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Patterns of movement and orientation during caching and recovery by Clark's nutcrackers, *Nucifraga columbiana*

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Clark's nutcrackers regularly store large numbers of pine seeds and remember the locations of the cached seeds. Although they are very accurate, they do make some errors during recovery. In an attempt to determine whether any behaviours during caching predicted the occurrence of errors during recovery, we videotaped Clark's nutcrackers while they cached and recovered seeds under laboratory conditions. We used the videotapes to develop complete, quantitative descriptions of caching and recovery behaviour, with an emphasis on body orientation and directions of movement. During caching, the birds showed the greatest change in their orientation and direction following cache creation. During cache recovery, in contrast, body orientation changed most following successful recovery of a seed. When orientation while making a cache was compared with orientation when recovering the same cache, orientations were similar more often than would be expected by chance. However, this consistency of direction was not related to the accuracy of cache recovery, indicating that such consistency is not necessary for accurate cache recovery. The location in which the birds chose to place their caches was the only variable that predicted the location of probes during recovery.

Clark's nutcrackers, *Nucifraga columbiana*, store large amounts of food every autumn and accurately recover this food during winter and spring. Many experiments have demonstrated that nutcrackers use spatial memory to relocate their caches (Balda 1980; Vander Wall 1982; Kamil & Balda 1985). Several experiments in which landmarks were moved or removed between caching and recovery have demonstrated that cache site memory is based on visual cues provided by landmarks (Balda 1980; Vander Wall 1982; Balda & Turek 1984). In nature, nutcrackers cache in highly variable, montane habitats, which undoubtedly provide a rich array of potential landmarks such as cliffs, trees, boulders and rocks. However, very little is known about how nutcrackers, or other caching birds, actually use the information provided by landmarks to relocate their cached food. The general purpose of the experiment reported here was to conduct a detailed, descriptive study of caching and recovery to begin to investigate this problem.

Many hypotheses have been proposed to account for the use of landmarks for orientation by animals, including piloting (Griffin 1952), triangulation (Bossema 1979), and the vector sum model (Cheng 1989). One such hypothesis for animals such as nutcrackers that need to keep track of many locations

simultaneously might be called the 'snapshot' theory (Cartwright & Collett 1983). During caching, the bird could look at the landmarks visible from the cache site and retain an image of this view. Then, during recovery, it could attempt to match what it sees to the remembered image. This type of mechanism appears to play a role in the ability of honeybees to relocate food sources (Cartwright & Collett 1983). One prediction of the snapshot hypothesis of cache site memory is that the bird should tend to approach the cache site from the same direction during caching and recovery because the view from a site depends on body orientation. Bossema (1979; see also Bossema & Pot 1974) tested this idea with European jays, *Garrulus glandarius*. He found that jays used the same direction of approach to the cache during recovery as they had during caching more than expected by chance. However, this is only weak evidence for the snapshot hypothesis, as there are many potential reasons for such a finding. For example, some objects may prevent certain directions from being used, or favourite perches or paths may promote the use of similar directions of approach to some cache sites. Therefore, one of our specific purposes in the design of the current experiment was to extend Bossema's approach by not only correlating directionality during caching and recovery, but also by attempting to

correlate consistency of the directionality of approach with accuracy. This would provide a more exacting test of the snapshot hypothesis in seed-caching birds than the data of Bossema (1979) provides.

Another purpose was to try to determine why nutcrackers remember some cache sites better than others. Kamil & Balda (1990) controlled access to cache sites during cache recovery. With this technique, they were able to establish that some sites were remembered better than others (as defined by number of errors) and that these better remembered sites were recovered first. But when Kamil & Balda (1990) forced nutcrackers to use the same sites repeatedly across successive cache-recovery cycles, there was no consistency in either recovery order or memorability among these cache sites. This finding suggests that physical differences between sites are not responsible for the variation in memorability. An alternative reason for this variation in the strength of memory for different cache sites is that variation in behavior during caching results in variation in memorability. For example, if the time spent creating caches varies, nutcrackers could remember longer-visited sites better. This would be analogous to the effects of requiring extra time or responses to the sample during operant matching-to sample tasks. Such added time in the presence of the sample improves the accuracy of performance after a retention interval (Roberts 1972; Sacks et al. 1972). This possibility has not been tested directly. Therefore, as part of our descriptive analysis, we searched for aspects of caching behaviour that might accurately predict characteristics of recovery behaviour, particularly recovery accuracy.

In the past, we have used two general methods for studying the cache recovery behaviour of nutcrackers. Both methods involved the use of a room with discrete cache sites defined by sand-filled holes in the floor, each of which was either available or fitted with a cap during an experimental session. In one method, termed 'free' recovery (e.g. Kamil & Balda 1985; Balda & Kamil 1989), birds cache with a limited number of the cache sites available, and with all holes available during recovery. In the second method, 'termed cluster' recovery (e.g. Kamil & Balda 1993; Bednekoff et al. 1997), only a limited number of holes are available during each recovery session. These holes are arranged in small clusters of six holes each, one of which may contain a cache. Free recovery has the advantage of putting as few constraints on the birds' movements as possible. During cluster recovery, movement paths may be partially determined by positioning of clusters. However, with cluster recovery, it is possible to assign errors to particular cache sites (errors that occur within the cluster containing that cache). Therefore, we examined caching and recovery behaviour under both conditions.

Methods

Subjects

Four wild-caught Clark's nutcrackers of unknown sex served as subjects in this experiment. These birds were captured as adults and had undoubtedly cached and recovered food in the wild. All four of the birds had been in the laboratory for at least 5 years and had participated in numerous experiments. However, the present experiment was the first performed by these birds in this experimental room. They were individually housed in large, metal cages and were fed a mixed diet of sunflower seeds, pinyon pine nuts, cracked corn, turkey started, pigeon pellets and mealworms (*Tenebrio* larvae). Birds were also provided with water, a vitamin supplement and oyster shells. During the duration of the experiment, birds only received pine seeds while in the experimental room and were deprived of all food for 24 h before each caching and recovery session. Birds were maintained on a constant 10:14 h light:dark cycle.

Experimental Room

The study was conducted in a room measuring 3.12 X 3.61 m with a raised plywood floor in the Avian Cognition Laboratory at Northern Arizona University. There were 238 5.1-cm diameter holes drilled into the floor, 20.3 cm apart (centre to centre) and arranged in 14 rows (numbered 1-14) and 17 columns (labelled A-O). Each hole contained a tightly fitting paper cup that could either be filled with sand of a uniform texture or capped with a snug wooden plug. The sand-filled cups and the wooden plugs were approximately level with the plywood floor. There were 32 landmarks such as rocks, boards, pipes, cans, sticks and plastic containers on the floor, and six posters on the walls. These stimuli were present throughout all sessions of the experiment.

A large rectangular feeder with a slotted top and false floor was placed in the centre of the room. At the start of a caching session, we placed 121 seeds in the slots of the feeder. When the desired number of caches had been made, a solenoid connected to the false floor was activated and the remaining seed fell through the slots to the bottom of the feeder, making them inaccessible.

The birds entered and left the experimental room through a porthole in one wall. This porthole connected directly to the bird's home cage, which was carried to and from the housing room for each experimental session. This wall also contained an entrance door and a one-way glass window through which the birds were observed.

Procedures

Birds were tested individually under two conditions that differed in how cache sites were presented during recovery sessions. During one condition (free) all holes in the room (N=238) were open during all recovery sessions. In the other condition (cluster), each cache

site was presented as a member of a 2#3 cluster of open holes. The order of presentation of the conditions was counterbalanced across birds. Birds first cached and recovered their caches under one condition, then cached and recovered under the other condition, with 22–25 days between the last recovery session of the first condition and the first caching session of the second.

Caching sessions did not differ for the two conditions. Under both conditions, birds were allowed into the experimental room to create caches with the seeds (N=121) provided on the feeder. During caching, 60 (of the 238) holes were filled with sand and the others were plugged. Different sets of 60 holes were used for the two conditions, counterbalanced across birds. Birds were allowed to continue caching until they made 15 caches or remained inactive for 20 min. On two occasions, birds made less than 13 caches in a single session and were allowed back in the room 2 days later to continue caching. Everything remained the same on the second session except all holes in which the birds had previously cached were now plugged and all signs of digging were removed. On one occasion it was not possible to stop a bird in the midst of an intensive caching bout and 17 caches were created. One bird made only three caches and then stopped all caching behaviour. This trial was eliminated from analysis.

Recovery sessions followed caching sessions by 9–12 days. To limit within-session satiation effects, we allowed each bird to recover one-third of its caches during each of three recovery sessions scheduled 1 day apart. During one set of recovery sessions (cluster), we randomly selected one-third of the cache sites for presentation during each recovery session. Each cache site was presented as one hole of a six-hole cluster (2#3 matrix). Clusters were arranged so that the correct hole (cache site) was at a different position within the cluster for each of the clusters. Clusters were separated by at least one row and one column of holes wherever possible and no hole was ever used in more than one cluster. Thus, for example, a bird that had made 15 caches would, during each cluster recovery session, be presented with five 2 X 3 clusters, each of which included a cache site. On a few occasions, birds placed their caches in a pattern that prevented the testing of all cache sites during recovery sessions.

For the other set of recovery sessions (free), all 238 holes were opened in the room during recovery. During both types of recovery sessions, only one seed was present in each cache site, to reduce satiation effects. (Balda et al. 1986, demonstrated that this reduction in cache size has no effect on recovery behaviour.)

Observational scoring categories

All sessions were videotaped through a one-way window, using a Panasonic PV-520 video camera, Panasonic NV-8200 video cassette recorder and Sanyo

DS20030 monitor. The tapes were then played back and scored. Each time a bird either made or recovered a cache, or visited an empty hole during recovery, the following information was taken from the videotape.

(1) The identity of the cache site (by column letter and row number).

(2) The time of the visit, in minutes and seconds from the beginning of the session. A visit was defined as having occurred whenever the bird's beak came into contact with the sand in the hole.

(3) Approach direction (APP): the direction in which the body was moving when the bird arrived at the site. All directional information was scored in eight categories, north (0°), northeast (45°), east (90°), and so forth.

(4) Begin direction (BEG): the direction of the body at the moment probing began.

(5) End direction (END): the direction of the body at the moment the last probe ended.

(6) Leave direction (LV): the direction in which the bird moved to leave the site.

(7) The number of probes: the number of times the bill came into contact with the substrate at the site. If one probe had already occurred, the next probe was counted only if either the head came fully upright or if a seed was obtained between successive contacts.

(8) The number of seeds cached.

(9) Time spent at cache site: the time in seconds from arrival at the site until departure from the site. This was scored in three components: time between arrival and the onset of probing, time spent probing (from first to last probe), and time between the last probe and departure. Each component was given a minimum score of 1 s, so the minimum possible score for total time spent at a site was 3 s.

Interobserver reliabilities

Two observers independently scored four sessions (two caching and two recovery) and their results were compared to determine interobserver reliability. In all cases for all categories, agreement between the observers was 90% or higher. In addition, both observers scored all of the tapes, and wherever differences occurred, they both observed the tape in question and resolved their differences. (The differences between observers, when they occurred, were small, for example when the bird's orientation was on the border between directions or it wasn't clear whether or not a particular head movement resulted in the bird actually touching the substrate.)

Data reduction and statistical analyses

Many of our analyses compared the direction of movement or body orientation at two different times. For these analyses, we calculated 'directional consistency scores'. As described above, we recorded the orientation of the bird four times during each visit to a cache site by classifying the orientation into one of eight 45° segments.

To compare orientation during any two segments, we used the absolute value of the result of subtracting the orientation of the bird during the second segment from the orientation during the first segment. The absolute value of the results of this subtraction could range from 0 to 315° (in 45° increments). A result of 0 represented cases in which the two orientations were in the same segment; results of either 45 or 315° represented cases in which the two orientations were in segments that were next to each other, and were combined into a single 45° category (since 315° is 360° minus 45°); results of either 90 or 270° represented cases in which the two orientations were separated by a single segment, and were combined into a single 90° category; and so forth.

In a number of cases, we used repeated measure ANOVAs to analyse aspects of our results. Although the exact nature of the ANOVAs depended upon the dependent variable being analysed, in all cases, we computed mean values for each bird for each condition being analysed (across either all caching episodes or all recoveries, across all sessions), and used these values in the ANOVA. In other words, the individual birds were the units of the analysis. Thus, dependent variables that may have been discrete, or even dichotomous, on an episode-by-episode basis were continuously distributed for the ANOVAs. Subsequent tests were carried out only following significant F ratios, and Fisher's least significant difference (LSD) test was used.

Results

Caching Behaviour

During caching sessions of the free-choice condition, birds made a mean \pm SE of 14.00 ± 1.87 caches, placing 4.55 ± 1.13 seeds per cache. They made a mean of 5.02 ± 1.04 probes in 10.02 ± 2.36 s at each of the cache sites. During the caching sessions of the cluster condition, each bird made 15 ± 0.00 caches, placing 5.89 ± 1.46 seeds per cache. They made a mean of 5.89 ± 1.37 probes in 14.11 ± 5.89 s at each cache site. There were no significant differences in caching behaviour in any of these measures between the free and the cluster conditions (paired t tests: NS in all cases).

Recovery Behaviour

During free-choice recovery sessions, the birds made a mean \pm SE of 1.82 ± 0.38 probes at holes containing seeds and 1.44 ± 0.28 probes at incorrect holes, spending a mean of 3.96 ± 0.25 s at holes containing seeds and 3.11 ± 0.11 s at incorrect holes. During cluster condition recovery sessions, the birds made a mean of 2.40 ± 0.28 probes at holes containing seeds and 1.42 ± 0.27 probes at incorrect holes, spending a mean of 4.69 ± 0.66 s at correct and 3.34 ± 0.34 s at incorrect holes. These data were analysed with two-way repeated measures ANOVA, with recovery condition (free versus cluster) and type of site (correct

versus incorrect) as independent variables. The only significant effect was that the birds spent more time at correct sites than at incorrect sites ($F_{1,3}=16.14$, $P=0.03$) and their tendency to make more probes at correct sites approached significance ($F_{1,3}=6.80$, $P=0.08$).

Recovery Accuracy

Any visit to an empty hole was considered an error; visits to holes containing seeds were considered correct. Repeated visits to holes within the same recovery session (after the first visit) were omitted from the analysis. During the recovery sessions of the free-choice condition, with all 238 holes available, the nutcrackers recovered their caches more accurately than would be expected by chance. The birds made a mean of 1.62 ± 0.26 errors per successful recovery, with an overall accuracy (probability that a probe was directed at a site containing a seed) of 0.38. During cluster recovery sessions, with only six holes open for each cache, caches were also recovered more accurately than would be expected by chance, with a mean of 0.85 ± 0.36 errors per recovery, yielding an overall accuracy of 0.54. This difference in accuracy was not statistically significant (paired t test: NS).

Directionality during Caching and Recovery

We carried out one set of analyses to examine within session patterns of orientation and movement during caching and during recovery sessions. We carried out another set of analyses to compare patterns observed during caching sessions with those observed during recovery sessions. In both cases, the observed patterns were very similar during both the free and cluster conditions, and preliminary analyses revealed no significant differences between these two conditions. Therefore, we combined the directional data from the free and cluster conditions for these analyses of directionality.

Orientation within caching and recovery sessions

To analyse changes in orientation during sequences of caching and recovery behaviour, we calculated a directional consistency score comparing each stage in the sequence with the next. We calculated scores separately for caching and recovery, comparing orientation when approaching the site with orientation at the start of probing (APP"BEGIN), the start of probing with the end of probing (BEGIN"END), and the end of probing with the direction of leaving the site (END"LV).

In general, the birds maintained a consistent pattern of orientation during both caching and recovery, changing direction primarily when leaving the site (Fig. 1). We analysed these data with a repeated measures ANOVA of the mean amount of change in orientation for each measure. We performed separate analyses for caching and recovery. There were significant differences in the amount of change in orientation both during caching ($F_{2,6}=48.33$, $P<0.001$), and recovery ($F_{2,6}=156.48$, $P<0.001$).

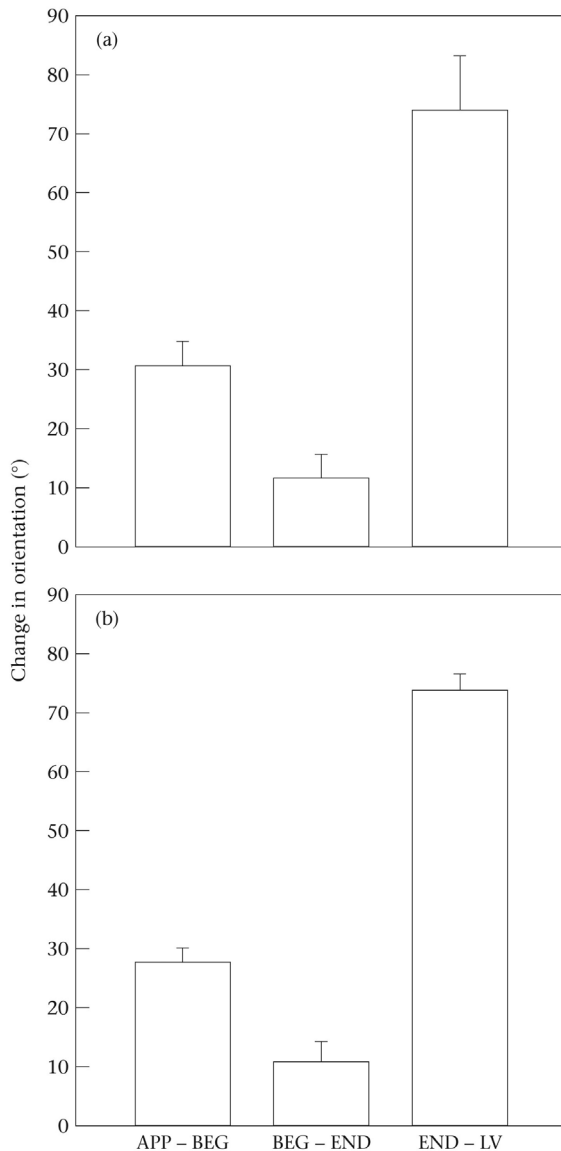


Figure 1. Consistency in direction during caching (a) and recovery (b). Each bar shows the average number of degrees of change in orientation from: APP-BEG: approaching the site to beginning to probe; BEG-END: beginning to probe to the end of probing; and END-LV: the end of probing to leaving the site.

Subsequent Fisher's LSD tests revealed that each of the three stages differed significantly from the others ($P < 0.01$). The birds maintained the most consistent orientation during actual probing, and changed orientation most between the completion of probing and leaving the site.

During recovery sessions, there were some differences in changes in body orientation between correct sites and incorrect sites. These differences were most evident between the beginning of probing and just prior to leaving the site. The birds changed their body orientation more during recoveries at correct sites than during probing at incorrect sites during both the

free ($F_{1,2} = 21.42$, $P < 0.05$) and cluster recovery sessions ($F_{1,3} = 27.89$, $P < 0.01$).

Directional consistency between caching and recovery

To determine whether there was any relationship between the orientation the birds tended to use during the recovery of a cache and the orientation they had used during its creation, we calculated directional consistency scores comparing approach, the beginning of probing, the end of probing, and leaving each site during recovery with orientation at the same point in the sequence during caching at each cache site. In addition, because of the results obtained with bees (Cartwright & Collett 1983), we compared the direction of leaving the site during caching with the direction of approach during recovery. Given our system of calculating directional consistency, if orientation during caching and during recovery were random with respect to each other, scores of either 8° or 180° would be expected to occur with a probability of 0.125, and scores of 45° , 90° , or 135° with a probability of 0.25.

We analysed the distribution of these directional consistency scores (Fig. 2) in two ways. First, we used chi-square tests to determine the significance of the differences between the overall distributions and chance. The observed distributions differed from chance for approaching a site, beginning probing, and at the end of probing ($P < 0.001$ in all cases), but not for leaving a site (NS). Then we carried out more focused tests, using the binomial distribution to determine whether orientation was exactly the same (scores of 0) during caching and recovery more often than would be expected by chance. These analyses showed that the same orientation was used significantly more often than would be expected by chance when approaching the site and at the beginning and end of probing ($P < 0.001$ in all cases), but not when leaving the site (NS), and that there was no significant relationship between the direction in which the nutcrackers left the site after caching and the direction from which they approached the site during recovery (NS).

Predictors of recovery accuracy

Is there any measure of behaviour at a particular site during caching that predicts the accuracy of cache recovery at that site? To answer this question, it is necessary to have a measure of accuracy that can be applied site by site. For cluster recoveries, such a measure is the number of errors within a cluster before recovery of the cache within that cluster. For free recoveries, the best measure available is the number of errors preceding each recovery. This measure assumes that the errors occurring before a particular recovery can be assigned to that recovery. Here, we use these site-by-site measures of accuracy to assess the extent to which caching behaviour or directionality predicts recovery accuracy. In these

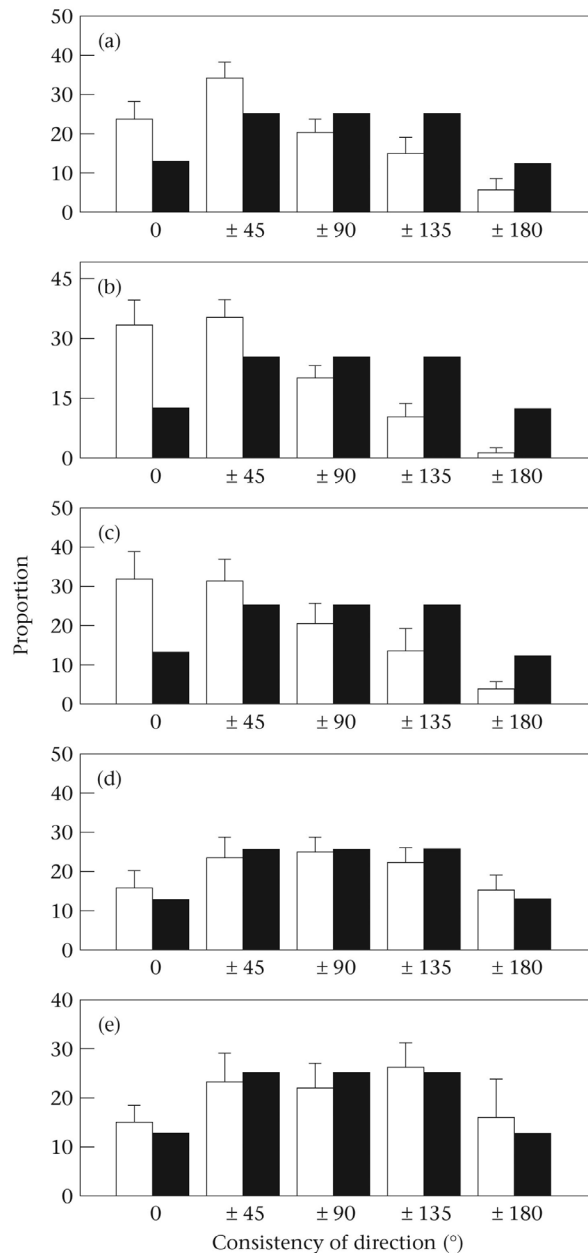


Figure 2. Consistency in direction between caching and recovery. h: Observed distributions of the amount of difference between caching and recovery; μ : expected value. Distributions of directional consistency are shown for (a) approach to the site, (b) begin probing, (c) end of probing, (d) leaving the site and (e) leaving the site after caching versus approaching the site during recovery.

analyses, we examined free and cluster results separately because of the different error measures that were used.

In one set of analyses, we examined the effects of directional consistency between caching and recovery on the number of errors made during recovery. Each cache recovery was classified into one of two categories based on the directional consistency shown by the bird while caching and recovering at that site. If the cache behavior and the recovery behaviour occurred with body orientations that were in the same segment a consistency

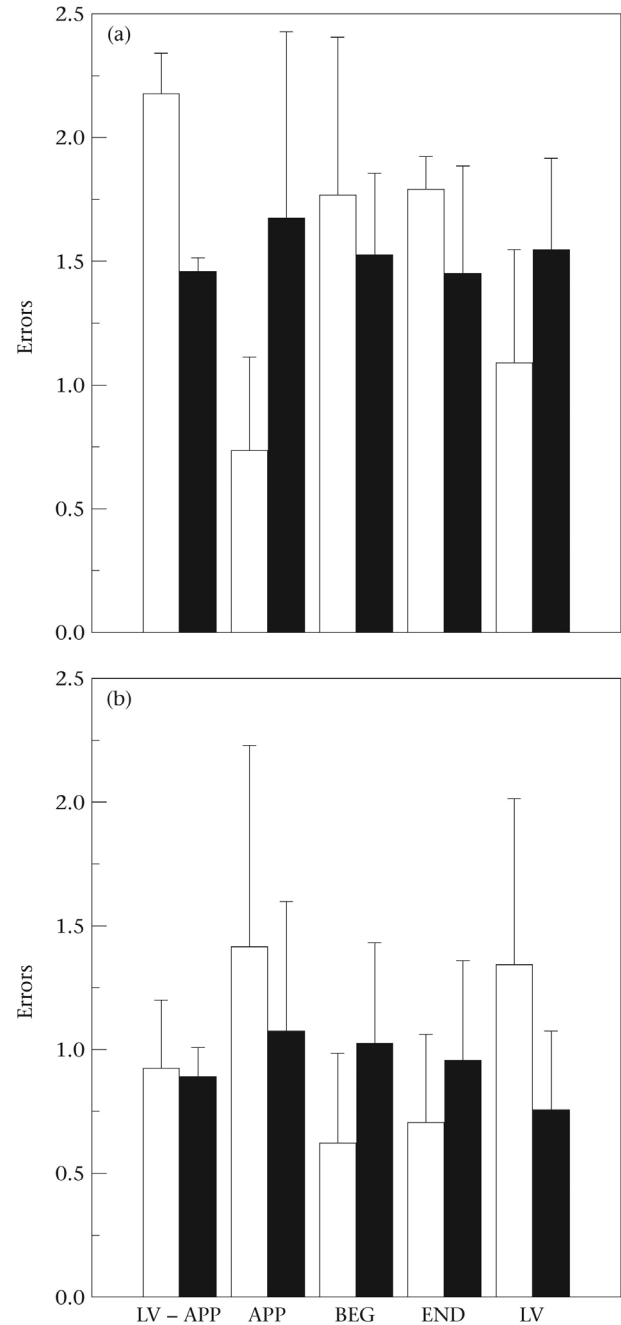


Figure 3. The relationship between the number of recovery errors and directional consistency. The number of errors made at sites when the same direction (h) and different directions (i) were used during caching and recovery. Data are given separately for (a) free and (b) cluster conditions, and for each of the five directional measures (APP: approach; BEG: begin; END: end; LV: leave; LV-APP: comparison of the leave direction during caching with the approach direction during recovery).

score of 0°), then the recovery was assigned to the directionally consistent category. Otherwise, it was assigned to the inconsistent category. (An additional set of analyses in which directional consistency was defined as a consistency score of ± 45) yielded results very similar to the results of these analyses.) We calculated the mean

number of errors for each category and compared the error rates for the two categories with one-way repeated measures ANOVA. We carried out five such analyses: for approach, begin caching, end caching, leave, and a comparison of leave direction during caching with approach during recovery, for free testing and for cluster testing. No significant differences were found in any of these 10 ANOVAs (see Fig. 3). The birds made the same number of errors when they used different orientations during caching and recovery as they did when using the same orientation during caching and recovery.

In another set of analyses, we categorized each cache recovery on the basis of the number of errors associated with that recovery. In free recoveries, the low-error category included all recoveries with zero or one errors while during cluster recoveries, the low-error category was defined as those recoveries with zero errors. (These definitions differ because the mean number of errors was higher in the free condition.) We then used one-way repeated measure ANOVA to compare these categories on seven behaviours including number of probes made during caching, number of seeds placed in the cache, total time spent at the cache site during caching, and the four measures of directional consistency. No significant effects were found (see Fig. 4). There were no consistent differences in caching behaviour between sites later recovered with few errors and those later recovered with more errors.

Finally, we did a series of power analyses (Cohen 1988) on the ANOVAs we used to evaluate predictors of recovery accuracy. The power of a statistical test is a function of the size of the effects one is attempting to detect. Therefore, in those cases where the number of errors made was the measure, we specified an effect size of more than two errors. That is, we calculated the probability of our statistical tests detecting an effect in which inconsistent directional approach added two errors to the birds' performance. There were 10 such analyses, with powers ranging from 0.07 to 0.59, with a median of 0.16. In those analyses in which other measures were used, we used the 'moderate' effect size of 50%. That is, we calculated the probability of detecting an effect in which caches recovered with few errors differed from the others by 50%. There were 16 of these analyses, and power varied from 0.06 to 0.37 with a median of 0.18.

Discussion

The nutcrackers used the same direction of approach to a site during cache recovery as they had used during creation of that cache 25–35% of the time, more often than would be expected by chance. They also tended to maintain the same body orientation at the site during recovery as they had during caching. This result replicates that of Bossema (1979) with European jays. However, the implication of this finding, that such use

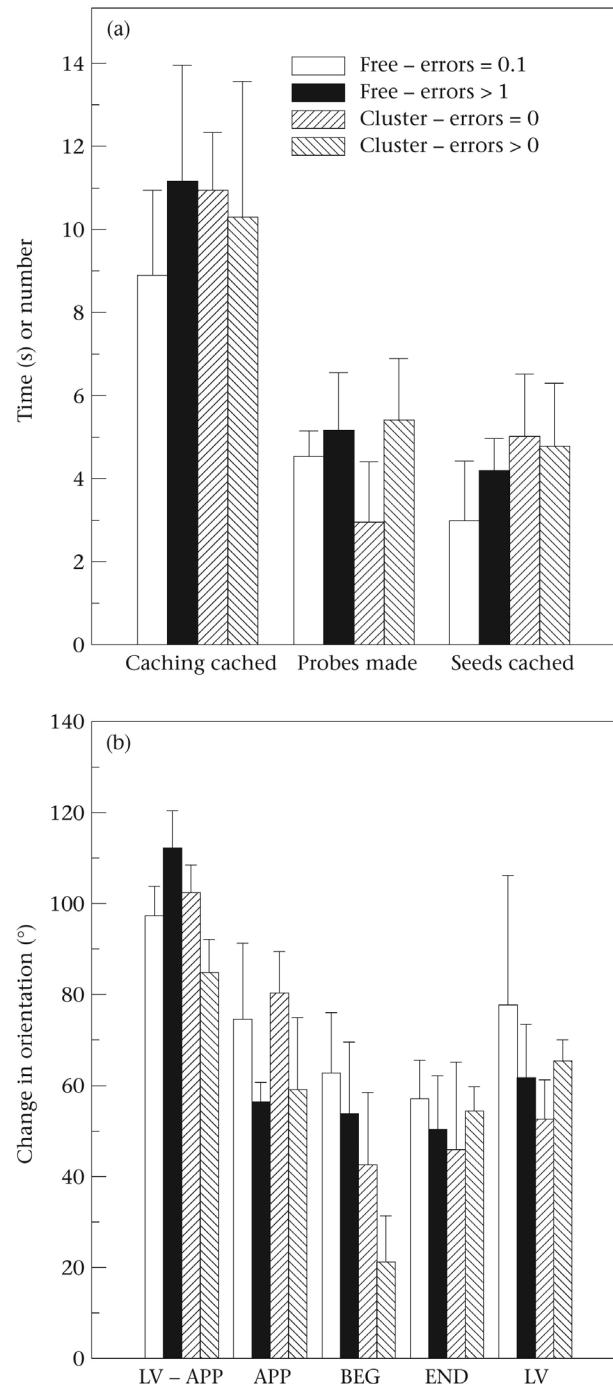


Figure 4. (a) Mean number of seconds spent caching, mean number of cache probes and mean number of seeds cached at sites as a function of number of errors made during recovery for both free and cluster conditions. (b) Mean caching-recovery change in direction as a function of number of errors made during recovery for both free and cluster conditions.

of the same orientation during caching and recovery plays an important role in accurate cache recovery, is clearly not supported by the data from this experiment. Although the birds were more directionally consistent than expected by chance, they approached a cache site from a different direction than that used when creating

the cache 65–75% of the time. If consistency of direction is important to accurate recovery, then such inconsistent approach should have been associated with less accurate performance. This was not the case. None of the analyses of the relationship between directional consistency and accuracy of cache recovery found any effects that even approached significance.

One objection that could be raised is that this conclusion rests on a series of negative results, of failures to reject the statistical null hypothesis. While this is true, the data are fairly convincing. (1) The results of the power analyses indicated that although some of our tests had low power, many were quite respectable in terms of power. Furthermore, one must consider the combined power of these tests, 26 in all. It seems unlikely that there could be a strong relationship between directional consistency and recovery accuracy and yet none of these tests proved significant. (2) When the results of the relevant analyses are examined qualitatively, there is not even an apparent pattern. In the analyses of errors as a function of directionality (Fig. 3), about half are in the direction of a positive association between directional consistency and recovery accuracy, the remainder in the opposite direction. A similar pattern holds for the analyses of directional consistency (Fig. 4b). This pattern argues against a biologically significant effect that was too small to be detected in the current data set. (3) Although the results of this set of analyses were uniformly negative, there were a number of similar analyses of other aspects of the data that were significant. Particularly striking is the finding that when we divided visits to sites into categories based upon whether they were correct or incorrect, significant differences in directionality were found for both types of recovery sessions. We also found significant patterns of changes in body orientation within caching and recovery sessions. Significant results such as these suggest that the design of the study and the precision of the data we collected were sufficient to detect differential patterns of directionality where they exist. (4) The negative results of our statistical tests are consistent with more subjective impressions gained when, through the use of videotape, we were able to watch cache creation and recovery at a particular site sequentially. There were many instances in which a bird clearly used a very different direction of approach and body orientation during recovery than during caching, and did so without making any recovery errors. It is clear that nutcrackers can accurately recover their caches without retracing the path they used during caching or aligning their body in the same direction at any point during probing of the site. We conclude that it is very unlikely that there is an important relationship between directional consistency and the accuracy of cache recovery.

Although this is a simple result, it has important implications for understanding the cognitive

mechanisms underlying accurate cache recovery in this species. It demonstrates that the birds probably do not use any simple 'snapshot matching' of landmarks to relocate caches. The ability to relocate sites from varying directions suggests that these locations are remembered in terms of the relationship between individual sites and landmarks. This, in turn, strongly implies that nutcrackers possess an internal representation of the caching area. If this representation maintains some of the geometric relationships among landmarks, then it could legitimately be called a cognitive map (Gallistel 1990).

The current study took a descriptive, nonexperimental approach. Therefore, the data do not lend themselves to detailed analysis of the nature of the internal representation being used by the nutcrackers, nor can they be used to determine which geometric relationships between cache sites and landmarks and/or between landmarks are used by the birds. Nevertheless, these results offer a strong rationale for detailed, experimental studies investigating the role of geometric relationships in spatial memory and orientation in Clark's nutcrackers (e.g. Kamil & Jones 1997).

This study also provides a more quantitative picture of the details of caching and recovery behaviour than was previously available. Several aspects of this picture are of particular interest. The behaviour is rapid. Not only do nutcrackers cache quickly, but they spend relatively little time, 10–12 s, at each cache site, roughly 2 s per seed cached. Considering how well they remember cache sites, this is impressive. Visits to cache sites during recovery are also very rapid, averaging 3–4 s.

It seems reasonable to think of a change in direction as an indicator of the end of one behavioural sequence and the beginning of the next. The directional analyses within caching and recovery sessions showed that the birds generally maintained the same orientation while approaching and probing in a site, with the greatest change in direction when leaving. This pattern suggests that the act of caching or recovering seeds marks the end of one of the components into which caching and recovery behaviour is organized. In a previous study (Balda & Kamil 1989), we found that nutcrackers dispersed their caches throughout the room, apparently at random. The movement pattern seen here during caching is consistent with that earlier observation. During recovery sessions, the change in direction when leaving the site probably represents a shift from locating the cache to consuming the recovered seed. This interpretation is supported by the finding that the birds changed direction more following successful recoveries than following unsuccessful visits to empty sites.

Finally, the only factor that predicted where the birds would search during recovery was where the birds buried their seeds. No other behaviour measured during caching sessions could account for any of the variation

in cacherecovery accuracy among sites. Thus we believe it is unlikely that variation in caching behaviour is responsible for differential memory for cache sites. Our earlier study (Kamil & Balda 1990) demonstrated that variation in physical characteristics are probably not responsible for variation in cache-recovery accuracy. We still have no answer to the question of why some sites are remembered better than others.

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