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FIVE COLLEGE
DEPOSITORY

COMPARATIVE SPATIAL MEMORY IN BIRDS

A Dissertation Presented

by

DEBORAH JEAN OLSON

Submitted to the Graduate School of the
University of Massachusetts in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

September 1989

Psychology

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COMPARATIVE SPATIAL MEMORY IN BIRDS

A Dissertation Presented

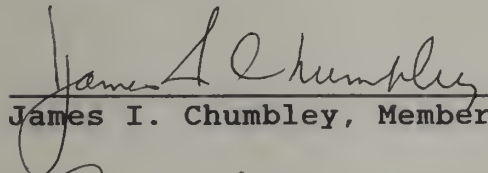
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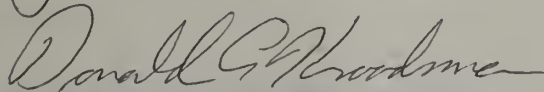
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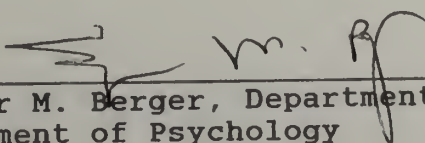
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ABSTRACT

COMPARATIVE SPATIAL MEMORY IN BIRDS

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The spatial memory abilities of Clark's nutcrackers (Nucifraga columbiana) and scrub jays (Aphelocoma coerulescens), were tested using an operant spatial nonmatching-to-sample procedure. These birds use spatial memory to recover cached food and differ in their dependence on the cached food as part of their diet. In Experiment 1 nutcrackers, scrub jays and pigeons (Columbia liva) were tested. Each trial consisted of a sample presentation, a retention interval, and a two choice test. Correct responding depended on remembering the sample location. The Clark's nutcrackers remembered the sample location longest; but, no differences were found between the scrub jays and pigeons. In Experiment 2 memory load (number of to-be-remembered locations) and retention interval were varied. Nutcrackers and scrub jays were tested. Nutcrackers consistently performed better than scrub jays. These results are correlated with species differences in food-caching and recovery.

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CHAPTER 1

INTRODUCTION

Spatial memory in food-caching birds has been studied empirically in controlled laboratory settings using members of two families, the Paridae (e.g. chickadees, Parus articapillus, Sherry, 1984; marsh tits, Parus palustris, Shettleworth & Krebs, 1982; Sherry, Krebs & Cowie, 1981) and the Corvidae (e.g. gray jays, Perisoreus canadensis, Bunch & Tomback, 1986; nutcrackers Nucifraga columbiana, Kamil & Balda, 1985; Vander Wall, 1982; nutcrackers, pinyon jays, Gymnorhinus cyanocephalus, & scrub jays, Aphelocoma coerulescens, Balda & Kamil, in press). These experiments have found that spatial memory is used to successfully locate cached food. The experiments presented in this paper focus on the ability of food-caching members of the Corvidae family to use spatial memory in an operant task. The operant paradigm was chosen because it is not related to food recovery and will extend our knowledge about food-caching and its relation to the ability to use spatial memory.

The use of a single paradigm for studying animal memory has limited value if the goal is to understand how memory processing has been influenced by evolutionary history. The effect of evolution on memory processing and the development of specific and/or general memory processing abilities has been proposed previously (e.g.

Sherry & Schacter; 1987). What this means for research programs, especially comparative research, is that a multi-task approach must be employed to study memory processing. This approach is not new (e.g. Hodos & Campbell, 1969) but is once again beginning to be emphasized. Kamil (1988) has suggested guidelines that properly employed will result in a solid research program and allow valid comparisons about memory processing to be made between species.

The two most important ideas that can be taken from Kamil (1988) are: (1) there must be some reason for choosing the species that are to be compared, such as their phylogeny and/or ecology, and (2) the validity of the differences and/or similarities found between the species must be verified by using more than one task. The comparative research on spatial memory that is reported in this paper is based on the use of these guidelines. It is necessary, therefore, to give a brief description of the two species that were used, the Clark's nutcracker (Nucifraga columbiana) and the scrub jay (Aphelocoma coerulescens), and the results of previous research using these birds. Both species are members of the family Corvidae and store (cache) pine nuts (Pinus species) for future use.

The Clark's nutcracker depends on seed caches as the major winter food source (Vander Wall & Balda, 1981). Nutcrackers have unique morphological adaptations for

harvesting and caching pine nuts. Their bills are lengthened and pointed, allowing the birds to begin harvesting pine seeds before the pine cones have ripened and fallen to the ground (Vander Wall & Balda, 1981). The nutcrackers also have a specialized pouch that allows them to carry up to 90 seeds to a cache location (Vander Wall & Balda, 1977; Bock, Balda & Vander Wall, 1973). These birds breed early and use the caches of pine nuts as the major portion of the nestling diet (Vander Wall & Balda, 1981; Mewaldt, 1956).

Scrub jays appear to be less dependent on caches than Clark's nutcrackers and do not have the morphological adaptations of the nutcrackers. Their bill is short and they do not begin harvesting pine seeds until the cones have ripened and fallen to the ground (Vander Wall & Balda, 1981). In contrast to nutcrackers, scrub jays do not use pine nuts as a major food source of their winter diet or of the nestling diet (Vander Wall & Balda, 1981).

Balda (1980a) first tested a single Eurasian nutcracker, Nucifraga caryocatactes, and found that the bird was able to recover caches it had made in a dirt floor aviary. Vander Wall (1982) found that individual nutcrackers are better at recovering their own caches than caches of other birds, even when they are able to observe another bird caching, and that recovery of caches is impaired when spatial cues are shifted. Kamil & Balda (1985) used a more controlled testing situation that

eliminated the ability of the birds to control where caches were made. This procedure decreased the probability that the birds would be able to create caches in locations they favored (increasing the probability of retrieving due to factors other than memory) and increased the probability that spatial memory would be used during cache recovery. These authors found under these conditions nutcrackers were still able to accurately recover their own caches. In addition, Balda & Kamil (in press) have found that in the controlled laboratory test nutcrackers and scrub jays tend to distribute their caches over large areas rather than clumping caches in limited areas. This result indicates that clumping caches is not a strategy that is used by either species to aid in cache recovery.

These results show that both species use spatial memory to recover caches, but they differ substantially in their dependence on cached food. Controlled cache recovery experiments indicate there are species differences in ability to recover caches. Kamil & Balda (in press) found that Clark's nutcrackers have a higher cache recovery accuracy than scrub jays.

The spatial memory abilities of nutcrackers do not appear to be limited to situations involving cache recovery. Kamil & Balda (1988) tested nutcrackers in a radial maze analogue. The performance of the nutcrackers was above chance at delays up to 6 hours. The delay

intervals obtained by nutcrackers were much longer than the delay intervals obtained by pigeons, Columba livia, in similar radial maze analogue tasks. Spetch & Honig (1988) found that the performance of pigeons was above chance up to delay intervals of 32 min. Previously research testing pigeons in radial maze analogues had obtained good performance with delays that were less than 5 min (Spetch & Edwards, 1986; Roberts & Van Veldhuizen, 1985). Whether the differences are related to species differences or to differences in experimental procedures are not known, because a comparative test using both species has not been done. However, such differences in spatial memory ability seem likely.

The research reported in this paper focused on the spatial memory abilities of nutcrackers, scrub jays and pigeons using an operant spatial nonmatching paradigm. These experiments were designed to test the hypothesis that spatial memory is better in species that use spatial memory to recover cached food even when the tests do not involve cache recovery.

CHAPTER 2

EXPERIMENT 1

Introduction

Previous knowledge about the foraging ecology of nutcrackers and scrub jays allowed testable predictions about species differences in laboratory cache recovery experiments to be made. These predictions, that cache recovery accuracy would be better for nutcrackers than scrub jays, have been empirically tested and the results confirm the predictions (Kamil & Balda, in press). Similar predictions about species differences in spatial memory ability can be made for operant spatial nonmatching-to-sample.

The spatial memory abilities of Clark's nutcrackers, scrub jays and pigeons were tested in the first experiment using the operant spatial nonmatching-to-sample task. Pigeons were included because of the literature that already exists about their memory abilities. If the need to remember cache locations for long periods of time is important for birds that cache and recover food, then non-caching birds should retain spatial information for shorter times than caching birds. The memory duration of spatial information for caching birds should be correlated

with their dependence on cached food. This would mean the nutcrackers should be able to remember spatial information longer than the scrub jays. The resulting rank order for retention of spatial information (from longest to shortest retention) would be: Clark's nutcrackers, scrub jays and pigeons.

Method

Subjects

Three species of birds, two corvids (Clark's nutcrackers and scrub jays) and one columbid (domestic pigeon) served as subjects. The birds had free access to water and were maintained between 80% and 90% of their free feeding weights with controlled daily feedings at the end of each experimental session. The housing rooms for all species were maintained on a 14/10 hr light/dark cycle.

Clark's nutcrackers

Three wild-caught adult Clark's nutcrackers of unknown age served as subjects. One bird died months after the completion of the experiment and sex was determined during the necropsy. This nutcracker, Scarface, was a female. Sex was unknown for the other two nutcrackers, Greta and Marcel. The birds were captured from the San Francisco peaks of Arizona. Each bird was individually housed in a commercial bird cage 73.5 cm x 48

cm x 48 cm (HxLxW). The maintenance diet consisted of pine nuts, turkey starter, sunflower seeds, mynah pellets, mealworms (Tenebrio larvae) and a powdered vitamin supplement.

Marcel had participated in spatial memory experiments using the cache-recovery procedure (Balda & Kamil, 1986; Kamil & Balda, 1985). Between October, 1984 and December, 1984 the nutcrackers were used to establish the procedures used in the current study. The data reported here for the nutcrackers were collected during 1985.

Scrub jays

Four wild-caught adult scrub jays of unknown age served as subjects. The sex of three birds was unknown. The fourth bird, Yellow, died after the completion of the experiment and the results of the necropsy showed this bird was a male. The jays were captured from the Albuquerque, New Mexico area. They were maintained on the same diet as the nutcrackers. Each of the jays was individually housed in a commercial bird cage 45.5 cm x 35 cm x 35 cm (HxLxW). All of the jays had participated in a cache recovery experiment (Kamil & Balda, in press). The data for the scrub jays were collected during 1986.

Pigeons

Four White Carneaux pigeons of unknown sex served as subjects. The pigeons were retired breeders obtained from the Palmetto Pigeon Plant, Sumter, South Carolina. They were maintained on Purina turkey grower #2, whole corn and

pigeon grit. They were individually housed in standard pigeon cages 29 cm x 38.3 cm x 23 cm (HxLxW). The pigeons were experimentally naive at the start of the experiment. The data for the pigeons were collected during 1985.

Apparatus

The apparatus was constructed of sheet metal sides, 38 cm high, fit together to form a trapezoid. The length of each nonparallel wall was 61.2 cm. The lengths of the long and short parallel walls were 76 cm and 26 cm respectively. The cover for the top of the apparatus was constructed of 1.2 cm hardware cloth and was hinged to the longest parallel. The cover contained a centrally located speaker to present white noise. A mirror was mounted over the top of the apparatus to facilitate observation of the birds. Indirect lighting to the apparatus was provided by a 15 watt bulb located 78 cm behind the shortest parallel. The light was directed away from the apparatus towards a wall and was reflected towards the interior of the apparatus.

The front intelligence panel (the longest parallel) contained a horizontal line of four round pecking keys. Only the two center keys were used for the present experiment. Each key was 3.1 cm in diameter. The center of each key was 7.6 cm from the panel top and 30.4 cm from the floor. The distance between adjacent keys was 20.3 cm

(center to center). The center of each outside key was 7 cm from the outside edge. The keys were illuminated for stimulus presentations by a 28V light covered with a red plastic cap.

The rear intelligence panel (the shortest parallel) contained one key and a food cup. The key was centrally located between the panel edges with the same diameter and distance from the apparatus floor and ceiling as the front keys. The feeder opening was 5 cm x 4.5 cm (HxW). The center of the opening was 20 cm from the top of the panel, 18 cm from the bottom, 8.5 cm from the left side and 17.5 cm from the right side. The feeder extended 3.6 cm beyond the panel and had a 2 cm lip around the cup. Reinforcers were delivered into the cup by a Davis Universal Feeder Model #310.

Perches were provided for the nutcrackers and jays to allow them to view the keys at approximately eye level. Each perch (one front and one rear) had a diameter of 1.2 cm, was parallel to and 8.3 cm from the intelligence panel. It was raised 16.5 cm above the floor. For the pigeons, a false floor made of 1.2 cm hardware cloth and 8 cm high allowed them to view the keys at approximately eye level.

A Northstar computer was used to program all stimulus events for each session and record the data of each trial.

Procedure

Pretraining

Prior to the start of the experiment each bird received six stages of keypeck training. One nutcracker, Marcel, was the first bird to be trained in the apparatus. The data for this bird have been excluded from the averages for pretraining, because the final pretraining procedures were established using this bird. This preliminary testing extended the pretraining procedures for this nutcracker.

Habituation. This stage familiarized the bird with the apparatus and the location of food. Habituation lasted until the bird was freely eating the reinforcers that had been placed in the illuminated feeder. Reinforcers for each species were pieces of the preferred items from the diet (pine nuts for nutcrackers, mealworms for scrub jays, and corn for pigeons). These sessions ended after 1 hr or when all reinforcements had been eaten. The nutcrackers required an average of 2 days. The scrub jays required an average of 3 days and the pigeons required an average of 3.25 days.

Magazine training. During magazine training reinforcers were presented on a variable time 90 sec schedule. The feeder was illuminated during reinforcement presentation only. This stage ended when the bird was eating the reinforcers when presented. The

nutcrackers required an average of 2.5 days. The scrub jays required an average of 1 day, and the pigeons required an average of 1.5 days.

Shaping. The method of successive approximations was used to train the birds to peck the two center keys on the front panel. Sessions ended after the presentation of 36 reinforcers. Shaping was completed when the bird was able to finish one session without the help of the experimenter. The nutcrackers required an average number of 2.5 days. The scrub jays required an average of 11.25 days and the pigeons required an average of 3 days.

Trial sequence training. All birds received only one session for each of the next three stages. Each session consisted of 36 trials with a 30 sec inter-trial-interval (ITI).

Two sessions were used to introduce a fixed ratio, FR, requirement (FR2 for session 1 and FR4 for session 2). Each trial consisted of illuminating one of the four front keys. The key was extinguished and a reinforcer was presented when the FR requirement had been completed.

The next stage introduced the use of the rear key. At the start of a trial the rear key was illuminated. One response to the rear key darkened the rear key and illuminated one of the four front keys. The front key was extinguished and a reinforcer was presented after the completion of five responses (FR5).

The final stage simulated an experimental trial. This session started with the sequence of trial events from the previous stage, but only the two center keys on the front panel were used. The rear key was illuminated after the completion of the FR requirement on the illuminated front key. One response to the rear key extinguished that key and illuminated the front key that had not been the key used for the FR requirement. One response to the illuminated key extinguished that key and ended the trial with the presentation of a reinforcer.

Acquisition

The sequence of events during the trial are shown in Figure 1. Each trial began with the illumination of the rear key. One response to the rear key darkened the key and illuminated one of the center keys (the sample) on the front panel. The order of sample presentations was based on sequences taken from Fellows (1967). The bird was required to make five responses (FR5) to the sample key (an FR2 was used with pigeon 325 and an FR3 was used with pigeon 350). Completion of the FR requirement darkened the sample key and illuminated the rear key. One response to the rear key darkened the rear key and illuminated both center keys (the two choice test). A response to either of the center keys extinguished both key lights. The choice was correct if the response was to the key that had not served as the sample. An incorrect choice was a response to the sample key. Correct choices were followed

by reinforcement and a 30 sec ITI. Incorrect choices were followed by the ITI. A session ended after 36 reinforcements had been received; however, if 72 trials had been completed and the criterion of 36 reinforcements had not been met the session was ended. Baseline training for each bird continued until a criterion of 85% correct for three consecutive days had been reached.

Delay training

Session length and trial events for delay training were exactly the same as during acquisition with the following exception. After the sample presentation a delay was introduced on the rear key. The delay was a pre-programmed time (see below for details) during which responses to the rear key had no consequences. The choice stimuli were illuminated when one response was made after the unsignalled end of the programmed delay had timed out. The delay length was titrated based on the outcome of the preceding trial. If the choice response on the preceding trial was correct, the delay was incremented by 0.1 sec. Delays following incorrect choice responses were decreased by 0.3 sec. The delay was not allowed to change by more than ± 2.5 sec in any single session. The session length was the same as during acquisition until the delay length required sessions that were longer than 1 hr. When this occurred the session length was limited to approximately 1 hour.

The titration procedure was chosen because there was no way to determine in advance what the performance of the birds would be. Titration has the advantage of being sensitive to the behavior of the individual and allows the delay to be adjusted continuously for each individual. It also has the advantage of maintaining choice performance fairly high, in this case 75% correct, so the bird will not extinguish responding or fail to begin trials due to lack of reinforcement. A procedure using a preset number of delay intervals that are constantly repeated would not be as sensitive to the behavior of individual birds.

The first session began with a programmed delay of 0 sec. Thereafter, the delay for the first trial of the next session was the same as the delay for the last trial of the previous session. Delay training ended after a minimum of 3000 trials had been completed. Delay training was extended for some of the scrub jays and pigeons.

Results

Definition of dependent measures

The following measures were subjected to analysis for comparisons between species and/or within species. (1) Start time, the time from the onset of the rear key light at the completion of the ITI to the first peck. (2) Sample time, the time required to complete the FR requirement on the sample key. (3) Delay time, the time between the sample presentation and the two choice test.

Two delay times were recorded for each trial, the programmed delay and the actual delay. The programmed delay was the scheduled delay time based on the titration procedure. The actual delay was the programmed delay plus the time to make the final peck on the rear key after the programmed delay had ended. The average difference between the actual and programmed delays was less than 1.0 sec for the nutcrackers, less than 0.8 sec for the scrub jays and less than 1.3 sec for the pigeons. Unless otherwise specified all analyses using delay times are reported for the programmed delay, because no differences between analyses using either programmed and actual delay were found. (4) Peck rate, the number of pecks during the delay interval divided by the number of seconds for that delay interval. (5) Choice time, the time required to peck one key during the two choice test. A significance level of 0.05 was used for all statistical analyses.

Data analysis

Acquisition

The last three days of baseline training were analyzed to determine if there were any differences between species prior to the start of delay training. Separate ANOVAs were performed for start time, sample

time, actual delay (because the programmed delay was 0 sec), and choice time with species and subjects within species as factors. There were no significant differences among species on any of these measures (see Table 1).

Delay training

The average delays for individual birds were calculated for blocks of 100 trials. The nutcrackers tolerated delays of 50 - 80 sec by the end of the experiment, the scrub jays tolerated delays of 7 - 44 sec, and the pigeons achieved delays of 0.5 - 25 sec. Table 2 lists the number of delay trials each bird received and the delay for the final session. Pigeon 343 received fewer than 3000 trials because this bird either failed to start a session or completed less than 10 trials on 19 of the last 24 sessions. Pigeon 350 received two other sample FR requirements (FR5 and FR10) after completion of 3000 trials with a FR3.

The previous experience with delay training during the development of the titration procedure for two of the nutcrackers, Greta and Marcel, did not appear to have any positive effect in the present experiment. The one nutcracker, Scarface, that did not have any previous experience with delay training, achieved higher delays than the two experienced birds.

In order to quantitatively analyze these data given the differing number of trials completed by each bird, averages for four blocks of 500 trials each were obtained.

The four blocks consisted of the data from the first 1000 trials (two 500 trial blocks) and from the last 1000 trials (two 500 trial blocks).

The average delays tolerated by each species were subjected to an ANOVA with species, subjects within species, and blocks as factors. There were significant differences between the species, $F(2,8)=6.32$, $p<.02$. As shown in Figure 2, nutcrackers consistently performed better than the other two species. Subsequent t -tests showed that this species difference in performance was significant during the first 500 trials for nutcrackers vs scrub jays, $t(5)=3.12$, $p<.05$, and for nutcrackers vs pigeons, $t(5)=4.05$, $p<.01$. There was no significant difference between the scrub jays and the pigeons during the first block, $t(6)=-0.29$, $p>.05$. There was also a significant overall increase in programmed delay across blocks of trials, $F(3,24)=20.9$, $p<0.001$. The change in delay interval between blocks was larger for nutcrackers than for either scrub jays or pigeons resulting in a significant two way interaction of species and block, $F(6,24)=4.91$, $p<.002$.

Proactive interference

Separate analyses were carried out for each species to determine if there was any effect of proactive interference on performance within a session. The first, middle and last five trials of each session were used to measure the performance during a session. The data from

the last 20 sessions in which at least 20 trials were completed were used for analysis. If there was any effect of proactive interference, the percentage correct should decrease as the session progressed.

ANOVA's for each species were performed using session blocks and subjects as factors. The results of these analyses show that there was no evidence of proactive interference for any species. There was no significant change in percentage correct as the session progressed for any of the species.

Additional analyses

Although this experiment did not attempt to manipulate ITI and sample time, other research has shown that these variables affect the ability to remember a sample stimulus (Wilkie, 1984; Grant & Roberts, 1976; Roberts & Grant, 1974). The start time and sample time were determined by the behavior of the birds in the present study. These two variables and the peck rate during the delay interval were subjected to analysis for each species to determine if there were any changes in the birds' behavior that could have had an effect on choice performance and influenced the delay interval.

Averages for four blocks of 500 trials were obtained for each species for both start time and sample time. The same four blocks were used as for the delays that are

shown in Figure 2. The data for each species were subjected to separate ANOVAs using blocks and subjects as factors.

The start time for nutcrackers did not change, but sample time did increase during the course of the experiment, $F(3,6)=6.25$, $p<.03$. No significant changes for either the start time or sample time were obtained for the scrub jays. The pigeons showed an increase in start time as the experiment progressed, $F(3,9)=5.63$, $p<.02$. The change in sample time for pigeons was not significant, although this effect did approach significance $F(3,9)=3.26$, $p=.07$. There was no significant change in peck rate for any of the species.

Discussion

Two of the three predictions about species differences in ability to remember spatial information were supported. The nutcrackers retained information about spatial locations longer than either scrub jays or pigeons. This difference in spatial memory between nutcrackers and scrub jays is consistent with the findings of Balda & Kamil (in press) for the cache recovery task using a single delay test. The difference in the spatial memory ability between the nutcrackers and pigeons is also consistent with the literature for the radial maze paradigm for nutcrackers (Balda & Kamil, 1988) and pigeons (Spetch & Honig, 1988; Spetch & Edwards, 1986; Roberts & Van Veldhuizen, 1985).

The retention intervals achieved by the pigeons in the present experiment and the performance of pigeons in other experiments using operant spatial memory tasks (Wilkie, 1984; Smith et al., 1982) were very similar. This similarity suggests that there was nothing peculiar about the present task that could explain the superior performance achieved by the nutcrackers. The absence of any difference between the retention intervals achieved by scrub jays and pigeons raises some doubt about whether caching alone can be used as a reliable predictor of differences in spatial memory abilities.

The underlying assumption made was that in caching birds that use spatial memory to recover caches the evolution of cache recovery might have been associated with the development of some specialization of the spatial memory system. However, it appears that this hypothesis may not always accurately predict differences between two or more species' ability to retain spatial information. No differences were obtained between the scrub jays, the least specialized caching bird, and the pigeons, the noncaching bird. However, differences in ability to retain spatial information were found between the nutcrackers, highly specialized and dependent on caching, and the pigeons in the current experiment and in the radial maze task (Balda & Kamil, 1988). It may be that dependence on the use of spatial information alone may be enough to predict species differences in ability to retain

spatial information. The relationship between natural caching and spatial memory abilities certainly needs to be tested further, perhaps using the radial maze or some other spatial memory test.

The results of this experiment along with the radial maze experiments (Balda & Kamil, 1988) and the comparative cache recovery experiments (Balda & Kamil, in press) indicate that, at least for the species used in the current experiment, some aspects of the natural history can be used to accurately predict species differences in spatial memory abilities. However, some methodological details might have affected the relative performance of the species.

The operant nonmatching-to-sample task uses multiple trials per session. One possible effect of multiple trials would be for proactive interference to cause choice accuracy to decrease as the session progressed and subsequently cause a decrease in the achieved delay length. If there was evidence for proactive interference for some species and not others, the species differences in performance may have been due to proactive interference. There was no evidence that choice accuracy was affected by proactive interference during the session for any species, making it very unlikely that the species differences were due to the effects of proactive interference within a session. Although there was not any evidence of within session proactive interference, this does

not rule out the possibility that proactive interference was occurring. Proactive interference may have occurred between sessions. The effect of between session proactive interference on performance would be the same as within session proactive interference, a decrease in choice accuracy that would result in decreasing the delay interval. Even if between session proactive interference was occurring, the results of this experiment would not change if the effect were the same for all species.

Changes in the behavior of the birds would lead to differences in the length of exposure to the sample stimulus or the ITI also might have affected the achieved retention interval for a species. Several experiments have found that these variables affect choice performance in various tasks. Grant & Roberts (1974) have shown that in a delayed matching-to-sample paradigm choice performance improves when the ITI is lengthened. Roitblat & Harley (1988) have shown that the performance of rats in a spatial memory task using a starburst maze is better with long ITIs. Sample duration also affects choice performance. Wilkie (1984) found that the performance of pigeons in an operant spatial memory task was better with longer exposure to the sample stimulus. The current study did not attempt to manipulate the ITI or stimulus

duration. These times were controlled by the birds so a trial would always begin when the bird was ready and no limits were set for the completion of the FR requirement for the sample time.

The duration of the ITI could be increased by delaying responding to the start key and the duration of the sample time could be increased by taking longer to complete the FR. Either of these behaviors by the birds could result in better retention of the sample. These changes in behavior could improve choice performance and result in increasing the retention interval. The pigeons were the only species that showed a significant increase in start time. They also tended to increase the sample time. The sample time did lengthen for the nutcrackers, but the duration of the sample remained shorter than for either the scrub jays or the pigeons. The scrub jays showed no changes for either of these times. Therefore if any species benefitted from an increase in ITI and sample time it was the pigeons. These results indicate that the retention intervals achieved by the species were not differentially affected by stimulus duration or ITI.

The results of this experiment indicate that the species differences in the spatial operant nonmatching-to-sample task do not appear to be related to any strategy or procedural difference in the current experiment. The

ability of nutcrackers to remember spatial information is outstanding when compared to scrub jays and pigeons and is consistent with their foraging ecology.

Although there were no differences between the retention intervals for the scrub jays and the pigeons, the lack of any species differences should be viewed with caution. The retention interval for the pigeon 343 was much longer than the other three pigeons. During the final block the retention interval for this bird was over 30 sec for four of the five 100 trial blocks. This bird began taking longer to start trials and complete the FR requirement as the retention interval increased. Since the bird responded correctly during the choice test the delay always increased because of the titration procedure. The behavior of this bird during the trial combined with the constant increase in delay interval resulted in fewer reinforcements for this bird during a session and eventually the bird would not even start the first trial during a session. Observations showed that this bird was bobbing and weaving its head in front of the key during sample presentations. The behavior of this pigeon is suggestive that this bird may have been doing something different than the other pigeons that helped improve performance. Whether responding during the choice test was guided by spatial memory, some other type of memory, behavior during the sample presentation or a combination of memory and behavior is unclear.

Table 1. Correct trial averages for last three days of acquisition for each species in Experiment 1. All times are in secs.

SPECIES	% correct	Start time	Sample time	Actual delay	Choice time
Nutcrackers	92.5	9.4	9.0	4.4	2.4
Scrub Jays	89.9	4.2	11.3	3.5	3.5
Pigeons	89.4	6.6	8.7	3.3	2.8

Table 2. Total number of delay trials and final delay for each bird during titration in Experiment 1.

<u>SPECIES</u>	<u># TRIALS</u>	<u>DELAY (SEC)</u>
Nutcrackers		
Greta	4108	50.5
Marcel	3075	65.0
Scarface	3166	80.2
Scrub Jays		
Blue	4384	10.5
Red	3024	44.6
Violet	4361	24.5
Yellow	3091	7.2
Pigeons		
P325	3526	10.7
P343	2169	24.4
P345	3691	25.0
P350	5078	0.5

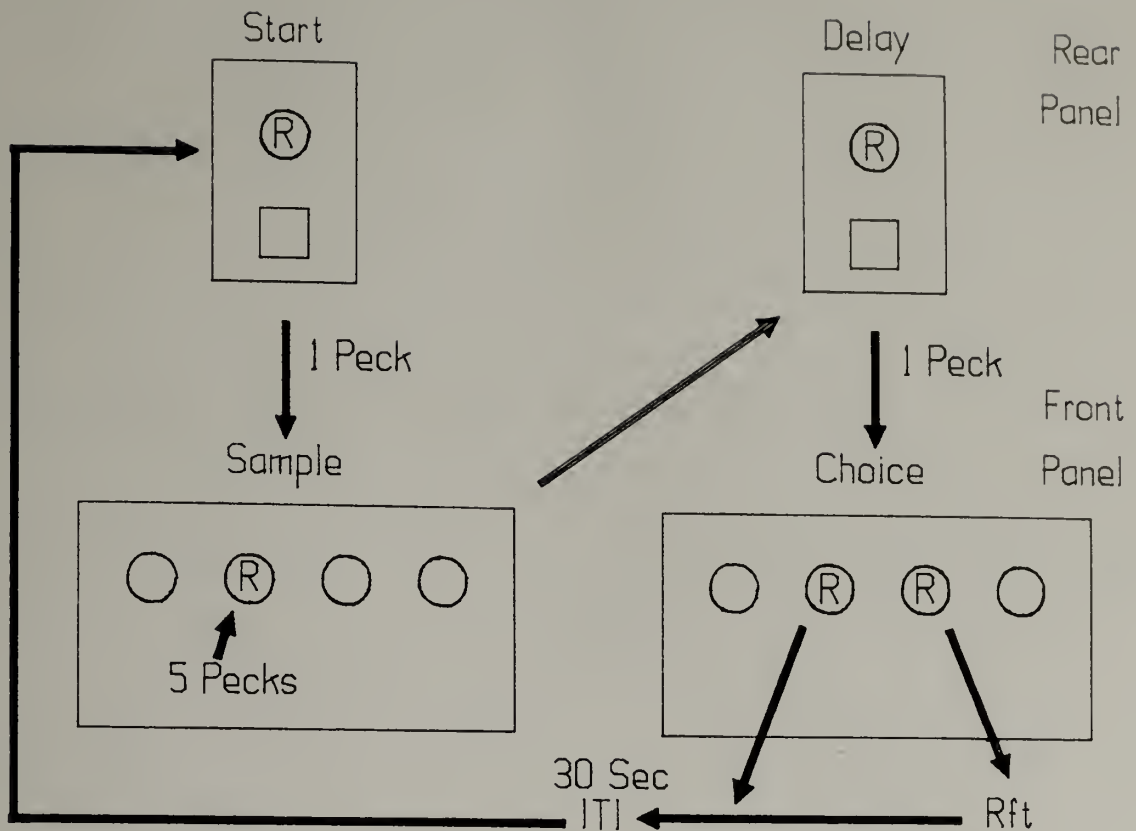


Figure 1. Flow diagram for a spatial nonmatching-to-sample trial for Experiment 1. The birds were required to move between the rear panel (the top panels in the figure) and the front panel (the bottom panels in the figure) during the trial. The circles inside the panels represent the pecking keys. The square box inside the rear panel represents the feeder used for presenting reinforcers. The arrows indicate the flow of events during the trial. Trial stages are labelled above the panels. The keys were illuminated with a red key light (R). The response requirement is shown below the rear panels for the start and delay stages and inside the front panel for the sample stage. The one peck shown for the delay stage had to occur after the delay had timed out. The response requirement for the choice panel was one peck to either of the illuminated keys. A reinforcer was presented if the key that had been pecked was not the key presented as the sample.

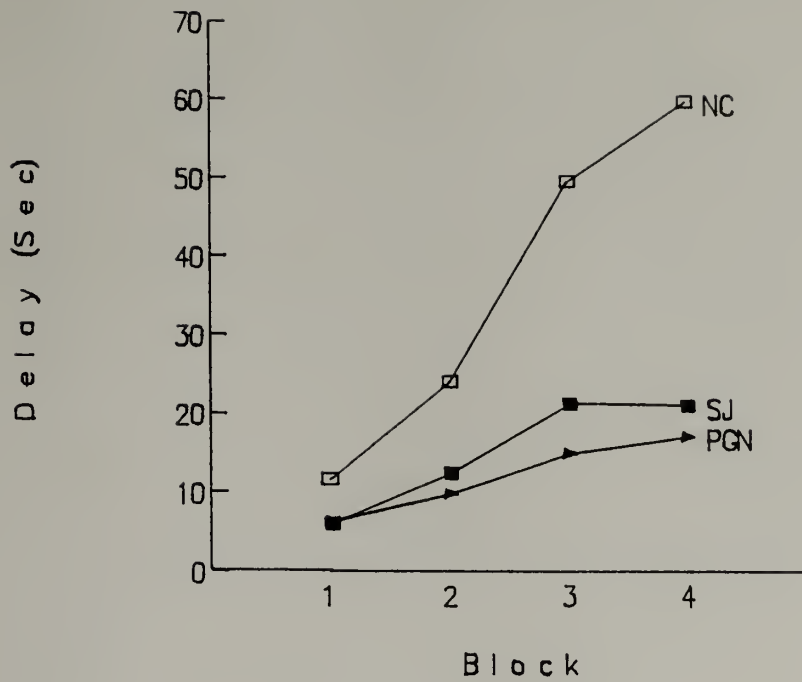


Figure 2. Average retention interval (delay) during titration for nutcrackers (NC), scrub jays (SJ) and pigeons (PGN) in Experiment 1. Each block represents the average retention interval for 500 trials. Block 1 and block 2 were the first 1000 trials of titration. Block 3 and block 4 were the last 1000 trials of titration.

CHAPTER 3

EXPERIMENT 2

Introduction

The most important result of Experiment 1 was the large species difference in duration of spatial memory ability among the closely related corvids, nutcrackers and scrub jays. The differences in the spatial memory ability of nutcrackers and scrub jays in operant nonmatching and in comparative tests of cache recovery (Balda & Kamil, in press) correlate with the ecological differences in the degree of dependence on cached food. One of the major purposes of Experiment 2 was to extend the results of Experiment 1 using fixed retention intervals.

The other major purpose was to determine if there were differences in the number of spatial locations (memory load) that each species can remember. Nutcrackers harvest between 22,000 and 33,000 pine seeds (Tomback, 1977; Vander Wall & Balda, 1977) and the average cache size is approximately 4 seeds (Vander Wall & Balda, 1981). A single nutcracker will create between 5000 and 8000 cache sites. Scrub jays harvest about 6,000 pine seeds (Balda, 1980b) with only 1 seed per cache (Vander Wall & Balda, 1981). Although the number of caches may be about equal, nutcrackers are extremely dependent on their caches. The caches are the major food source for an individual bird and more importantly for the nestling diet (Vander Wall & Balda, 1981). In contrast, scrub jays do

not depend on the caches as a their major food source or for the nestling diet (Vander Wall & Balda, 1981). The difference in dependence on caches for survival may mean that the nutcrackers are able to remember more spatial loacations than the scrub jays.

Increasing the number of spatial locations presented during the sample stage allows more than between species comparisons to be explored. Kamil & Balda (1985) found that when nutcrackers attempt to recover caches from holes that did not contain seeds, the errors tended to occur close to holes that contained a cache. Wilkie & Summers (1982) found that in operant spatial matching-to-sample pigeons make more errors when the choice keys are near neighbors. Based on these results, both nutcrackers and scrub jays should make more errors as the distance between the choice keys decreases.

Primacy and recency effects can also investigated by increasing the number of spatial locations. Kamil & Balda (1985) found that the order of cache recovery by nutcrackers is uncorrelated with the order in which caches were created. In contrast, Wright et al. (1984) found that choice performance by pigeons is affected by the postion of an item in a list. Items presented at the beginning or end of the list are remembered better than

items presented in the middle of the list. Whether nutcrackers and scrub jays in the operant spatial task will show an effect of presentation order cannot be predicted a priori, but the results will be interesting for either outcome.

Nutcrackers and scrub jays were tested with varying retention intervals and memory loads. The memory load was varied by sequentially illuminating either one, two or three spatial locations on the front panel as the sample. The bird was required to complete two responses while the key was illuminated. The duration of each stimulus was controlled by illuminating the key for 4 seconds. Memory was tested by varying the retention interval and using a two choice test.

Method

Subjects

Four Clark's nutcrackers and four scrub jays served as subjects. The birds were maintained as in Experiment 1. Two of the nutcrackers, Greta and Marcel, and two of the scrub jays, Red and Violet, from Experiment 1 served. Two naive birds of each species served. The naive birds were captured as adults in the same areas as described in Experiment 1.

The naive birds did not have any prior experience with operant procedures. The nutcrackers, Adolph and Johann, had served in a cache recovery experiment (Kamil & Balda, 1985) and in a radial maze experiment (Balda &

Kamil, 1988). The scrub jays, Green/Red and Orange/Blue, had served in a cache recovery experiment (Balda & Kamil, in press). All birds were tested simultaneously and the data were collected between October, 1987 and May, 1989.

Apparatus

The apparatus of Experiment 1 was used with one modification. An infrared photocell was mounted to the apparatus to detect the presence of a bird on the front perch.

Procedure

Pretraining

The pretraining procedures described in Experiment 1 were used for the naive birds. All eight birds received 1 day of the final stage of trial sequence training from the pretraining sequence.

Acquisition

The purpose of the acquisition stage was to train the birds to the nonmatching task with different numbers of sample stimuli. The birds were first trained with 1 sample, then with 2 samples, then with 3 samples. The delay between the sample presentation and the choice test was 0 sec. Throughout, each session lasted for 36 trials.

At the start of each stage the duration of the last location started at 8 sec. The stimulus duration was gradually decreased to 4 sec over four or five days. Data collection began when the stimulus duration for all samples reached 4 sec.

Sample size 1. The sequence of events for a trial are shown in Figure 3. A trial began with the illumination of the rear key. One response to the rear key darkened that key. The sample stimulus presentation began when the bird landed on the front perch. One of the four keys on the front panel was illuminated for 4 sec. The bird was required to complete two responses to the illuminated key. (If the response requirement was not completed, the trial was aborted and the ITI began. A 30 sec penalty was added to the normal 30 sec ITI for aborted trials.)

After the 4 sec sample presentation the rear key was illuminated. One response to the rear key darkened the rear key and two keys on the front panel (the sample location and another location) were illuminated. One response to either key darkened both locations. If the nonsample key was chosen, a reinforcer was presented, the feeder light remained on for 8 sec and was followed by a 30 sec ITI. If the sample key was chosen, the ITI began immediately.

This stage continued until a performance criterion of three consecutive days at or above 85% correct responses and at or less than 11% aborted trials. was met or for a maximum of 75 days.

Sample size 2. The trial sequence for this stage was the same as that used for sample size 1 with the following exception. The sample presentation consisted of two different spatial locations. The locations were presented sequentially so the effects of primacy and recency could be analyzed. Each location was illuminated for 4 sec and the two peck requirement was in effect for each location. The choice test stimuli consisted of one of the two sample locations and one of the two remaining spatial locations. The criterion for ending this stage was the same as for sample size 1.

Sample size 3. The same trial sequence was used as in the previous stages, except the sample consisted of the sequential presentation of 3 different spatial locations. The duration of stimulus presentations and the response requirement were the same as the previous stages. The choice test consisted of one of the sample locations and the remaining location. The criterion for ending this stage was the same as for the previous stages.

Baseline

This stage began after acquisition of sample size 3 had been finished and lasted for 36 sessions. During this stage all three sample size conditions were used, with the

sample size varying between sessions. The presentation of sample sizes was randomized in blocks of six sessions, with each sample size presented twice in each block. The presentation of any one sample size was limited to no more than two consecutive days. This constraint remained in effect for the duration of the experiment.

Short delay exposure

This stage lasted for six sessions. The sequence of events during each trial was changed by adding a short delay between the sample presentation and the choice test. The delay started when the rear key was illuminated after the presentation of the last sample location. The end of the delay was not signalled and ended with the first response to the rear key after the scheduled time had elapsed. These constraints on the delay remained the same throughout the experiment. Three delay intervals (0 sec, 5 sec, 10 sec) were used and the delay varied within sessions. The delay intervals were randomized for blocks of six trials using two presentations of each interval per block. Twelve blocks of delay intervals were generated with the constraint that no more than two consecutive trials could have the same delay interval. The order of delay presentation for trials was the same for all sample sizes.

Delay testing

This stage was the same as the previous stage except that four delay intervals (0 sec, 10 sec, 20 sec, 30 sec)

were used. The delay intervals were randomized in blocks of four trials and 72 blocks of delay intervals were generated. The same delay orders were used for testing each sample size.

Stimulus sequences

Lists of 288 trial sequences were generated for each sample size. All locations were used equally often as a member of the sample for each sample size. Blocks of trials for the sample presentation were generated based on the minimum number of unique sample combinations that could be presented once per block. There were four trials per block for sample size one and sample size three. There were six trials per block for sample size two. All possible variations were used for each sample size and were not repeated until each variation had been used.

All locations were used equally often in choice test pairs. For sample size one a location was not used for more than three consecutive choice tests and could not be the correct or incorrect location for more than two consecutive trials. For sample size two and sample size three a location was not used for more than five consecutive choice tests and could not be the correct or incorrect location for more than four consecutive trials.

The training for each sample size began with the first trial in the sequence for that sample size list. Each successive session for that sample size list started with the next trial in the sequence. When trial 288 was

reached the next trial restarted the list. At the start of delay testing the starting trial for each sample size sequence was reset. The starting trial for sample size one was 216, for sample size two it was 1, and for sample size three the starting trial was 144.

Results

Definition of dependent measures

There were three types of trial outcomes. An aborted trial was a trial for which the peck requirement was not completed during the illumination of one of the sample stimuli. A completed trial was a trial for which a choice response had been made. A completed trial was correct if the nonsample key had been pecked and was incorrect if the sample had been pecked. The following variables were subjected to analysis: (1) Percentage correct, the total number of correct choices divided by the total number of completed trials. (2) Percentage abort, the total number of aborted trials divided by the total possible trials. (3) Start time, the time to peck the rear key and move to the front of the box to initiate the beginning of the sample presentation. The average start time was calculated by adding the start time for all completed trials and dividing by the total number of completed trials. (4) Actual delay, the programmed delay plus the time required to make the final peck after the designated interval had elapsed. The average for the actual delay was calculated for each programmed delay by adding the

actual delay for completed trials for the programmed delay and dividing by the total number of trials completed for the programmed delay. (5) Peck rate, the total number of pecks made during the programmed delay divided by the total number of completed trials for the programmed delay. (6) Choice time, the time from the onset of the choice stimuli until one of the choice stimuli had been pecked. The average choice time for the programmed delay was the total choice time for completed trials for that programmed delay divided by the total number of completed trials for that particular delay. A significance level of 0.05 was used for all analyses. Significant main effects and interactions were analyzed using an analysis of variance. The Newman-Keuls test was used for subsequent analyses which were carried out following significant F -ratios.

Data analysis

Acquisition

One scrub jay, Red, required smaller changes to bring the sample duration from 8 sec to 4 sec than the other birds. This change in procedure was needed for sample size one only. If the decrement in sample duration was too large, this bird would begin the trial but fail to meet the peck requirement necessary to complete the trial.

All birds met the performance criterion of a minimum percentage correct of 85% and a maximum percentage abort of 11% for three consecutive sessions for sample size one.

An ANOVA was performed for the number of days required for acquisition for sample size one with species and subjects within species as factors. There were no significant species differences for the number of sessions completed for sample size one.

One nutcracker, Greta, met the performance criterion for sample size two and one nutcracker, Johann, met the performance criterion for sample size three. All other birds received at least 75 sessions for these sample sizes. The number of days for individual birds for each sample size are shown in Table 3. Figure 4 shows the performance for percentage correct and percentage abort for the last three days of each acquisition stage for each species.

Baseline

The data for each bird were averaged for each sample size for blocks of two consecutive sessions. There were six blocks for each sample size. Five separate ANOVAs were performed with species, subjects within species, sample size and blocks as factors. The variables subjected to analysis were: (1) percentage correct, (2) percentage abort, (3) start time, (4) actual delay and (5) choice time. There were no significant interactions between species, sample size, and blocks for any of the five variables.

Significant main effects were obtained for all three factors for percentage correct. The performance of

nutcrackers was consistently better than the performance of scrub jays, $F(1,6)=6.99$, $p<.04$, (Figure 5).

Performance significantly decreased as the sample size increased, $F(2,12)=34.1$, $p<.001$, (Figure 5). Subsequent analysis showed that there were significant differences in percentage correct for all sample sizes. There was a significant effect of block, $F(5,30)=2.57$, $p<.05$. This effect was due to a small decrement in performance for the first three blocks (81.3%, 80.1%, 80.0%). Performance increased during block 4 and block 5 then decreased for block 6 (83.5%, 84.5%, 81.4%).

The only other significant effect was an increase in the probability of aborting as the sample size increased, $F(2,12)=12.8$, $p<.001$. The percentage abort for sample size one was 6.7%. For sample size two the percentage abort was 13.4%, and the percentage abort for sample size three was 21.4%.

The group averages for the start time, actual delay and choice time are shown in Table 4. No significant differences were obtained for species or sample size for any of these times during baseline.

Delay testing

Preliminary data analyses found that performance did not change as delay testing proceeded. Therefore data from the entire delay testing stage were used. The data for each bird were averaged for blocks of six sessions resulting in four quarters for each sample size. The

variables subjected to analysis were: (1) percentage correct, (2) percentage abort, (3) start time, (4) actual delay and (5) choice time. Five separate ANOVA's were performed with species, subjects within species, sample size and delays as factors.

The performance for each species at each sample size is shown in Figure 6. As during baseline training the performance of nutcrackers was better than the performance of scrub jays, $F(1,6)=8.6, p<.03$. Performance varied as a function of sample size, $F(2,12)=17.64, p<.001$. The percentage correct for sample size one, 73.5%, was higher than the other sample sizes. There were no differences in percentage correct between sample sizes two and three, 68.6% for both sample sizes. Performance also varied as a function of delay, $F(3,18)=22.9, p<.001$, (Figure 7). As the delay interval increased performance decreased. Subsequent analysis showed there were no differences in percentage correct for the 20 sec and the 30 sec delays. The percentage correct for all other delay comparisons were significantly different.

The only significant two way interaction was for sample size x delay, $F(6,324)=4.65, p<.001$, (Figure 8). The decrease in performance between the 0 sec and 10 sec delays was larger for sample size one than for the other two sample sizes. The species x sample size x delay interaction approached significance, $F(6,324)=1.9, p=.08$. This interaction, as shown in Figure 9, indicates that

there were no differences in the performance of nutcrackers and scrub jays for the 0 sec delay at sample size one. The performance of nutcrackers tended to be better than the performance of scrub jays at all other sample sizes and delays.

The only significant main effect for percentage abort was for sample size, $F(2,12)=65.5$, $p<.001$. The probability of aborting increased as the sample size increased. The percentage abort for sample size one was 10.6%, for sample size two the percentage abort was 19.9%, and for sample size three the percentage abort was 29%. The only significant two way interaction was for species x sample size, $F(2,12)=4.11$, $p<.05$, (Figure 10). The probability of aborting as sample size increased rose faster for scrub jays than for nutcrackers. The three way interaction did not approach significance, $p=.5$.

There were no significant main effects or interactions for start time or actual delay. Significant main effects were found for peck rate and for choice time. Peck rates were analyzed only for the delays that were scheduled to be longer than 0 sec. Peck rate increased as the sample size increased, $F(2,12)=8.36$, $p<.01$, and as the delay increased, $F(2,12)=31.3$, $p<.001$. The peck rate ranged from 0.83 pecks per sec for sample size one to 0.89 pecks per sec for sample size three. The peck rate for

the delay intervals ranged from 0.75 pecks per sec for the 10 sec delay to 0.94 pecks per sec for the 30 sec delay. There were no significant interactions for peck rate, all p 's $> .6$.

There was only one significant effect for choice time. Choice time increased as the delay interval increased, $F(3,18)=10.2$, $p < .001$. The choice time ranged from 2.4 sec for the 0 sec delay to 3.4 sec for the 30 sec delay.

Additional analyses

The data from the delay testing were subjected to three additional analyses. These analyses focused on the effects of proactive interference, the distance between choice keys, and primacy -- recency effects. In this section only statistics involving these factors are presented. Other F -ratios were redundant with those already presented for delay testing.

Proactive interference. The last 12 sessions for each sample size were used for this analysis. If performance during the session was affected by proactive interference, the result would be a decrease in percentage correct as the session progressed. Each session was divided into three blocks of 12 trials each. The percentage correct and percentage abort were calculated for each session block in the same manner as described for the session percentages.

Two ANOVAs were performed with species, subjects within species, sample size and blocks as factors. No significant main effect of block or two way interactions with block for percentage correct were found. There was a significant three way interaction for species x sample size x block, $F(4,24)=5.72$, $p<.003$, (Figure 11). The effect of proactive interference on the performance of nutcrackers was most obvious for sample size three. The performance of scrub jays was more variable during the session, with the middle of the session tending to have the poorest choice accuracy. The difference in performance for the sample sizes was replicated $F(2,12)=12.3$, $p<.002$, with sample size one still having the the highest, choice accuracy 73.8%. However, the percentage correct for sample size three, 70.6% was higher than the percentage correct for sample size two, 67.8%.

Percentage abort did not change over the session, $p>.1$. There was a significant two way interaction of sample size x block, $F(4,24)=6.7$, $p<.001$, (Figure 12). The only sample size that showed an increase in the probability of aborting over the course of the session was sample size three. There was a significant species x sample size x block interaction, $F(4,24)=4.0$, $p<.02$, (Figure 13). The probability of aborting for nutcrackers tended to decrease over the session, with the exception of

block 3 for sample size three. The probability of aborting for the scrub jays tended to decrease for block 2 for sample size one and sample size two and increased over the session for sample size three.

Distance between choice keys. The data were averaged across all sessions of delay testing for each sample size. The percentage correct and the choice time for correct trials were obtained for each distance and delay for each bird. There were three possible distances between the test keys: 0, 1 or 2 intervening keys for any choice test. Two ANOVA's were performed with species, subjects within species, sample size and delay as factors.

Performance decreased as the distance between choice keys increased, $F(2,12)=32.0$, $p<.001$. The percentage correct as the distance between choice keys increased from 0 to 2 intervening keys was: 66.2%, 73%, 77%. There were no significant interactions of distance between choice key on choice accuracy.

There was no significant effect of distance between choice keys on choice time. The choice time for the two species was affected differently by the distance between choice keys, $F(2,12)=4.5$, $p<.04$, (Figure 14). The choice time of the nutcrackers remained fairly constant, but the choice time of the scrub jays decreased as the distance between the choice keys increased.

Primacy recency effects. The data were averaged across all sessions of delay testing for sample size two and sample size three to determine if choice behavior was influenced by position of the sample in the list (list position) during the presentation of the sample items. A primacy effect would produce best performance for the sample presented first. A recency effect would produce best performance for the sample presented last. The percentage correct and correct choice time for each list position as a function of the sample choice stimulus was calculated for each programmed delay. Two ANOVA's were performed for each sample size with species, subjects within species, list position and delay as factors. There was no significant main effect or interactions with list position for the choice time analyses for sample size two and sample size three.

For sample size three, list position affected the choice performance, $F(2,12)=5.0$, $p<.03$. Choice accuracy was highest, 71.8%, for the last list position presented. Choice accuracy was lower for the first two list positions, but there were no differences between the percentage correct for these list positions, 67.1% and 67.4%. There was a significant interaction of list position x delay, $F(6,36)=6.8$, $p<.001$ (Figure 15). There

was a large decrease in choice accuracy for the last list position between the 0 sec and 10 sec delay. Choice accuracy for the first two list positions was unaffected by delay.

The results of the analysis for sample size two were similar to the results for sample size three. As in the case of sample size three the last list position had a higher choice accuracy, 71.7%, than the first list position, 65.6%, ($F(1,6)=10.3, p<.02$). There was also a significant list position x delay interaction, ($F(3,18)=6.8, p<.002$), (Figure 16). Choice accuracy for the last list position remained constant for delays above 0 sec, but choice accuracy for the first list position continued to decrease as the delays increased.

For both sample size two and sample size three performance on the last list position was superior to the other list positions. An analysis was performed to determine if there was any correlation between memory load and performance on the last list position. The number of items that are held in memory could differentially affect how well the last position is remembered, even though this position is always remembered best. The percentage correct for the last list position for each sample size was subjected to analysis with species, subjects within

species, sample size and delay as factors. There was no significant difference in the percentage correct for sample size one, 73.5%, sample size two, 71.7%, or sample size three, 71.8%.

Discussion

The results of this experiment support the findings of Experiment 1 and confirm the predictions that were made about species differences for memory load. The performance of nutcrackers was better than scrub jays regardless of sample size or delay. The superior performance of the nutcrackers was evident during the baseline condition, when no memory delay was imposed, and persisted through delay testing. These differences were not due to species differences in time to start a trial, time to make the last response to complete the delay interval, peck rate during a delay interval or choice time.

There was one behavioral difference, besides the difference in choice accuracy, between nutcrackers and scrub jays. The scrub jays were less willing to complete trials with increasing sample size during delay testing. The probability of aborting increased as the sample size increased for both species, but the increase in probability of aborting rose faster for scrub jays than nutcrackers. This species difference was not evident during the baseline condition when the delay was always 0 sec. The increase in the probability of aborting for the

scrub jays may have been due to the poorer ability of these birds to remember the sample. When the memory load was increased and coupled with an unknown delay interval this reduced percentage correct, thereby reducing reinforcement rate, which may have forced the scrub jays to abort more trials.

There were changes in the behavior of the birds that were not due to species differences, but were due to the effect of delay. Choice accuracy decreased as the delay increased. Choice time also increased as the delay interval increased. These results suggest there were no differences between nutcrackers and scrub jays in the rate at which memory for the sample decays. It is unlikely that the birds were able to predict what the delay interval was going to be on a particular trial, since there was no effect of delay on probability of aborting a trial.

Increases in memory load (sample size) decreased choice accuracy, but did not affect choice time. The lack of any choice time differences as a function of memory load is inconsistent with the human literature (Sternberg, 1966). This inconsistency may be due to the fact that times were accurate only to 0.1 sec.

The performance of nutcrackers was relatively unaffected by increases in sample size, especially at the short delay. This result is in contrast to the findings with pigeons in operant spatial matching-to-sample

procedures. Wilkie & Summers (1982) found that the performance of pigeons decreased when the sample size was increased from one sample to three samples. The performance of nutcrackers and scrub jays on sample size three was above chance for all retention intervals including the 30 sec delay. Smith et al. (1982) found that pigeons were able to maintain performance at above chance levels for less than 10 sec when presented with three simultaneous spatial locations. These findings indicate there may be species differences in spatial memory ability between scrub jays and pigeons when memory load and retention interval are varied.

Although the performance of nutcrackers and scrub jays decreased as the sample size increased, especially after longer retention intervals, the most recently presented sample was remembered equally well regardless of sample size or retention interval. These results for memory load are more similar to those for operant tasks than for cache recovery tasks. Kamil & Balda (1985) did not find any evidence of primacy or recency effects during cache recovery for nutcrackers. However, Wright et al. (1984) found primacy and recency effects for pigeons using picture stimuli. These effects were found with lists of four items and retention intervals under 6 sec. Longer list lengths or shorter retention intervals might produce primacy effects for nutcrackers and scrub jays. Further research is needed to determine whether the recency effect

is due to differences between the operant and cache recovery procedures or whether spatial information is encoded and/or retrieved differently depending on the task.

Consistent with the findings in Experiment 1, there was no effect of proactive interference during the session. In the current experiment neither the choice accuracy or the probability of aborting changed. This constant probability to abort a trial is important for two reasons. First, it indicates that there was no change in the motivation of the birds to either start or complete trials during the course of a session. Second, if there had been an increase in aborting as the session progressed this could have possibly increased the choice accuracy as the session progressed since there would have been longer times between trials.

Choice performance, however, was affected by the distance between choice keys. Performance was worst when the test keys were adjacent and improved with increasing distances between the keys. This is consistent with cache recovery experiments with nutcrackers (Kamil & Balda, 1985) and operant spatial matching-to-sample with pigeons (Wilkie & Summers, 1982).

The choice time of nutcrackers and scrub jays was affected differently as the distance between the test keys increased. The distance between choice keys had very little effect on the choice time of nutcrackers. The choice time of scrub jays decreased with increasing distances between the choice keys. Why these behavioral differences exist need to be explored further.

Table 3. Number of days completed by individual birds during the acquisition stage for each sample size (SS) in Experiment 2.

	<u>SS1</u>	<u>SS2</u>	<u>SS3</u>
Nutcrackers			
Adolf	41	79	75
Greta	47	63	75
Johan	34	75	43
Marcel	27	79	75
Scrub Jays			
Red	39	75	75
Violet	28	75	77
Green/Red	55	75	75
Orange/Blue	47	75	75

Table 4. Averages for completed trials during baseline for each species in Experiment 2. All times are in secs.

SPECIES	Start time	Actual delay	Choice time
Nutcrackers	4.8	2.2	2.2
Scrub Jays	5.1	2.6	2.2

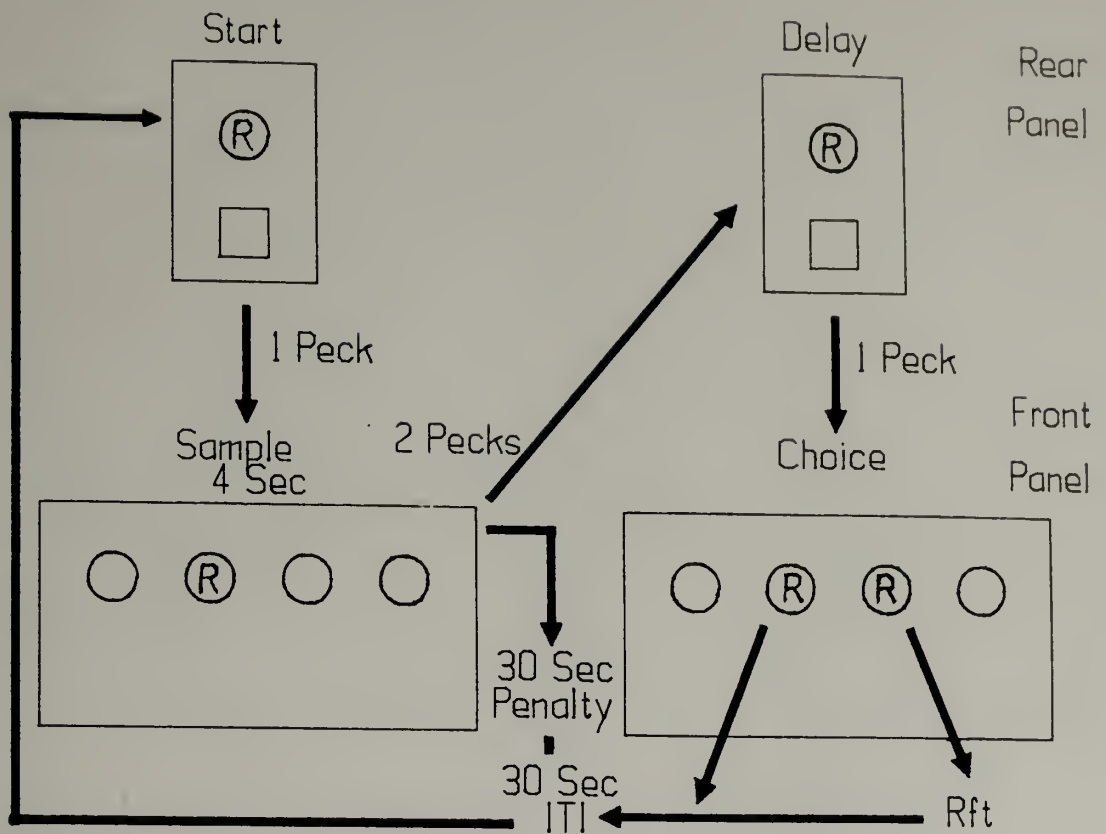


Figure 3. Flow diagram for a spatial nonmatching-to-sample trial for Experiment 2. The birds were required to move between the rear panel (the top panels in the figure) and the front panel (the bottom panels in the figure) during the trial. The circles inside the panels represent the pecking keys. The square box inside the rear panel represents the feeder used for presenting reinforcers. The arrows indicate the flow of events during the trial. Trial stages are labelled above the panels. The keys were illuminated with a red key light (R). The response requirement is shown below the rear panels for the start and delay stage. The one peck for the delay stage had to occur after the delay had timed out. The two peck response requirement for the sample stage (the bottom left panel) had to occur within 4 sec after the key was illuminated or the trial was terminated. The response requirement for the choice panel was one peck to either of the illuminated keys. A reinforcer was presented if the key that had been pecked was not the key presented as the sample.

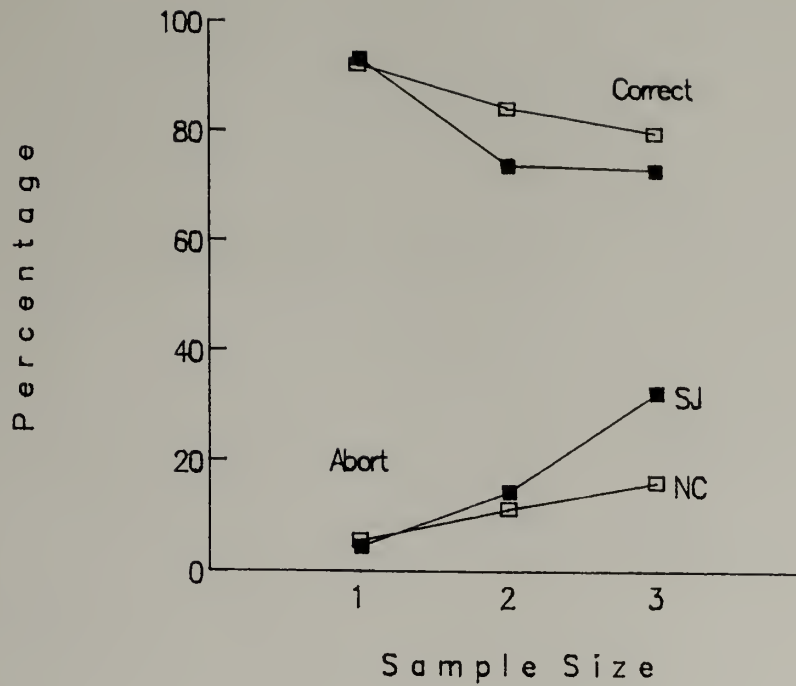


Figure 4. Performance of nutcrackers (NC), and scrub jays (SJ) as a function of sample size (number of to-be-remembered locations) for the last three days of acquisition in Experiment 2. The percentage correct represents trials that terminated after the two choice test. The percentage abort represents the trials which terminated before the two choice test.

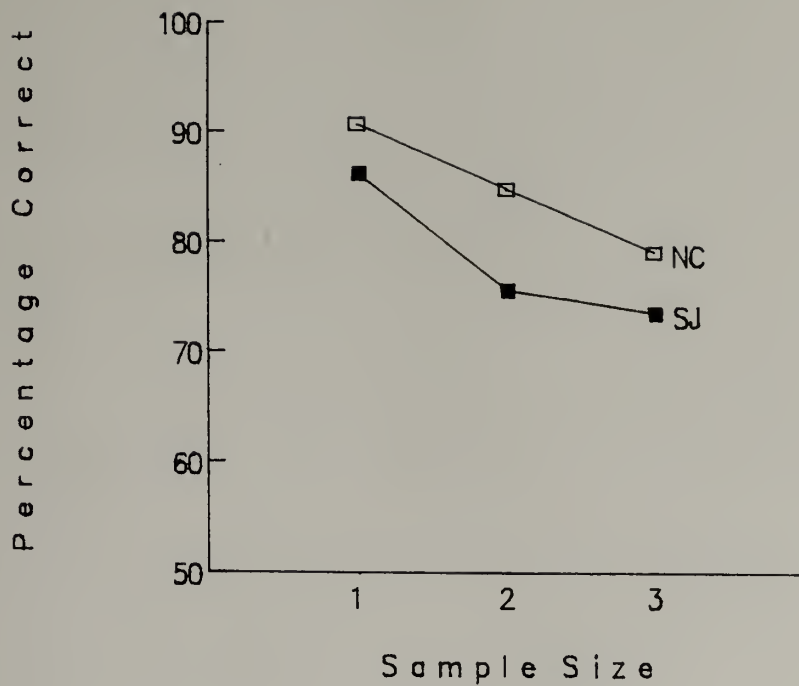


Figure 5. Performance of nutcrackers (NC), and scrub jays (SJ) as a function of sample size (number of to-be-remembered locations) during baseline in Experiment 2. Sample size was varied between sessions. The percentage correct represents performance on trials that terminated after the two choice test. There was no significant interaction between species and sample size.

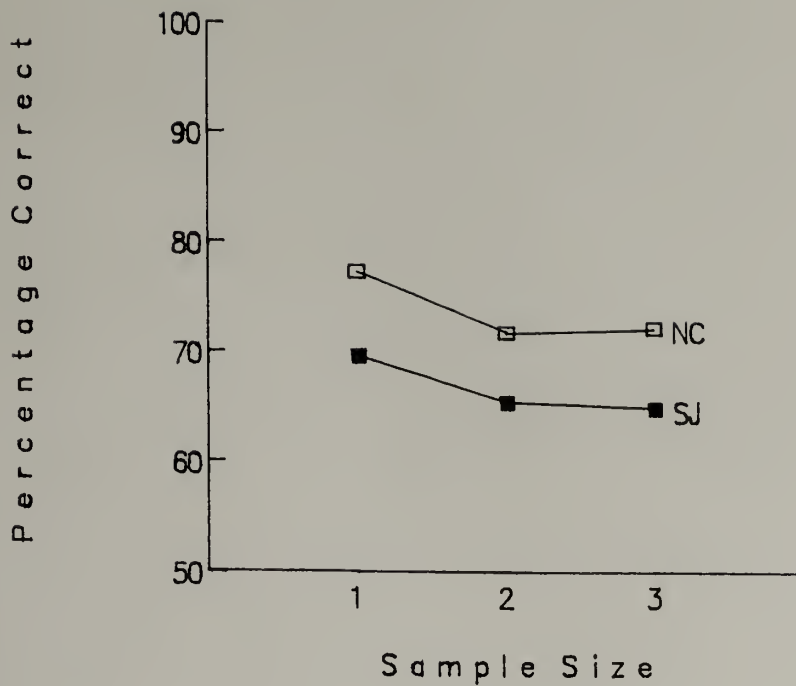


Figure 6. Performance of nutcrackers (NC), and scrub jays (SJ) as a function of sample size (number of to-be-remembered locations) during delay testing in Experiment 2. The percentage correct represents performance on trials that terminated after the two choice test. There was no significant interaction between species and sample size.

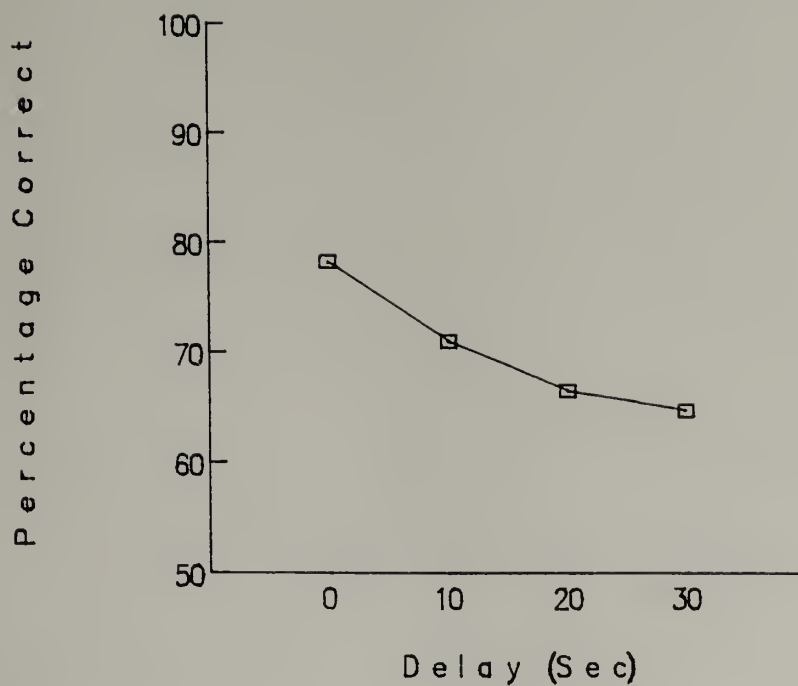


Figure 7. Performance as a function of retention interval (delay) during delay testing in Experiment 2. The percentage correct represents performance on trials that terminated after the two choice test.

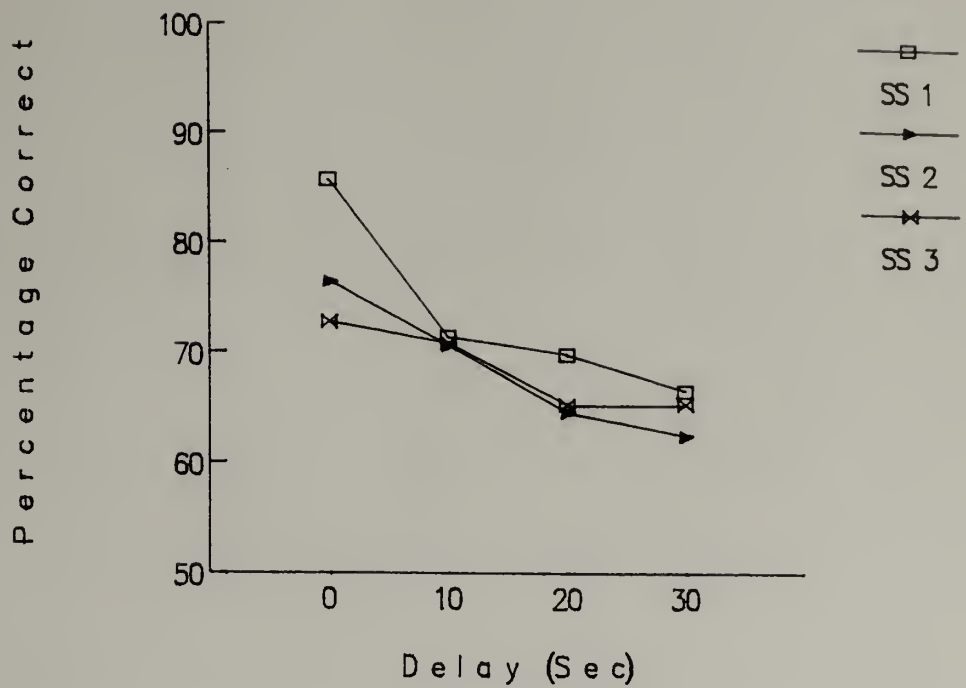


Figure 8. Performance as a function of sample size (SS), number of to-be-remembered locations, and retention interval (delay) during delay testing in Experiment 2. The percentage correct represents performance on trials that terminated after the two choice test.

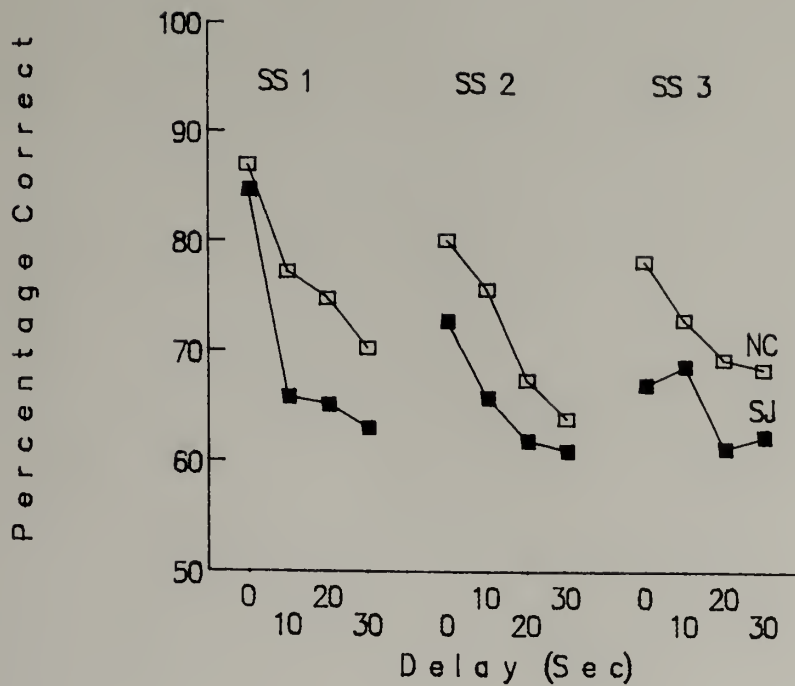


Figure 9. Performance of nutcrackers (NC), and scrub jays (SJ) as a function of sample size (SS), number of to-be-remembered locations, and retention interval (delay) during delay testing in Experiment 2. The percentage correct represents performance on trials that terminated after the two choice test. The three way interaction approached significance, $p=.08$.

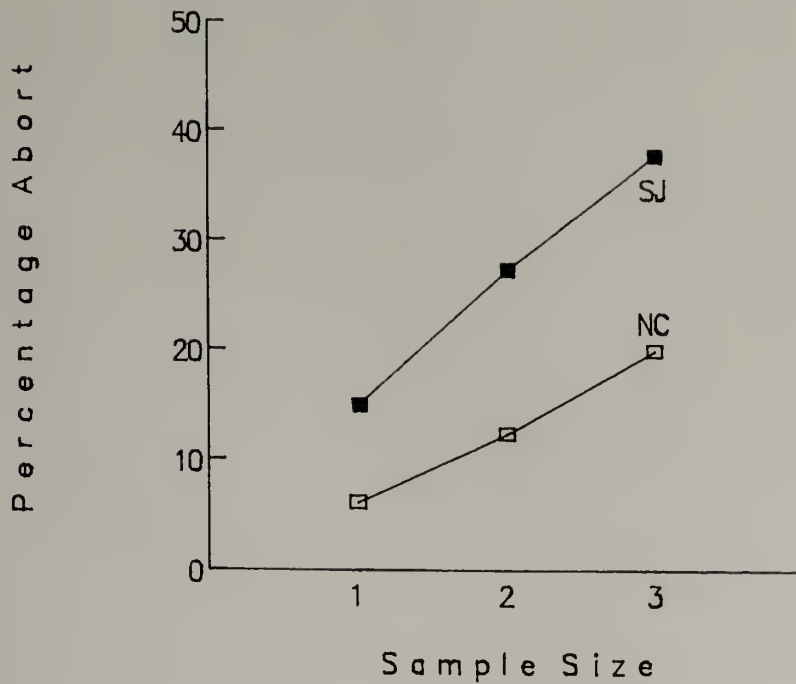


Figure 10. Performance of nutcrackers (NC), and scrub jays (SJ) as a function of sample size (number of to-be-remembered locations) during delay testing in Experiment 2. The percentage abort represents the trials that terminated before the presentation of the two choice test. There was a significant interaction between species and sample size.

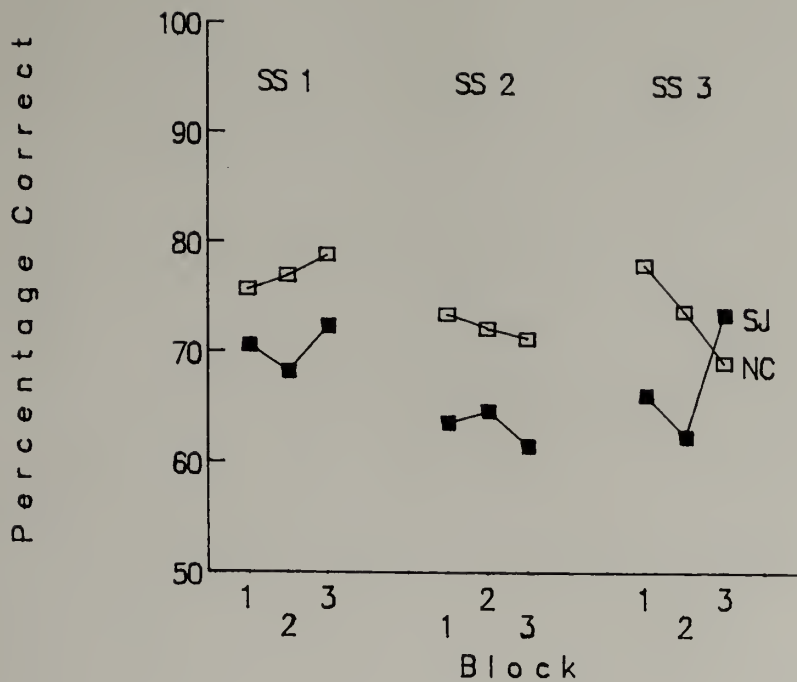


Figure 11. Performance of nutcrackers (NC), and scrub jays (SJ) as a function of sample size (SS), number of to-be-remembered locations, and trials into the session (block) during delay testing in Experiment 2. Sessions were divided into three 12 trial blocks. The percentage correct represents performance on trials that terminated after the two choice test. The three way interaction was significant.

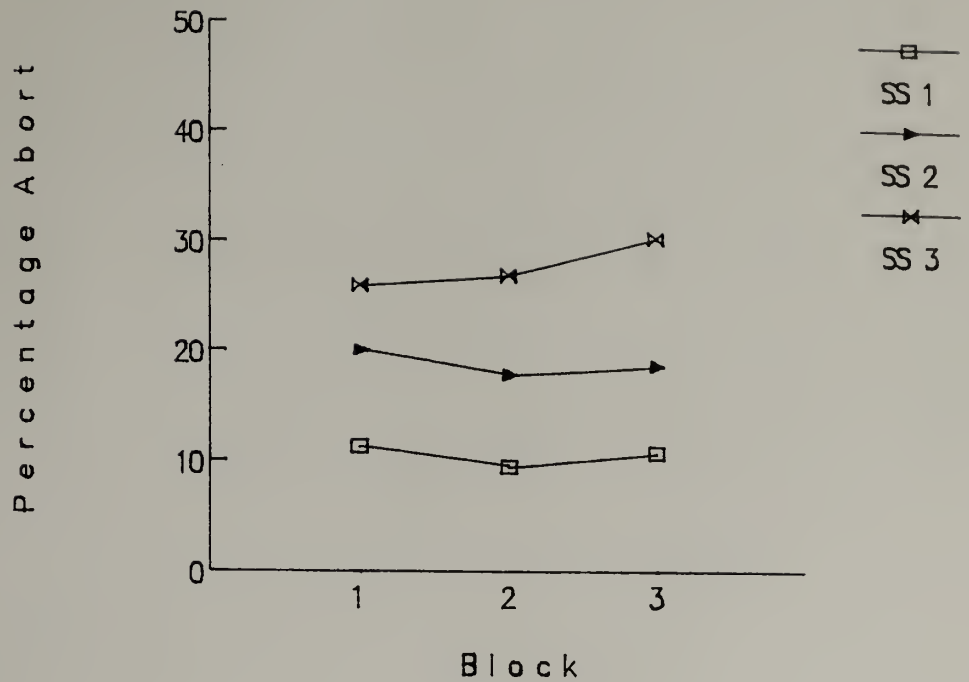


Figure 12. Performance for each sample size (SS), number of to-be-remembered locations, as a function of trials into the session (block) during delay testing in Experiment 2. Sessions were divided into three 12 trial blocks. The percentage abort represents trials that terminated before the presentation of the two choice test. There was a significant interaction between sample size and block.

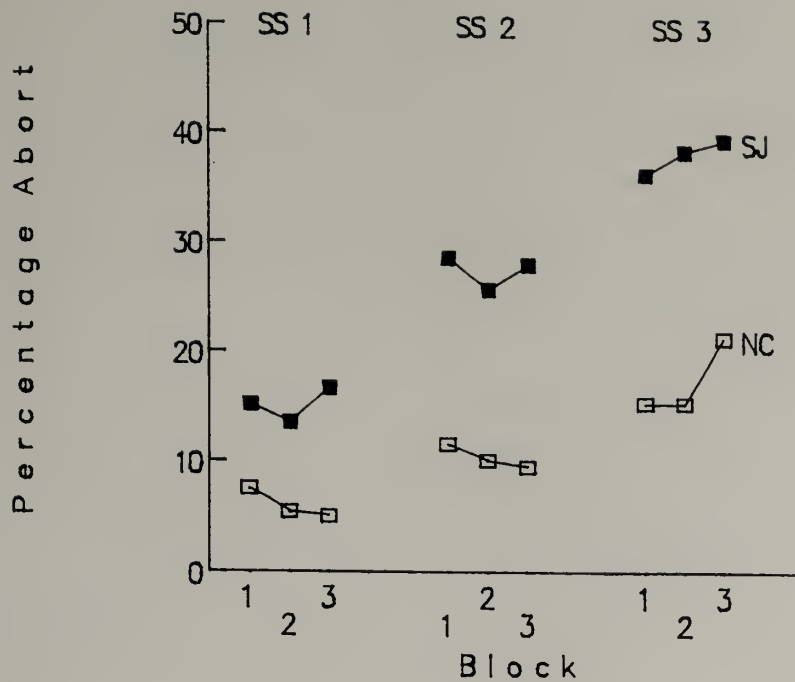


Figure 13. Performance of nutcrackers (NC), and scrub jays (SJ) as a function of sample size (SS), number of to-be-remembered locations, and trials into the session during delay testing in Experiment 2. Sessions were divided into three 12 trial blocks. The percentage abort represents trials that terminated before the presentation of the two choice test. There was a significant three way interaction.

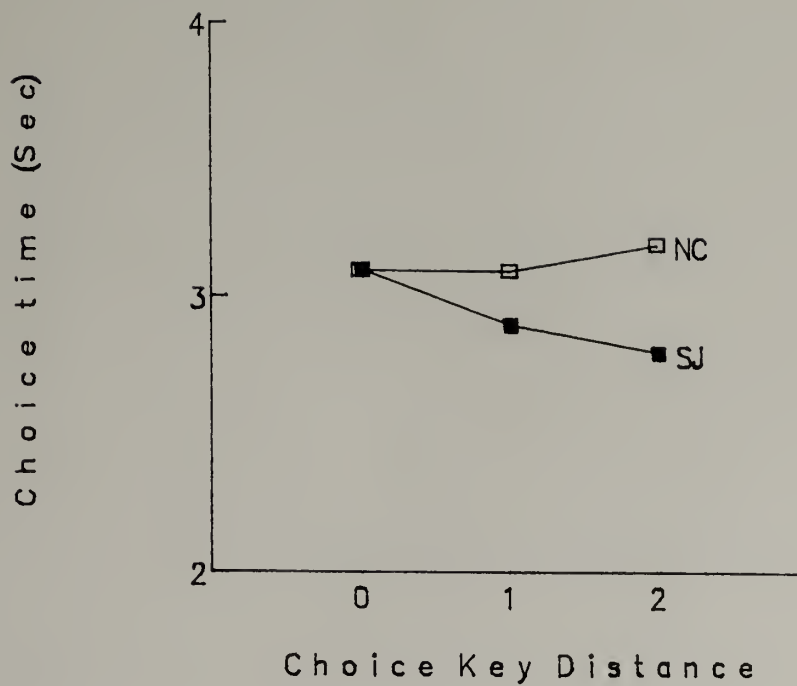


Figure 14. Time to peck one of the keys in the two choice test (choice time) by nutcrackers (NC), and scrub jays (SJ) as a function of the number (distance) of keys between the the two stimuli during delay testing in Experiment 2.

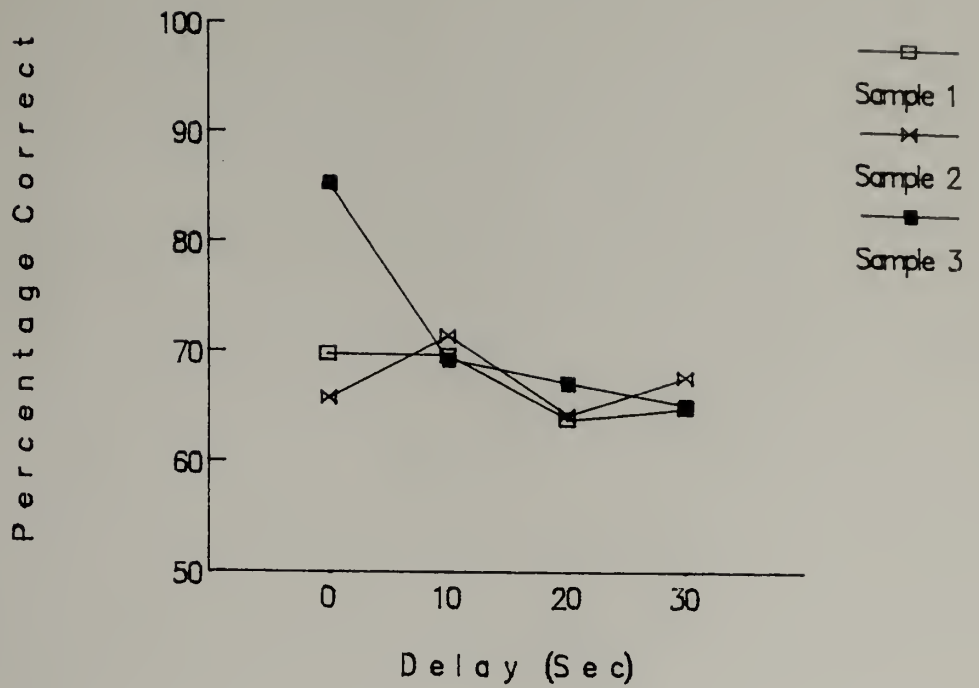


Figure 15. Performance when there were three to-be-remembered locations as a function of list position (sample) and retention interval (delay) during delay testing in Experiment 2. The percentage correct represents performance on trials that terminated after the two choice test.

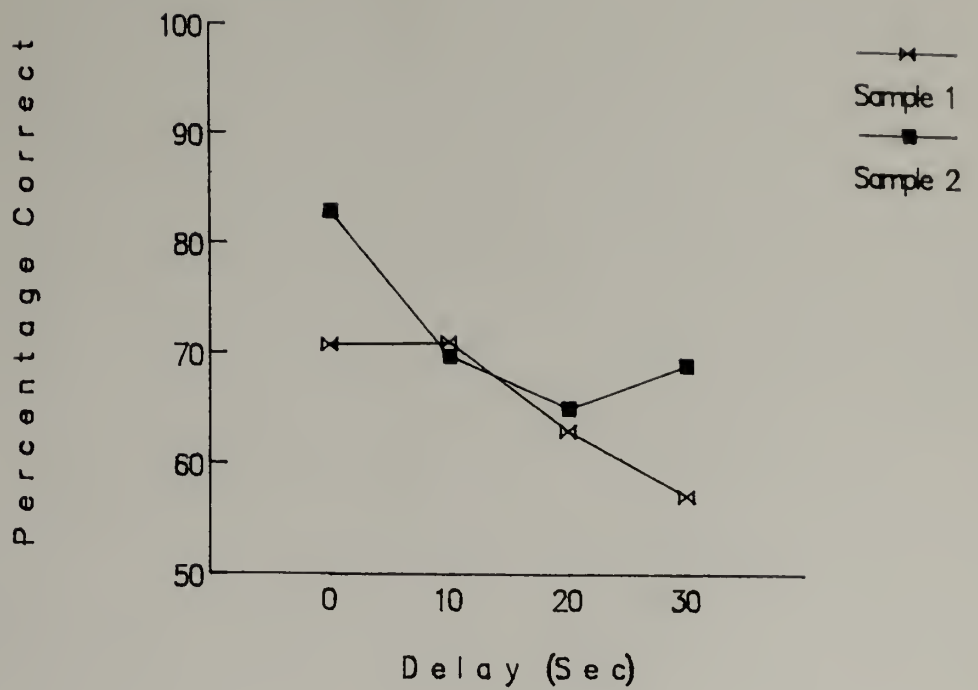


Figure 16. Performance when there were two to-be-remembered locations as a function of list position (sample) and retention interval (delay) during delay testing in Experiment 2. The percentage correct represents performance on trials that terminated after the two choice test.

CHAPTER 4

GENERAL DISCUSSION

This research has focused on memory for the spatial location of stimuli using operant nonmatching-to-sample. There are several relevant theoretical issues: (1) the role of natural history in empirical research, (2) the nature of memory systems, (3) differential rates of acquisition, and (4) the relationships between interference, stimulus duration and memory.

Natural history and empirical research

The predictions about species differences in spatial memory relied on prior knowledge about the natural history of the nutcrackers and scrub jays. The idea that natural history should be used to guide research has been used extensively in biology and is not new to psychology. The encouragement for psychologists to use a variety of species is not new, but has often been ignored (Hodos & Campbell, 1964; Beach, 1950). Recently there has been a resurgence of interest in using evolution and natural history to guide research (Kamil, 1988; Rosenzweig & Glickman, 1985; Shettleworth, 1985). Theoretical papers have attempted to show how these concepts might be important. For example, Crawford (1989) stressed that evolutionary theory and the use of evolutionary principles

can and should be used to make predictions and testable hypotheses about human behavior. However, evolution and natural history must be used properly. This is true whether the research is concerned with a single species or with comparisons between species.

Comparative research particularly requires the greatest caution. Mackintosh et al. (1985) have advocated using multiple tasks to determine species differences. They argue that the role of evolution should not be considered until species differences have been documented. This guideline, if applied, would result in undirected comparative work, as has too often characterized comparative psychology in the past. Many classes and/or orders of species would need to be tested on many different tasks without any a priori reasons for choosing those species. Evolutionary and natural history explanations would, perforce, be used only in a post hoc manner as happens too often.

The guidelines presented by Kamil (1988) suggest a way to give direction to programs of comparative research on learning and/or memory, although these guidelines may also be applied to research with a single species. As indicated in the introduction the two most important aspects of these guidelines are (1) an a priori reason for choosing the species and (2) using more than one task to test for species differences.

If these guidelines are followed, they will allow research programs to focus on the similarities and differences between species. We will begin to understand the relationship between the process of natural selection and the ability of animals to learn about their environment. This understanding will help to discern how and why there are differences in the ability of species to learn and/or remember information.

This approach is in direct contrast with that of Macphail (1985a, 1985b). According to Macphail no species differences in "intelligence" have been demonstrated among nonhuman vertebrates (MacPhail, 1985a). Macphail reaches this conclusion because of his approach to what are often called contextual variables. In any single experiment, species differences need not be due to species differences in ability. They could be due to the context of the experiment being more appropriate for one species than another. Although MacPhail is correct in following Bitterman (1965) in identifying this problem, his approach, like Bitterman's is doomed to fail. It requires eliminating all possible contextual variables and, as Kamil (1988) has pointed out, this is equivalent to trying to prove a null hypothesis.

Nonetheless, the contextual variable problem must eventually be surmounted. In order to accomplish this goal, Kamil (1988) suggested the approach based upon the use of multiple tasks to compare species selected on the

basis of their ecology. If species differences are found to be consistent across a variety of tasks, the probability that species differences are due to contextual variables is decreased. Therefore, our confidence in the validity of the species difference as differences in cognitive ability are increased. If a sufficient number of independent tests based on different techniques produce consistent results, contextual variables will have been almost eliminated as an explanation for species differences.

It would be difficult to use contextual variables as an explanation for the spatial memory differences between the nutcrackers and other birds that appear in a growing body of empirical evidence. Field work has shown that there are species differences in dependence on cached food (Vander Wall & Balda, 1981) and indicate that the nutcrackers remember cache locations for months (Tomback, 1980). Laboratory research has found that nutcrackers use spatial memory to locate caches they have previously made (Kamil & Balda, 1985; Vander Wall, 1982) and that memory for cache locations is better for the nutcrackers than the scrub jays (Balda & Kamil, in press). Finally, the radial maze work that has been done with nutcrackers (Balda & Kamil, 1988) shows that their ability to use spatial information is not limited to cache recovery and indicates that there may be differences between the nutcrackers and the pigeons.

In this context the species differences reported here are particularly significant. The operant task is dramatically different from the field situation, from the laboratory cache recovery situation, and from the radial maze analogue, yet there were species differences. The performance of nutcrackers was better for longer retention intervals and for larger sample sizes than the performance of the scrub jays. These consistent species differences across very different paradigms offer strong support for the conclusion that species differ in the ability to remember spatial information.

Nature of memory systems

The concept of different types of memory systems for different types of knowledge has been suggested in both the human (ie. Tulving, 1985; Craik, 1985) and animal (Honig, 1978) literature. Those scientists who study animals have suggested that information that is held for short periods of time is stored in short term or working memory. Information that is held for long periods is stored in long term or reference memory. Long term memory has been further subdivided in the human literature into procedural memory, the rules to solve problems and various other types of memory, all which have some common feature of memory of events. This distinction has arisen because it is possible to learn the rules of the task without any memory for the specific events (see Schacter, 1985; Maki, 1979).

Sherry & Schacter (1987) have proposed that some types of memory have evolved because of specific environmental problems that some animals confront. If existing memory systems could not efficiently resolve the problem, specific memory systems might evolve. One system these authors cite as a specific memory system concerns song in birds. They present the hypothesis that there may be a specific memory system that has evolved in food caching birds, although they indicate that there is not enough evidence yet to confirm this fact.

A memory system is defined by the rules that operate on the acquisition, retention and retrieval of information. In order for memory systems to be different, they must show differences in acquisition, retention and retrieval, although there may be some overlap between systems. Although a new memory system may evolve to handle some environmental problem, it is also possible that an existing system would be flexible enough to be used in the new situation.

This raises a central question: If a spatial memory system had already evolved in birds, would a separate system for cache recovery have evolved in caching specialists? It is too soon to answer this question definitively, but some trends have begun to emerge. First, the spatial memory abilities of the nutcrackers are not limited to the caching situation. If a specialized memory system for caching food has evolved in the

nutcrackers, then this system is not so specialized that it is limited to cache and recovery. Second, nutcrackers are able to remember spatial information, in several different spatial tasks, for long periods of time when compared to other birds. However, even for the nutcrackers, there are differences in performance across tasks. Whether this is due to the constraints imposed by the task or to differences in how the information is encoded and/or retrieved has yet to be determined. If the differences are due to differences in information encoding and/or retrieval this finding would be quite interesting. It would imply that there is flexibility for how information is stored depending on how that information is acquired.

Determining whether the differences in the performance of nutcrackers across tasks are due to the task or to the storage and/or retrieval of information will require further research. Spatial information that is encoded for cache sites, locations visited in the radial maze and locations presented in operant nonmatching-to-sample task (Experiment 2) can be considered to be a list, since to-be-remembered spatial locations are encountered sequentially. If the information is stored as a list and spatial cues can be used to improve retrieval, then performance in the operant procedure might be expected to be poorer than the cache recovery and the radial maze, because there are fewer

spatial cues available. Alternatively the large number of trials used per session in the operant task may be producing enough proactive interference so that retrieval of information is affected, even though no effect of proactive interference within a session was found in Experiment 1 or Experiment 2.

Vauclair (1985) has proposed that spatial information that is obtained sequentially can be available for simultaneous use if spatial capacities are highly organized. Vauclair suggests that food storing birds might be able to access memories of cache locations simultaneously rather than sequentially. This ability to recode spatial information, if it exists, would account for the lack of primacy or recency effects during cache recovery in the nutcrackers (Kamil & Balda, 1985). If a system like this did exist and could be adapted for use in the the operant task this might also account for the lack of primacy effects in Experiment 2.

There are two more likely explanations that might explain why there were no primacy effects in Experiment 2. First, there may not have been enough samples to be able to get the primacy effect. Second, Wright et al. (1984) have found the the primacy effect in pigeons is most evident with delays under 6 sec. If the primacy effect in tasks using operant procedures is this short in all avian species, even the shortest actual delay, generally a minimum of 2 sec, may have been too long to obtain the

primacy effect for the nutcrackers and scrub jays. Nonetheless the ability to recode spatial information remains an interesting hypothesis for the nutcrackers.

Differential rates of acquisition

There are two ways in which the nutcrackers, scrub jays and pigeons could have shown species differences in rates of acquisition in Experiment 1. First, there could be differences between the species. Shettleworth (1985) has suggested that the cache recovery abilities of birds such as the nutcracker or the chickadee might enable them to show faster acquisition on spatial tasks when compared to other noncaching birds. Second, contextual variables present in the apparatus might have affected the species differentially, resulting in differences in rates of acquisition. Although the number of days spent in acquisition were not analyzed for Experiment 1, because of the slightly different procedures, the number of days in acquisition was 36 days for nutcrackers, 35.8 days for scrub jays and 31 days for pigeons. It is apparent that the cache recovery ability of nutcrackers and scrub jays did not enable them to learn the spatial nonmatching-to-sample task faster than pigeons in Experiment 1.

The results of Experiment 2 indicate that dependence on cached food is uncorrelated with the rate of acquisition in the operant task. There were no differences between the number of days spent in each stage of acquisition for nutcrackers and scrub jays.

The caching abilities of nutcrackers and scrub jays did not give these birds any advantage in learning the spatial nonmatching task. This does not necessarily lead to the conclusion that caching will not have any effect on learning for all tasks.

There was no attempt to manipulate contextual variables in either experiment. Therefore, there is no way to determine if any species did use contextual variables, resulting in an increased rate of acquisition. If contextual cues had been used by any species, this might change the conclusions that were made about the correlation between the natural ecology and rate of acquisition.

Relationships between interference, stimulus duration, and memory

One way evolution could affect memory systems is by affecting the ability of the system to resist interference from outside sources. During experimental tests this would be revealed by changes in proactive and retroactive interference. The analyses of proactive interference for Experiment 1 and Experiment 2 showed there was no effect of proactive interference during the session. It is

possible that information in spatial memory may be resistant to interference. This would be advantageous if survival was dependent on remembering spatial information. The cache recovery of the nutcrackers appears to be resistant to interference when multiple cache sessions have been used (Kamil & Balda, 1985).

There may also be differential effects of interference based on the modality of the information and possibly the memory system that is used. The effect of differential interference depending on modality may have an evolutionary basis. As pointed out above, the more relevant the information is to survival, the more resistant it might be to interference. Spatial information is probably important to almost all animals and could be expected to be equally resistant to interference for all species.

There is some indication that the performance of pigeons appears to be differentially affected by interfering events depending on the modality. Performance is affected differently by retroactive interference depending on whether the modality is color matching-to-sample (ie. Maki et al, 1977; see also Grant, 1988) or spatial matching-to-sample (Wilkie, 1984). When the interfering event is the onset of an unexpected light, choice accuracy in color matching-to-sample decreases. But unexpected light does not effect choice accuracy in spatial matching-to-sample. The effect of retroactive

spatial events on performance in spatial matching-to-sample depends on the relationship between the to-be-remembered information and the interfering event. Wilkie (1984) found that using irrelevant spatial keys as the retroactive event did not effect performance. When the retroactive event was one of the keys for the choice test performance was affected during the choice test. If the key was the to-be-correct choice, performance was improved and if the key was the to-be-incorrect choice, performance was decreased.

Memory for the stimulus has generally been shown to improve with longer exposure to the to-be-remembered stimulus for color matching-to-sample (Roberts & Grant, 1974) and spatial matching-to-sample (Wilkie, 1983). If there is no upper limit for stimulus exposure, the performance of the pigeons in Experiment 1 should have been superior when compared with other experiments. The average stimulus duration was 16 sec for the pigeons. But, the retention intervals achieved by the pigeons in Experiment 1 did not differ significantly from other experiments using pigeons in spatial matching-to-sample (Wilkie, 1984), where the stimulus durations are generally between 1 sec and 5 sec. The lack of differences between the performance of pigeons in the experiments indicates there may be duration after which longer exposure does not result in any improvement of performance.

This would be true if there was an interval at which complete transfer of information to memory was achieved. If this were the case, longer exposure to the stimulus may not affect memory for that stimulus. The complete transfer of information would allow for better retention with a strong memory trace, therefore increasing the accuracy. This raises at least two interesting questions. First, are there differences between species and/or modalities for complete transfer of information to memory. Second, for birds that cache and recover food, what role if any would this have on their performance during cache recovery.

Conclusion

One advantage of the current experiments was that the same procedure was used for all species. This eliminates the problem of trying to make comparisons and draw conclusions about species differences when slightly different procedures have been used. These procedures can also be used to test different modalities, such as color, with no changes in the procedure except to use colors as sample and choice stimuli. This will allow for direct comparisons between different modalities and increase the validity of the results.

Retention of spatial information was superior for nutcrackers when compared to either scrub jays or pigeons. The nutcrackers were able to remember more spatial locations than scrub jays. The number of spatial

locations nutcrackers will be able to remember in the operant nonmatching-to-sample has not yet been determined. Both the better retention of spatial information and ability to remember more spatial locations were predicted based on the foraging ecology of the species. The results show that dependence on spatial memory in the natural environment was a good predictor of species differences. When combined with the results of comparative cache recovery experiments (Balda & Kamil, in press) and radial maze research, they provide strong evidence for the existence of species differences in spatial memory.

REFERENCES

- Balda, R. P. (1980a). Recovery of cached seeds by a captive Nucifraga caryocatactes. Z. Tierpsychol., 52, 331-346.
- Balda, R. P. (1980b). Are seed-caching systems co-evolved? In R. Nohring (Ed.), Acta XVI Congressus Internationalis Ornithologicic (pp. 1185-1191). Berlin: Deutsche Ornithologen-Gesellschaft.
- Balda, R. P., & Kamil, A. C. (1988). The spatial memory of Clark's nutcrackers (Nucifraga columbiana) in an analogue of the radial maze. Animal Learning & Behavior, 16, 116-122.
- Balda, R. P., & Kamil, A. C. (in press). A comparative study of cache recovery by three corvid species. Animal Behaviour.
- Beach, F. A. (1950). The snark was a boojum. American Psychologist, 5, 115-124.
- Bitterman, M. E. (1965). Phyletic differences in learning. American Psychologist, 20, 396-409.
- Bock, W. J., Balda, R. P., & Vaner Wall, S. B. (1973). Morphology of the sublingual pouch and tongue musculature in Clark' nutcracker. Auk, 90, 491-519.
- Bunch, K. G., & Tomback, D. F. (1986). Bolus recovery by gray jays: An experimental analysis. Animal Behaviour, 34, 754-762.
- Craik, F. I. M. (1985). Paradigms in human memory research. In L. Nilsson, & T. Archer (Eds.), Perspectives on Learning and Memory (pp 179-222). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Crawford, C. B. (1989). The theory of evolution: Of what value to psychology?. Journal of Comparative Psychology, 103, 4-22.
- Grant, D. G. (1988). Sources of visual interference in delayed matching-to-sample with pigeons. Journal of Experimental Psychology: Animal Behavior Processes, 14, 368-375.
- Grant, D. S., & Roberts, W. A. (1976). Inhibition in pigeon short-term memory. Journal of Experimental Psychology: Animal Behavior Processes, 2, 1-16.

- Fellows, B. J. (1967). Chance stimulus sequences for discrimination tasks. Psychological Bulletin, 67, 87-92.
- Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. Psychological Review, 76, 337-350.
- Honig, W. K. (1978). Studies of working memory in the pigeon. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), Cognitive Processes in Animal Behavior (pp 211-248). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Kamil, A. C. (1988). A synthetic approach to the study of animal intelligence. In D. W. Leger (Ed.), Comparative Perspectives in Modern Psychology: Nebraska Symposium on Motivation, Vol. 35 (pp 257-308). Lincoln, Nebraska: University of Nebraska Press.
- Kamil, A. C., & Balda, R. P. (1985). Cache recovery and spatial memory in Clark's nutcrackers. Journal of Experimental Psychology: Animal Behavior Processes, 11, 95-111.
- Mackintosh, N. J., Wilson, B., & Boakes, R. A. (1985). Differences in mechanisms of intelligence among vertebrates. In L. Weiskrantz (Ed.), Animal Intelligence (pp53-65). Oxford: Clarendon Press.
- Macphail, E. M. (1985a). Vertebrate intelligence: The null hypothesis. In L. Weiskrantz (Ed.), Animal Intelligence (pp 37-51). Oxford: Clarendon Press.
- Macphail, E. M. (1985b). Ecology and intelligence. In N. Weinberger, & J. McGaugh (Eds.), Memory Systems of the the Brain (pp 279-286). New York: Guilford Press.
- Maki, W. S. (1979). Discrimination learning without short-term memory processes in pigeons. Science, 204. 83-85.
- Maki, W. S., Jr., Moe, J. C., & Bierley, C.M. (1977). Short-term memory for stimuli, responses, and reinforcers. Journal of Experimental Psychology: Animal Behavior Processes, 3, 156-177.
- Mewaldt, L. R. (1956). Nestling behavior of the Clark nutcracker. The Condor, 58, 3-23.
- Roberts, W. A., & Grant D. S. (1974). Short-term memory in the pigeon with presentation time precisely controlled. Learning & Motivation, 5, 393-408.

- Roberts, W. A., & Van Veldhuizen, N. (1985). Spatial memory in pigeons on the radial maze. Journal of Experimental Psychology, 11, 241-260.
- Roitblat, H. L., & Harley, H. E. (1988). Spatial delayed matching-to-sample performance by rats: Learning, Memory, and proactive interference. Journal of Experimental Psychology: Animal Behavior Processes, 14, 71-82.
- Rosenzweig, M. R., & Glickman, S. E. (1985). Comparisons of learning abilities among species. In N. Weinberger, J. McGaugh & G. Lynch (Eds.), Memory Systems of the Brain (pp 296-307). New York: Guilford Press.
- Schacter, D. L. (1985). Multiple forms of memory in humans and animals. In N. Weinberger, J. McGaugh & G. Lynch (Eds.), Memory Systems of the Brain (pp 351-379). New York: Guilford Press.
- Sherry, D. (1984). Food storage by black-capped chickadees: Memory for the location and contents of caches. Animal Behaviour, 32, 451-464.
- Sherry, D. F., Krebs, J. R., & Cowie, R. J. (1984). Memory for the location of stored food in marsh tits. Animal Behaviour, 29, 1260-1266.
- Sherry, D. F., & Schacter, D. L. (1987). The evolution of multiple memory systems. Psychological Review, 95, 439-454.
- Shettleworth, S. J. (1985). Food storing by birds: Implications for comparative studies of memory. In N. Weinberger, J. McGaugh & G. Lynch (Eds.), Memory Systems of the Brain (pp 231-250). New York: Guilford Press.
- Shettleworth, S. J., & Krebs J. R. (1982). How marsh tits find their hoards: The roles of site preference and spatial memory. Journal of Experimental Psychology: Animal Behavior Processes, 8, 354-375.
- Smith, J. P., Attwood, J. C., & Niedorowski, L. (1982). Delayed choice responding by pigeons when correct response is not predictable from the sample stimulus. Journal of the Experimental Analysis of Behavior, 37, 57-63.
- Spetch, M. L., & Edwards, C. A. (1986). Spatial memory in pigeons (Columba livia) in an "open-field" environment. Journal of Comparative Psychology, 100, 279-284.

- Spetch, M. L., & Honig, W. K. (1988). Characteristics of pigeons' spatial working memory in an open-field task. Animal Learning & Behavior, 16, 123-131.
- Sternberg, S. (1966). High-speed scanning in human memory. Science, 153, 652-654.
- Tomback, D. F. (1977). Foraging strategies of the Clark's nutcrackers. Living Bird, 16, 123-161.
- Tomback, D. F. (1980). How nutcrackers find their seed stores. The Condor, 82, 10-19.
- Tulving, E. (1972). Episodic & semantic memory. In E. Tulving & W. Donaldson (Eds.), Organization of memory (pp 381-403). New York: Guilford Press.
- Tulving, E. (1985). How many memory systems are there? American Psychologist, 40, 385-398.
- Vander Wall, S. B. (1982). An experimental analysis of cache recovery in Clark's nutcrackers. Animal Behaviour, 30, 84-94.
- Vander Wall, S. B., & Balda, R. P. (1977). Coadaptions of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecological Monographs, 47, 89-111.
- Vander Wall, S. B., & Balda, R. P. (1981). Ecology and evolution of food-storage behavior in conifer-seed-caching-corvids. Z. Tierpsychol., 56, 217-242.
- Vauclair, J. (1985). A comparative approach to cognitive mapping. In P. Ellen, & C. Thinus-Blanc (Eds.) Cognitive Process and Spatial Orientation in Animal and Man (pp. 89-96). Dordrecht, The Netherlands: Martinus Nijhoff Publishers.
- Wilkie, D. M. (1983). Pigeons spatial memory: Matching of key location. Journal of the Experimental Analysis of Behavior, 40, 143-151.
- Wilkie, D. M. (1984). Pigeons spatial memory: IV. Effects of intertrial interval manipulation on delayed matching of key location. Canadian Journal of Psychology, 38, 178-195.

Wilkie, D. M., & Summers, R. J. (1982). Pigeon's spatial memory: factors affecting delayed matching of key location. Journal of the Experimental Analysis of Behavior, 37, 45-56.

Wright, A. A., Santiago, H. C., Sands, S. F., & Uricuioli, P. J. (1984). Pigeon and monkey serial probe recognition: Acquisition, strategies, and serial position effects. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), Animal cognition (pp. 353-373). Hillsdale, NJ: Erlbaum Associate.

BIBLIOGRAPHY

- Balda, R. P. (1980a). Recovery of cached seeds by a captive Nucifraga caryocatactes. Z. Tierpsychol., 52, 331-346.
- Balda, R. P. (1980b). Are seed-caching systems co-evolved? In R. Nohring (Ed.), Acta XVI Congressus Internationalis Ornithologicic (pp. 1185-1191). Berlin: Deutsche Ornithologen-Gesellschaft.
- Balda, R. P., & Kamil, A. C. (1988). The spatial memory of Clark's nutcrackers (Nucifraga columbiana) in an analogue of the radial maze. Animal Learning & Behavior, 16, 116-122.
- Balda, R. P., & Kamil, A. C. (in press). A comparative study of cache recovery by three corvid species. Animal Behaviour.
- Beach, F. A. (1950). The snark was a boojum. American Psychologist, 5, 115-124.
- Bitterman, M. E. (1965). Phyletic differences in learning. American Psychologist, 20, 396-409.
- Bock, W. J., Balda, R. P., & Vaner Wall, S. B. (1973). Morphology of the sublingual pouch and tongue musculature in Clark' nutcracker. Auk, 90, 491-519.
- Bunch, K. G., & Tomback, D. F. (1986). Bolus recovery by gray jays: An experimental analysis. Animal Behaviour, 34, 754-762.
- Craik, F. I. M. (1985). Paradigms in human memory research. In L. Nilsson, & T. Archer (Eds.), Perspectives on Learning and Memory (pp 179-222). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Crawford, C. B. (1989). The theory of evolution: Of what value to psychology?. Journal of Comparative Psychology, 103, 4-22.
- Grant, D. G. (1988). Sources of visual interference in delayed matching-to-sample with pigeons. Journal of Experimental Psychology: Animal Behavior Processes, 14, 368-375.
- Grant, D. S., & Roberts, W. A. (1976). Inhibition in pigeon short-term memory. Journal of Experimental Psychology: Animal Behavior Processes, 2, 1-16.

- Fellows, B. J. (1967). Chance stimulus sequences for discrimination tasks. Psychological Bulletin, 67, 87-92.
- Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. Psychological Review, 76, 337-350.
- Honig, W. K. (1978). Studies of working memory in the pigeon. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), Cognitive Processes in Animal Behavior (pp 211-248). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Kamil, A. C. (1988). A synthetic approach to the study of animal intelligence. In D. W. Leger (Ed.), Comparative Perspectives in Modern Psychology: Nebraska Symposium on Motivation, Vol. 35 (pp 257-308). Lincoln, Nebraska: University of Nebraska Press.
- Kamil, A. C., & Balda, R. P. (1985). Cache recovery and spatial memory in Clark's nutcrackers. Journal of Experimental Psychology: Animal Behavior Processes, 11, 95-111.
- Mackintosh, N. J., Wilson, B., & Boakes, R. A. (1985). Differences in mechanisms of intelligence among vertebrates. In L. Weiskrantz (Ed.), Animal Intelligence (pp53-65). Oxford: Clarendon Press.
- Macphail, E. M. (1985a). Vertebrate intelligence: The null hypothesis. In L. Weiskrantz (Ed.), Animal Intelligence (pp 37-51). Oxford: Clarendon Press.
- Macphail, E. M. (1985b). Ecology and intelligence. In N. Weinberger, & J. McGaugh (Eds.), Memory Systems of the the Brain (pp 279-286). New York: Guilford Press.
- Maki, W. S. (1979). Discrimination learning without short-term memory processes in pigeons. Science, 204, 83-85.
- Maki, W. S., Jr., Moe, J. C., & Bierley, C.M. (1977). Short-term memory for stimuli, responses, and reinforcers. Journal of Experimental Psychology: Animal Behavior Processes, 3, 156-177.
- Mewaldt, L. R. (1956). Nestling behavior of the Clark nutcracker. The Condor, 58, 3-23.
- Roberts, W. A., & Grant D. S. (1974). Short-term memory in the pigeon with presentation time precisely controlled. Learning & Motivation, 5, 393-408.

- Roberts, W. A., & Van Veldhuizen, N. (1985). Spatial memory in pigeons on the radial maze. Journal of Experimental Psychology, 11, 241-260.
- Roitblat, H. L., & Harley, H. E. (1988). Spatial delayed matching-to-sample performance by rats: Learning, Memory, and proactive interference. Journal of Experimental Psychology: Animal Behavior Processes, 14, 71-82.
- Rosenzweig, M. R., & Glickman, S. E. (1985). Comparisons of learning abilities among species. In N. Weinberger, J. McGaugh & G. Lynch (Eds.), Memory Systems of the Brain (pp 296-307). New York: Guilford Press.
- Schacter, D. L. (1985). Multiple forms of memory in humans and animals. In N. Weinberger, J. McGaugh & G. Lynch (Eds.), Memory Systems of the Brain (pp 351-379). New York: Guilford Press.
- Sherry, D. (1984). Food storage by black-capped chickadees: Memory for the location and contents of caches. Animal Behaviour, 32, 451-464.
- Sherry, D. F., Krebs, J. R., & Cowie, R. J. (1984). Memory for the location of stored food in marsh tits. Animal Behaviour, 29, 1260-1266.
- Sherry, D. F., & Schacter, D. L. (1987). The evolution of multiple memory systems. Psychological Review, 95, 439-454.
- Shettleworth, S. J. (1985). Food storing by birds: Implications for comparative studies of memory. In N. Weinberger, J. McGaugh & G. Lynch (Eds.), Memory Systems of the Brain (pp 231-250). New York: Guilford Press.
- Shettleworth, S. J., & Krebs J. R. (1982). How marsh tits find their hoards: The roles of site preference and spatial memory. Journal of Experimental Psychology: Animal Behavior Processes, 8, 354-375.
- Smith, J. P., Attwood, J. C., & Niedorowski, L. (1982). Delayed choice responding by pigeons when correct response is not predictable from the sample stimulus. Journal of the Experimental Analysis of Behavior, 37, 57-63.
- Spetch, M. L., & Edwards, C. A. (1986). Spatial memory in pigeons (Columba livia) in an "open-field" environment. Journal of Comparative Psychology, 100, 279-284.

- Spetch, M. L., & Honig, W. K. (1988). Characteristics of pigeons' spatial working memory in an open-field task. Animal Learning & Behavior, 16, 123-131.
- Sternberg, S. (1966). High-speed scanning in human memory. Science, 153, 652-654.
- Tomback, D. F. (1977). Foraging strategies of the Clark's nutcrackers. Living Bird, 16, 123-161.
- Tomback, D. F. (1980). How nutcrackers find their seed stores. The Condor, 82, 10-19.
- Tulving, E. (1972). Episodic & semantic memory. In E. Tulving & W. Donaldson (Eds.), Organization of memory (pp 381-403). New York: Guilford Press.
- Tulving, E. (1985). How many memory systems are there? American Psychologist, 40, 385-398.
- Vander Wall, S. B. (1982). An experimental analysis of cache recovery in Clark's nutcrackers. Animal Behaviour, 30, 84-94.
- Vander Wall, S. B., & Balda, R. P. (1977). Coadaptions of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecological Monographs, 47, 89-111.
- Vander Wall, S. B., & Balda, R. P. (1981). Ecology and evolution of food-storage behavior in conifer-seed-caching-corvids. Z. Tierpsychol., 56, 217-242.
- Vauclair, J. (1985). A comparative approach to cognitive mapping. In P. Ellen, & C. Thinus-Blanc (Eds.) Cognitive Process and Spatial Orientation in Animal and Man (pp. 89-96). Dordrecht, The Netherlands: Martinus Nijhoff Publishers.
- Wilkie, D. M. (1983). Pigeons spatial memory: Matching of key location. Journal of the Experimental Analysis of Behavior, 40, 143-151.
- Wilkie, D. M. (1984). Pigeons spatial memory: IV. Effects of intertrial interval manipulation on delayed matching of key location. Canadian Journal of Psychology, 38, 178-195.

Wilkie, D. M., & Summers, R. J. (1982). Pigeon's spatial memory: factors affecting delayed matching of key location. Journal of the Experimental Analysis of Behavior, 37, 45-56.

Wright, A. A., Santiago, H. C., Sands, S. F., & Uricuioli, P. J. (1984). Pigeon and monkey serial probe recognition: Acquisition, strategies, and serial position effects. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), Animal cognition (pp. 353-373). Hillsdale, NJ: Erlbaum Associate.

