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# Performance of Four Seed-Caching Corvid Species in Operant Tests of Nonspatial and Spatial Memory

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## Abstract

The performance of 4 seed-caching corvid species was tested using 2 different operant nonmatching tasks. These species differ in their dependence on stored food, and differences in spatial memory tests have been correlated with better performance by the more cache-dependent species. Acquisition and retention of a color non-matching-to-sample task was tested in Experiment 1. Acquisition of the color task was not correlated with cache dependence, and no differences between species in performance during memory testing were found. Acquisition and retention of an operant spatial non-matching-to-sample task was tested in Experiment 2. Species differences in the spatial task were found for acquisition and during retention testing. The influence of natural history on the evolution of memory is discussed.

In recent years, comparative studies of spatial memory have focused on species that vary in the extent to which they depend on stored food. This approach has been used most extensively with two families of birds within which species vary in the extent of this dependence—parids and corvids. Within the parids, some species cache, whereas others do not, and experiments with parids have tested the hypothesis of better performance on spatial memory tasks for caching species than noncaching species. Results have largely been mixed, generally showing only small differences in performance (Healy & Krebs, 1992; Hilton & Krebs, 1990; Krebs, Healy, & Shettleworth, 1990). Brodbeck (1994) and Clayton and Krebs (1994) have trained birds by using simultaneous presentation of spatial and nonspatial cues and then tested with these cues dissociated. Storing parids (Brodbeck, 1994; Clayton & Krebs, 1993) and storing corvids (Clayton & Krebs, 1993) used spatial cues first and then nonspatial cues. The nonstoring species did not show any preference for cue type and used both types of information equally (Brodbeck, 1994; Clayton & Krebs, 1993).

In contrast with parids, most corvid species cache, but they vary in the extent of their dependence on cached food. Comparative experiments have focused on differences in spatial memory that might correlate with the degree of dependence among four species, nutcrackers (*Nucifraga columbiana*), pinyon jays (*Gymnorhinus cyanocephalus*), scrub jays (*Aphelocoma coerulescens*), and Mexican jays (*A. ultramarina*). Perhaps it is surprising that despite the fact that all species cache, large differences have been found in performance during several spa-

tial tasks. One purpose of the present experiment was to test these corvid species for differences in performance during a nonspatial task.

The variation among these four species in dependence on cached food is associated with differences in their habitats and natural history. Clark's nutcrackers live at high elevations and are dependent during the winter on pine seeds (*Pinus spp*) cached during late summer and early fall (Vander Wall & Balda, 1981). These cached pine seeds are the major component of their diet during the winter and into spring, including much of the breeding season. Pinyon jays live at slightly lower elevations but are also dependent on cached pine seeds during the winter and spring (Vander Wall & Balda, 1981). Scrub jays of western North America, in contrast, live at lower elevations than nutcrackers or pinyon jays. Although they do cache food, this cached food is a relatively minor part of their diet (Vander Wall & Balda, 1981). Less is known about the food-storing behavior of the Mexican jay, but they do cache food and live at somewhat higher elevations than do scrub jays (J. Brown, personal communication, September 15, 1993).

These differences in natural history also correlate with species differences in morphological adaptations associated with the harvest and storage of food. For example, nutcrackers possess a sublingual pouch in which they can transport as many as 90 pine seeds, whereas pinyon jays have an expandable esophagus in which they can carry up to 35 or 40 pine seeds (Vander Wall & Balda, 1981). Neither scrub jays nor Mexican jays can carry more than a few pine seeds at a time.

These differences in natural history, morphology, and dependence on cached food have led us to predict that the more cache-dependent species—nutcrackers and pinyon jays—would perform better on spatial memory tasks than the less cache-dependent species—scrub jays and Mexican jays. Most of our data support this hypothesis. Balda and Kamil (1989) used a cache-recovery paradigm to compare the retrieval accuracy of nutcrackers, pinyon jays, and scrub jays. They found that scrub jays were less accurate during cache recovery than either nutcrackers or pinyon jays. Olson (1991) found that nutcrackers remembered spatial locations longer than did scrub jays in an operant spatial non-matching-to-sample task. Kamil et al. (1994) compared the performance of the four species in a radial maze analog. Acquisition of the radial task was quicker and asymptotic performance was higher for nutcrackers and pinyon jays than for scrub jays and Mexican jays. When retention intervals were varied, performance of nutcrackers and pinyon jays continued to be better than performance of the other two species for retention intervals of less than 3 hr, although these species differences disappeared after longer delays between 3 hr and 24 hr.

These results clearly support the hypothesis of species differences in spatial memory correlated with species differences in dependence on cached food. Furthermore, these differences are not limited to tasks involving cache recovery, implying that a specific selective pressure—ability to accurately retrieve cached food—produced general species differences in cognitive abilities. However, one major issue that remains to be addressed is whether these differences are limited to the spatial sphere or are more general. This is an important issue. Suppose that the pattern of species differences we have obtained in previous experiments with spatial tasks are also obtained with nonspatial tasks. This might imply that the differences we have found are not particularly related to cache recovery. For example, one could argue that nutcrackers and pinyon jays perform better during experiments simply because they adapt to the laboratory better than do scrub jays or Mexican jays.

In the first experiment we address this issue using an operant color non-matching-to-sample task designed to be as similar as possible to the spatial task used by Olson (1991). The species used for these experiments were nutcrackers, pinyon jays, Mexican jays, and western scrub jays. If the effects of evolution on memory processing have not been limited to spatial memory, then the same pattern of species differences observed in our previous work should be found. However, results indicating either no species differences or a different pattern of species differences during this nonspatial task would indicate that the selective pressures associated with relocating a position in space have affected spatial information processing differently than nonspatial information processing. Experiment 2 was carried out to determine whether differences in spatial memory would be obtained using the same birds from the first experiment. The spatial experiment allowed us to compare performance of the same birds in a spatial and nonspatial task, increased the number of corvid species tested in an operant spatial task, and provided acquisition data for the spatial task that was not available to Olson (1991).

## Experiment 1

### Method

#### Subjects

Four nutcrackers, 4 pinyon jays, 3 Mexican jays, and 4 scrub jays served as subjects. All birds were captured as adults with the exception of 2 hand-reared scrub jays. The birds were maintained at between 85% and 95% of their free-feeding weights with controlled daily feedings after completing experimental sessions. They were maintained on a diet of turkey starter, sunflower seeds, parrot pellets, mealworms (*Tenebrio* larvae), and pine seeds (*Pinus* species). Water was always available in the home cage. Reinforcers for the experimental sessions were pieces of the preferred items in the diet (pine seeds for nutcrackers and pinyon jays, mealworms for scrub jays and Mexican jays). Preference was determined by observing the order items were taken by birds when fed the daily diet. All species were maintained on a 14:10 light-dark cycle.

The birds varied in the amount of time they had been in captivity and in their previous experimental histories, but none of the birds had been tested with operant procedures. The nutcrackers had been maintained in captivity for 4 to 7 years. One nutcracker had participated in sun compass orientation experiments, and all birds had participated in cache recovery experiments and radial maze experiments. The pinyon jays had been maintained in captivity for 1 to 6 years; 2 of them were experimentally naive, and 2 had participated in a radial maze experiment. The Mexican jays had been maintained in captivity for 2 years and were experimentally naive. The scrub jays had been maintained in captivity for 1 to 5 years; 2 of them were experimentally naive, 1 had participated in a cache recovery experiment and a radial maze experiment, and 1 had participated only in a radial maze experiment.

Each bird was housed individually in the colony room. Cages were arranged so that some-species birds were always within visual contact. Different-sized parrot cages served as the home cage. Nutcrackers and Mexican jays (weights = 117–160g) were maintained in large cages, pinyon jays (weights = 91–103 g) in medium cages, and scrub jays (weights = 72–95 g) in small cages.

#### Apparatus

Four operant chambers were used. One chamber was used only for key-peck training. The front panel contained a row of four pecking keys. The rear panel contained a single pecking key and a food cup for presenting food (see Olson, 1991, for more detail).

The other three operant chambers were used for experimental sessions and were constructed to be as similar as possible. The chamber walls were constructed from sheet metal and were 50.3 cm × 35.5 cm × 45.2 cm (L × W × H). Each chamber was covered by a hardware cloth lid that could easily be removed.

A speaker for white noise presentation was mounted on one long wall. The remaining long wall contained a door with a peephole placed in the middle of the wall.

The short walls served as the front and rear panels. The front panel contained a touch frame (Carroll Touch Model 8001-4117-01). The frame was mounted on the inside of the

chamber, centered on the panel with the bottom of the frame 11.5 cm from the apparatus floor. The touch frame was fitted with a 0.625 cm piece of Plexiglas mounted on springs so that the Plexiglas moved slightly when pecked. A houselight was mounted above the touch frame. Perches for the front panel were located 6 cm above the floor. One perch was 5 cm from the bottom of the frame for scrub jays. The other perch was 8 cm from the bottom of the frame for the other three species. An infrared beam was located parallel to the perch to monitor when the bird arrived at the perch.

The rear panel contained a 2.5 cm diameter pecking key 16.5 cm above the floor and 3 cm from the wall with the door, a centrally located feeder 3 cm above the floor, and a feeder light located at the same position as the houselight on the front panel. Additional perches were added for pinyon jays and scrub jays to allow them to reach the rear key.

A monitor was located against the outside of each chamber and positioned so that the display area was within the boundaries of the Plexiglas area of the touch frame. Two chambers were equipped with NEC MultiSync II monitors. Two Epson Equity I+ computers with EGA cards for the color monitor were connected to two chambers. The third chamber was equipped with a NEC Multisync monitor and an Epson Equity III computer containing a Targa 16 videographics board. Stimulus events for the sessions were programmed to appear on the MultiSync monitors. Each computer was equipped with a monochrome monitor used to monitor session events.

#### *Procedure*

*Habituation and magazine training* – Habituation and magazine training, see below, were conducted in either the key box or touch frame boxes. The same box was used for habituation and magazine training for an individual bird.

Habituation sessions consisted of placing the appropriate reinforcer for the species—8 pine seeds or 10 mealworms—in the illuminated food cup. Sessions ended either after the bird ate all reinforcers or 1 hr had elapsed. Habituation sessions continued until the bird ate all reinforcers within 10 min.

Magazine training sessions consisted of 36 trials with the appropriate reinforcer presented on a variable-time 75 s schedule. This stage ended when the bird ate the reinforcers when presented.

*Keypeck shaping* – All birds were trained to keypeck in the key box after completing magazine training. Hand shaping was done using the method of successive approximation using a single front key illuminated with a blue keylight. Sessions lasted for 36 reinforcers or 1 hr and were continued until the bird was pecking on its own for the entire session. All subsequent sessions ended after 36 reinforcements had been presented. The number of responses (fixed ratio, FR) and intertrial interval (ITI) were increased over sessions to a final FR 5 and ITI 30 s. The final stage in this box introduced the rear key. Each trial began with the illumination of the rear key. One peck to the rear key darkened that key and illuminated the front key. The trial then proceeded as in the previous stage.

*Touch-monitor training* – When first introduced to the touch frame chambers, all birds required some hand shaping at FR 1 without the ITI. Once the bird was pecking, the FR and ITI were increased and the rear key was introduced, using the same stages as the previous phase.

*Acquisition* – Following completion of touch-monitor training, the birds were assigned to one of the three experimental chambers. Four birds were assigned to two chambers, and 7 birds were assigned to the third (TARGA) chamber. (At least 1 bird of each species was tested in each chamber). A trial began when the yellow light illuminated the rear key. One peck to this key extinguished the light, and the bird was required to move to the touch frame panel. The sample presentation was initiated when the bird broke the infrared beam along the front perch. The sample was a 2 cm circle, red or green, outlined in white. This was presented against a black background on the monitor and was displayed in the center of the touch frame-monitor. The height at which the stimuli were presented on the monitor varied for each species so the stimuli were presented at approximately eye level. The heights (measured from the bottom of the monitor screen) were 4.5 cm for scrub jays, 6 cm for pinyon jays, and 8.5 cm for nutcrackers and Mexican jays. The first peck directed at the sample after 4 s cleared (blackened) the monitor screen and the yellow rear key was illuminated. One peck to the rear key extinguished the light, and the two choice stimuli were simultaneously presented on the monitor. A red and green circle each outlined by white were presented simultaneously against a black background and were separated by 10 cm (edge to edge). Two pecks directed to either circle cleared the display to black. The trial was correct if the bird pecked the nonsample color and incorrect if the sample color was pecked. Correct choices were followed by the delivery of a reinforcer. A 15-s ITI began after reinforcement on correct trials and immediately following the choice on incorrect trials. If the bird failed to peck at the sample before 16 s had elapsed, the trial ended and was recorded as an incomplete trial. After an incomplete trial, the monitor display was cleared, and the ITI began immediately. An additional 30 s was added to the ITI following incomplete trials. Each session ended after 36 reinforcements, 72 trials, or 50 min. In the case of the time constraint, the session did not end until the trial in progress had been completed.

Three birds failed to learn the task using the 4-s sample duration. The sample duration was increased to 8 s for these birds after at least 147 sessions had been completed. The increased exposure was done to facilitate learning. A correction procedure was also used for birds that were choosing one side during the choice test for at least 25 sessions. The correction procedure was in effect for 11 sessions. During the choice test, if the incorrect choice was chosen, the choice stimuli were cleared and then displayed again. This retest procedure continued until the bird chose the correct stimulus.

Acquisition ended when either a performance criterion or a date criterion was met. The performance criterion was based on an average of 85% correct for the last four sessions (omitting incomplete trials). The second criterion was made necessary by the move of the laboratory from the University of Massachusetts to the University of Nebraska-Lincoln. Any bird that had not met the performance criterion by November 22, 1991, was stopped on this date. Regardless of which criteria was used, all birds were put back on free feed after completing this stage.

The stimulus sequences for each session were arranged independently for each experimental chamber, but the same sequence constraints were used for all chambers. Sequences were randomized in blocks of four trials so each color would ap-

pear equally often as the sample and equally often on the right or left side during the choice test in each block of four trials. In addition, the same color could not appear as the sample color on more than three consecutive trials. The test stimuli were arranged so that within the block of four trials the correct location for each color sample appeared once on the left and once on the right. Eighteen blocks were constructed at the start of the day.

*Reacquisition* – Following the move to Nebraska, the birds were maintained for several weeks on a free-feeding schedule, and then their weights were reduced to 85% of their free-feeding weights and the experiment was restarted. Two operant chambers were used. The 7 birds that had been assigned to the TARGA chamber were reassigned to the two chambers.

The trial procedure was the same as in Experiment 1, and the 8-s minimum stimulus time for the sample presentation was used throughout the experiment. The end-of-session criterion was changed to 32 reinforcements, 64 trials, or 45 min to be able to test all 15 birds daily in the two chambers.

Each bird received a minimum of 20 reacquisition sessions. A less strict performance criterion was adopted for reacquisition, at or above 70% for 9 out of 10 consecutive sessions. One scrub jay failed to meet this criterion, and reacquisition ended for this bird when it had completed 50 sessions.

*Titration* – Titration testing began immediately after reacquisition. A retention interval was introduced between the end of the sample presentation and the choice test. The retention interval was imposed while the rear key was illuminated, and the end of the interval was not signaled for the bird. The rear key remained lit until the first peck after the retention interval had timed out. The choice test stimuli continued to be presented as soon as the terminal peck had been completed. Titration ended when the bird had completed at least 3,000 trials that ended with the choice test.

A within-session titration procedure was used to adjust the retention interval between trials. The titration values were chosen so the retention interval would increase as long as performance between trials remained above 66% correct. If the choice had been correct on Trial  $N - 1$ , the interval was incremented by 0.1 s for Trial  $N$ . If the choice had been incorrect on Trial  $N - 1$ , the interval was decremented by 0.2 s for Trial  $N$ . If Trial  $N - 1$  was incomplete, there was no effect on the retention interval for Trial  $N$ .

The retention interval for the first trial of a session was the same as the retention interval for the last trial of the preceding session. If the first trial retention interval was less than 10 s, the retention interval was not allowed to change by more than  $\pm 1$  s. If the first trial retention interval was greater than or

equal to 10 s, the retention interval was not allowed to change by more than  $\pm 2$  s.

*Data analyses* – Unless otherwise mentioned, only the trials that ended in completion of the choice test were used in the analyses. Analyses for percentage data were also repeated using arcsine transformations. There were no differences between the analyses for either measure, so the percentage data are reported for all experiments. One-way between-group analyses of variance (ANOVAs) and two-way mixed (Species  $\times$  Trial Block) ANOVAs were used as appropriate. Subsequent contrasts were only carried out following significant  $F$  ratios, with an alpha level of .05.

## Results

Species differences were obtained during acquisition of the color non-matching-to-sample task, but few species differences were obtained during reacquisition or titration. Pinyon jays and Mexican jays acquired the task faster than did scrub jays.

The number of sessions for each species during habituation, magazine training and the various shaping stages are shown in Table 1.

*Acquisition* – All but 3 birds—2 scrub jays and 1 nutcracker—met the 85% correct acquisition performance criterion before the cutoff date. To analyze speed of acquisition, the number of trials required to meet the 85% criterion were calculated for each bird. (The 3 birds not meeting criterion were assigned the number of trials actually completed.) There was a significant difference between species in the number of trials to criterion,  $F(3, 11) = 4.64$ ,  $p < .05$  (Figure 1). Scrub jays showed slower acquisition when compared with pinyon jays and Mexican jays.

Asymptotic performance was analyzed by examining performance during the last four sessions each bird, including those that did not meet the performance criterion, received during acquisition. There were no differences between the species in either percentage correct,  $F(3, 11) = 1.47$ ,  $p > .10$ , or in the probability of failing to complete a trial ( $F < 1$ , range = 0.6–3.0%).

Five variables were examined that measured speed of responding. These were start time (latency to peck the illuminated rear key after the ITI); move time (time taken to go from the rear of the apparatus and break the infrared beam for sample presentation); sample duration (time sample illuminated); retention interval (time rear key was illuminated between end of sample and presentation of choice stimuli); and choice time (latency to make 2 pecks at one of the choice stimuli). The data from the last four sessions for each bird were used to compare

**Table 1.** Mean Number of Sessions Spent in Each Stage During Training in Experiment 1

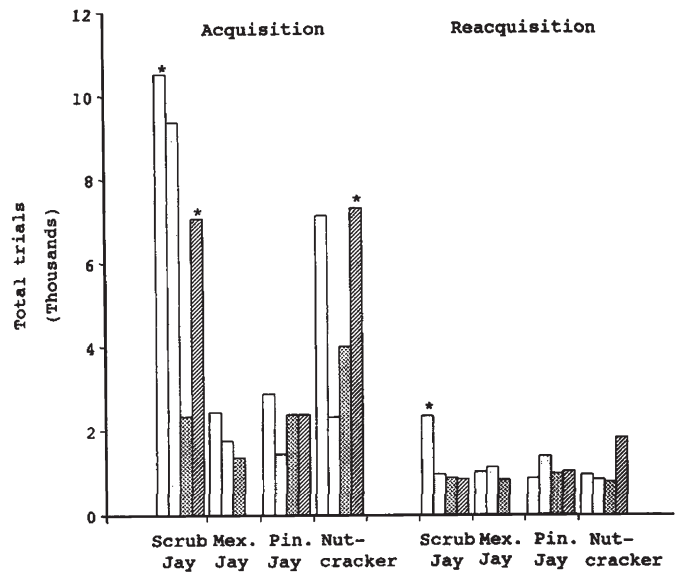
Stage	Scrub jays		Mexican jays		Pinyon jays		Nutcrackers	
	<i>M</i>	Range	<i>M</i>	Range	<i>M</i>	Range	<i>M</i>	Range
Habituation	6.0	1-19	6.0	3-9	4.0	2-9	3.2	1-6
Magazine training	3.5	2-7	9.0	2-19	1.8	2-3	2.2	1-3
Key shaping								
Hand	8.2	2-19	9.7	8-11	16.5	5-25	8.0	5-11
On own	5.0	4-6	6.7	3-12	6.5	4-12	6.8	3-15
Touch screen								
Hand	7.8	3-19	11.3	4-15	5.5	3-12	5.8	4-10
On own	3.2	5-25	13.7	10-18	16.8	8-41	5.3	9-21

performance between the species for these times, and one-way ANOVAs were carried out (Table 2). Move time was longer for pinyon jays than for the other three species by about 1 s,  $F(3, 11) = 7.95, p < .01$ , and choice time was shorter for nutcrackers,  $F(3, 11) = 4.56, p < .05$ .

**Reacquisition** – At the beginning of reacquisition, 8 of 15 birds were responding quite accurately during the first reacquisition session (Figure 2). There were no significant differences among the species in the number of reacquisition trials (analysis included the number of trials completed by the bird that failed to meet the behavioral criterion,  $F < 1$ , Figure 1). The percentage correct and percentage incomplete trials were averaged for the last 10 sessions, and two separate ANOVAs were performed. There were no differences between the performances of the species for either of these variables (percentage correct,  $F(3, 11) = 1.64, p > .1$ , percentage incomplete trials  $F < 1$ ).

The speed-of-responding variables were subjected to separate Species  $\times$  Session ANOVAs (Table 3). There were no significant species differences or Species  $\times$  Session interactions. Although there was some variation in start time,  $F(9, 99) = 2.03, p < .05$ , and choice time,  $F(9, 99) = 5.54, p < .01$ , across sessions there was no consistent trend over the course of reacquisition. Start time and choice time appeared to have stabilized by the final three sessions.

**Titration** – To analyze performance during titration testing, the data for each bird were divided into 30 blocks with 100 trials per block. (Two birds did not complete 3,000 trials. These birds were both Mexican jays, and they completed 2,900 and 2,100 trials. For these birds, the averages obtained for the last completed block were assigned to the remaining blocks.) Unless otherwise mentioned, the retention intervals subjected to analyses are for the programmed retention interval (which is slightly lower than the actual experienced retention interval because of the terminal peck requirement).



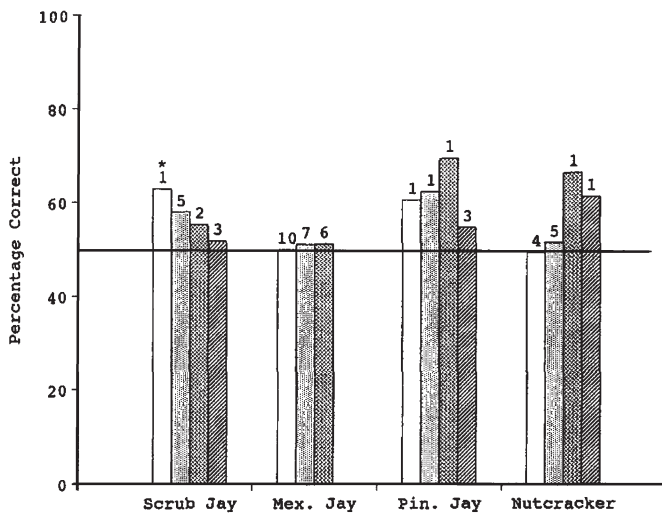
**Figure 1.** Number of trials completed through the criterion stage during color non-matching-to-sample acquisition and reacquisition for individual birds for each species. The asterisk indicates birds that did not meet the behavioral criterion.

The average retention interval by block is shown for each species in Figure 3. The retention interval programmed during any given trial is a direct function of the results of previous trials, so that blocks are not independent. Therefore, separate ANOVAs for each block were performed to determine whether there were any species differences within blocks. There were significant species differences for Blocks 1 through 7. Pinyon jays and Mexican jays had longer retention intervals. Scrub jays had shorter retention intervals than did either Mex-

**Table 2.** Mean Latencies for Within-Trial Events During the Last Four Sessions During Color Acquisition and Reacquisition for Each Species in Experiment 1

Variable	Scrub jays		Mexican jays		Pinyon jays		Nutcrackers	
	M	SE	M	SE	M	SE	M	SE
<b>Acquisition</b>								
Start time	87.1 <sup>a</sup>	82.46	8.4	4.07	9.4	2.88	14.4	6.05
Move time	1.2	0.01	1.1	0.01	2.4	0.29	1.0	0.01
Sample time	6.8	0.63	5.0	0.01	5.0	0.18	5.7	0.43
Retention interval	2.3	0.33	2.6	0.29	2.1	0.10	2.2	0.32
Choice time	2.7	0.28	3.5	0.22	3.5	0.19	1.7	0.11
Average number of session trials	42.5	—	40.6	—	39.3	—	43.1	—
<b>Reacquisition</b>								
Start time	5.5	0.61	5.6	0.84	15.6	2.40	10.4	1.68
Move time	1.5	0.01	1.3	0.22	2.3	0.17	1.3	0.15
Sample time	9.1	0.01	9.0	0.01	9.3	0.10	8.8	0.00
Retention interval	3.1	0.74	2.2	0.10	4.1	0.94	3.0	0.31
Choice time	2.8	0.13	2.8	0.01	3.0	0.15	1.7	0.01
Average number of session trials	41.0	—	38.1	—	33.9	—	39.2	—

<sup>a</sup> This long start time was due to one session for 1 scrub jay with few trials and very long start times. The average start time excluding this session was 4.7 s.



**Figure 2.** Performance during the first reacquisition session of color non-matching-to-sample reacquisition for individual birds for each species. Number above the bar represents the first reacquisition session in which the percentage correct was at or above 60% and the line at 50% represents chance performance. The asterisk indicates the bird that did not meet the behavioral criterion for reacquisition.

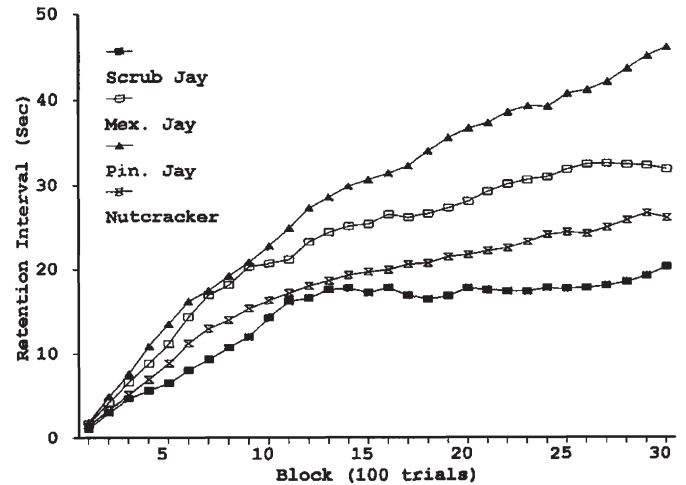
ican jays or pinyon jays throughout these blocks. Comparison of the retention intervals between nutcrackers and pinyon jays found differences between Blocks 2 through 6, and there were no differences between the retention intervals for nutcrackers and Mexican jays. After the first 700 trials, no species differences in retention interval were found.

The highest retention interval obtained, the block the interval occurred in, and the final retention interval were subjected to separate ANOVAs. There were no differences between the species for any of these measures (all  $p$ 's > .10). All species obtained the highest retention interval prior to the last block (range = 23–29).

Four speed-of-responding variables (start time, move time, sample duration, and choice time) were averaged for blocks of 500 trials and subjected to four separate ANOVAs using group as the within-subjects variable and block as the between-subjects variable. No main effect of species or interaction of Species  $\times$  Block was obtained for any of these measures. As titration proceeded, start time increased from 10.7 s to 49.3 s from the first 500 trials to the final 500 trials,  $F(5, 55) = 3.22$ ,  $p < .05$ . The sample duration increased as titration proceeded from 9.3 s to 9.9 s,  $F(5, 55) = 6.90$ ,  $p < .001$ , and choice time increased from 2.6 s to 3.3 s,  $F(5, 55) = 37.15$ ,  $p < .001$ .

## Discussion

The species differences for acquisition of a nonspatial operant color task differed considerably from the radial maze analog (Kamil, Balda, & Olson, 1994). In that experiment, speed of acquisition correlated quite well with dependence on stored food, with the two most dependent species, nutcrackers and pinyon jays, performing better during acquisition than the less



**Figure 3.** Performance of each species during color non-matching-to-sample titration. Data are presented as averages of blocks of 100 trials.

dependent species, scrub jays and Mexican jays. In the current experiment, these species differences were not replicated. Although the slowest-learning species, scrub jays, is not heavily dependent on cached food, the two species that acquired the task most rapidly include both the cache-dependent pinyon jay and the less dependent Mexican jay.

The results of titration testing were very different from those obtained in comparative studies of spatial tasks with these species. By the end of 3,000 trials of titration of spatial non-matching-to-sample, nutcrackers were tolerating delays of approximately 60 s, whereas scrub jays could only tolerate delays of about 12 s (Olson, 1991). In the present study, nutcrackers and scrub jays never performed at different levels. Furthermore, in previous spatial studies, species differences among the four species tested in the current experiment have correlated well with degree of dependence on stored food. Pinyon jays and nutcrackers recovered caches more accurately than did scrub jays (Balda & Kamil, 1989) and acquired the radial maze analog more rapidly than did either scrub jays or Mexican jays (Kamil, Balda, & Olson, 1994). Performance following a retention interval in nonspatial non-matching-to-sample does not show the same pattern of species differences.

Although speed of acquisition and retention interval did not correlate well with dependence on stored food, it seems to correlate with their social organization. Although pinyon jays and Mexican jays live in relatively permanent flocks or groups (Brown, 1963; Marzluff & Balda, 1992), Clark's nutcrackers and scrub jays live in pairs. Birds that live in a relatively constant, close social structure may attend not only to the spatial distribution of the group, but also to nonspatial variables that would allow an individual bird in the group to recognize other members of the group.

## Experiment 2

The failure to find any differences in memory ability in the color non-matching-to-sample task suggests that evolution has acted differently on spatial memory than it has on nonspatial memory. During Experiment 2 the birds from Experiment 1 were tested with procedures very similar to the spatial non-matching-to-sample task used by Olson (1991) to collect spatial data from the same birds used in the color experiments. In addition, this experiment provided operant spatial data from pinyon jays and Mexican jays for the first time.

### Method

#### Procedure

**Acquisition** – The subjects and apparatus of Experiment 1 were used during Experiment 2, except 1 Mexican jay was dropped because of poor health. One week after completing Experiment 1, the birds started acquisition of the spatial non-matching task. The trial events were the same as described in Experiment 1, with several exceptions. First, the color stimuli presented on the monitor were replaced with white circles presented on a black background. The diameter of the circles remained 2 cm. Second, the center location was eliminated. The sample stimulus was either one of two spatial locations. The spatial locations used for the sample presentation and for the two choice tests were the locations used during the choice test for the color non-matching-to-sample task. Third, the retention interval imposed between the sample presentation and choice test was removed so that the first response to the rear key illuminated the choice stimuli. Each session ended after 36 reinforcements, 72 trials, or 45 min, whichever came first. Acquisition was stopped when the bird had reached a criterion of either a 4-day average of 85% correct or better or 7,000 trials without reaching the behavioral criterion.

**Titration** – Titration began with the next session after acquisition was completed. The procedure used for titration was the same as in Experiment 1. Titration ended for most birds after at least 3,000 trials had been completed. Four birds (1 Mexican jay, 2 pinyon jays, and 1 nutcracker) completed at least 1,700 trials, and titration was stopped for them when the number of completed trials per session was consistently fewer than 10.

**Color retest** – Once titration had been completed, memory for the color nonmatching task was tested. Each bird received five sessions using the procedure described for reacquisition in Experiment 1.

### Results

Nutcrackers acquired the operant spatial task more rapidly than did either scrub jays or pinyon jays. Nutcrackers also performed much better than did the other three species during titration testing.

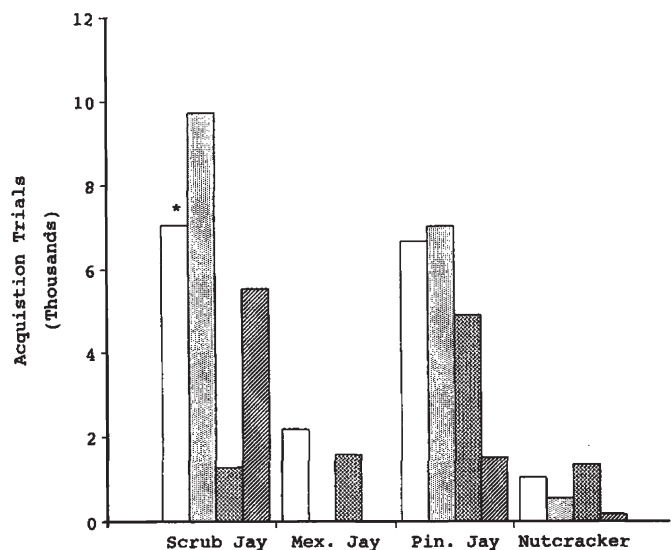
There was a significant difference among species in the number of trials required to meet criterion during acquisition,

$F(3, 10) = 3.88, p < .05$  (Figure 4). Subsequent contrasts found that nutcrackers required fewer trials than did either scrub jays or pinyon jays,  $p < .05$ , and the difference between Mexican jays and scrub jays approached significance,  $p = .08$ . Analysis of speed-of-responding variables (as Experiment 1) from last four criterion acquisition sessions found no differences between the species in start time, move time, sample duration, acquisition-retention interval, or choice time (Table 3).

Because all birds completed at least 1,700 trials, the block by block analysis of titration performance used these 1,700 trials (Figure 5). Data for these trials were averaged in blocks of 100 trials, and the programmed retention intervals for each block subjected to separate ANOVAs as in Experiment 1. There were no species differences during Blocks 1 through 6. However, there was a significant difference in every block thereafter. These effects were entirely due to the longer retention intervals displayed by nutcrackers.

Performance following retention intervals was also evaluated by examining the longest retention interval achieved. For each bird, the data from all completed trials were averaged for blocks of 100 trials, and the average achieved retention interval was calculated for each block. The highest value was then selected as representative of the best performance of the bird and subjected to a one-way ANOVA. A significant difference among the species was once again obtained,  $F(3, 10) = 3.96, p < .05$ . The maximum retention interval for nutcrackers was longer than the retention intervals obtained by scrub jays and pinyon jays, but it did not differ from Mexican jays.

Because the data obtained in the first 17 blocks were generally representative of the species, four within-trial times were analyzed for these blocks (as in Experiment 1, except that the retention interval was excluded). Mixed Species  $\times$  Block ANOVAs were performed. Significant effects were found for sample duration and choice time only.



**Figure 4.** Number of trials completed through the criterion stage during spatial non-matching-to-sample acquisition for individual birds for each species. The asterisk indicates the bird that did not meet the behavioral criterion



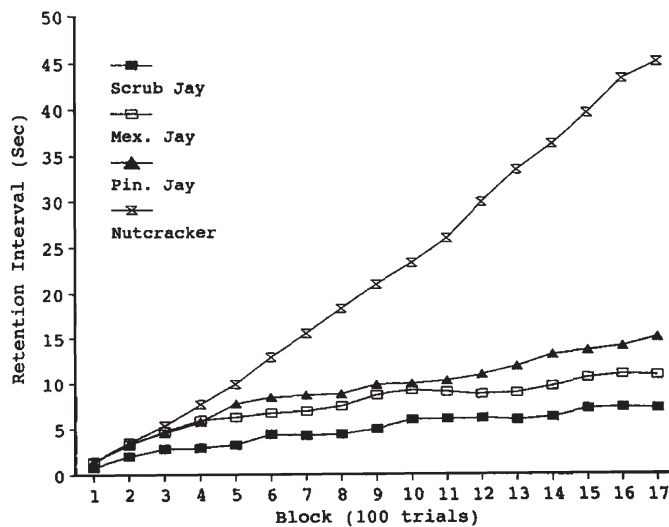
**Table 3.** Mean Latencies for Within-Trial Events During the Last Four Sessions During Spatial Acquisition for Each Species

Variable	Scrub jays		Mexican jays		Pinyon jays		Nutcrackers	
	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>
Start time	3.8	0.49	2.5	0.62	47.0 <sup>a</sup>	18.21	8.3	1.82
Move time	1.3	0.01	0.8	0.08	1.5	0.21	1.0	0.01
Sample time	9.2	0.12	8.7	0.00	9.6	0.24	8.9	0.01
Retention interval	2.5	0.16	1.9	0.18	2.1	0.16	3.5	0.62
Choice time	3.1	0.19	2.2	0.23	2.5	0.27	2.0	0.32
Average number of session trials	46.5	—	42.9	—	37.1	—	40.7	—

<sup>a</sup>The long start time was due to 1 pinyon jay. Range for this bird was 64.5–225.9 s.

As titration proceeded, sample duration increased,  $F(16, 160) = 6.00$ ,  $p < .001$ , from 9.0 s to 9.7 s. There was no significant main effect for species, but there was a significant Species  $\times$  Block interaction,  $F(48, 160) = 1.56$ ,  $p < .05$ . Sample duration for Mexican jays and nutcrackers increased about 1 s from the first to last block, but the increase for pinyon jays and scrub jays was less than 0.5 s. Choice time increased as titration progressed,  $F(16, 160) = 4.68$ ,  $p < .001$ , from 2.4 s to 3.2 s. There were no differences between the species, nor was there a significant Species  $\times$  Block interaction.

Performance during the color retest was subjected to an ANOVA using species as the within variable and session as the between variable. Due to experimenter error, 1 scrub jay failed to receive the color retest sessions, so only 3 scrub jays completed the color retest. The only significant effect was an improvement in performance across sessions,  $F(4, 36) = 4.75$ ,  $p < .01$ . To determine whether performance for the first session was above chance (50%), this session was subjected to a two-tailed  $t$  test. Four  $t$  tests were performed, one for each species. The performance of all species was found to be above chance (all  $p$  s  $< .05$ ).



**Figure 5.** Performance of each species during spatial non-matching-to-sample titration. Data are presented as averages of blocks of 100 trials

## Discussion

These results complement those of Olson (1991) in several ways. First of all, the species differences between nutcrackers and scrub jays in performance following a delay was replicated under somewhat different circumstances. Although Olson (1991) used pecking keys and naive birds, the current experiment used a touch frame with a monitor display and birds that had been previously trained on a nonspatial task. Although the nonspatial training may have affected the results of the current experiment, three of the four species performed at lower levels during spatial titration than during nonspatial titration, the species differences between nutcrackers and scrub jays are very consistent with those found by Olson (1991), even with the differences in experimental history and procedure.

Second, the addition of two species, pinyon jays and Mexican jays, provided an additional test of the hypothesis that species differences on this task would correlate with degree of dependence on cached food. The results supported the hypothesis, but the differences between nutcrackers and pinyon jays were somewhat surprising. These species have performed similarly during both cache recovery (Balda & Kamil, 1989) and the radial maze analog (Kamil et al., 1994). Thus the operant task produced a pattern different from that of these other two tasks.

There are many possible sources for this variation in the pattern of species differences across tasks. For example, although cache recovery and the radial maze analog are open-room tests, the operant procedures involve a more impoverished stimulus situation. In addition, the potential for proactive interference is much greater in the operant task, with many trials per day, than during the radial maze analog, with one trial per day. However, it is important to note that the overall pattern of results from the three spatial tasks is consistent with the cache dependence hypothesis. The most specialized species, nutcrackers, consistently performed as well as or better than the other species. The next most specialized species, pinyon jays, consistently performed as well as nutcrackers in two of the three tasks. And the least specialized species, scrub jays and Mexican jays, consistently performed poorly.

These species differences can also be compared to the pattern of species differences in brain structure. Basil, Kamil, Balda and Fite (in press) found that hippocampal volume (relative to either body size or telencephalon volume) was largest in nutcrackers, of intermediate size in Mexican jays and pinyon jays, and smallest in scrub jays. If the hippocampal volume was solely a function of dependence on cached food, then pinyon jays should have ranked much higher than Mexican jays, especially since pinyon jays acquired the radial maze analog faster than Mexican jays (Kamil et al., 1994) and pinyon jays perform very accurately during cache recovery (Balda & Kamil, 1989). The operant spatial data for pinyon jays provide the first case in which pinyon jays perform relatively poorly on a spatial task. This result is consistent with the hippocampal data obtained for pinyon jays.

## General Discussion

The results of these experiments, combined with those of earlier comparative spatial experiments with these species, strongly suggest that the pattern of species differences is different for spatial than for nonspatial tasks. Although there is some variation in the details, in general there have been species differences during spatial experiments that correlate quite well with dependence on cached food. In contrast, during nonspatial experiments the species differences obtained were not correlated with cache dependence. This pattern of results has two important, broad implications. First, these data greatly strengthen the hypothesis that variation in performance on spatial tasks reflects the extent of dependence on cached food in these species. Second, these data indicate that evolution has acted differently on processing of spatial and nonspatial information among these corvids.

Results with parids also support the hypothesis that evolution has acted differently on processing of spatial and nonspatial information. There are differences in neural substrates between caching and noncaching species in both genera (Basil et al., in press; Healy & Krebs, 1992; Krebs, Sherry, Healy, Perry, & Vaccarino, 1989). The volume of the hippocampal formation of caching species is generally larger than the volume of noncaching species. Further, within the corvid species, the volume of the hippocampal formation is correlated with cache dependence, the more cache dependent species have larger hippocampal volumes.

Differences in neural substrate and natural history indicate there should be differences at the behavioral level. The cache dependent corvids consistently perform better on spatial tasks than the noncache dependent species (Balda & Kamil, 1989; Kamil et al., 1994; Olson, 1991). Caching parids consistently perform better on spatial tasks than noncaching parids, although the effects tend to be smaller than for corvids (Healy & Krebs, 1992; Hilton & Krebs, 1990; Krebs, Healy, & Shettleworth, 1990). One experiment allows direct comparison between parids and corvids. Clayton and Krebs (1994) have compared the performance of caching and noncaching parid and corvid species. When spatial and nonspatial cues, color, were dissociated in test trials caching species used spatial informa-

tion first and then nonspatial, but noncaching species used either type of information equally.

The results of these experiments on nonspatial and spatial memory demonstrate the value of comparative cognitive research with closely related species selected on the basis of differences in natural history. Such research is necessary to understand the evolution of cognitive abilities and can yield valuable information about the structure of cognitive systems.

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