPERIMENT 1

Method

Subjects. The 3 nutcrackers used in this experiment (Adolph, Hans, and Johann) had been captured as adults and had been held in captivity for 3 years. They had served in several experiments on cache recovery (Balda et al., 1986; Kamil & Balda, 1985). They were maintained in large metal cages on a mixed diet of sunflower and piñon (pine) seeds, cracked corn, mealworms, popcorn, and mice. The birds were deprived of pine seeds for 48 h, and of all food for 18 h, prior to all sessions.

Experimental room. The experiment was conducted in a 3.4 × 3.4 m room with a plywood platform floor raised above the original floor. There were 180 5.5-cm-diam holes drilled in the plywood floor, separated by 23.5 cm center to center. During the present experiment, only eight of these holes, arranged in a circle, were used. The other holes were capped with wooden plugs. Each hole contained a tight-fitting paper cup filled with fine sand. Visual stimuli were provided by rocks and boards located on the floor and posters placed on the walls. A central perch, 1 m high, was located above the circle of holes so that all eight holes could easily be seen from it (see Figure 1). The birds were observed through a one-way window located high on one wall. This wall also contained the port through which the birds entered and left the room.

Pretraining. The birds had been habituated to the room and trained to leave it at a signal (flashing room lights and tapping on the window) during previous experiments. Pretraining sessions were conducted on successive days and lasted no longer than 35 min per bird. A bird was allowed into the experimental room with all eight holes open. Each hole had an exposed pine seed resting on the surface of the sand. The session ended when the bird had located and eaten all of the seeds. Within six trials, all 3 birds were removing the seeds within 10 min. During the next stage, each hole contained a seed buried under the sand by the experimenter. All 3 nutcrackers learned to remove and eat buried seeds within 10 min in only two sessions.

Memory testing. During this phase of the experiment, each trial consisted of two parts, the preretention stage and the postretention stage. When the bird entered the room for the preretention stage, only four of the holes were open, each containing one buried seed. The four open holes were selected randomly for each trial, with the restriction that no more than two of the open holes be adjacent. The birds were allowed to dig up and eat each seed and were then signaled to leave the room. The 5-min retention interval then began. The bird spent this interval in its home cage outside the room. During the retention interval, the experimenter entered the room, cleaned up all signs of earlier digging, and opened the four remaining holes, each of which contained one buried seed.

After the retention interval, the bird was allowed back into the experimental room. All eight holes were now open. Seeds were available only in the four holes not visited during the preretention stage. Visits to these holes were considered correct responses; visits to the holes emptied during the preretention stage were considered errors.

Sessions were conducted 3 days per week, 48 h apart. After 10 sessions, the room was rearranged by placing more rocks and logs

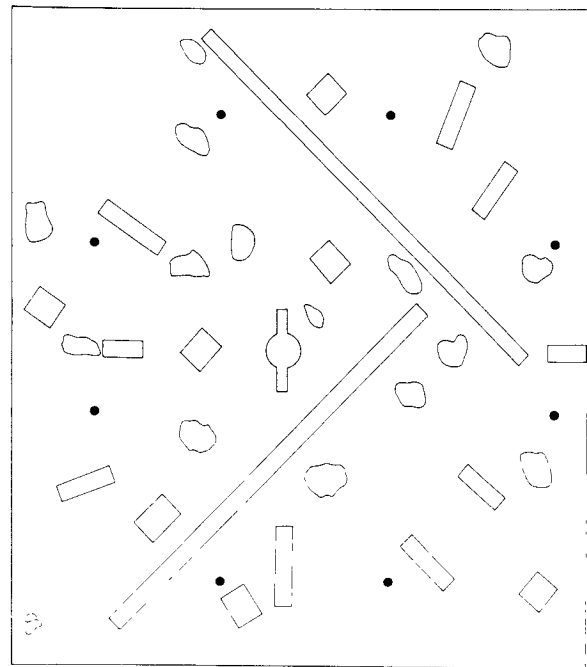


Figure 1. A diagram of the experimental room. The black dots represent the eight holes used in these experiments. The other objects present were a feeder (in the center of the room, not used in these experiments), logs, posts, and rocks.

around the holes, making it more difficult for the birds to move directly from one hole to the next. The final arrangement is shown in Figure 1. The birds received 12 additional sessions with the new room configuration.

Results and Discussion

The birds readily went to the floor and dug in the holes during both the preretention and postretention stages of each trial throughout the experiment. The birds very rarely visited the same hole twice during either stage of a trial. Throughout all of the postretention tests of memory testing there was only one repeat visit to a hole previously probed during the same postretention test. This avoidance of repeat visits to holes visited earlier during the postretention stage may have been based not on memory, but on the avoidance of holes with signs of digging. Therefore, all analyses of the data omitted second visits within a stage, and chance probabilities were calculated based upon sampling without replacement. Given sampling without replacement, a bird choosing at random would require an average of 3.2 errors to find all four seeds during the postretention phase.

The mean number of errors required to find all four seeds during the postretention stage was lower than would be expected by chance throughout the experiment (Table 1). However, performance was mediocre until the room was rearranged after Session 10. During the first 10 sessions, the birds had a strong tendency to move directly from one hole to the next, resulting in frequent choices of adjacent holes. After the room was rearranged,

Table 1
Mean Number of Errors Required by Each Bird to Find All Four Seeds During Experiment 1

Bird	Trials			
	1-5	6-10	11-16	17-22
Adolph	2.4	2.6	1.7	1.3
Hans	3.2	2.8	1.5	1.5
Johann	2.4	3.4	1.5	2.8

this tendency was reduced, because the objects added to the room made it more difficult to move directly from one hole to the next. There was a sudden and substantial decrease in the average number of errors immediately after the change was made. Performance during the last 12 trials was clearly better than would be expected by chance ($p < .05$ in all cases, Kolmogorov-Smirnov tests on the data of each bird). Pooling across birds, all four seeds were found with no error or one error on 50% of the trials. If the birds were choosing randomly, performance this accurate would be expected by chance only 7.1% of the time.

These results indicate that this analogue to radial arm testing has promise. The analogy to retention tests in the radial maze is very close. In memory tests in the radial arm maze, animals are allowed to choose (either forced choice or free choice) some subset of arms of the maze, then a retention interval is imposed, and then the animals are tested with all arms available. Except for the substitution of holes in the floor for maze arms, the procedures are virtually identical. Circumstances beyond our control forced suspension of radial arm maze testing for 10 months, after which Experiment 2 was begun. In Ex-

periment 2, the effects of retention intervals of up to 24 h were tested.

EXPERIMENT 2

Method

Four nutcrackers were tested. Three were the subjects used in Experiment 1. The fourth bird, Newkirk, had been captured as an adult 1 year before Experiment 2 began, had served in one cache recovery experiment, and was pretrained following the procedures used in Experiment 1. The other 3 birds had been in no experiments between Experiments 1 and 2.

The experimental room was set up as at the end of Experiment 1. Each bird was tested at retention intervals of 5, 15, 45, 90, 180, 360, and 1,440 min. Testing at each interval up to 180 min continued until the bird's accuracy was stable over three consecutive sessions. The birds received 6 to 13 sessions at each of these retention intervals. All birds received extended testing (13-18 sessions) at 360 min and 8 sessions at 1,440 min. Beginning with the 45-min retention tests, all 4 birds were given preretention exposure before any bird received the postretention test. During retention testing up to 1,440 min, the birds were tested three times per week, on Mondays, Wednesdays, and Fridays. During the 1,440-min (24-h) testing, each bird was tested twice per week. Preretention stages were given on Mondays and Thursdays; postretention tests on Tuesdays and Fridays. All procedures and conditions not specified for this experiment were as in Experiment 1.

Results

The birds responded readily during both the preretention and postretention stages of each trial throughout the experiment. They very rarely visited the same hole twice during either stage of a trial. During all postretention tests, there were a total of seven (<0.3%) repeat visits to holes previously probed during the same postretention test. As

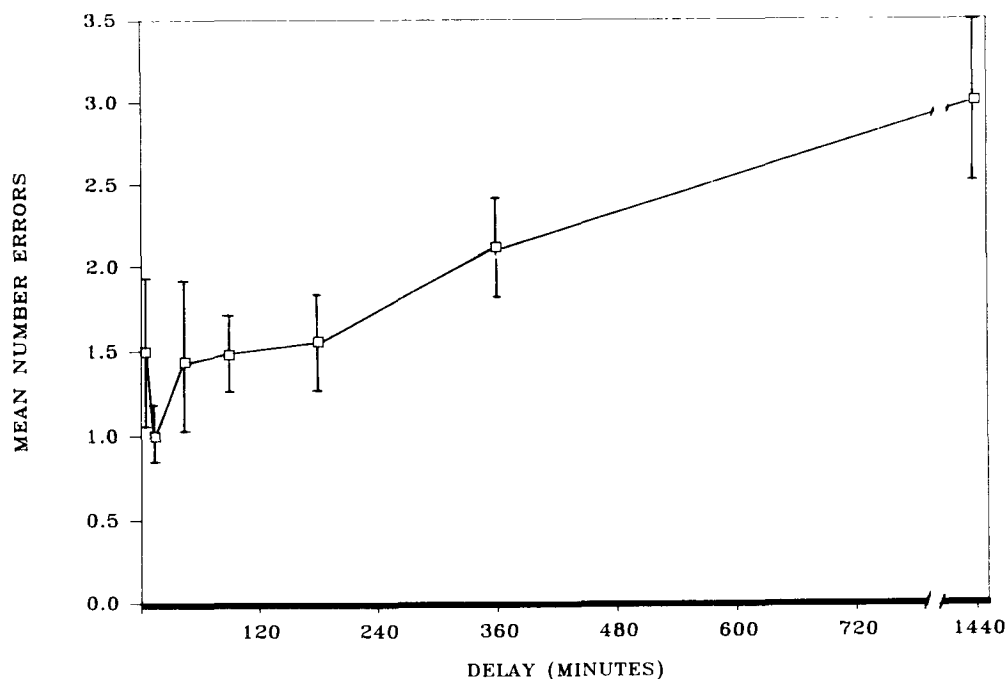


Figure 2. The mean number of total errors ($\pm SE$) to find all four seeds during the last four sessions at each retention interval.

in Experiment 1, analyses of the data omitted second visits within a stage, chance probabilities were calculated based upon sampling without replacement, and 3.2 errors would be expected before finding all four seeds by chance during the postretention stage.

The nutcrackers consistently made less than 3.2 errors before finding all four seeds at delays from 5 to 360 min (Figure 2, Table 2). Except for particularly accurate performance during the 15-min testing, the birds consistently cleared the maze with about 1.5 errors through 180 min. After 24 h, performance was very close to what would be expected by chance. When the chi-square approximation to the Kolmogorov-Smirnov test (Pratt & Gibbons, 1981) was used to pool results across birds, performance was above chance ($p < .05$) after all retention intervals except 24 h. Analysis of variance of these data indicated a significant effect of retention interval [$F(6, 18) = 3.80, p < .01$]. A subsequent Dunnett's test, comparing performance after all intervals with performance after 5 min, revealed that only the 1,440-min test was significantly different from performance at either 5 or 15 min ($p < .05$).

Table 2
Summary of Individual Performance During the Last Four Sessions of Each Stage of Experiment 2

Retention Interval (min)	Mean Total Errors	Mean Errors, First 4 Choices	Number of Sessions
Adolph			
5	1.00	0.50	8
15	0.75	0.50	13
45	1.75	1.00	8
90	2.00	1.50	8
180	1.25	1.00	10
360	1.75	1.00	18
1,440	3.25	1.75	8
Hans			
5	0.50	0.50	8
15	0.75	0.75	13
45	0.00	0.00	8
90	1.25	1.00	8
180	1.25	1.00	10
360	2.00	1.25	17
1,440	3.00	2.00	8
Johann			
5	2.25	1.00	8
15	0.75	0.50	13
45	2.00	0.50	8
90	2.25	0.50	8
180	2.25	1.00	10
360	3.00	1.67	18
1,440	1.75	1.75	8
Newkirk			
5	2.25	1.25	9
15	1.75	1.00	9
45	2.00	1.00	9
90	1.67	1.00	6
180	1.50	1.00	11
360	1.75	1.00	13
1,440	4.00	2.00	8

A similar picture emerges from examination of the accuracy of the first four choices after the retention interval. Chance behavior would result in an average of 2 errors in the first four choices. The nutcrackers consistently made fewer than 2 errors in their first four choices, except during the 1,440-min test (Figure 3). When the performance of all birds was pooled using the chi-square approximation, performance was significantly above chance ($p < .05$) after all retention intervals except 1,440 min. Analysis of variance indicated that there were significant differences in performance after different retention intervals [$F(6, 18) = 6.00, p < .01$]. Subsequent Dunnett's tests indicated that only performance during the 1,440-min test was significantly different from performance at either 5 or 15 min ($p < .05$).

We also examined the relationship between the order in which each available hole was chosen during the preretention phase and the probability of an error's being directed toward that location after the retention interval. Many more errors than would be expected by chance were directed at the hole visited first during the preretention phase [$\chi^2(3) = 42.67, p < .001$]. Overall, 43.8% of errors were directed at the hole chosen first during the preretention phase. This "reverse primacy" effect probably reflects the effects of preferences for particular holes. If the hole chosen first during the preretention phase is a preferred hole, then one might expect it to be more likely to be visited later in the trial, especially if some forgetting has occurred. This hypothesis is supported by an analysis of the order of hole choice during the preretention phase. All of the nutcrackers had strong preferences for one or two holes. When the frequency of first choice of each hole was compared to what would be expected by chance based on how often each hole was made available during preretention phases, all of the nutcrackers showed highly significant preferences [$\chi^2(7) > 100, p < .001$] for each bird. The most preferred holes were Holes 3-6. These holes were located near the port through which the birds entered and left the room, and were also near the observation window and the door through which the experimenters entered the room.

Analysis of the postretention choice patterns of the nutcrackers showed that they tended to choose adjacent holes (± 1) more often than would be expected by chance (adjacent holes were chosen an average of 51.3% of the time, versus 28.6% expected by chance). There was no consistent relationship between retention interval duration and the frequency of choice of adjacent holes. However, it should be noted that during 24-h testing, two of the birds did show frequent runs of choosing adjacent holes. For Adolph, 87.5% of the 24-h sessions contained four or more consecutive choices of adjacent holes; for another bird, Newkirk, this figure was 75%.

Discussion

It is clear that the nutcrackers used spatial memory to perform accurately during postretention interval testing.

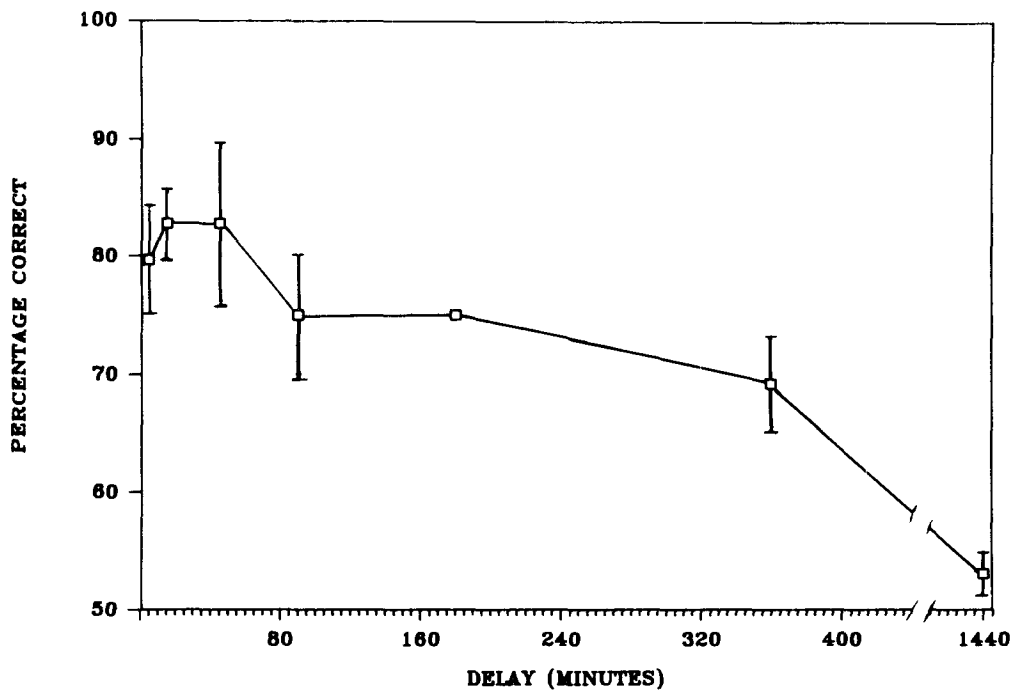


Figure 3. The mean percentage correct ($\pm SE$) during the first four choices during the last four sessions at each retention interval.

Although they showed some tendency to make more choices of adjacent holes than would be expected by chance, this tendency cannot account for accurate performance when forced choice procedures were used. Furthermore, their accurate postretention interval performance could not have been based on physical cues left on the floor. Beginning with the 45-min condition, all 4 birds received preretention testing before any bird received postretention testing. Thus, birds were entering the room for postretention testing after other birds had been tested. Yet performance remained high.

The most important result of this experiment is that the birds remembered visited locations with virtually no forgetting for at least 180 min, but showed very little retention after 24 h. These results stand in marked contrast both to the performance of nutcrackers in cache recovery tests and to the performance of pigeons in analogous procedures.

In comparison with the results of cache recovery experiments, the performance observed in this experiment is unimpressive. For example, high accuracy levels after retention intervals of 10–15 days, with 25–30 cache sites to be remembered, have routinely been observed in nutcrackers (Kamil & Balda, 1985). This difference could reflect methodological differences between the two methods for testing spatial memory. The most important difference is probably that in radial arm tests, the set of locations to be remembered changes on each trial, whereas the same set of sites is remembered throughout a single cache recovery experiment. Proactive interference is more likely to affect performance in radial maze tests. Another difference is that cache recovery tests require the birds

to return to visited locations, whereas radial maze tests require the birds to avoid previously visited sites.

The differences between the results of cache recovery experiments and those of the present radial arm maze experiments could also be the result of the use of different memory systems in the two tasks. In the present experiments, the experimenters created the caches and the birds had to remember the locations from which seeds had been removed. In cache recovery experiments, the bird remembers the locations where it had buried seeds. If some special behavior is used by the birds when creating a cache, behavior that "imprints" the location in memory, this mechanism may not have been elicited by radial arm maze tests.

Another methodological difference between cache recovery and maze-analogue tasks suggests a way to test for possible differences in the memory systems used in the two tasks. In cache recovery experiments, nutcrackers have difficulty avoiding visits to previously emptied cache sites (Balda et al., 1986). But in the present experiment, emptied sites were precisely what the birds avoided. It would be particularly interesting to conduct an experiment identical to the one reported here, but in which the birds were forced to cache in four sites chosen by the experimenters during the preretention stage of each trial. If the results of such an experiment were dramatically different from those of the present experiment, this would support the hypothesis of different memory systems (Sherry & Schacter, 1987). Shettleworth and Krebs (1986) found some differences in the ability of chickadees to remember stored versus encountered seeds. However, these differences probably reflect methodological effects

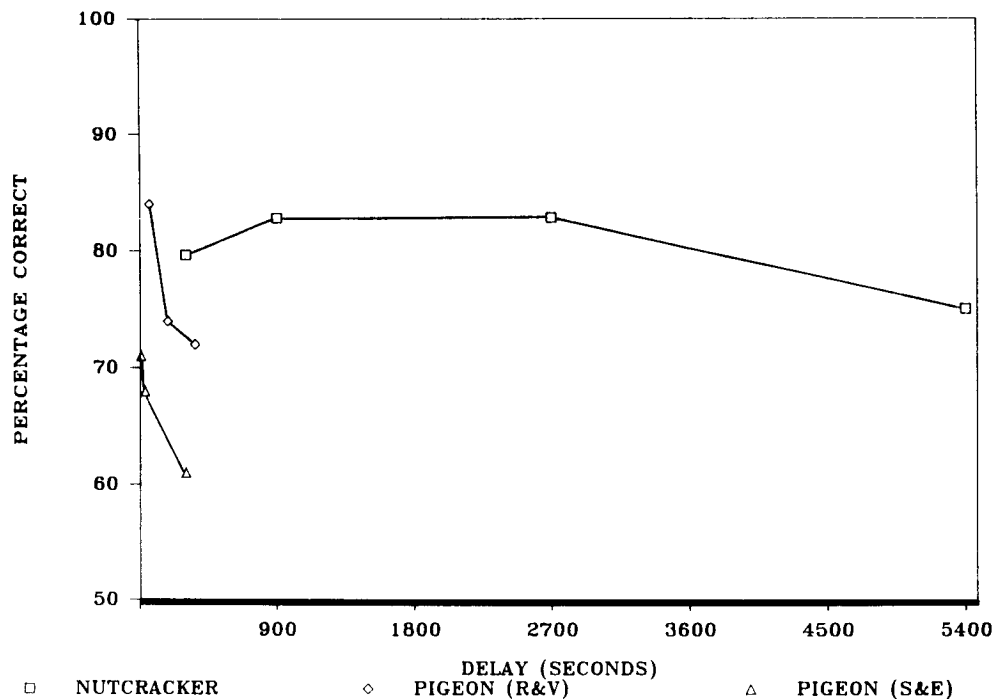


Figure 4. The mean percentage correct during the first four choices during the last four sessions after retention intervals of 300, 900, 2,700, and 5,400 sec. Results from two experiments with pigeons are also shown, the open-field experiment of Spetch and Edwards (1986) and the maze experiment of Roberts and Van Veldhuizen (1985).

rather than any special memorial status for the location of stored seeds.

The nutcrackers forgot preretention locations much more slowly than have pigeons in similar experiments. Both Roberts and Van Veldhuizen (1985) and Spetch and Edwards (1986) found significant retention loss within 5 min. As shown in Figure 4, the slopes of the forgetting curves are very similar for the two pigeon studies, but both of these slopes are very different from that observed in the present study. It is, of course, very difficult to interpret such species differences (e.g., Macphail, 1982, 1985). It is possible that pigeons could perform better at long retention intervals when tested with different procedures.

In spite of these difficulties, it would be a mistake to ignore the possibility of a dramatic difference in spatial memory between nutcrackers and pigeons. Such a difference might represent a phylogenetic difference between corvids and columbids. This idea is supported by the findings of Wilson and Boakes (1985), who found that jackdaws (another corvid) remembered the occurrence of food better than did pigeons when tested with a conditional discrimination in an operant chamber. But any difference between nutcrackers and pigeons may also reflect some adaptive specialization of memory associated with cache recovery. That is, the source of any possible differences between the spatial memory of pigeons and that of nutcrackers may be attributed to either ecological or phylogenetic variables. In view of the substantial logical

and methodological problems that confront comparative research on memory, resolution of these issues will require comparative testing of many species in different settings (Kamil, in press). The results of this experiment demonstrate that radial maze analogues can productively be used to study spatial memory in seed-storing birds.

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