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Alan Kamil
University of Nebraska - Lincoln, akamil1@unl.edu

Russell P. Balda
Northern Arizona University, Russell.Balda@nau.edu

Deborah J. Olson
University of Nebraska - Lincoln

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Performance of Four Seed-Caching Corvid Species in the Radial-Arm Maze Analog

Alan C. Kamil, School of Biological Sciences and Department of Psychology, University of Nebraska–Lincoln

Russell P. Balda, Department of Biological Sciences, Northern Arizona University

Deborah J. Olson, School of Biological Sciences, University of Nebraska–Lincoln

Corresponding author — Alan C. Kamil, School of Biological Sciences, Manter Hall, University of Nebraska–Lincoln, Lincoln, Nebraska 68588-0118; email akamil2@unl.edu

Abstract

Four seed-caching corvid species were tested in an open-room analog of the radial-arm maze. During Experiment 1, the species more dependent on stored food, Clark's nutcrackers *(Nucifraga columbiana)* and pinyon jays *(Gymnorhinus cyanocephalus),* acquired the task more quickly and to higher accuracy levels than either scrub jays *(Aphelocoma coerulescens)* or Mexican jays *(A. ultramarina).* During Experiment 2, performance after retention intervals was tested. When intervals of 30-210 min were tested in ascending order, species differences observed during acquisition were again obtained. However, when intervals of 5-300 min were tested in random order, the species differed only at shorter intervals. During Experiment 3, only nutcrackers gave any indication of performing above chance after a 24-hr retention interval. Results support the hypothesis of species differences in spatial information processing that correlate with dependence on stored food.

Previous research has demonstrated a correlation between dependence on stored food and performance during two different behavioral tests of spatial memory. Clark's nutcrackers (*Nucifraga columbiana*) and pinyon jays (*Gymnorhinus cyanocephalus*) recover their caches more accurately than scrub jays (*Aphelocoma coerulescens*) during controlled laboratory tests (Balda & Kamil, 1989). Nutcrackers also perform better than scrub jays during spatial nonmatching to sample in an operant chamber (Olson, 1991). Other experiments have shown that nutcrackers perform very accurately in an open room analog of the radial maze (Balda & Kamil, 1988; Olson, Kamil, & Balda, 1993). However, no direct comparative study of seed-caching corvids in the radial maze has been reported.

The study of species differences in cognitive abilities presents particular logical and methodological problems. Differences obtained during any single experiment may be due either to cognitive differences between species or to the effects of contextual variables (Bitterman, 1965; Macphail, 1982). Contextual variables lead to the problem that between-species variance in any single experiment may reflect a coincidental effect of some detail of the experimental paradigm. For example, if the stimuli or rewards are more suited to one species than another, a species difference can result in the absence of any actual species difference in learning or cognitive ability. One strategy for circumventing this problem is provided by the synthetic approach, which requires multiple testing of several species under different experimental paradigms (Kamil, 1988). If consistent species differences are found across very different tasks, with different response requirements and discriminative stimuli, then the likelihood that some contextual variable is responsible for the species differences becomes remote. This experiment extends earlier work by testing species differences among four seed-caching corvids in another spatial task, an analog of the radial maze.

The four species were selected for study on the basis of several considerations, namely, performance during previous studies of spatial memory, their natural history, and the phylogenetic relation. Numerous studies have examined the spatial memory of Clark's nutcrackers because of their natural history. In the fall nutcrackers cache tens of thousands of pine seeds in thousands of different, scattered locations. The birds depend on this stored food throughout the winter and spring. Many studies have shown that nutcrackers use spatial memory to recover their stored seeds (see Kamil & Balda, 1990, for review).

In comparison, scrub jays of western North America store less food and are much less dependent on it (Vander Wall & Balda, 1981). In a comparative study, Balda and Kamil (1989) found that scrub jays recovered their cached seeds less accurately than nutcrackers. This suggested that nutcrackers and scrub jays might differ in their spatial memory abilities, but many other interpretations were possible. Subsequently, Olson (1991) found that nutcrackers performed much better than scrub jays in an operant spatial nonmatching-to-sample experiment. This lent further support to the idea that nutcrackers have better spatial memory than scrub jays. However, additional tests with these two species in other paradigms need to be carried out to further test the hypothesis.

Two other species were included in the study. Mexican jays (*Aphelocoma ultramarina*; formerly known as gray-breasted jays) are congeners of scrub jays. Although less is known of their natural history than for the other birds, they do live at somewhat higher elevations than scrub jays and have been observed to cache at high rates in the fall (J. L. Brown, personal communication, September 15, 1993). The inclusion of Mexican jays allowed the collection of data on another *Aphelocoma* species whose natural history differed somewhat from that of the scrub jay.

Pinyon jays were included for two reasons. Although pinyon jays also live at high elevations and are heavily dependent on cached pine seeds, their range is lower than that of nutcrackers, and they are somewhat less dependent on their caches (Ligon, 1978; Vander Wall & Balda, 1981). During a comparative test of cache recovery accuracy (Balda & Kamil, 1989), pinyon jays performed as well as nutcrackers in one condition and better than nutcrackers in another. However, they tended to place their caches close together in tight clusters. This suggested that their recovery accuracy may have been partially aided by area-restricted search. The inclusion of pinyon jays in this study allowed further investigation of their spatial abilities in a context in which area-restricted search could not play a role.

In addition to the differences in natural history, there are also differences in the relative size of the hippocampal formation among these birds (Basil, Kamil, Balda, & Fite, in press). When the ratio of hippocampal volume to telencephalon volume was calculated for each of these four species and compared on the regression line of this ratio for a wide variety of New and Old World corvids (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Sherry, Vaccarino, Buckenham, & Herz, 1989), nutcrackers had the largest relative hippocampal volume.

We carried out three experiments with these species. In the first experiment the performance during acquisition of the radial maze task was investigated. In the second experiment the performance after different retention intervals up to 5 hr was studied. During the third experiment the performance after a 24-hr retention interval was examined.

Experiment 1

Method

Subjects — Twenty-four birds, 6 of each of four species (*Nucifraga columbiana, Gymnorhinus cyanocephalus, Aphelocoma coerulescens,* and *A. ultramarina*), served in this experiment. All of the birds had been captured as adults and had undoubtedly cached and recovered food in the wild. They were all naive to both the experimental room and to radial-maze analog procedures but did vary somewhat in previous experience in the laboratory. The scrub jays had been captured 1–5 years before the experiment began. Three of the scrub jays were naive, and 3 had served in both cache-recovery experiments (Balda & Kamil, 1988) and operant experiments (Olson, 1991). The Mexican jays had been captured 3 years earlier and had served in one cache-recovery experiment. Four of the 6 pinyon jays had been captured 2 years earlier and served in a cache-recovery experiment. The other two pinyon jays had been captured 1 year earlier and were experimentally naive. All 6 nutcrackers had been captured 6 months earlier and were experimentally naive.

All birds were individually housed in large cages and maintained on a 10:14-hr light–dark cycle. They were maintained at 85%–90% of their free-feeding weight throughout the experiment by controlled daily feeding. The standard diet for all species consisted of pinyon pine seeds, mealworms (*Tenebrio* larva), pigeon pellets, sunflower seeds, turkey starter, cracked corn, and a vitamin supplement. The diet fed in the home cage was adjusted to take into account the rewards received during experimental sessions.

Apparatus — The experiment was conducted in a 3.6 m wide × 2.7 m high × 3.2 m long room with a plywood floor that had 12 holes drilled in it. One wall contained a door, a one-way window, and a porthole. The porthole served as the entry and exit to the room for the birds. Spatial cues were provided by posters placed on the remaining three walls and by objects placed on the floor (e.g., rocks, wooden logs, cinder blocks, etc.). Many objects were placed between adjacent holes to discourage direct movement from one hole to the next. The 12 holes, numbered in clockwise order, were 5.1 cm in diameter and were arranged in a circle that was centered in the room. The distance between the center of adjacent holes was 58.4 cm. Each hole could be fitted with either a sand-filled paper cup or a wooden plug. A perch was placed in the room so that it was centered in front of the one-way mirror (distances from center of perch to north, east, south, and west walls were 2.0, 1.6, 1.6, and 1.5 m, respectively). Because the perch was not located in the center of the floor, the distance between the perch and each of the holes was not uniform. However, the perch-to-hole distances, center to center, ranged from 107.9 to 119.9 cm. The room was illuminated by four fluorescent fixtures. In addition, a small spotlight was positioned above the perch and controlled by a separate switch.

Procedures — Experiment 1 was divided into three stages, habituation, pretraining, and acquisition. Throughout the experiment all birds were treated identically except that scrub jays and Mexican jays received meal worms as rewards during test sessions, whereas nutcrackers and pinyon jays received pinyon pine seeds. This difference was introduced because scrub jays and Mexican jays are not as specialized on pine seeds as the other two species, and previous work (Olson, 1991) had shown that mealworms serve as effective rewards for the two *Aphelocoma* species. The pine seed rewards given to the nutcrackers and pinyon jays were removed from the shells to increase the speed with which trials could be conducted. Experimental sessions were conducted 6 days per week.

During the first session of habituation, all holes in the room were capped, and there was no food; the birds were allowed to explore the room for 30 min. Then the light in the room was turned off so that illumination came only through the exit porthole. If the bird did not leave the room on its own, the experimenter entered the room and encouraged the bird to exit through the porthole (such encouragement was generally necessary only for the first few sessions). During the second habituation session, six rewards were placed on the floor of the room in a circle around the feeder. The protocol for the experiment was to allow the birds to remain in the room until they recovered the six rewards or until 15 min had elapsed without any activity. As all birds ate the seeds, pretraining began during the next session.

During the first pretraining session, 8 holes were open on the floor, and one reward was placed on top of the sand in each open hole. During the second pretraining trial, a different set of 8 holes was open, and the reward was buried about half-

way down into the sand. During the third and fourth pretraining sessions, different sets of 8 holes were open, and the reward was completely buried in the sand in each hole. The protocol for pretraining was to allow the birds to remain in the room until they had harvested the eight rewards or 15 min of inactivity had elapsed. However, all birds found and consumed all available rewards without causing the 15-min inactivity criterion to be invoked. These four sessions completed pretraining, and acquisition testing began with the next session.

Throughout the 60 sessions of acquisition, each session consisted of two parts, a preretention stage and a postretention stage, separated by a 5-min retention interval. During the preretention stage each bird was allowed into the room, where 4 open holes each contained a buried reward. These holes were selected randomly with the restriction that there were never 3 or more adjacent holes. This stage continued until the bird had found and eaten all four rewards. Once the last reward had been found, the lights in the room were turned off, and the bird returned to its home cage. The experimenter entered the room, cleaned up all signs of digging, opened 4 randomly selected new holes, and buried a reward in each new hole. After the 5-min retention interval was over, postretention testing began. When the bird reentered the room, there were 8 open holes, the 4 original holes that were now empty and the 4 new holes that each held a reward. The postretention stage continued until one of three criteria was met: The bird recovered the four rewards, probed 6 unique holes, or was inactive for 10 min. The limit on the number of holes visited was imposed to ensure that errors resulted in a reduction in the number of rewards obtained during the session. In those cases when the 10-min inactivity criterion was met, the session was terminated, and a substitute session was conducted later in the week.

Results

All 24 birds completed habituation and pretraining in 6 sessions. During the experiment all of the birds readily entered and left the room, took seeds out of holes during the preretention phase of each trial, and chose among the available holes during the test phase of each trial. The percentage of correct responses during the first four choices of each trial was used to assess choice accuracy. (Repeat visits to the same hole were omitted from the analysis because signs of previous digging provided cues of the previous activity. These visits were very rare in any case). With 8 holes, 4 of them correct, presented on each trial, chance performance with this measure was 50%.

Accuracy throughout the experiment was analyzed by partitioning performance into 12 blocks of five trials each and by subjecting the data to Species × Block mixed analysis of variance (ANOVA). (All data for percentage of correct responses collected during these experiments were also subjected to the logit transformation, but as this made no difference in the results of any analysis, only analyses of the raw data are presented). There were significant species differences, F (3, 20) = 5.21, $p < .01$, a significant improvement in performance across blocks, F (11, 220) = 23.20, $p < .001$, and a significant Species × Block interaction, F (33, 220) = 2.23, $p < .01$. All four species performed at approximately the same accuracy levels during the first block of training but rapidly diverged: Nutcrackers and pinyon jays performed at higher levels than either scrub jays or Mexican jays (Figure 1).

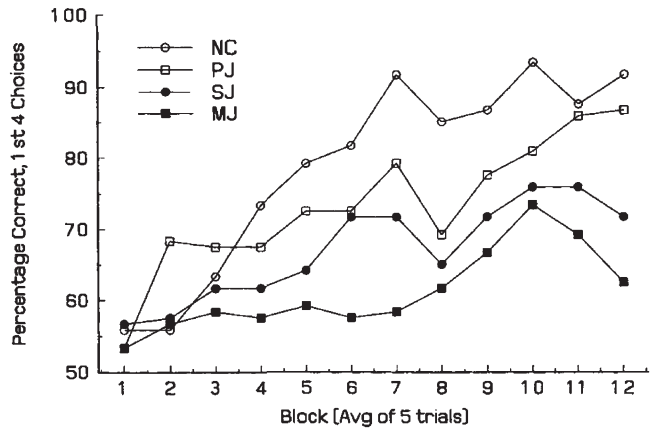

Figure 1. Mean percentage of correct responses during the first four choices of each trial for each species during each block of Experiment 1. (NC = Clark's nutcracker; PJ = pinyon jay; SJ = scrub jay; and MJ = Mexican jay.)

Asymptotic levels of performance were analyzed by examining the percentage of correct responses during the first four choices of each test during the last 3 blocks of the experiment. The results of this analysis showed that there were significant species differences during the last 3 blocks, F (3, 20) = 6.57, $p < .01$, but that neither the effect of block, F (2, 40) < 1, nor the Species × Block interaction, F (6, 40) = 1.60, $p > .15$, were significant. Subsequent Newman-Keuls tests indicated that nutcrackers did not differ significantly from pinyon jays, pinyon jays did not differ significantly from scrub jays, and scrub jays did not differ significantly from Mexican jays, but all other pairwise species differences were significant ($p < .05$).

The speed with which the radial maze task was acquired was analyzed by calculating the number of blocks each bird required to reach a criterion of two consecutive blocks with an accuracy of 80% or better. (Any bird that failed to reach this level was assigned a score of 12.) Analysis of these data (Figure 2) revealed a significant difference between the species, F (3, 20) = 4.72, $p < .02$. Subsequent Newman-Keuls tests revealed that nutcrackers reached criterion significantly faster than either scrub jays or Mexican jays, but no other species differences were significant.

The choice patterns of the four species were analyzed by examining the sequence of the choices of the last 15 sessions of the experiment. The most frequent choice of all four species was the adjacent holes (Figure 3), but the strength of this tendency varied among species, F (3, 20) = 4.25, $p < .05$. A subsequent Newman-Keuls test showed that Mexican jays chose adjacent holes more often than the other species, which did not differ ($p < .05$).

Discussion

There were species differences in both the speed with which the radial maze task was acquired and in the levels of performance achieved at the end of Experiment 1. The results of this experiment were consistent with earlier comparative

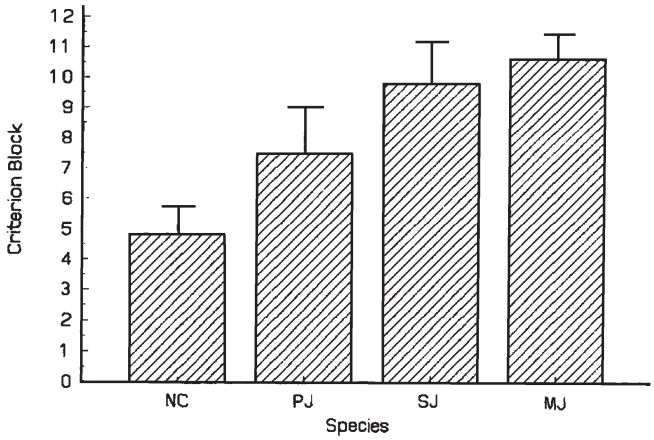

Figure 2. Mean number of blocks each species required to reach criterion during Experiment 1. (NC = Clark's nutcracker; PJ = pinyon jay; SJ = scrub jay; and MJ = Mexican jay.)

research on spatial memory. Pinyon jays and nutcrackers performed better than scrub jays, the same result found during cache recovery (Balda & Kamil, 1988). Also, as found for operant nonmatching to sample (Olson, 1991), nutcrackers performed better than scrub jays.

Pinyon jays performed as well as nutcrackers. Although pinyon jays took slightly longer to reach criterion and performed at somewhat lower levels at asymptote, these differences were rather small. Despite the differences in natural history and hippocampal size between nutcrackers and pinyon jays, there were no differences in performance during acquisition.

The performance of Mexican jays was very similar to that of scrub jays. They performed at slightly lower levels than scrub jays throughout acquisition and showed a greater tendency to choose adjacent holes. This is consistent with both the close phylogenetic relationship between these congeners and with the similar sizes of their hippocampuses. However, it does indicate that the differences in natural history between the *Aphelocoma* species do not result in differences in radial maze acquisition.

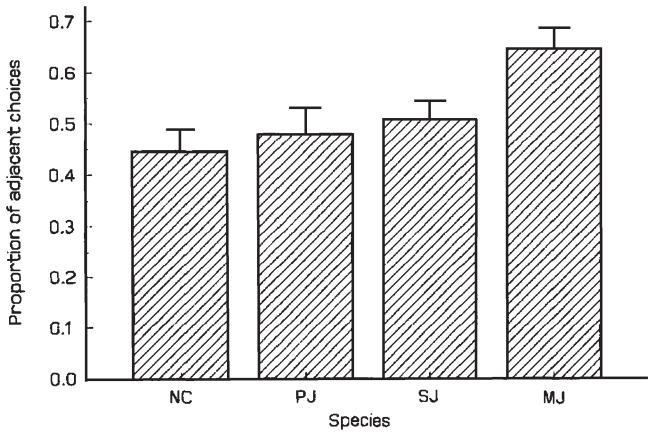

Figure 3. Mean proportion of choices that were directed towards adjacent holes by each species during the last 15 sessions of Experiment 1. (NC = Clark's nutcracker; PJ = pinyon jay; SJ = scrub jay; and MJ = Mexican jay.)

Experiment 2

Previous research with nutcrackers (Balda & Kamil, 1988) found that they perform well after retention intervals of 4–6 hr in the radial maze. However, no data have been reported on the performance of pinyon jays, scrub jays or Mexican jays. The purpose of Experiment 2 was to investigate the performance of all four species after different retention intervals between the end of the preretention stage of the trial and the beginning of the test stage.

Method

Subjects and apparatus — The birds that were trained and tested during Experiment 1 served in Experiment 2, except that two birds were dropped for health reasons. One scrub jay was dropped at the beginning of the experiment. One Mexican jay was dropped at the start of the second phase, the random series retention intervals. The experimental room and radial maze were the same as the one used during Experiment 1.

Procedure — All procedures during Experiment 2 were identical to those used during Experiment 1 except the duration of the retention interval. The experiment was divided into two phases. The first phase was designed to introduce the subjects to extended retention intervals and to obtain preliminary data for each species at several intervals. Therefore, an ascending series of retention intervals was used. During the ascending series, four intervals, 30, 60, 120, and 210 min, were used. Each interval was presented for 10 consecutive sessions.

After the 40 sessions of ascending retention intervals, a random series, during which the retention interval varied randomly from day to day, was begun. Because the data from the ascending series indicated that all of the species performed above chance after the 210-min interval, a longer retention interval was included. The birds received four retention intervals, 5, 60, 180, and 300 min, in a randomized block design so that each set of four sessions included all intervals in random order. This testing was continued for 80 sessions.

Results

The percentage of correct responses during the first four choices of each trial was the basic dependent variable examined throughout retention testing. The birds continued to perform above chance throughout the ascending series of retention testing (Figure 4). These data were analyzed by dividing testing at each retention interval into two blocks (to test for changes in performance with experience at each interval) and carrying out a Species × Retention Interval × Block ANOVA. There were significant species differences, F (3, 19) = 3.80, $p < .05$. Performance declined as the retention interval increased, F (3, 57) = 15.21, $p < .001$. Neither the effect of block, F (1, 19) = 3.30, $p < .10$, nor any of the interactions was significant.

More extensive analyses of the random series testing during the second phase were carried out. First, the entire data set was analyzed by dividing the experiment into 5 blocks of

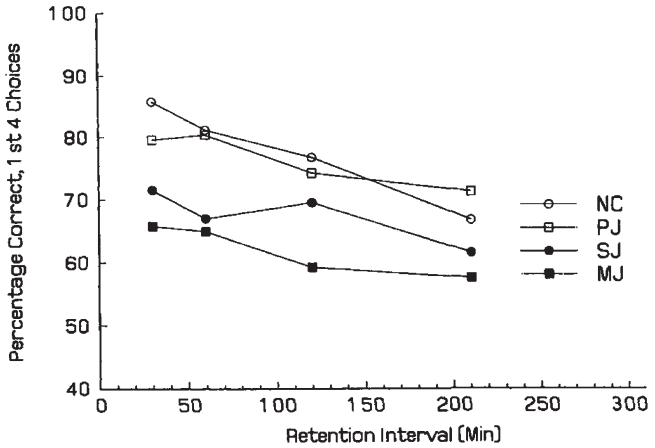

Figure 4. Mean percentage of correct responses during the first four choices of each trial for each species at each retention interval during the ascending test series of Experiment 2. (NC = Clark's nutcracker; PJ = pinyon jay; SJ = scrub jay; and MJ = Mexican jay.)

16 trials (4 at each retention interval) for a Species × Retention Interval × Block ANOVA. This analysis indicated a small but significant improvement in performance across blocks, F (4, 72) = 2.67, $p < .05$, but none of the interactions with block were significant. Therefore, performance during the last two blocks was selected for further analysis of asymptotic performance after the retention intervals. The results indicated a significant species difference, F (3, 18) = 3.55, $p < .05$, a significant decline in performance as the retention interval increased, F (3, 54) = 94.65, $p < .001$, and a significant Species × Retention Interval interaction, F (9, 54) = 3.19, $p < .01$ (Figure 5). To investigate further the nature of this interaction, the data from each retention interval were subjected to separate ANOVAs. The results

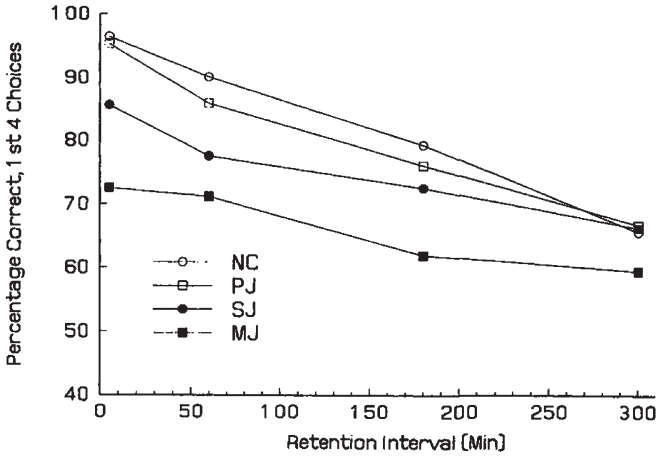

Figure 5. Mean percentage of correct responses during the first four choices of each trial for each species at each retention interval during the random order test series of Experiment 2. (NC = Clark's nutcracker; PJ = pinyon jay; SJ = scrub jay; and MJ = Mexican jay.)

indicated that there were significant species differences after 5 min, F (3, 18) = 8.38, $p < .01$, and after 60 min, F (3, 18) = 3.85, $p < .05$, but not after either 180 min, F (3, 18) = 2.12, $p > .10$, or 300 min, F (3, 18) < 1.

Discussion

As in previous radial-maze analog experiments with nutcrackers (Balda & Kamil, 1988; Olson et al., 1993), performance declined as retention interval increased, but remained well above chance even after 5-hr retention intervals. Balda and Kamil (1988) found nutcrackers performed at 71% correct after 6 hr, and Olson et al. (1993) found performance at 62% after 7 hr. Those results are fairly comparable with the ones observed in the nutcrackers in this study.

There were substantial differences in overall levels of performance between the ascending series and the random series. Because the primary purpose of the ascending series was to introduce longer delays and our major aim during this experiment was to obtain comparative data in a random series, comparisons between the two series are difficult. However, accuracy was clearly higher during the random series. This is especially clear in data from the 60-min retention interval tests common to both series. In addition, the pattern of species differences obtained during the two series of retention tests were different. During the ascending series, there were consistent species differences parallel to those found during acquisition. In contrast, during the random series the species differences were observed only at the shorter retention intervals and disappeared after longer retention intervals.

The reason for the differences between the ascending series and the random order series is not clear. It may be due to the additional experience the birds had received between the beginning of the ascending series and the start of the random series. In order to examine this possibility more closely, behavior during the first block of random series testing was analyzed separately. The results of this analysis showed that even during Block 1, the species were most different at the shortest retention intervals, and the Species × Retention Interval interaction was significant, F (9, 54) = 2.43, $p < .02$. This argues against the additional training interpretation but is not conclusive. Another explanation of the difference between the two series could be the direct result of procedural differences. Perhaps species differences are found when the length of the retention interval is predictable but not when it is unpredictable. Alternatively, if a retention interval longer than 210 min had been included in the ascending series, the results of this series may have also shown no species differences at longer retention intervals.

The most direct interpretation of the data from the random series is that while scrub jays and Mexican jays do not either encode or retrieve spatial information as well as nutcrackers and pinyon jays, they forget this information less rapidly. This is consistent with the larger species differences at shorter retention intervals. It is also consistent with the species differences during acquisition. There are other possibilities. Floor effects can produce the pattern of results obtained. This seems unlikely in this case because all species were well

above chance after the 5-hr interval, and the retention curves are clearly not parallel throughout the range of intervals tested. Other possible explanations include differential performance factors or interference effects. However, these all seem less likely than the direct interpretation, that is, smaller species differences after longer retention intervals under the conditions of the second phase of Experiment 2. These results suggest that during random series tests of retention intervals in the radial maze task, the more seed-dependent species, nutcrackers and pinyon jays, forget spatial location faster, although they initially remember locations better, than the less specialized species.

Experiment 3

Balda and Kamil (1988) found that nutcrackers performed slightly above chance after a 24-hr retention interval. Olson et al. (1993) conducted more extensive 24-hr retention testing and found consistent above chance performance, especially when testing was conducted with a longer intertrial interval. The purpose of Experiment 3 was to test all four species after a 24-hr retention interval.

Method

The subjects that completed Experiment 2 served in Experiment 3, except that 1 scrub jay was dropped for health reasons. During Experiment 3, all procedures were identical to those of Experiment 2 except that a retention interval of 24 hr was used and the intertrial interval was 48 hr. Thus, for example, a bird received the preretention stage on Monday, the postretention stage at the same time on Tuesday, then the next preretention stage on Thursday, and the next postretention stage on Friday. This testing continued for 18 sessions.

Results

In terms of the percentage of correct responses in the first four choices, all four species performed slightly above chance (51%–54% correct; Figure 6). The results were analyzed by dividing the experiment into two 9-trial blocks and conducting a Species × Block ANOVA. Neither of the main effects nor the interaction were statistically significant (*ps* > .40 for all cases). The performance of each species during each half of the experiment was compared to chance with two-tailed *t* tests (Table 1). Only the performance of the nutcrackers during the second half of the experiment was significantly above chance.

An additional analysis examined the percentage of correct responses of all choices (up to six were possible on each trial) with a Species × Block ANOVA. There were no overall effects of species or block (*ps* > .10). However, nutcrackers and pinyon jays improved from the first half of the experiment to the second half, whereas scrub jays and Mexican jays did not, which was shown by a significant Species × Block interaction, $F(3, 17) = 3.40$, $p < .05$.

Discussion

As in previous studies of 24-hr retention by corvids (Balda & Kamil, 1988; Olson et al., 1993) and by parids (Hilton & Krebs, 1990) in the radial maze, above-chance performance was found, but the difference between what was expected by chance and the observed performance was rather small. Balda and Kamil (1988) reported accuracies between 50% and 56% for individual nutcrackers. Olson et al. (1993) conducted two series of 24-hr tests. In the first series, trials were conducted three times per week, and accuracies ranged between 47.4% and 62.9%. In the second series, trials were conducted once per week, and accuracies ranged from 52.8% to 61.1%. Hilton and Krebs (1990) reported mean accuracies of 56.2% and 56.9% for two storing parid species, marsh tits and coal tits, and means of 51.9% and 53.8% for two nonstoring species, great tits and blue tits.

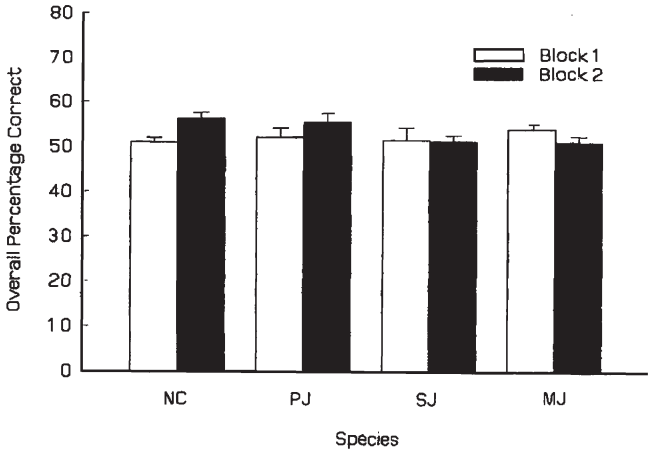

Figure 6. Mean percentage of correct responses of all choices for each species during the first and second blocks of Experiment 3. (NC = Clark's nutcracker; PJ = pinyon jay; SJ = scrub jay; and MJ = Mexican jay.)

Table 1. Mean Percentage of Correct Responses for Each Specieson the First Four Choices of Each Trial After the 24-Hr Retention Interval for Each Half of Experiment 3

Species	Pct of correct responses	Probability for *t* test
Nutcracker		
First half	49.5	.58
Second half	54.2	.04
Pinyon jay		
First half	50.0	1.00
Second half	52.9	.11
Scrub jay		
First half	51.4	.60
Second half	51.4	.39
Mexican jay		
First half	53.3	.24
Second half	49.9	.97

Although the results of Experiment 3 do not indicate that any of these species perform very well after 24 hr, there are interesting hints that nutcrackers and pinyon jays may perform at levels higher than those we observed with sufficient training. The nutcrackers performed above chance during the second half of the experiment, and both pinyon jays and nutcrackers improved in overall accuracy from the first to the second half of the experiment.

General Discussion

There are three major results of these experiments. First, the species most dependent on stored food, Clark's nutcrackers, acquire the radial-maze task more rapidly and to a higher asymptotic level than the less dependent Mexican and scrub jays, although pinyon jays are intermediate between the nutcrackers and the two *Aphelocoma* species. Second, nutcrackers and pinyon jays also perform better than Mexican jays and scrub jays during an ascending test of retention and after short retention intervals in random-order testing. This difference disappears, however, after a 300-min retention interval during random series tests. Third, performance after 24-hr retention intervals was only slightly above chance, although there were indications that the performance of nutcrackers and pinyon jays might improve with further testing.

At one level these results complement the other available comparative data on these species. Nutcrackers and pinyon jays recover cached seeds more accurately than scrub jays (Balda & Kamil, 1989). Nutcrackers perform better than scrub jays during retention testing in an operant spatial task (Olson, 1991). Thus the acquisition and ascending retention test results add additional support to the hypothesis that there are species differences among North American corvids in performance during spatial tasks that are correlated with dependence on cached seeds. Furthermore, these results confirm those of Olson (1991) in demonstrating that these species differences are not limited to tasks that involve the recovery of cached seeds. The selective pressures associated with dependence on the accurate recovery of cached food affected the spatial abilities of these species in a manner general enough to influence performance on a variety of spatial tasks.

At another, more detailed level, however, one aspect of our results is puzzling. The random presentation of retention intervals appears to be the best test of retention in the radial arm maze. Unlike the ascending series, it does not confound amount of training with retention interval. During the random series phase of Experiment 2, the species differences were largest at short retention intervals and disappeared after long retention intervals. This pattern stands in marked contrast to what seems to be the most logical expectation based on natural history. If these species differ in memory ability, then one ought to expect the species differences to be greatest after longer retention intervals.

Hilton and Krebs (1990) claimed to have found this pattern of larger species differences after longer retention intervals in their study of radial-maze performance by seed-storing marsh and coal tits and nonstoring great and blue tits. They carried out two sets of data analyses. First, the performance of each species was compared with chance performance after 24-hr retention intervals. The results were mixed: The food-storing marsh and coal tits and the nonstoring blue tits were all significantly above chance, but the nonstoring great tits were not. Then, the species were grouped according to whether or not they were storers. The storers were significantly above chance after 24 hr, and the nonstorers were not. Finally, a Storer–Nonstorer × Retention Interval ANOVA was carried out. The critical Species × Retention Interval interaction, however, was not significant (reported as $p < .06$, one-tailed). Thus a direct comparison of the performance of nonstorers with that of nonstorers after 24 hr was never carried out, and the one direct ANOVA failed to obtain significant differences. Any conclusion that storing parids forget less rapidly than nonstoring parids is premature.

Nonetheless, it may well be the case that the pattern of significant species differences under long retention intervals will be found in parids, but not in corvids, in the radial maze. Any differences in the patterns of results between Hilton and Krebs's (1990) study and our study may be due to different patterns in parid and corvid families. However, in a study of corvids, Olson (1991) also reported species differences correlated with dependence on stored food that are larger after longer retention intervals. She found that nutcrackers and scrub jays did not differ at short retention intervals but did so when long retention intervals were introduced. This held with two different methods of presenting retention intervals, that is, titration and random order presentations of fixed retention intervals similar to those used in this study. Although both operant and radial maze studies have found species differences among corvids that are correlated with dependence on cached food, there appears to be some kind of complex interaction with task characteristics. This raises some interesting issues.

The spatial nonmatching operant task used by Olson (1991) differs in many ways from the procedures of this experiment. For example, the procedures differ in the nature of the stimuli, in the overt responses required, and in the number of trials per day. Thus, there are many methodological differences that may be responsible for the differing patterns of results.

In the past we have tended to interpret species differences in performance during spatial memory tasks to reflect species differences in spatial memory abilities (Balda & Kamil, 1989; Olson, 1991). However, this may have been too restrictive. In order to respond accurately after a retention interval, an animal must have attended to the relevant stimuli, coded the information presented by those stimuli, retained the coded information, retrieved the information from storage, and utilized the information. Differences in performance, including species differences, may be due to differences at any or all of these stages of information processing. Thus the differences among corvids in spatial information processing may well be multidimensional. This implies that species may differ at many stages of the processing of spatial information.

Different tasks undoubtedly differ in the extent to which they are sensitive to different stages of information processing. For example, one task may be more demanding in terms of coding information, whereas another is more demanding in

terms of retaining information. Such differential task sensitivity, paired with multidimensional differences among species, can lead to the type of complex pattern of comparative results obtained across different experimental paradigms.

For example, suppose that the operant task is particularly demanding in terms of retention of information. Given the massed presentation of trials, this may well be the case. Then, the results obtained by Olson (1991) may reflect species differences in ability to retain the spatial information. This is consistent with her finding of species differences only after the task was made more demanding by increasing either the retention interval or the amount of information to be retained. In contrast, the radial-maze task may put more emphasis on attention to and coding of spatial information. This is consistent with the finding of species differences in acquisition but not in rate of forgetting during random series testing. Then, if the species differ in both coding and retention, but these differences become apparent only under difficult conditions, the results in hand make sense. In the operant task, differences are most apparent when retention intervals are increased. In the radial-maze task they are most apparent during acquisition and after short retention intervals when differences in initial coding are most important.

This must not be regarded as the only possible explanation of the pattern. Rather, it is an example of how taking a broad information-processing perspective can help us understand species differences in cognition. This argument strongly suggests that species differences during many different types of spatial tasks merit investigation. For example, Brodbeck (1994) recently found that seed-caching chickadees and nonseed-caching juncos differ in the extent to which their choice behavior is controlled by spatial stimuli in an ambiguous-cue task. The seed-caching birds were more likely to follow spatial cues than the nonseed-cachers.

Another issue raised by these data concerns the relation between natural history, hippocampal volume, and performance during spatial tasks among seed-caching corvids. When the results obtained from nutcrackers are compared with those obtained from the two *Aphelocoma* species, the pattern that emerges is wholly consistent. Nutcrackers are more dependent on cached food, possess a number of morphological specializations, have a larger hippocampus, and perform better during cache recovery and operant spatial- and radial-maze studies than the *Aphelocoma* species.

However, when the differences in natural history are more modest, as in the comparison between nutcrackers and pinyon jays, the pattern of results is less clear. Nutcrackers appear to be more dependent on stored food than pinyon jays and possess a greater degree of morphological specialization for the harvesting and storage of pine seeds, yet the two species have performed at equivalent levels in studies of cache recovery and of radial maze performance. It may be argued that the species do not differ because the differences in natural history are rather small, as both species are heavily dependent on the recovery of stored food during the winter. The problem is that there is no objective, external gauge by which to judge how much of a difference is sufficient to produce differences during behavioral tests. This problem is compounded by the likelihood that different behavioral tests differ in their sensitivity to species differences.

Although the tests of spatial information processing conducted to date have failed to find any differences between nutcrackers and pinyon jays, volumetric measures of the hippocampal formation have found differences. A comparative analysis of hippocampal volume (Basil et al., in press) indicates that pinyon jays have a smaller hippocampus than nutcrackers. This may reflect an inadequacy of volume as a measure of the functioning of the hippocampal formation during spatial tasks. Alternatively, it may be an indication that other spatial tasks, which make different demands of the subjects, such as operant spatial nonmatching, will reveal differences between pinyon jays and nutcrackers.

These complications arise because the relations between natural history, hippocampal formation, and performance during spatial tasks among seed-caching corvids are complex. Further studies of the natural history, behavioral capabilities, and neuroanatomy of these species are needed. It will be especially useful to learn more about the natural history of dependence on cached food in these species and to test more varied aspects of spatial information processing in different tasks. Overall, however, the results of our experiment, especially when considered in conjuction with the results of comparative operant tests (Olson, 1991), offer considerable support for the hypothesis that the use of memory to recover stored seeds has favored some kind of general spatial memory ability among seed-caching corvids.

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