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Tests for Cognitive Mapping in Clark's Nutcrackers (*Nucifraga columbiana*)

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Abstract

In these experiments, the authors examined the nature of the spatial information that Clark's nutcrackers (*Nucifraga columbiana*) use during navigation and whether this information is represented in the form of a cognitive map. In Experiment 1, nutcrackers were able to use distal cues to locate a small hidden goal. In Experiments 2 and 3, nutcrackers were given the opportunity to develop a map of a room by viewing local subsets of the landmarks in the room at a goal during training. During transfer tests, nutcrackers were presented with a landmark panorama that was not previously seen at the goal. Of 3 nutcrackers that had learned the relationship between distal cues and the goal, 3 were able to locate the goal during transfer, indicating they may have developed a cognitive map. Experiments 4 and 5 suggest that the simpler mechanism of vector integration may have been used by some nutcrackers during the transfer tests.

There are several navigational systems (e.g., dead reckoning, motor response learning) that appear to be ubiquitous across a broad range of species (for reviews, see Gallistel, 1990; Healy, 1998; Redish, 1999; Shettleworth, 1998). One spatial system that has been frequently studied is navigation by landmarks (Cheng & Spetch, 1998). Objects that remain in the same place can serve as landmarks to guide an animal toward a goal that remains fixed with respect to these cues. The nature of the spatial information animals encode from landmarks is currently being investigated. A large body of evidence indicates that animals encode vectors between landmarks and a goal (e.g., Cartwright & Collett, 1983; Collett, Cartwright, & Smith, 1986). The summing or integration of these separate vectors specifies the location of the goal (e.g., Cheng, 1988, 1989, 1990; Kamil & Cheng, 2001). For example, Cheng (1988) trained pigeons to find a hidden goal at a constant place with respect to an array of landmarks. During tests in which some landmarks were shifted, birds searched at locations between the original training location of the goal and the position of the goal as defined by the shifted landmarks. The magnitude of the shift in search was dependent on the algebraic summation of the specific landmark-goal vectors and the weight given to each of the shifted landmarks. Although it is clear that landmark-based information plays an important role in navigation, debate continues as to how spatial information, particularly about landmarks, is acquired and organized by animals (Shettleworth, 1998).

A *cognitive map* can be defined as an internal representation of the geometric relationships among the important landmarks in an organism's environment (O'Keefe & Nadel, 1978; Tolman, 1948). Organisms encounter costs (e.g., predatory, metabolic) when navigating from one site to the next. Individuals with more efficient or flexible navigational systems would have a navigational advantage. Landmarks organized

into a map might not only specify previously encountered goal-landmark geometries but could also be used to generate novel travel routes among locations (Gould, 1986; O'Keefe & Nadel, 1978), thereby increasing navigational flexibility and reducing travel costs.

Although the idea that animals use cognitive maps to navigate may be conceptually appealing, it has proven extremely difficult to establish the existence of cognitive maps in animals (e.g., Bennett, 1996; Dyer, 1991; Wehner & Menzel, 1990). An important concern is that researchers who have found support for cognitive mapping have generally failed to consider that other simpler mechanisms of navigation may be used by the animals during navigation (Bennett, 1996). For example, Gould (1986) reported that bees could take a novel route to locate a feeder, indicating the use of a cognitive map; yet similar and more controlled experiments have found that these bees may have been using the local features of the landmark environment (e.g., beacons) to locate the goal (Dyer, 1991).

Recently, Benhamou (1996) carried out an ingenious water maze study that tested for cognitive mapping in rats after he had apparently controlled for navigation by other simpler spatial systems. Benhamou trained rats to locate a goal placed in a fixed location in a partially enclosed water maze that provided rats with a limited visual panorama of the room that they could use to locate the goal during training. During transfer tests, the opening to the apparatus was rotated so that rats observed a view of landmarks and the room that had been encountered previously, but never at the goal location. A correct solution appeared to require rats to integrate the landmark-goal relationships learned during training within the framework of a map of the room and the visual panorama observed during transfer. The rats were unable to accurately navigate to the goal during transfer tests, indicating that they were unable

to develop or use a cognitive map. Although rats need to navigate effectively in their environment, the evolutionary cost of developing a cognitive map may far exceed their navigational requirements. Hence, tests for cognitive mapping in a species that has an exceptional spatial cognitive demand would be of interest.

The Clark's nutcracker (*Nucifraga columbiana*) appears to be an ideal choice for tests of cognitive mapping, as its impressive spatial cognitive abilities have been well investigated over the past 2 decades. Clark's nutcrackers cache up to 33,000 pine seeds in thousands of locations several kilometers from the collection site (Balda & Kamil, 1998). Nutcrackers rely almost exclusively on the recovery of these caches during the winter and early spring as their primary energy source for survival (Giuntoli & Mewaldt, 1978). A large body of experimental evidence indicates that nutcrackers have a spatial memory for the location of caches made previously (for a review, see Balda & Kamil, 1998). Spatial memory for a cache site, however, may only be part of a broader spatial system (Shettleworth, 1998; Shettleworth & Hampton, 1998) adapted for the efficient recovery of a large number of spatially dispersed caches. In recent tests, researchers have examined how nutcrackers may be using landmarks to navigate and return to a goal location (e.g., Kamil & Jones, 1997, 2000). Here, we report the results of tests in which we examined the nature of the spatial information Clark's nutcrackers use during search for a hidden goal and whether or not it conforms with the use of a cognitive map.

Experiment 1

A number of researchers have explored the use of local and distal spatial cues during search for a hidden goal (Alyan & Jander, 1994; Biegler & Morris, 1996; Roberts & Pearce, 1999; Spetch & Edwards, 1988). Landmarks that are in the immediate vicinity are *local cues*, whereas landmarks farther away provide *distal information*. These terms are somewhat arbitrary and likely vary with respect to the ecology of a species. To further operationalize and to invalidate either local or distal information, these researchers often keep the relationship between the goal and one set of cues constant while varying the relationships between the goal and the other set of cues randomly (e.g., Collett et al., 1986).

Although nutcrackers are able to attend to distal information during local landmark navigation (Gould-Beierle & Kamil, 1996), perhaps including the geometry of the room (Cheng, 1986), it has yet to be determined if nutcrackers can use the features of a room to accurately return to a small and hidden goal. Experiment 1 was designed to accomplish three goals. First, we wanted to determine if nutcrackers could use the features of an open room to locate a small buried goal. Second, 5 of the 10 nutcrackers selected for this study had prior experience using local cues to find a buried goal (Kamil & Jones, 1997). The other 5 nutcrackers were experimentally naive. These different experimental histories allowed us to examine whether nutcrackers that had previous experience using local cues would perform differently than naive birds during a task using the features of the room alone. Finally, in preparation for tests of cognitive mapping, we wanted to provide all nutcrackers with experience in using relatively more distal cues and in following the open-room testing procedures.

Method

Subjects

The birds were 10 Clark's nutcrackers (*Nucifraga columbiana*) that had been trapped as adults and subsequently housed individually in a colony of other individually housed birds at the University of Nebraska-Lincoln. Nutcrackers were fed a daily combination of turkey starter, sunflower seeds, meal worms, and a vitamin supplement. During the experiment, nutcrackers were maintained at 85% to 90% of their free-feeding weight.

Experimental Room and Apparatus

Testing was conducted in 4.4 × 3.0-m experimental room that was as spatially homogenous as possible. All four walls of the room were painted light beige, and all removable landmarks were taken out of the room. The experimenter could move between the observation area and the experimental room through a large door located in the east wall. Nutcrackers were trained to enter and leave the experimental room through a small sliding door located to the south of a large door in the east wall. A holding cage that had an opening in one side was placed next to the sliding door, and it temporarily housed nutcrackers during the experimental sessions. Animal bedding was distributed evenly on the floor (6 to 8 cm depth) of the experimental room and was retained by a wood beam (15 cm tall). The experimental room had four 70-W fluorescent light fixtures that provided even illumination. A closed-circuit video camera (Panasonic Model WV-BL200), the body of which was hidden within the ceiling of the room, was connected to a VCR (Panasonic Model AG-1730) and used to monitor and record behavior during a session.

Procedures

Birds were assigned to either a naive or experienced group on the basis of their previous experimental history (see above). All nutcrackers underwent identical training and testing procedures, as identified below.

Familiarization. Two familiarization sessions were conducted per day. Each session began when a nutcracker was individually transported by hand from the colony to the holding cage. Following a 1-min habituation period, the sliding door was opened, and the bird was able to enter the experimental room. Most birds flew from the perch in the holding cage through the door and landed directly onto the surface of the experimental room. Some birds occasionally flew in a loop around the room for 5 to 10 s and landed on the substrate or the barrier. Birds were then allowed up to 15 min to locate four pine seeds placed on a gray camera lens cap (3 cm diameter) situated on the surface of the substrate. The position of the lens cap was randomly determined before the start of each session. Most birds typically found the goal within the first couple of minutes of the start of the trial. Immediately after the bird found and consumed the last of four pine seeds or after the 15-min time limit had passed, the houselights were turned off. The light in the observation area illuminated the opening to the sliding door and served as a guide during departure. If the bird did not return immediately to the holding cage after the lights were turned off, the experimenter entered the room and gently directed the bird towards the sliding door. The sliding door was then closed and the room was prepared for the next session. Familiarization continued until a bird found all eight seeds (four from each session) for 3 consecutive days, and it lasted for a total of 5 days (10 sessions).

Acquisition. Following familiarization, each nutcracker experienced one four-trial acquisition session per day. During each of the first three trials, the lens cap with two pine seeds on top of it was placed at the goal location. The lens cap and the seeds were partially buried 1 to 2 cm into the animal bedding, so that one quarter of the lens cap could be seen. The nutcracker was released into the experimental room through the sliding door. After either 50 digs (see below) had been made, 10 min had passed, or the last seed

was consumed, the houselights were turned off, and the nutcracker was allowed to exit through the sliding door. The sliding door was closed, and during a 2-min intertrial interval (ITI), the experimenter entered the room, restocked the goal, and swept the substrate to remove any markings. Before the start of the fourth trial (the test), the experimenter completely buried the lens cap and seeds at the goal location during the ITI. The nutcracker was then released into the room and allowed to search for the hidden goal. Previous experiments with nutcrackers in our laboratory have indicated that these birds do not use olfactory cues to accurately locate a hidden goal. The goal was always 1.5 m west of the retaining wall and 1 m south of the north wall during all four trials of the session. Acquisition proceeded for 10 five-session blocks.

Measures and Analysis

From a videotape record of each session, we determined the Cartesian $\{x, y\}$ position of each dig and of the goal with respect to the room. An *individual dig* was defined as the point at which a nutcracker first placed its beak into the substrate. The coordinates of each dig and the goal were calculated using video playback software that could freeze an image from a section of the videotape from each session on a computer screen. A cursor on the screen was placed over the critical image (e.g., beak in substrate), and the room coordinate of the dig was recorded. The position of each of the first 20 digs made during the test was determined, and the absolute distance of each dig from the goal location was calculated and averaged. This measure was used as an indicator of search accuracy for the first experiment.

An analysis of variance (ANOVA) using group (naive vs. experienced) as a between-subjects factor and block and bird as a repeated factors was used to examine for reliable differences between the groups across acquisition. Alpha was set at .05 for reliable effects for all experiments.

Results

Accuracy improved across blocks of acquisition for both the naive and experienced groups, $F(9, 72) = 9.29, p < .01$ (Figure 1). This improvement in accuracy appeared to increase steadily until Block 4, after which performance remained stable. The naive group was initially less accurate than the exper-

rienced group, as revealed by a reliable Group \times Block interaction, $F(9, 72) = 2.52, p < .01$. Fisher's least significant difference (LSD) multiple-comparison tests found that the groups differed during Blocks 1 and 2 ($ps < .05$), but that they were not reliably different after Block 2 ($ps > .05$ in all cases).

Discussion

The results from Experiment 1 indicate that nutcrackers are able to use the features of an open-room environment (e.g., corners) to locate the position of a hidden goal that is fixed with respect to the room. Whereas previous studies have indicated that nutcrackers attended to the features of an open room during navigation (e.g., Gould-Beierle & Kamil, 1996), the current study required nutcrackers to use these features to return to a small and discrete location. The results are consistent with research documenting the ability of other animals to use distal information to locate a goal (Biegler & Morris, 1996; Margules & Gallistel, 1988; Spetch & Edwards, 1988).

Experiment 2

While moving from one location to the next, animals experience local subsets of the landmarks in an environment. Simultaneous viewing of these landmark clusters may be impeded by distance or by barriers between them. Over time, local subsets of landmarks may be incorporated into a broader map of the environment that encodes the geometric relationships among the individual components. While at a goal, an animal might encode in a map landmarks in its current visual panorama. Later, if the animal is some distance from the foraging site, it could use the current landmark panorama to specify its position within the map and infer the relative distance and direction to the goal location, even when the landmarks at the goal are not currently in view. The second experiment is, in many respects, an open-room test of such a scenario. If

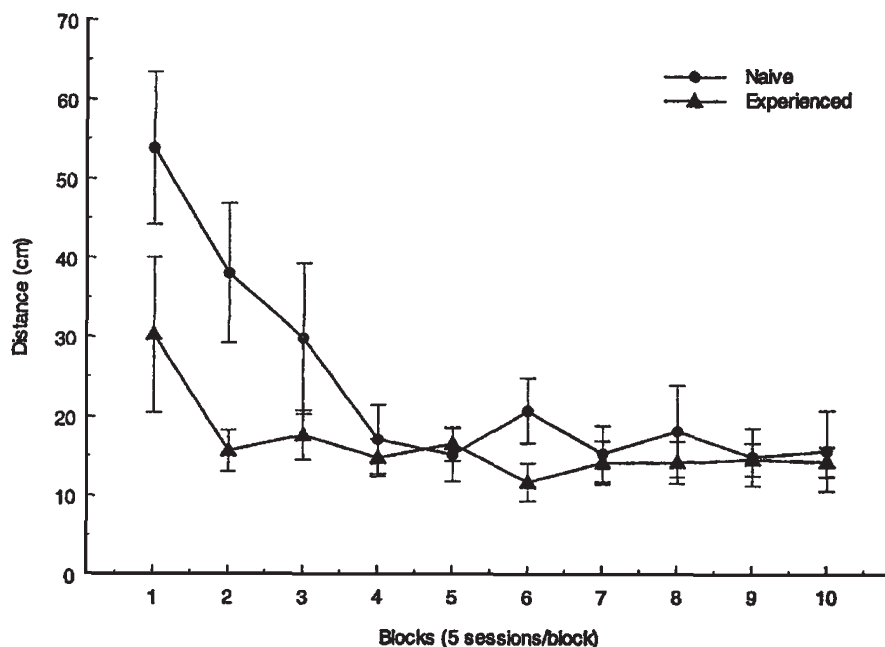


Figure 1. The mean absolute distance of digs from the goal during acquisition for both the experienced and naive groups in Experiment 1.

nutcrackers are able to develop and use a cognitive map, then they should be able to determine their current position using landmarks previously stored in the map. Subsequently, they should be able to infer the direction and distance to the location of a hidden goal even when all landmarks viewed previously at the goal are hidden from view (Benhamou, 1996). Therefore, in Experiment 2, we tested the birds with an apparatus that could be rotated to block certain views of the room from the goal while allowing other views. During tests, birds were examined for their ability to integrate a currently viewed landmark panorama within the framework of a cognitive map to accurately locate a hidden goal.

In Experiment 2, we also examined how preexposure to a landmark array would affect performance on a spatial test. An animal that is able to encounter all the landmarks in an environment at one time or has a greater period of exposure to subsets of landmarks (Prados, Redhead, & Pearce, 1999) might have an advantage in its ability to generate or use a map.

Method

Animals

In Experiment 2, we used 9 of the 10 nutcrackers that completed Experiment 1. One nutcracker (Rei) died before the start of the sec-

ond experiment. A necropsy of the carcass failed to reveal any conclusive findings as to the cause of the death. Birds were maintained as described in Experiment 1.

Experimental Room

Testing and the balance of training were conducted in a 4.4- × 3.0-m room similar to that used in Experiment 1 (Figure 2A). Animal bedding was dispersed on the floor at a depth of 6 to 8 cm.

Apparatus and Landmark Array

The apparatus was a steel cylinder (diameter = 132 cm; height = 154 cm) positioned upright on the floor near the geometric center of the room (Figure 2B). An opening located along 90° of the curved wall of the apparatus allowed access into the interior. The apparatus was secured on top of a large lazy-Susan-style wheel built into the floor of the room. The apparatus could be rotated (see below) so that the opening provided different panoramas of the room from inside while limiting others. Animal bedding was dispersed on the floor of the apparatus at a depth similar to that of the experimental room. A goal was located 38 cm from the geometric center of the interior of the apparatus and at a fixed bearing of 320° from due north. Although the apparatus could be rotated during the experiment, the position of the goal was always in the same {*x*, *y*} location with respect to the room. The lens of a closed-circuit camera was fitted into a small hole created in the center of the roof of the apparatus and was recessed from the in-

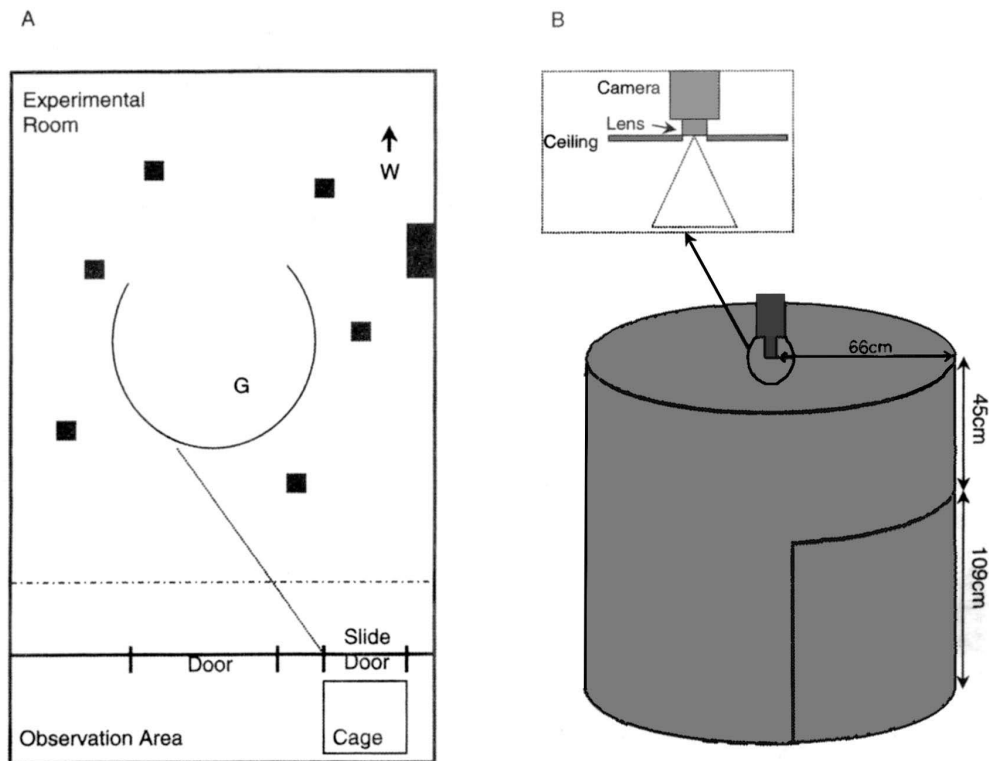


Figure 2. **A:** A top-down diagram of the room used for the balance of training and testing in Experiment 2. The six polyvinyl chloride landmarks are indicated by the small filled squares. The large filled rectangle adjacent to the north wall shows the position of an electrical conduit that ran from the floor to the ceiling of the room. The five posters placed on each of the four walls are represented by the dashed lines. The location of the apparatus is depicted by the semicircle in the center of the room. The dotted diagonal line between the apparatus and the sliding door shows one of two possible positions of the curtain (attached to the south side of the sliding door in this example). G indicates the position of the goal (approximately 40° clockwise from due north and 38 cm from the center of the apparatus). The dotted horizontal line represents the wood beam. The diagram is not drawn to scale. **B:** A diagram of the cylindrical apparatus showing the opening. The mounting of the camera above the apparatus is shown in the inset.

ner surface of the ceiling (see inset of Figure 2B). The dark coloration of the ceiling combined with the dark coloration of the recessed camera lens made the lens difficult to detect.

Six unique landmarks made of polyvinyl chloride (PVC) pipes were dispersed around the apparatus. The landmarks varied in width (3 to 6 cm) and height (30 to 60 cm) and were painted different colors. Some landmarks had horizontal or vertical stripes. The position of the landmarks was fixed with respect to the room. Five posters of varying sizes were also placed on the walls of the room. To ensure that every nutcracker had equal exposure to all of the landmarks, we used a large cloth curtain to direct nutcrackers to pass through either the north or south half of the room before entering the apparatus. The corners of the curtain abutted the east face of the apparatus and were attached to the ceiling and floor. The other end of the curtain could be attached to the east wall to either the north or south of the sliding door.

Procedure

Preexposure. Birds in the naive and experienced groups (Experiment 1) were randomly reassigned into two groups: a preexposure group ($n = 4$) and a room-naive group ($n = 5$). The room-naive group continued acquisition as described in Experiment 1 for an additional 5 days in the original room, whereas the second group began preexposure procedures in the room prepared for the second experiment. For the second group, all posters and landmarks were positioned in the room as described previously, but the apparatus and curtain were absent. Preexposure procedures were similar to the familiarization procedures used in Experiment 1. No pine seeds were ever placed at the goal location. One session of preexposure was conducted per day for 5 consecutive days.

Training. Following additional training in the old room or preexposure procedures in the new room, both groups were combined, and the cylindrical apparatus and the curtain were placed in the experimental room used in Experiment 2. An individual bird was transported from the home cage to the holding cage and allowed 1 min to habituate. A session consisted of two trials. During the first trial of the session, the sliding door was opened, and the nutcracker was released into the room. The lens cap and two seeds were partially buried at the goal location inside the apparatus. The trial concluded when the bird either located and consumed the second seed, made 25 digs, or failed to locate the seeds within 5 min. Our experience in the first experiment indicated that most birds found the seeds within approximately 25 digs, so this limit was used rather than the 50 dig limit used previously. The end of the trial was signaled by immediately turning off the houselights and allowing the bird to leave the room through the sliding door. Most birds consistently found the goal within the 1st minute, so the time limit rarely came into effect. During a 2-min ITI, the lens cap and two seeds were completely buried at the goal location, and the surface of the substrate in the room and the apparatus was swept with a broom so that the surface was even.

Following the ITI, the second trial began, and the bird was again released into the room. After the nutcracker entered the apparatus and located and consumed the seeds or if the trial limits had been met, the houselights were turned off, and the nutcracker was allowed to exit. The direction nutcrackers were forced to travel around the apparatus (using the curtain) during their departure in the second trial was randomly determined before each phase of a session and was balanced across sessions in a block. The surface of the animal bedding was swept with a broom so that the surface was even after each trial and between sessions. All birds encountered 2 training sessions per day. Training continued for six 16-session blocks.

Before the start of each training session, the apparatus was rotated so that the right edge of the opening (from inside the apparatus) was positioned at one of four training orientations (see O1–O4, Figure 3A). The same orientation was used for both trials of a session, and orientations were randomly selected and balanced within a block. Rotating the apparatus served several functions. First, rotations provided different views of the landmark and room panorama from the goal. Each training orientation provided a 90° panorama of the landmarks

and the room. The panoramas at adjacent training orientations overlapped with each other by 67°. Combined, the four orientations provided nutcrackers with approximately a 170° view of the room panorama from within the apparatus as it was rotated across sessions. Rotations were also intended to limit the use of simpler mechanisms of navigation, such as dead reckoning (e.g., Etienne, 1992), in which the animal would only need to use egocentric cues. Finally, rotating the apparatus served to dissociate locations of the goal based on distal and local information.

We defined *distal information* as those cues outside the apparatus (e.g., posters, PVC landmarks) whose spatial relationships were fixed with respect to the goal and the room. Since distal cue–goal relationships were fixed, a landmark outside the apparatus viewed from multiple orientations (Figures 3B, Diagram 1, and 3B, Diagram 2) could be used during different sessions to locate the goal. In contrast, *local cues*, defined as the spatial relationships between the goal and some feature of the apparatus (e.g., the edge of the opening), were not informative from one session to the next because the apparatus–goal relationships changed. For example, if a nutcracker encoded a local vector from one edge of the opening to the goal during one session of training (Figure 3B, Diagram 1), the application of that same local vector during another session in which the apparatus was rotated (Figure 3B, Diagram 2) would direct the bird to an incorrect or apparatus-defined location of the goal. In this case, rotation of the apparatus between training sessions would lead to a displacement of search by an amount equivalent to the degree of rotation between training orientations. During the early stages of acquisition, nutcrackers might erroneously use local information and dig at locations other than the goal. However, we anticipated that nutcrackers would learn to use distal information from landmarks outside the apparatus (Figure 3B, Diagram 1), because navigational vectors to these landmarks were the same regardless of how the apparatus was rotated (Figure 3B, Diagram 2).

Transfer tests. These trials were designed as tests of cognitive mapping to determine where the birds would search when they only had a new view of the room panorama and landmarks from the goal. One transfer test was conducted per bird per day for 3 consecutive days following training. Before the start of the transfer test, the opening of the apparatus was rotated to Transfer Orientation T1/O5 (Figure 3A), providing nutcrackers with a panorama of landmarks that had been experienced previously but never from the goal location. No pine seeds were used during the transfer tests. The session began when an individual bird was transported from the home cage and allowed 1 min to habituate to the holding cage. The sliding door was then opened, and the nutcracker was released into the room. The trial concluded either when the bird made 25 digs or when 5 min had passed. The conclusion of the trial corresponded with the houselights being turned off and the bird being allowed to leave the room through the sliding door. The surface of the animal bedding was swept with a broom after each test.

If nutcrackers develop a cognitive map, then they should have encoded into the map the position of the goal in the room and its relationship to the subset of landmarks viewed during training. During transfer tests, when landmarks previously seen at the goal are blocked from view (as in Position A in Figure 3B, Diagram 3), the birds should be able to determine their current position in the room using the landmarks from the transfer panorama. Using the map, they should be able to determine the geometric relationship between the landmarks in the transfer panorama, the landmarks in the training panorama, and the encoded position of the goal (Positions B and C in Figure 3B, Diagram 3). Finally, they should be able to infer the distance and direction to the goal location using the map (Position C in Figure 3B, Diagram 3).

Alternatively, nutcrackers might search for the goal using four separate local vectors, each paired with a local cue for each training orientation (Diagrams 1 and 2 of Figure 3B show one local vector paired with O1; see Position D in Figure 3B, Diagram 3, for all four applied to T1). If birds learn four separate local solutions, then they might be expected to dig at one of four apparatus-defined locations of the goal (Positions A1 through A4, Figure 3B, Diagram 3). Each of the four ap-

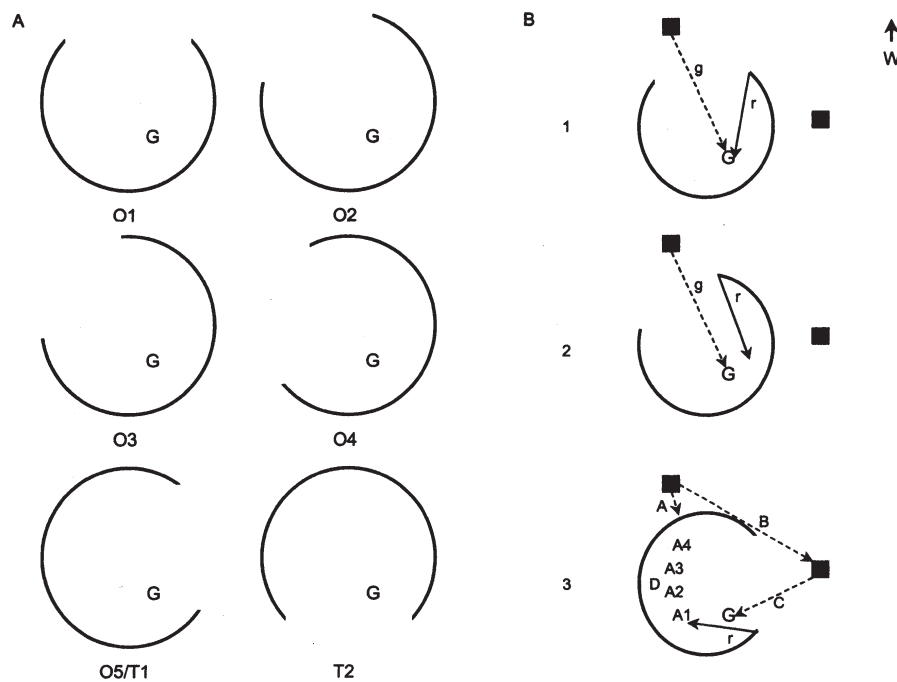


Figure 3. A: A top-down diagram showing each of the training (O1, O2, O3, O4) and transfer test (O5/T1, T2) orientations in the room during Experiment 2. The orientation of the apparatus and its opening is depicted by semicircles. G indicates the position of the goal. B: Three top-down diagrams showing the relationship between the goal (G), the landmarks (filled squares), and the apparatus (semicircles) during Experiment 2. Diagram 1: The opening of the apparatus at Training Session O1, showing a panorama of landmarks from inside the apparatus. The r indicates the angle of the local vector in this example relative to the side wall of the apparatus and the goal. The g depicts a potential global vector between a landmark and a goal. Diagram 2: During a subsequent session, the apparatus has been rotated to another training orientation (O2) in this example. The local vector encoded during Training Orientation O1 is no longer a reliable indicator of the goal location, as the local cue (i.e., the apparatus opening) has rotated between sessions, and search based on this local vector leads to search at an apparatus-defined location of the goal. Only g remains the same across these training orientations. Diagram 3: During transfer testing, the apparatus has been rotated and blocks the view of the previously viewed landmark panorama. The diagram shows the determination of a bearing to the goal using a landmark panorama that had never been seen previously at the goal, but that had been encoded into a broader map of the room during training (see text). A1, A2, A3, and A4 represent the locations of the apparatus-defined locations of the goal (one encoded during training at Training Orientations O1, O2, O3, and O4 and applied to the opening of the apparatus during testing at Transfer Orientation T1). The A, B, and C identify the metric relationships that could have been used during the transfer test (see text). The diagram is not drawn to scale

paratus-defined locations during testing at T1 reflects the application of one of the four local vectors to a local cue (e.g., right edge of the opening of the apparatus) during transfer.

Measures and Analysis

A virtual Cartesian grid, generated for geometric analysis of the data, was laid over the room and the floor of the apparatus. As in Experiment 1, we determined the Cartesian $\{x, y\}$ position of digs made inside the apparatus, the geometric center of the apparatus, and the goal. The results from Experiment 1 and previous studies with nutcrackers (Kamil & Jones, 1997) have shown that the first five digs made in the room are representative of search for a hidden goal. Hence, in Experiment 2, we used data from the first five digs made during a test to generate two measures of accuracy. For each session, the absolute distance of each of the first five digs from the goal was determined and then averaged. Similarly, we calculated the absolute acute angular deviation between due north, the center of the apparatus, the x, y location of each of the first five digs, and the position of the goal in a session, and averaged them. These data were subject-

ed to statistical analyses, as described below. All maps depicting performance were constructed using the average location of the first five digs in a session.

Results

Training

Two birds (Uli, New) were dropped from the study because of their inability to consistently and accurately locate the goal during training. Two ANOVAs were used to compare the performance of the room-naive and room-experienced groups during acquisition. Each analysis used group as a between-groups factor, and block and bird as repeated factors. The first ANOVA used distance as a dependent measure, and the second used angular deviation as a dependent measure. Because the performance of the room-naive and room-experienced groups did not differ when considering either distance, $F(1, 5) = 2.05, p = .22$, or angular deviation, $F(1,$

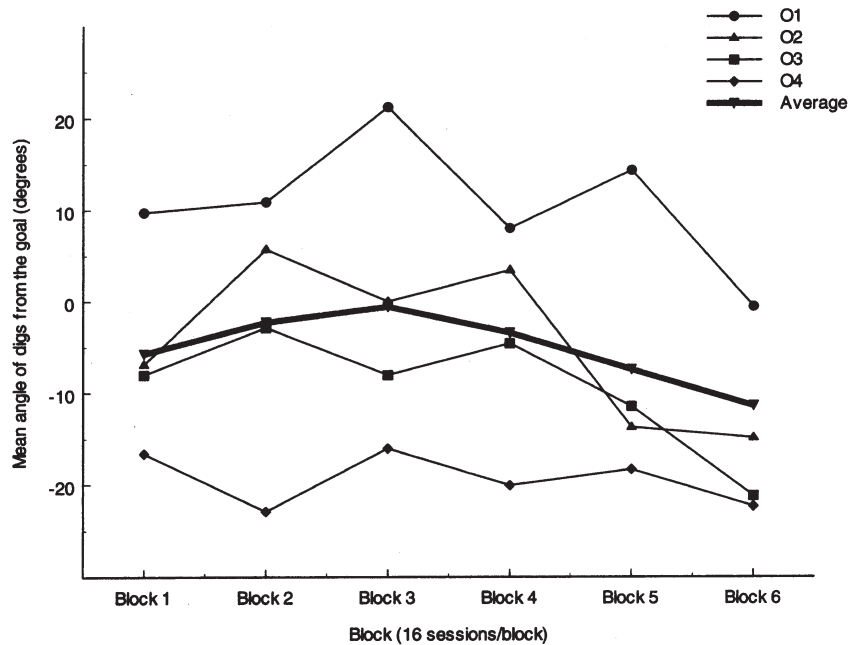


Figure 4. The mean acute angular deviation (in degrees) of digs from the goal location across blocks of training for each training orientation during Experiment 2. Negative values represent deviations clockwise from the goal location, whereas positive values represent angular deviations counterclockwise from the goal. Training orientations are represented by O1, O2, O3, and O4.

5) = 1.56, $p = .27$, as measures, these groups were combined for all subsequent analyses.

Using a second set of analyses, we examined whether nutcrackers were using distal or local information during their search for the goal. If nutcrackers had been using local features of the apparatus to locate the goal, then the mean angular deviation of digs should have been different during training across orientations. To assess for the use of distal or local information, we performed two ANOVAs, one using angular deviation as a dependent measure and the other using distance as a dependent measure, with both analyses using block, training orientation, and bird as repeated factors. The angular deviation of digs appeared to be similar with Orientations O2 and O3 (Figure 4), but both of these were different than the angular deviation of digs with Orientations O1 and O4. Correspondingly, the analysis revealed a reliable effect of training orientation, $F(3, 18) = 28.49$, $p < .01$. Subsequent LSD comparisons confirmed that the angular deviation of digs was similar for Orientations O2 and O3 ($p > .05$), but that the angular deviation of digs at O4 was shifted clockwise when compared with O2 and O3 ($ps < .05$). Likewise, the angular deviation during testing at O1 was shifted counterclockwise when compared with testing at Orientations O2 and O3 ($ps < .05$). The accompanying analysis using distance as a measure revealed a similar pattern of results and will not be reported here. A map of the mean location of digs during the last block of training (Figure 5A) indicates that most nutcrackers dug just northwest (counterclockwise) of the goal location.

Transfer

Two sets of analyses were conducted. The first compared accuracy across all birds at the end of acquisition with accuracy

during transfer tests. A repeated-measures ANOVA with bird, session, and condition (training or transfer) as factors was conducted with distance as a dependent measure. A second, identical ANOVA was performed, but with angular deviation as a dependent measure. In contrast to the last block of acquisition, the distribution of digs on these tests tended to be concentrated near apparatus-defined locations of the goal (Figure 5B). The analysis using distance revealed that the mean distance, $F(1, 6) = 51.37$, $p < .001$, and angular deviation, $F(1, 6) = 62.13$, $p < .001$, of nutcrackers' digs was significantly larger during each of the three transfer tests than during the last 3 days of training.

Discussion

Our transfer tests for cognitive mapping required that nutcrackers learn to use distal landmarks provided in the room to locate the goal during training. If, however, nutcrackers had been using local features of the apparatus, then the mean angular deviation of digs should have been different during training at consecutive orientations. Generally, this was the case, as the mean angular deviation of digs and the distance of digs from the goal were different for most orientations. Nutcrackers may have tried to align their position with the center of the opening of the apparatus to locate the goal. During training at Orientations O2 and O3, when the center of the opening of the apparatus was more closely aligned with the goal (see Figure 3A), the angular deviation of their digs was very accurate. When training was conducted at Orientations O1 and O4, however, the goal was somewhat displaced counterclockwise and clockwise, respectively, in relation to the center of the opening. Consistent with this interpretation, birds dug counterclockwise of the goal during training at O1 and clockwise of the goal during training at O4.

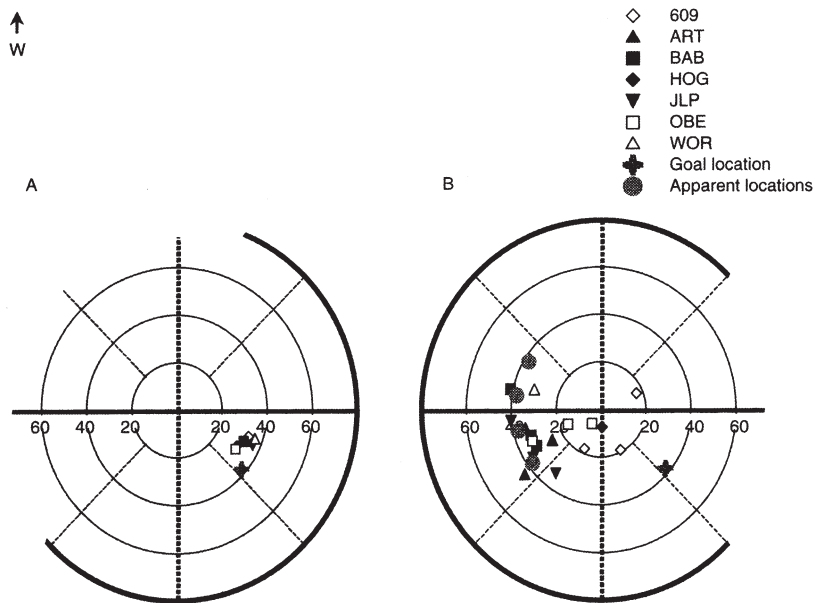


Figure 5. A: The mean position of digs for each bird (represented by 609, ART, BAB, etc.) across the last eight trials of Block 6 during training in Experiment 2. B: The average location of digs for each bird during each of the three transfer tests in Experiment 2. The apparatus-defined locations of the goal are represented by the large solid circles. The four apparatus-defined locations ranged from 129° to 60° counterclockwise from due west and 38 cm from the center of the apparatus during transfer tests. The bold semicircles represent the wall of the apparatus. The panorama of the room available to birds while inside the apparatus across training or during transfer tests is indicated by the space between the two ends of the bold semicircles.

Transfer tests examined the extent to which nutcrackers could use distal information and its application in the formation of a metric map. Most nutcrackers used local information provided by the features of the apparatus (e.g., the opening) during transfer and searched in the vicinity of the apparatus-defined locations of the goal. This finding is consistent with the apparent failure of most nutcrackers to use distal cue-goal relationships during training.

Experiment 3

Nutcrackers' ability to recognize and use distal cue-goal relationships is a critical facet of the transfer tests as an assay for cognitive mapping. In Experiment 2, adjacent orientations were separated by 23°. This degree of separation may have been insufficient to dissociate local and distal information. Alternatively, nutcrackers may have learned to discriminate local and distal cues but weighted local information more prominently following the relatively large change in the goal-landmark panorama during transfer. Therefore, in Experiment 3, we increased the range of orientations used during training to increase the probability of nutcrackers learning the dissociation between local and distal information. The birds were trained with five orientations, each of the four original training orientations (O1, O2, O3, and O4) plus the transfer orientation used in Experiment 2 (Orientation T1).

Method

Subjects and Apparatus

In Experiment 3, we used 5 of the birds that had completed the first and second experiments. Before completing the third experiment,

2 additional birds died (609, Wor). Again, a necropsy of the carcasses failed to reveal any conclusive findings as to the cause of the death. The birds were maintained as described previously. The room and landmarks were identical to those used in the previous experiments.

Procedures

The training and transfer testing procedures were nearly identical to those used in Experiment 2. Two important exceptions were that (a) the transfer test orientation used in Experiment 2 (T1) now was included as one of five training orientations (see Figure 3A, T1/O5, and Figure 3B), and (b) the second series of three transfer tests were conducted at a new transfer orientation (T2) that provided a view of the room that nutcrackers had never seen from the goal. The curtain was removed before transfer testing. Training proceeded for five blocks, each having 10 sessions, and was followed by three single unrewarded transfer tests.

Measures and Analysis

The measures used in Experiment 3 were similar to those used in the second experiment. As in Experiment 2, separate analyses were conducted for training and transfer.

Results

Training

To examine for changes in accuracy across training, we conducted two ANOVAs, one using distance and the other angular deviation as a dependent measure. Each analysis used block, training orientation, and bird as repeated factors. Nutcrackers' accuracy generally improved as training progressed. The distance (Figure 6A) of nutcrackers' digs from the goal de-

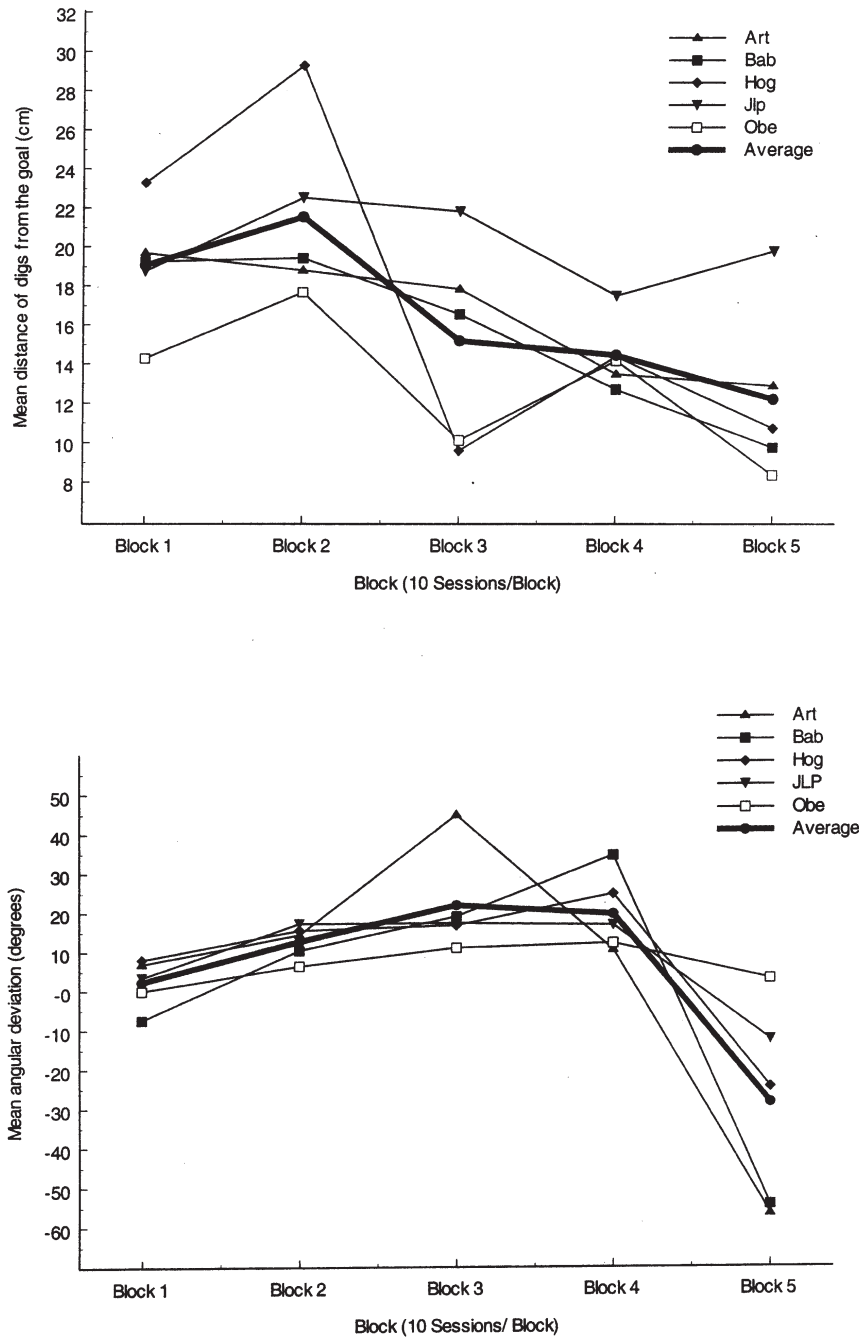


Figure 6. Top panel: The mean distance (in centimeters) of digs from the goal location during training at each of the four training orientations during Experiment 3. Bottom panel: The mean acute angular deviation (in degrees) of digs from the goal location across blocks of training for each training orientation during Experiment 3. Nutcrackers' names are Art, Bab, Hog, and so forth.

clined across acquisition, $F(4, 16) = 4.69, p < .01$. In contrast, the angular deviation of digs from the global goal location (Figure 6B) was relatively small and stable throughout the first four blocks but was rotated clockwise slightly during the final block of testing. Consistent with this trend, ANOVA revealed a significant effect of block when angular deviation was a dependent measure, $F(4, 16) = 5.69, p < .01$. However, as can be seen in Figure 7A, although the center of digging was rotated slightly from the goal, the mean distribution of digs

nearly overlapped the global goal location during the end of acquisition.

Transfer

As in Experiment 2, we compared accuracy across all birds at the end of acquisition with accuracy during transfer tests. A repeated measures ANOVA with bird, session, and condition (training or transfer) as repeated factors was conducted, with

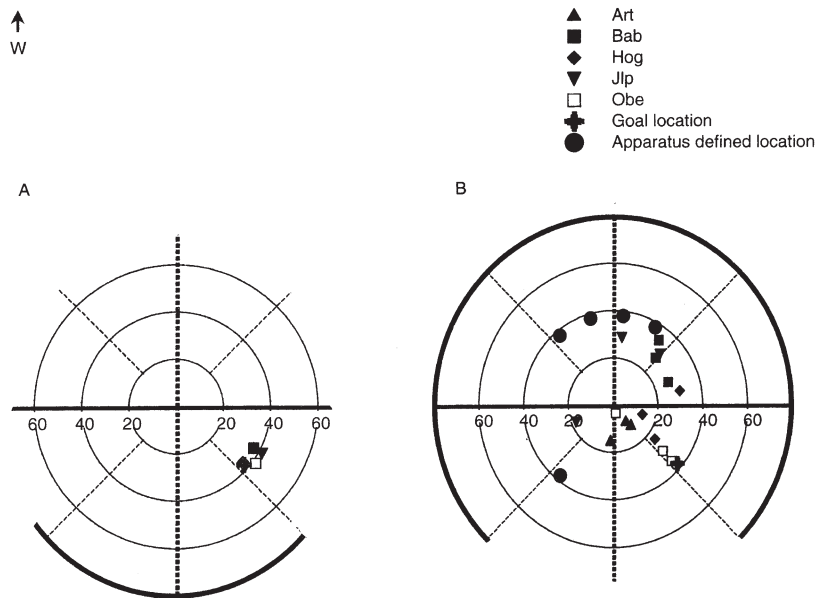


Figure 7. **A:** The mean position of digs for each nutcracker (represented by Art, Bab, Hog, etc.) across the last eight trials of the last block of training during Experiment 3. **B:** The mean location of digs for each bird during each of the three transfer tests of Experiment 3. The bold semicircles represent the wall of the apparatus. The panorama of the room available to birds while inside the apparatus across training or during the transfer test is indicated by the space between the two ends of the semicircles.

distance as a dependent measure. A second identical analysis was also performed with angular deviation as a dependent measure. Although the distance of nutcrackers' digs during transfer was larger than that observed during the end of training, $F(1, 4) = 18.17, p < .05$, the mean angular deviation of digs during transfer was not significantly different from that during training, $F(1, 4) = 4.23, p = .11$.

Using a second set of analyses, we examined performance on a bird-by-bird basis using paired measures for both distance and angular deviation. The distance and angular deviation of each dig was determined from the goal location, as well as from the mean position of each of the first four apparatus-defined locations (mean of the apparatus-defined locations). Because the distribution of most digs tended to be focused either near the first four local locations or near the goal during transfer, we did not include the fifth local location in the estimation of the mean apparatus-defined location of the goal. The paired measures for both distance and angular deviation were summed across the three transfer tests, and a paired Wilcoxon t or Student's t test (when normality was not violated) was used to test for reliable differences in performance.

Of the 5 nutcrackers, 3 (Obe, Hog, and Art) directed their search toward the correct location of the goal during transfer (Figure 7B). The analyses of both distance and angular deviation supported this pattern. The distance of 3 (Obe, Hog, and Art) of the 5 nutcrackers' digs was significantly smaller when measured from the goal location than when measured from the mean apparatus-defined location (ps ranged from .05 to .01). Similarly, the mean acute angular deviation of the digs made by Obe, Hog, and Art was significantly smaller when measured from the goal location than when measured from the mean apparatus-defined location (ps ranged from .05 to .01).

Discussion

Across all nutcrackers, the angular deviation of digs during transfer did not differ from that observed during the end of training. Likewise, 3 (Art, Hog, and Obe) of 5 nutcrackers in Experiment 3 dug in the vicinity of the goal during transfer tests, indicating that they had learned the relationships between distal landmarks and the position of the goal in the room. The improvement in search accuracy during transfer from the second experiment indicates that either the inclusion of the fifth training orientation (T1) or the extended period of training during Experiment 3 facilitated the discrimination of the local and distal landmark-goal relationships.

Although it might be tempting to conclude that these 3 nutcrackers (Art, Hog, and Obe) used a cognitive map to locate the goal during transfer tests, a number of observations suggest that this would be premature. Even though the distribution of digs was significantly closer to the goal than the mean apparatus-defined location (for 3 of 5 nutcrackers), only 1 nutcracker dug exactly at the goal location. This pattern of performance would appear to be in contrast with the notion that cognitive maps evolved for very accurate navigation. Likewise, during the course of testing, it appeared that nutcrackers rarely turned their heads and looked outside the apparatus at landmarks during moment-to-moment search for the goal. The use of landmarks during training and testing is an important aspect of the development and use of a cognitive map with respect to the current experiment.

Experiment 4

A critical component of the cognitive mapping hypothesis is the incorporation of landmarks from the environment into

a mental map. Our observations from Experiment 3 indicated that nutcrackers either may not have been using distal landmark information during moment-to-moment search for the goal or may have been encoding information about landmarks before entering the apparatus. In Experiment 4, we examined whether nutcrackers were using landmarks during moment-to-moment search for the goal. We hypothesized that if birds had encoded the position of landmarks into a map, the removal of some landmarks from the experimental room might disrupt navigation.

Method

Subjects and Apparatus

The birds, room, and landmarks were identical to those used in the previous experiment. The birds were maintained as described previously.

Experimental Design

We used a factorial design with landmark condition and goal panorama as variables. Landmark condition had two levels in which the distal landmarks (see below) could either be present or absent in the room during a session. There were also two levels of the goal panorama factor in which the orientation of the apparatus could be either at one of the training orientations (O1, O2, O3, O4, T1/O5) or at the transfer orientation (T2) during a session. Across all levels of both factors, birds experienced four conditions: landmarks present with the training panorama (LP: O1-T1/O5), landmarks present with the transfer panorama (LP: T2), landmarks absent with the training panorama (LA: O1-T1/O5), and landmarks absent with the transfer panorama (LA: T2).

Testing in Experiment 4 was conducted in two 4-day blocks. Each bird experienced one of the four conditions (LP: O1-T1/O5, LP: T2, LA: O1-T1/O5, LA: T2) in a session during each day of a block. All four of the conditions were used in a block for each bird, and the order in which birds experienced each of these conditions was randomly determined.

Procedures

Training sessions (Training Orientations LP: O1-T1/O5 and LA: O1-T1/O5). As in Experiments 2 and 3, for these days there were two trials per session and two sessions were conducted per day. Before the start of the first trial, the apparatus was rotated to one of the five training orientations. Landmark removal, when required, was performed before the start of the session on that day. In such cases, the PVC landmarks and posters were temporarily removed from the room. An individual bird was transported from the home cage to the holding cage and allowed 1 min to habituate. During the first trial of the session, the sliding door was opened, and the nutcracker was released into the room. The lens cap and two seeds were partially buried at the goal location inside the apparatus. The trial concluded when the bird either located and consumed the seeds, made 25 digs, or failed to locate the seeds within 5 min. During a 2-min ITI, the lens cap and two seeds were completely buried at the goal location, and the surface of the substrate in the room and apparatus was swept.

Following the completion of the 2-min ITI, the second trial began, and the bird was again released into the room. After entering the apparatus and locating and consuming the seeds or when the trial limits had been met, the houselights were turned off, and the nutcracker was allowed to exit. The direction nutcrackers were forced to travel around the apparatus (using the curtain) during their departure in the second trial was randomly determined before each phase of a session and was balanced across sessions in a block. The surface of the animal bedding was swept with a broom so that the surface was even after each trial and between sessions.

Transfer sessions (Transfer Orientations LP: T2 and LA: T2). Before the start of the transfer session, the opening of the apparatus was rotated to the transfer orientation (T2; Figure 3A), providing nutcrackers with a panorama of landmarks that had been experienced previously, but never with the goal. The pine seeds and lens cap were not used during these sessions. As during the sessions conducted with the training orientations in this experiment, the removal of the PVC landmarks and posters, when required, was performed before the beginning of the session on that day. The curtain was also removed during these sessions. The session began when an individual bird was transported from the home colony and allowed 1 min to habituate to the holding cage. The sliding door then was opened, and the nutcracker was released into the room. The trial concluded when the bird either made 25 digs or 5 min had passed. Immediately following the end of the trial, the houselights were turned off, and the bird was able to leave the room through the sliding door. The surface of the animal bedding was swept with a broom so that the surface was even after each test. One transfer session was conducted per day during days in which transfer tests were given.

Measures and Analyses

The method used to derive the measures of distance and angular deviation were identical to those described in Experiments 2 and 3. Two 2×2 repeated-measures ANOVAs were subsequently performed. The first used distance as a dependent measure, with landmark condition and goal panorama as group factors and bird and block as repeated factors. The second ANOVA used angular deviation as a dependent measure, landmark condition and goal panorama as group factors, and bird and block as repeated factors.

Results

Across orientations, the deviation of the mean angular deviation of digs was smaller when landmarks were present, $F(1, 4) = 14.14$, $p < .05$ (Figure 8A and 8B), than when they were absent (Figure 8C and 8D). No corresponding effect of landmarks was revealed in the analysis of distance, $F(1, 4) = 1.10$, $p = .35$. In general, nutcrackers were more accurate in locating the goal when they were presented with training panoramas (Figure 8A and 8C) than when they were presented with the transfer panorama (Figure 8B and 8D). In support of this effect, both the analysis of distance, $F(1, 4) = 21.55$, $p < .01$, and angular deviation, $F(1, 4) = 10.94$, $p < .05$, revealed a significant effect of orientation. For some nutcrackers (e.g., Art, Obe), there appeared to be a slight improvement in accuracy during transfer when landmarks were present (Figure 8A) than when they were absent (Figure 8C). No interaction between orientation and landmark condition was found in the analysis using distance, $F(1, 4) = 1.90$, $p = .24$, or angular deviation, $F(1, 4) < 1$, however.

Discussion

The removal of landmarks from the room resulted in a decline in accuracy regardless of the visual panorama birds had available to them during the session. This finding is consistent with the notion that nutcrackers had encoded the position of landmarks and were using them during search, perhaps within the framework of a map. Although landmark removal influenced the angular deviation of nutcracker digs, it did not significantly influence the distance of these digs from the goal. The estimation of compass bearing and distance to the goal may have been accomplished by two independent processes in which birds used two separate classes of information. Spe-

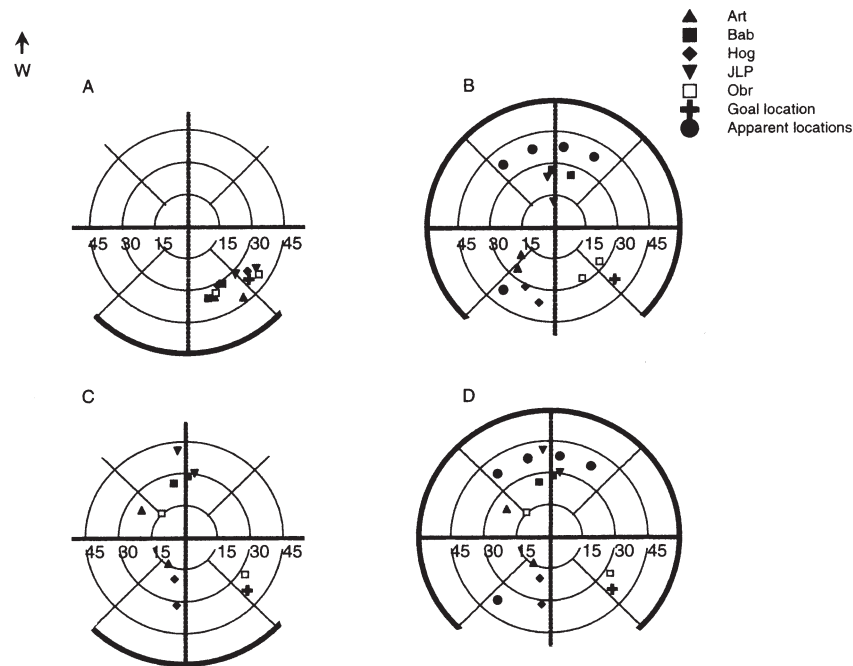


Figure 8. For Experiment 4, the distribution of digs for each nutcracker (represented by Art, Bab, Hog, etc.) during tests (A) with the landmarks in the room and the opening of the apparatus rotated to each of the training orientations used in Experiment 3 (O1, O2, O3, O4, O5/T1) or (B) at the second transfer test orientation (T2). The distribution of digs during tests without the landmarks in the room and the opening of the apparatus rotated to (C) each of the training orientations used in Experiment 3 (O1, O2, O3, O4, O5/T1) or (D) at the second transfer test orientation (T2). The bold semicircles represent the wall of the apparatus. The panorama of the room available to birds while inside the apparatus is indicated by the space between the two ends of the bold semicircles.

cifically, the geometric properties of the cylindrical apparatus provided strong cues in estimating the distance to the goal. Studies with rodents (Cheng, 1986; Margules & Gallistel, 1988) have shown that the geometry of the environment (e.g., apparatus) can be important in resolving the location of a goal. Nutcrackers could have aligned themselves at a constant distance from either the perimeter or the center of the apparatus or both. The determination of a navigational vector (Cheng, 1988) to the goal may have been accomplished, in part, by the nutcrackers' using landmark information outside the apparatus, as indicated by the effect landmark removal had on the angular deviation of search.

Additionally, there might have been a temporal component to the assessment of distance and angular deviation. Before entering the apparatus, nutcrackers may have used landmark information to determine a compass bearing to the goal. Once inside, nutcrackers may have calculated the distance to the goal using one of the approaches outlined above. This would be consistent with the fact that nutcrackers rarely looked outside the apparatus opening during moment-to-moment search for the goal.

Experiment 5

Local cues, such as the opening of the apparatus, may have been important for setting a navigational bearing toward the goal for some birds. The apparatus may have also

served as an important cue for all nutcrackers in determining the distance to reach the goal. If these cues from the apparatus played a role in search for the goal, then removal of the apparatus should disrupt navigation. In the following experiment, we examined the effects of local cue removal on search accuracy. We hypothesized that if birds have a map of the goal location with respect to landmarks in the environment, then they should search at the goal when the apparatus is removed.

Method

Subjects and Apparatus

The birds, room, and landmarks were identical to those used in the previous two experiments. The birds were maintained as described previously.

Procedures

Testing began 2 days following the last session in Experiment 4. Before testing, the entire apparatus and curtain were removed from the room. All other landmarks removed during Experiment 4 were returned to the room in their original location. The lens cap and two seeds were not used during these tests. An individual bird was transported from the home cage and allowed 1 min to habituate to the holding cage. The session began when the sliding door was opened and the nutcracker was released into the room. The trial concluded when the bird either made 25 digs or 5 min had passed. The houselights were turned off, and the bird was able to leave the room

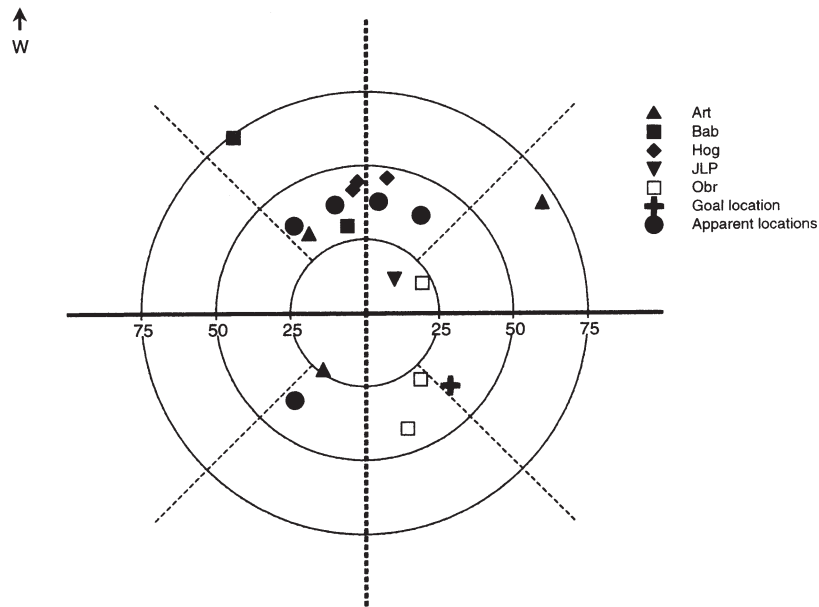


Figure 9. The location of digs for each nutcracker (represented by Art, Bab, Hog, etc.) during tests in which the apparatus and curtain were removed from the room during Experiment 5.

through the sliding door. One test was conducted per bird per day for 3 consecutive days.

Results

In a similar fashion to our analysis of transfer in Experiments 2 and 3, we compared accuracy across all birds when all landmarks were presented during training with orientations (LP: O1-T1/O5) in Experiment 4 with accuracy during the transfer tests in Experiment 5 when the apparatus was removed. An ANOVA with condition (training or transfer) as a factor and distance as a dependent measure was conducted. A second identical ANOVA was performed, but with angular deviation as a dependent measure.

As in Experiments 2 and 3, birds' performances were also compared individually. For each of the removal tests, the absolute distance of each dig from the goal location and the absolute distance of each dig from the mean apparatus-defined location were determined. The data from the three removal tests were averaged and subjected to paired Wilcoxon *t* or *t* tests (when normality was not violated). An identical set of analyses was performed for each nutcracker using the measure of angular deviation.

Although the distribution of digs during tests with the apparatus removed was more dispersed than either of the transfer test conditions in Experiments 2, 3, and 4, most nutcrackers dug near the apparatus-defined goal locations (Figure 9). Consistent with this trend, the results from the ANOVA revealed that the distance, $F(1, 30) = 42.12, p < .001$, and angular deviation, $F(1, 30) = 42.05, p < .001$, of nutcrackers' digs from the goal was significantly less during the training trials than during the removal tests. Only 1 nutcracker (Obe) continued to dig near the goal location following the removal of the apparatus ($p_s < .01$, both measures).

Discussion

If nutcrackers had been solely dependent on cues provided by the apparatus during navigation and not on distal landmarks or maps, then the removal of the apparatus should have completely disrupted search. This was generally not the case, as nutcrackers dug within the space previously occupied by the apparatus, and most dug near the apparatus-defined locations of the goal. The results from Experiments 4 and 5 indicate that nutcrackers encoded information about the landmarks and used this information during search for the goal. During the last 2 days of testing, some nutcrackers failed to dig within 5 min during some of the later tests. For these birds, either the removal of the apparatus or the effects of repeated unrewarded testing may have influenced search for the goal.

General Discussion

In these experiments, we have examined the nature of the spatial information Clark's nutcrackers use during navigation and, specifically, whether this information is represented so as to allow the navigational flexibility expected from the use of a cognitive map. To test for cognitive mapping in Experiments 2, 3, 4, and 5, we used a design similar to Benhamou's (1996), which required birds to learn distal landmark-goal relationships during training and encode them into a map of the room. During our transfer tests, which were the assays for cognitive mapping, birds were required to integrate a panorama of landmarks that had not been previously encountered at the goal with a map of the room. Birds initially failed to use distal goal-landmark relationships in the second experiment, as most birds searched for the goal using local cues provided by the apparatus. Thus, tests for mapping were uninformative, as only local relationships were used during search for the goal.

When the difference between erroneous local information and the correct distal information was made larger in the third experiment, 3 of 5 birds switched from using local information to using distal information when searching for the goal. During transfer tests, these same 3 birds dug at locations that were near the goal location. The results from this experiment suggest that nutcrackers that learned the distal landmark-goal relationships may have had a map that they used during the transfer test.

Although it may be tempting to conclude that these nutcrackers developed and used a cognitive map, there are some concerns. Even though the distribution of nutcrackers' digs was not reliably different across training and transfer conditions, the mean location of digging for some birds was not extremely close to the goal (Experiment 3). Surely if a cognitive map had evolved as a result of the pressure to search for small caches of pine seeds, then nutcrackers would be expected to be considerably more accurate across the transfer tests. Furthermore, if nutcrackers had indeed developed a map of the room, one would expect more birds to have dug at the goal location when the entire apparatus was removed during Experiment 5. All of the nutcrackers did dig in the region previously occupied by the apparatus, indicating that they were using landmarks and distal features of the room to dig at the approximate location of the goal (also see Experiment 1), but most failed to dig at the precise goal location. Although the current procedures were designed to specifically control for nonmapping strategies, these observations indicate to us that nutcrackers may have been using another strategy to find the goal.

The results of a similar study with humans (Gibson, 2001) suggest that another nonmapping strategy could have been used by the nutcrackers to locate the goal. In the current study, the center of the floor of the apparatus is the only point inside the apparatus that is equidistant from all points of the wall of the cylinder. This geometric feature may have been particularly salient to nutcrackers. Previous work has indicated that a goal is more accurately located when it is hidden in the center of a landmark array than when it is placed in a position that is at the same distance but is outside the perimeter of the array (Gibson & Kamil, 2001). During training, nutcrackers may have encoded a directional bearing from the center of the apparatus to the goal with respect to a compass bearing (e.g., due west). Using features of the room, including the landmarks, the birds may have obtained the compass bearing before entering the interior of the apparatus. During transfer, nutcrackers that dug near the goal location may have used the same navigational bearing but with respect to a different angle of approach to locate the goal. Because this alternative mechanism of navigation could be used to locate the goal, it is impossible to be certain that nutcrackers were able to use or develop a cognitive map (Bennett, 1996).

The results from Experiment 4 would seem to indicate that nutcrackers were using the landmarks in the room to set a compass bearing. If landmarks were being used for directional information, then their removal would be expected to disrupt performance. When landmarks were removed during Experiment 4, the angular deviation of nutcrackers' digs was significantly different than when the landmarks were present. In contrast, the distance of nutcrackers' digs did not differ when the landmarks were removed. Cues from the apparatus could

still be used to determine distance; that is, nutcrackers may have dug at the same distance from the wall of the apparatus regardless of the direction.

The use of the center of an array of items may be part of a larger navigational system that uses the geometry of the environment (Shettleworth, 1998) as information. Rats use the geometry of an apparatus during search for food (Cheng, 1986; Margules & Gallistel, 1988). Using the center of an array of landmarks may be computationally much easier than using information from arrays that do not have a clear center. For example, the navigational vectors from a goal placed in the center of an array of landmarks positioned on the perimeter of a circle have the same distance. The summation of the directional components could provide a powerful cue during navigation (Cheng, 1989). Kamil and Jones (1997) trained nutcrackers to locate a hidden goal that was centered on a line between two landmarks. During transfer tests in which the distance between the landmarks was different than that encountered during training, nutcrackers continued to dig at the center between the two landmarks. However, Spetch et al. (1997) has reported that pigeons do not use the center of an array of four landmarks placed at the corners of a square as a cue during search. One way to test whether nutcrackers were using the center of the apparatus during navigation in the current experiments would be to displace the apparatus from side to side in the room across sessions. The displacement would change the distance and the direction of the goal location (within the room) with the respect to the interior of the apparatus. If nutcrackers had been using the geometry of the apparatus during navigation, then they would be expected to dig at the same location inside the apparatus regardless of where the apparatus was moved in the room. More generally, tests might use landmark arrays that had different geometries to see whether animals still used the center to navigate.

Regardless of whether nutcrackers have cognitive maps, their performance during this dynamic task indicates considerable flexibility in the integration of spatial information. During Experiment 1, nutcrackers were able to use distal spatial cues provided by the room environment to locate a small hidden goal. Some nutcrackers may have also used similar cues to locate the goal during the tests in which the apparatus was removed (see the Discussion section, Experiment 5). The finding is consistent with other work with nutcrackers (Gould-Beierle & Kamil, 1996) and rats (e.g., Biegler & Morris, 1996) in implicating the use of distal room cues during search. In Experiment 2, nutcrackers used local cues provided by the apparatus (e.g., the opening) to attempt to locate the goal. During Experiments 3 and 4, nutcrackers learned to use distal cues provided by landmarks around the perimeter of the apparatus to help locate the goal. Finally, as previously mentioned, the geometry of the apparatus itself may have been particularly important in the determination of distance and perhaps the navigational bearing to the goal. Thus, a broad range of spatial information was encoded, and nutcrackers demonstrated the use of different sets of spatial information during different experiments and under different conditions. By the end of training, our nutcrackers were experienced with this spatial task. The nature of the spatial information used by animals during navigation likely may change with experience. In the future, researchers might address the nature of the interrelationships among these different spatial systems and the ways in which

experience may facilitate changes from one system to the next. Finally, it is clear that the spatial information encoded into and used by these multiple spatial systems is rich enough to account for the navigational behavior of nutcrackers. Thus reliance on more complex theoretical models, such as a cognitive mapping, may be unnecessary.

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