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Do Clark's nutcrackers demonstrate what-where-when memory on a cache-recovery task?

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Abstract

What-where-when (WWW) memory during cache recovery was investigated in six Clark's nutcrackers. During caching, both red- and blue-colored pine seeds were cached by the birds in holes filled with sand. Either a short (3 day) retention interval (RI) or a long (9 day) RI was followed by a recovery session during which caches were replaced with either a single seed or wooden bead depending upon the color of the cache and length of the retention interval. Knowledge of what was in the cache (seed or bead), where it was located, and when the cache had been made (3 or 9 days ago) were the three WWW memory components under investigation. Birds recovered items (bead or seed) at above chance levels, demonstrating accurate spatial memory. They also recovered seeds more than beads after the long RI, but not after the short RI, when they recovered seeds and beads equally often. The differential recovery after the long RI demonstrates that nutcrackers may have the capacity for WWW memory during this task, but it is not clear why it was influenced by RI duration.

Keywords What-where-when memory, Episodic-like memory, Clark's nutcracker, Cache recovery

Introduction

The purpose of the present experiment was to test for what-when- where (WWW) memory in Clark's nutcrackers. Clayton and Dickinson (1998) demonstrated WWW memory in Western scrub jays using a unique single-trial cache-recovery paradigm. Scrub jays were allowed to cache both perishable wax worms and non-perishable peanuts in small caching trays in their home cages. When presented with both trays after 4- or 124-h retention intervals, the birds preferred to recover and eat the wax worms. After several experiences during which a 124-h retention interval was followed by replacement of edible wax worms with rotten ones, the birds searched for normally non-preferred peanuts first, indicating that they had learned something about the perishability of the worms. This is a clear demonstration of WWW memory. The scrub jays must have used what information (worm or nut), where information (the spatial location of the cached item), and when information (duration of the retention interval) simultaneously to switch preferences and recover the appropriate foods after different retention intervals.

This WWW memory in scrub jays is consistent with some aspects of their natural history. They are scatter-hoarding corvids that typically cache perishable and nonperishable food items in their natural environment (Clayton and Dickinson 1998) and also use spatial memory to relocate their caches (Balda and Kamil 1989). Therefore, the ability to simultaneously remember what is in their cache, where it is, as well as when it was made could be useful to scrub jays in nature.

Zinkivskay et al. (2009) have also demonstrated WWW memory in another scatter-hoarding corvid, the magpie, using a larger-scale cache-recovery paradigm. Magpies, like scrub jays, cache many different kinds of food items, some of which become perishable over time.

The natural history of Clark's nutcrackers provides an interesting contrast with that of the Western scrub jay and magpie. Nutcrackers are more dependent on stored food in the wild (Balda 1980; Vander Wall and Balda 1981). In their natural environments, individual nutcrackers store up to 33,000 pine seeds in a given fall and rely almost exclusively on these caches for their winter diet (Balda 1987; Vander Wall and Balda 1981). Nutcrackers have also performed well in a series of different spatial tasks in the laboratory, outperforming other scatter-hoarding corvids including scrub jays (Balda and Kamil 1989; Kamil et al. 1994; Olson 1991; Olson et al. 1995; but see Gould-Beierle 2000). Nutcrackers, unlike scrub jays and magpies, appear to cache only pine seeds, which remain palatable for many months, especially during late fall and winter when the ground is cold. In the laboratory, they do not readily cache food items other than pine seeds (A. Kamil, personal observation). It is, therefore, quite possible that nutcrackers have experienced weaker selective pressure to remember the contents of a cache or the time at which it was made. This suggests that nutcrackers, despite their excellent memory for the location of caches, might remember neither the contents nor the time of creation of their caches.

The challenge in designing a cache-recovery WWW task with nutcrackers is that these birds will not reliably cache anything but pine seeds in a laboratory setting. Recently, however, Zinkivskay et al. (2009) developed a clever cache-recovery method to test WWW memory in magpies. They used a single food type that could be presented in two different colors during caching. Then, during recovery, either type could be made "inedible" by replacing it with a non-edible object (wooden bead) the same size and color as the cached items. In our experiment, nutcrackers cached pine seeds of two different colors, which were then made "inedible" as needed by being replaced with a wooden bead of the same color.

Another advantage to this experimental design is that it minimizes preferences for one food type over another which was shown in Clayton and Dickinson's (1998) scrub jays. Preferences can vary among individual birds and change over time, so using the same food item presented in two different forms (i.e., colors) the influence of individual and temporal differences in preferences are avoided. The design also allows for reverse contingencies, as both colors of seed can be made "inedible" depending on the retention interval associated with each color.

Methods

Subjects

Six Clark's nutcrackers (*Nucifraga columbiana*) were used. They were all captured in Colorado under appropriate state and federal permits in August between 1992 and 2000. All birds had previous experience in open room tasks, and five had also participated in operant studies. None of the past experiments investigated WWW memory. All six birds cached and recovered seeds in an open room with a woodchip bedding floor prior to this experiment to assess their willingness to cache and recover pine seeds in the laboratory environment. The birds were housed individually in 48 × 48 × 73 cm cages and maintained on a 14:10 light/dark cycle. They were maintained on a daily diet of parrot pellets, sunflower seeds, turkey starter, dried mealworms, and pine seeds. On days during which they were tested, they were fed after their caching or recovery session. In addition, they were not given access to pine seeds during the 2 days prior to a caching or recovery session. They had water and grit *ad libitum*. The training and experimental sessions were run January–April 2008 and October 2008–April 2009.

Pretraining (exposure to painted seeds)

Pine seeds were painted either red or blue with nontoxic acrylic paint (Palmer Prism Acrylic). Before the experiment began, the birds were given four pine seeds, two red and two blue, in their home cages during feeding time to make sure that the colors would not deter them from eating the seeds and to check for any color preferences. They readily ate the seeds, and no individual color preferences were apparent. This was assessed by giving them equal numbers of each color in their food dishes and recording which seeds were chosen first and which ones were eaten over the course of 20 days.

Testing room

The room in which the birds cached and recovered was 2.7 × 4.8 m. It had a raised 2.7 × 3.8 m wooden floor with an 11 × 16 grid of holes that were 5.5 cm in diameter and 20 cm apart. One hundred and forty-nine of these 176 holes were available to use in the experiment, since we excluded any of the holes on the edges. A plastic cup was inserted into each hole and filled with sand. A hole could be capped with a plaster of Paris plug that fit the top of the cup. Post-it notes with letters or numbers were placed along the three walls that surrounded the raised floor to act as a visual grid system for the experimenter to identify the location of any cache that the bird made. Posters on the walls and various objects on the floor were provided as potential landmarks. These landmarks were changed every trial (through both novel configurations and introduction of new items) so that the birds experienced a trial-specific environment for each cache-recovery session (Figure 1).

To start each session, birds were carried to the room by hand from their home cages and put into a holding cage (48 × 48 ×73 cm) that had an opening in the back that allowed exposure to a small, sliding door for entering the experimental room. The door was opened, and the birds flew into the room. The door was located underneath a smoked, plexiglass window for viewing the room. When a session was done, the lights in the room were shut off and the lights in the space where the cage was located were turned on with the sliding door open to the cage. Birds flew back into the cage at the end of their session. The sliding door to the room was shut, and they were carried by hand back to their home cages. A video camera located in the ceiling recorded each session.

Habituation to the room

Birds were allowed into the testing room with 6 unpainted seeds in a plastic food cup located in a central location on the floor. Landmarks were located on the floor and the walls. All holes were capped. The birds were left in the room until they ate all the seeds. This was done for 2 days in a row, with new configurations of landmarks or novel landmarks each day.

Training

All birds were given two cache and two recovery sessions with unpainted pine seeds in the testing room, one with a short retention interval (SRI) of 3 days between caching and recovery and one with a long retention interval (LRI) of 9 days between caching and recovery. This was done to assess their willingness to cache and recover in the room and introduce the two retention intervals that were going to be implemented in the experiment. Twenty-four seeds were placed in a plastic food dish near the center of the room. Thirty-three randomly selected holes were uncapped in the room (with the stipulation that they could not be on the edges next to each of the three walls in the caching area of the room). The birds were allowed to eat and/or cache those seeds until they were all gone. Then, the lights were turned off in the room, and the birds flew back to the holding cage. If the bird ate all 24 seeds and did not make a cache, 8 more seeds were put in the dish and the bird was allowed to go back into the room. This was continued until each bird made a minimum of 2 caches. The maximum number of caches was not limited. All birds met this criterion for each caching session. Afterward, they were brought back to the home cage and were returned to the experimental room either 3 or 9 days later to recover their caches. One seed was placed at each previous cache location, and all holes were uncapped in the room. They were allowed to search in the room until all caches were found.

Figure 1 Photograph of the experimental cache-recovery room.

Testing: Cache session

For testing purposes, the birds were divided into two groups. On test day 1, group 1 (Duck, Ignatius, and Petey) started with 24 *red* seeds in a plastic food dish near the center of the room. Group 2 (Myotis, Albert, and Six) started with 24 *blue* seeds in the dish. The starting seed color was alternated between the two colors during the February–April 2008 trials and randomized so that half of each trial type started with one color and half with the other color for the October 2008–April 2009 trials. For both groups, 33 random holes were uncapped in the room (with the same stipulation as above). The birds were allowed to eat and/or cache those seeds until they were all gone. At that point, the lights were turned off in the room and the birds flew back to the holding cage. If the bird ate all 24 seeds without caching, 8 more seeds of the same color were put in the dish and the bird was allowed to go back into the room. This continued until the bird cached. If the bird made one or more caches during their first bout in the room, the experimenter would cap any holes where a cache was made and record the grid location of the cache and the seed color. The same number of holes that had just been capped, chosen at random, would then be uncapped, 24 seeds of the opposite color would be placed into the food dish, and the bird would be allowed back into the room. This continued until the birds made a minimum of two caches of each color with no upper limit to the maximum caches that could be made. Between individual bird caching sessions, all seeds were removed from cups, seed shells were picked up, and any sand that was on the floor near the cups was cleaned up.

Testing: retrieval session

Group 1 birds were given a short retention interval (SRI) of 3 days between their first cache session and their first retrieval session and a long retention interval (LRI) during their next cache/retrieval session. Group 2 birds were given a LRI of 9 days first, then an SRI during their second set of cache/retrieval session. The retention intervals were randomized in pairs of trials for subsequent cache/retrieval session. For group 1 birds after a SRI, any red seed caches made during their cache session were replaced in the same location with one red wooden bead that was roughly the same size as a pine nut. Any caches made with blue seeds were replaced with one blue seed. For LRI sessions, the replacements were reversed so red seed caches were replaced with one red seed and blue seed caches were replaced with one blue, wooden bead. To control for color bias, group 2 birds had reversed color contingencies (see Figure 2).

For each recovery session throughout the experiment, each location in which the bird being tested had cached during the immediately preceding caching session was uncapped and contained either a seed or bead buried in the sand. A cluster technique (see Kamil et al. 1993) was implemented, with three holes next to each recorded cache location also being uncapped. These holes were randomly chosen with the stipulation that they had to form a square including the cache location (Figure 3). Empty clusters of four holes with no seeds that formed a square were also randomly opened according to the formula N (number of empty clusters) = ½ (number of blue clusters + number of red clusters). Thus, during each recovery session, the nutcracker was presented with a set of 2 × 2 clusters of uncapped holes.

Group	Day 1	3 Day SRI	9 Day LRI
1	Cache	Red Bead	Red Seed
		Blue Seed	Blue Bead
2	Cache	Red Seed	Red Bead
		Blue Bead	Blue Seed

Figure 2 A diagram of recovery contingencies. During caching, all birds cached seeds of *both colors*. During recovery, one color of caches was replaced with seeds and the other with beads. For example, group 1 birds recovered red seeds and *blue beads* after a short retention interval (*SRI*) while the reverse was true after a long retention interval (*LRI*).

Some of these clusters included a cache site with an appropriate item in it (bead or seed) while the remainder consisted of 4 empty holes in which the bird being tested had not cached.

Each bird was released into the room on their appropriate retrieval day, and each hole location was recorded in the order it was searched. The bird was left in the room until all seeds and beads were found. All seed shells and any sand that was on the floor near the cups were cleaned up before each recovery session began. When a bead was recovered during the first few trials, birds would throw the beads around, play with them, or try to open them. However, after the first few trials, they generally just dropped them as soon as they were recovered and ignored them.

During the first bout of testing sessions between February and April 2008, each bird was tested on three SRIs and four LRIs. During the second bout of testing sessions between October 2008 and April 2009, each bird was tested on six SRIs and six LRIs.

Results

The mean number of caches made per trial during the February–April 2008 trials was 9.28 (range 4–17), while the mean number of caches made per trial during the October 2008–April 2009 trials was 7.04 (range 4–13). There were no differences based on retention interval for either time period (paired t tests for February–April 2008: $t(5) = 1.283$, $P = 0.256$; October 2008–April 2009: $t(5) = -0.824$, $P = 0.448$).

Results will first be presented that establish the birds' spatial memory for the caches they made after both retention intervals. This will be followed by results addressing differences in the birds' WWW memory performance based on retention interval.

Accuracy of cache recovery

The nutcrackers accurately recovered their caches throughout the experiment by all three measures we analyzed. (1) They chose to first search in clusters containing a cache site more often than predicted by chance. If they chose clusters at random, we would expect the probability of first choice of non-empty clusters to be equal to the number of non-empty clusters divided by the total number of clusters. As shown in Table 1, they made significantly more first searches in non-empty clusters (regardless of palatability) than predicted by chance following both short (paired t test: $t(5) = 5.651$, $P = 0.002$) and long (paired t test: $t(5) = 6.092$, $P = 0.002$) retention intervals. (2) The first search within a non-empty cluster was consistently directed at the cache. If the birds chose holes within clusters at random, their first search

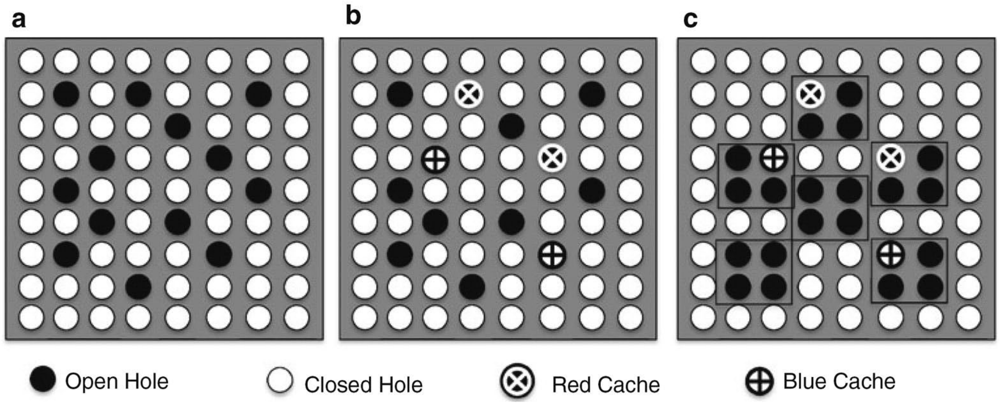

Figure 3 Diagram of experimental cache-recovery room. **a)** The available holes during a hypothetical caching session. **b)** Displays the actual caches made by a bird from the hypothetical caching session. **c)** Shows which holes would be open during the recovery session using the cluster technique. *Black boxes* are to highlight the clusters on the diagram and were not present in the actual room.

within a cluster would have been directed at the cache with a probability of 0.25 (since 1 of the 4 holes in the cluster contained an item). As shown in Table 2, the proportion of times the birds recovered an item on the first search within a cluster across the entire experiment was significantly more than predicted by chance in one-sample *t* tests for both the SRI ($t(5) = 3.43$, $P = 0.019$) and LRI ($t(5) = 3.01$, $P = 0.03$). (3) The nutcrackers also required relatively few probes to find a cache within a cluster. With one item hidden among four alternatives, the mean number of searches required to find the item (seed or bead) within each cluster if the bird was searching randomly is 2.5. One-sample *t* tests showed that the birds were significantly better than chance at recovering seeds ($t(5) = -3.04$, $P = 0.029$) and beads ($t(5) = –5.64$, $P = 0.002$) during the SRI. They were also better than chance at recovering seeds ($t(5) = –5.53$, $P = 0.003$) and beads ($t(5) = –3.15$, $P = 0.025$) during the LRI (Table 3). There was also no difference in the number of searches for a seed in each cluster between the two retention intervals (Paired samples *t* test: $t(5) = 0.75$, $P = 0.488$).

WWW memory

For all analyses of WWW memory in this section, the first short retention interval session and the first long retention interval session at the beginning of the experiment were excluded from the analysis because the birds had not yet had any opportunity to learn the episodic component of the task. The first short retention interval session and first long retention interval session in October 2008 (following the 5-month break in the experiment caused by factors beyond experimenter control) were also excluded from the analyses, due to potential relearning of the task.

Table 1. The proportion of times a non-empty cluster (containing a bead or a seed) was chosen first across the entire experiment.

	SRI		LRI	
	Observed	Expected	Observed	Expected
Bird				
Duck	1.0	0.714	0.90	0.667
Ignatius	1.0	0.655	0.90	0.632
Petey	1.0	0.652	0.88	0.644
Myotis	1.0	0.823	0.77	0.477
Albert	0.77	0.667	0.80	0.638
Six	0.77	0.604	0.77	0.707
Mean	0.923	0.686	0.837	0.628
P		< 0.001*		
<0.001*				

Individual bird data and means are included for both the short retention interval (SRI) and long retention interval (LRI) trials. *P* values are for paired samples *t* tests comparing observed with expected. Expected was calculated by dividing the number of non-empty clusters by the total number of clusters across the experiment for each bird.
* $P < 0.05$

Table 2. The proportion of first searches within a cluster that were to holes that contained an item (seed or bead) across the entire experiment.

	SRI	LRI
Bird		
Duck	0.30	0.31
Ignatius	0.47	0.42
Petey	0.48	0.34
Myotis	0.36	0.41
Albert	0.65	0.76
Six	0.33	0.45
Mean	0.44	0.46
P	<0.01*	<0.01*

Individual bird data and means are included for both the short retention interval (SRI) and long retention interval (LRI) trials. Chance is 0.25. *P* values are for one-sample *t* tests comparing proportions to chance.
* $P < 0.05$

Table 3. The mean number of searches it took for a seed and a bead to be found within a cluster.

	SRI		LRI	
	Seeds	Beads	Seeds	Beads
Bird				
Duck	2.57	2.22	2.15	2.41
Ignatius	1.79	1.80	1.67	2.10
Petey	2.10	1.43	2.00	1.88
Myotis	2.10	1.92	2.20	2.33
Albert	1.24	1.30	1.53	1.32
Six	1.94	1.72	1.74	1.94
Mean	1.96	1.73	1.88	2.00
P	<0.01*	<0.001*	<0.001*	<0.01*

Individual bird data and mean bird data are included for both the short retention interval (SRI) and long retention interval (LRI) trials. Chance is 2.5 searches. *P* values are for one-sample *t* tests comparing number of searches to chance.
* $P < 0.05$

Table 4. The mean rank of cluster type chosen (bead or seed) across the entire experiment (minus the first SRI and LRI sessions in the beginning and after the 5-month lay-off)

	SRI		LRI	
	Seeds	Beads	Seeds	Beads
Bird				
Duck	2.74	3.79	3.21	4.27
Ignatius	2.45	3.69	2.17	3.64
Petey	3.67	3.42	3.31	3.94
Myotis	4.04	3.79	4.48	3.69
Albert	4.52	3.79	4.41	4.18
Six	4.19	3.50	3.74	4.51
Mean	3.60	3.66	3.55	4.04
P		>0.05		<0.05*

Individual bird data and means are included for both the short retention interval (SRI) and long retention interval (LRI) trials. *P* values are for Wilcoxon signed rank tests comparing seeds to beads.
* $P < 0.05$

Table 5. The proportion of times a seed cluster was chosen first in a recovery session throughout the entire experiment (minus the first SRI and LRI sessions in the beginning and after the 5-month lay-off)

	SRI		LRI	
	Observed	Expected	Observed	Expected
Bird				
Duck	0.333	0.304	0.417	0.321
Ignatius	0.333	0.344	0.50	0.292
Petey	0.25	0.321	0.70	0.31
Myotis	0.833	0.327	0.433	0.31
Albert	0.417	0.357	0.35	0.291
Six	0	0.319	0.30	0.362
Mean	0.361	0.329	0.45	0.314
P		>0.05		>0.05

Individual bird data and means are included for both the short retention interval (SRI) and long retention interval (LRI) trials. *P* values are for paired *t* tests comparing observed with expected (LRI results approached significance with $P = 0.08$). Expected was calculated by dividing the number of seed clusters by the total number of clusters across the experiment for each bird.

A mean ranking analysis was used to investigate whether birds were more likely to choose seed clusters before bead clusters when looking at all searches. In this analysis, a "1" was given to the first cluster searched, a "2" was given to the second cluster searched, etc. Each rank was then assigned to the item type that was found there (either bead or seed). All the ranks for an item type were added and divided by the total number of that item type to account for the difference in numbers of caches made within sessions and between birds. There was a significant difference in rankings between seed and bead cluster recovery for the long retention interval only (Wilcoxon signed rank test SRI: $Z = -0.945$, $P = 0.345$; LRI: $Z = -1.977$, $P = 0.048$). So over the course of an entire recovery session, there was no difference in the order of recovery of seeds or beads after short retention intervals, but the birds were more likely to choose seed clusters before bead clusters after long retention intervals (Table 4).

An analysis of which type of cluster was chosen first in a recovery session (seed or bead) found that birds chose seed clusters first more than predicted by chance after the long RI (but not significantly) but not after the short RI (paired *t* test LRI: $t(5) = 2.18$, $P = 0.082$, SRI: $t(5) = 0.30$, $P = 0.78$). Table 5 shows that the birds' memory for which cluster contained seeds was moderately better than chance after 9 days but not significantly different than chance after 3 days.

WWW memory over time

We also looked at the proportion of seed and bead caches that were retrieved by the time all seed caches had been retrieved for the first 9 trials during short retention intervals and the first 9 (of 10) trials during long retention intervals (Figure 4). This analysis is analogous to that done by Zinkivskay et al. (2009) in their experiment on WWW memory in magpies. We ran a three-way analysis of variance with repeated measures and found a significant main effect of item (seed/bead; $F(1,3) = 17.89$, $P = 0.024$), showing that birds recovered significantly more seeds than beads overall. We also found that birds recovered a higher proportion of total items before all seeds were found during the SRI than compared with the LRI (although not significantly, main effect of retention interval: $F(1,3) = 8.93$ $P = 0.058$). There was no item 9 trial interaction ($F(8,24) = 1.08$, $P = 0.412$), demonstrating that the birds did not retrieve fewer beads as the trials increased (Figure 4). However, over the entire session, birds recovered a higher proportion of beads before recovering all of their seeds during the SRI compared with the LRI (although not significantly, item 9 retention interval interaction: $F(1,3) = 8.93$, $P = 0.058$). Therefore, the trend was for birds to recover more of their seed caches than their bead caches during the LRI.

Discussion

The Clark's nutcrackers in this experiment demonstrated that they remembered where they had cached red vs. blue pine seeds after the long retention interval. After the short retention interval, however, they failed to discriminate these sites. They also tended to recover more seeds than beads in general during the long retention interval. These patterns demonstrate what/where memory and a sensitivity to the duration of the retention interval. However, unlike the magpies Zinkivskay et al. (2009), the nutcrackers did not retrieve fewer beads over time as the experiment progressed.

The reason for this difference in performance as a function of retention interval duration is not clear. It was necessary to use retention intervals for at least several days duration. During caching sessions, nutcrackers eat many seeds before they begin to cache. This results in weight gain and reduced motivation to retrieve seeds that takes at least 48 h to start to dissipate. The duration of these intervals is much longer than that usually used during other tests of WWW memory in food-storing birds (Clayton and Dickinson 1998; Feeney et al. 2009; Zinkivskay et al. 2009). It should be remembered, however, that nutcrackers make long-term caches in the wild (Tomback 1980), unlike many other scatter-hoarding birds that make their caches for short-term use with retrieval after a matter of hours to a few days (Smulders et al. 2010). Nutcrackers have also demonstrated the ability to accurately remember spatial locations after very long retention intervals of up to 285 days after caching in a laboratory setting (Balda and Kamil 1992).

It is possible that there were differences in motivation level for WWW memory for each of the retention intervals. During a caching session, the birds sometimes ate as many as 45 seeds before beginning to cache. After the 3-day retention interval, while they did not have access to seeds for the 2 days prior to recovery, they may still not have been fully motivated to search for seeds. This low motivation may have continued into day 3 of the experiment, leading to more errors in searching. However, there were no differences in accuracy of recovering an item within a cluster between the 3- and 9-day retention intervals (Table 2), suggesting that if there were motivational differences as a function of retention interval duration, they were not reflected in general spatial accuracy. Memory for

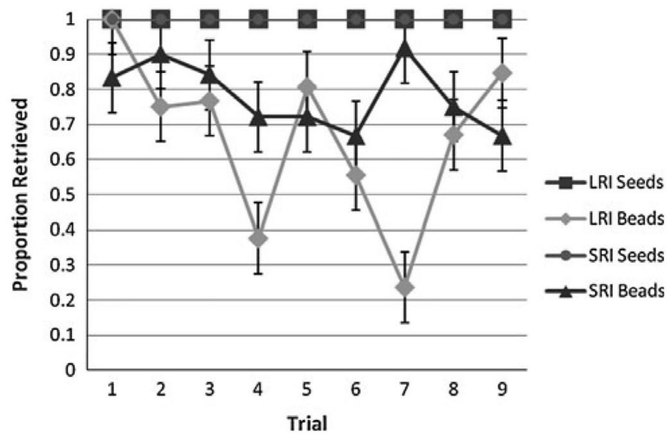

Figure 4 Proportion of seed and bead caches retrieved by the time all seed caches had been retrieved for all 9 of the short retention interval trials and the first 9 of the long retention interval trials. Birds always retrieved all of their seed caches for each trial, hence proportions of 1.0. *Error bars* represent standard errors of the mean.

whether a cache site would contain a seed or a bead (WWW memory) may have still been differentially affected by retention interval. After the 9-day-long retention interval, their motivation to search for seeds may have been higher due to the longer time period between eating a large number of seeds and later searching. Higher motivation to find caches may have resulted in a more accurate recollection of where seeds, but not beads, were located.

Due to the influences of differences in motivation based on the two retention intervals, it would be interesting to see whether setting the short retention interval to 9 days and increasing the long retention interval accordingly might yield different results. Alternatively, the retention intervals could be systematically varied to determine whether there is a short retention interval threshold for performance. If either of these aspects was influencing the current results, then one might hypothesize that the birds would show WWW memory for both retention intervals.

Another potential reason for differences between the two retention intervals might be the design of the experiment. If what the birds were learning is that certain food items do not go bad after 9 days (LRI), then logically they should not also go bad after 3 days (SRI). For example, a red seed might remain edible after 9 days, but it would be inedible (be replaced by a bead) after only 3 days. This might therefore affect performance on the short retention intervals negatively if information about edibility from a previous long retention interval affects SRI performance. In order to test this further, one might train birds with only short retention intervals between caching and recovery. If the factors mentioned in the previous argument influenced performance in the current study, then birds should perform better at retrieving edible seeds in a new study with only short RIs.

The differences in performance between the two retention intervals are very unlikely to be based on differences in encoding, because caching sessions were followed by either long or short retention intervals in random (unpredictable) order. One possibility is that recall may have been heavily influenced by primacy or recency effect after the short retention interval, but not after the long retention interval. Serial position effects have been seen in spatial list learning in black-capped chickadees (Crystal and Shettleworth 1994), but not in Clark's nutcrackers (Lewis and Kamil 2006). This would be interesting to test further.

Birds that were more accurate in general spatial memory (finding an item) were not also birds that showed significant preferences in finding a seed over a bead (Tables 1 and 5). This suggests that general spatial memory and what-where (and perhaps when) memory are different categories of memories and most likely are processed and retrieved differently. While spatial information is one of the components of WWW memory, the way "where" information is bound together with information about "what" and "when" may be subject to a different set of neurobiological processes during memory formation and retrieval. Five of the six birds demonstrated WWW-like memory during the LRI, but at least one of those birds also demonstrated WWW-like memory during the SRI (Table 5). Reasons for individual differences in memory during cache recovery could be based on many factors, including individual differences in how information is encoded, the types of cues used, or motivation and would be worth exploring.

The current results from the long retention interval in Clark's nutcrackers suggest that cached items may not have to show temporal degradation in their natural environment in order for information to be encoded and stored as WWW memory. The fact that the birds chose seeds over beads after the long retention interval demonstrates their ability to remember "what" and "where", while the absence of this effect after the short interval suggests that they may also be able to remember "when" after the long retention interval. We suspect that use of longer intervals, for example 6 versus 18 days, would lead to choice of seeds over beads at both intervals. Such an experiment would be useful for further exploration of WWW memory capabilities in these birds. It would also be interesting to see whether Clark's nutcrackers would also demonstrate this ability in non-caching tasks, like that of black-capped chickadees searching for food hidden by experimenters (Feeney et al. 2009) or an operant version of such a task.

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