The use of relative and absolute bearings by Clark's nutcrackers, *Nucifraga columbiana*

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Two groups of Clark's nutcrackers were trained to find buried seeds whose location was defined by a constant angle from two landmarks whose interlandmark distance and position in the room varied across trials. The first group had a landmark array that was always placed in the same orientation with respect to the walls, allowing the animals to use both relative and absolute bearings. The second group had a landmark array that rotated across trials so that only relative bearings could be used to locate the seeds. The birds in each group learned the task and transferred to new interlandmark distances both within and beyond the range of training distances. Results from these experiments indicate that nutcrackers can learn a geometric relationship that relies exclusively on relative bearings even though the use of absolute bearing yields more efficient search.

The hidden goal technique (Bossema & Pot, 1974) has been widely used to study how animals use landmarks to find a location (Bennett, 1993; Gould-Beierle & Kamil, 1996, 1998; Spetch, Cheng, & MacDonald, 1996; Spetch et al., 1997). Over many trials, food is hidden in a location that bears a constant spatial relationship to a set of landmarks. The landmarks themselves are moved about the experimental room while maintaining a constant relationship among themselves and with respect to the correct location. Once the problem has been learned, buried-seed trials in which the landmark array is manipulated are used to discern which aspect of the spatial relationship between the landmarks and the goal location control search. In most such experiments, the landmarks are presented at the same distance and direction from the goal throughout training (e.g., Bossema & Pot, 1974; Gould-Beierle & Kamil, 1996; Spetch et al., 1996; Spetch et al., 1997). A disadvantage of this procedure is that when experimenters alter landmark–landmark geometry during probe tests, goal–landmark geometry is also changed.

This led us (Kamil & Jones, 1997) to develop a modification of the hidden goal procedure in which the geometric relationship between the goal and the landmarks was held constant during training. In this original experiment, the distance between two landmarks varied throughout training and the goal was always placed halfway between the landmarks. Thus, the geometric relationship of halfway was maintained, but distance between the landmarks and between the goal and the landmarks varied. The

nutcrackers readily learned the task. When the landmarks were presented at novel interlandmark distances within the range with which they had been trained, birds continued to search halfway between the landmarks, demonstrating they had probably learned something about the geometric relationship between the goal and landmarks rather than memorizing the training configurations (but see Biegler, McGregor, & Healy, 1999, and the reply by Kamil & Jones, 1999).

We have subsequently extended these findings by training different groups of nutcrackers with different geometric principles governing the spatial relationship between goal and landmarks (Kamil & Jones, 2000). We found that nutcrackers could learn to find the point one-quarter of the way between two landmarks as well as halfway between. We also found that nutcrackers could learn to find the third point of a triangle, whose base was defined by the landmarks, when the goal was located at a constant direction (bearing or angle) from the landmarks while distance varied. The birds also generalized all three of these geometric rules to novel interlandmark distances, both within and outside the range of training distances.

Throughout the training stages of these experiments, the landmarks were always presented north and south of each other, parallel to two of the walls of the room and perpendicular to the other two. Therefore, the birds could have used either (or both) of two different methods of judging direction, absolute or relative bearings. Absolute bearings refer to a compass reading (e.g., north of the south landmark). Relative bearings refer to using the apparent angular distance between the landmarks and do not require reference to a compass (although they can be determined by comparing two compass directions). Rotating the landmark array would place these two types of bear-

ings in conflict. For example, suppose there are two landmarks located north and south of each other and that a goal is located northwest of one landmark and southwest of the other. If the landmark array is now rotated so that the landmarks are east and west of each other, the absolute bearings will not intersect. But there will still be a set of points at which the relative bearings are unchanged.

We found that when the landmark array was slightly rotated during probe tests, search occurred at locations that suggested the birds compromised between searching at the location predicted by relative bearings and the location predicted by the absolute bearings. However, when the landmark array was rotated 90° so that the landmarks were placed east and west of each other, the birds ignored relative bearings and searched at the location predicted by use of an absolute bearing from one landmark (Kamil & Jones, 1997, 2000). These results raise the question of whether or not Clark's nutcrackers can learn a geometric task that requires the use of relative bearings. The purpose of the present experiment was to compare the performance of a group of nutcrackers required to use relative bearings with that of a group that could use absolute bearings as well as relative bearings. We approached this problem by comparing the performance of a group trained with landmarks whose orientation rotated during training with that of a control group for whom the orientation of the landmarks was constant during training.

EXPERIMENT 1

Method

Subjects. Ten experimentally naive Clark's nutcrackers, randomly divided into two groups, served as subjects for all experiments. One bird died within the first 3 weeks of the initial training. The birds were individually housed at the University of Nebraska School of Biological Sciences in a colony room kept at 22° Celsius on a 14:10-h light:dark cycle. Throughout the course of the experiment the birds were kept at approximately 90% of their free-feeding weights by controlled daily feedings of turkey starter, sunflower seeds, parrot pellets, mealworms, pine seeds, and vitamin supplements. The birds had unlimited access to water and grit in their home cages.

Apparatus

The experiment was conducted in a 4.4 by 2.7 m observation room. The birds entered the room through a porthole on the east wall just below a smoked glass observation window with a drawn curtain. The observer entrance door was north of the porthole on the east wall. Behind the porthole, outside the observation room, was a holding cage in which the birds were kept between trials. A Panasonic video camera (Model WV-BL200) was mounted above the ceiling and connected to a video monitor and VCR (Model JVC BR-3200U). Subjects were observed through the observation window and on the video monitor. A 7-cm raised floor began 90 cm from the east wall, which was bordered by a 15-cm high edge. The wooden floor extended the width of the room to the west wall and was covered with a 2-cm layer of cellulose substrate. Four centrally located fluorescent lights illuminated the room.

There were two 40-cm high landmarks (blue and red PVC pipe 2.5 cm in diameter). The distance between the landmarks varied (in increments of 24 cm) from 36 to 108 cm during training and from 24 to 120 cm during transfer tests. The total area over which the landmark array was presented, measured from the center of the room, was ± 60 cm in the east–west direction and ± 40 cm in the north–south direction. Within this area there were 116 locations where the landmark array could be placed. The room was divided into four equal quadrants, and the array was placed in each quadrant once per day (Figure 1). Each day the placement of the apparatus within each quadrant was randomly assigned, as was the trial order of the quadrants. Sampling of positions was done randomly without replacement, ensuring that no bird received the same target position twice within a block of 116 trials (29 days).

Habituation

Habituation testing was conducted for two trials per day for 5 days. On each trial of the 1st day, two unshelled pine seeds were placed on the surface of the substrate on a 3.5-cm diameter plastic lid in the center of the room. Each bird entered the room through the porthole and the session continued until the seeds had been found. The following days, the substrate was placed in the lid completely covering the seeds. This procedure insured that the birds used the lid as a cue to seed location. For each trial following the 1st day, the lid was moved to various locations within the room.

Training

For each group the arbitrary line that connected the landmarks defined the base of a triangle. The third point of the triangle was the goal location. The goal was always placed at equal 45° angles from the base of the triangle and each landmark, thus creating a right triangle. The difference between the groups was in the orientation of the landmark array with respect to the room. For the unrotated group, the landmark orientation was always north–south so that the line connecting the landmarks was always parallel to the walls on the east and west sides of the room and perpendicular to the walls on the north and south. For the rotated group, five different landmark orientations were used: 0° (north–south, identical to the unrotated group) and rotated 30° and 60° clockwise and counterclockwise (Figure 1). The presentation of the rotated positions across training trials was organized into a completely randomized block design.

The birds were brought individually from their home cage to the holding cage outside the observation room. Initially, the lights in the holding room were off and the lights in the observation room were on. The sliding door in the porthole was opened, and a bird was allowed to enter the room. When the bird reached criterion for completing the trial, the observation room lights were turned off, the sliding door was opened, the holding room lights were turned on, and the bird flew back to the holding cage. Trials continued until the goal was located, 40 probes were made, or the bird had been in the room for 10 min. The definition of a probe was when the bird's beak came into contact with the substrate. If the bird was removed from the room prior to finding the seeds, it was not allowed another attempt at that position. After the completion of four trials, the bird was taken back to its home cage.

Four different interlandmark distances were used in training: 36, 60, 84, and 108 cm. Each interlandmark distance was presented in random order once a day, with the exception that each interlandmark distance must have been a buried-seed trial once out of every four buried-seed trials in a random order. For the first 30 days of training each bird had three training trials preceding one buried-seed trial. During the training trials, a part of the lid was exposed. During a buried-seed trial, the seeds and lid were buried, and the session was videotaped and analyzed to provide acquisition data. The buried-seed trials were organized into a completely randomized block design, and the interlandmark distances not in the buried-seed trial each day were randomly assigned to the training trials. After
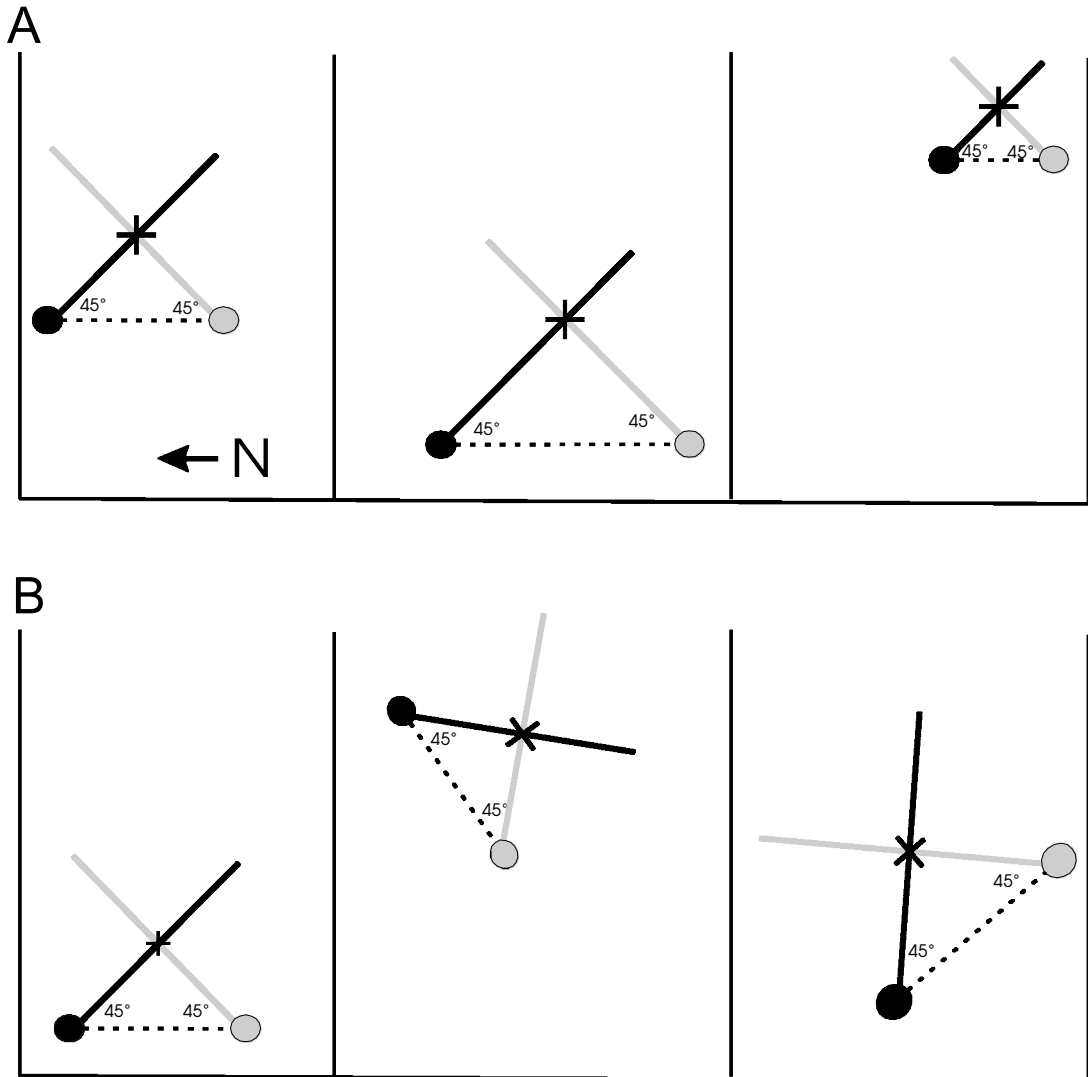
Figure 1. Diagrammatic representation of the position of the landmark array and goal position for three trials for each group. (A) The conditions for the unrotated group: Interlandmark distance varied; position in room varied but the landmark array always stayed in the same orientation with respect to the walls. (B) The conditions for the rotated group: Interlandmark distance varied; position in room varied and the orientation of the landmark array was rotated. Black circle: blue landmark. Gray circle: red landmark. Cross: location of the buried seed. Black line: relative bearing from the blue landmark. Gray line: relative bearing from the red landmark. Dashed line: hypothetical line that connects the landmarks.

30 days, two buried-seed trials per day on Trials 3 and 4 were presented for an additional 30 days. Finally, for 10 additional days all trials presented were buried-seed trials.

Beginning on Day 71 of training, we introduced one "no-seed" trial (probe trial) each day. For a probe trial, neither the lid nor the seeds were placed in the room, and the bird was removed from the room after five digs. This no-seed probe trial was randomly assigned to the second, third, or fourth trial each day. The introduction of the probe trial phase lasted for 8 days, during which each bird received two probe trials at each training interlandmark distance. A probe trial at each interlandmark distance was experienced prior to receiving a second probe trial at an interlandmark distance.

Determining Position of Probes and Data Analyses

To determine the position of the probes, each session was analyzed through a review of the videotaped trial on a Panasonic VCR (Model AG-1730) that allowed frame-by-frame playback and was attached to a TARGA videograph system. First the landmark and goal positions were recorded, and then each probe location was recorded using a digitizing pad. The bird's first 10 digs were recorded on buried-seed trials, and all 5 digs were recorded on probe trials. Each marked location was assigned an X and Y coordinate by the TARGA videograph system. For analysis, the coordinates for each of the first 5 digs were subtracted from those of the goal location and converted to centimeters. The absolute value of each error dis-

tance was then averaged. The X error was related to the error in the east–west axis, and the Y error was related to the error in the north–south axis (discussed below). From the average X and Y error for each day, total error distance was calculated by using the Pythagorean theorem. Data analysis was carried out by analyses of variance (ANOVAs); subsequent Fisher's LSD tests were carried out only after significant overall F ratios (with alpha ≤ .05).

Results

The training data were divided into 13 blocks of 10 buried-seed trials each and analyzed with a group × block repeated measures ANOVA. As the experiment proceeded, performance improved, resulting in a statistically significant effect of block [$F(12,84) = 44.79, p < .05$; Figure 2]. The unrotated group consistently performed with a higher level of accuracy than the rotated group, but this difference was not statistically significant [$F(1,7) = 5.10$, $p > .05$], nor was there any significant group × block interaction [$F(12,84) < 1$]. A subsequent Fisher's LSD revealed that there was no significant difference among Blocks 5–13.

Next we compared performance on no-seed trials with performance on trials with a seed buried at the goal. In this comparison, only the first two probes from each trial were included, because the birds usually found the seed within two to three probes on seed trials, and using more probes would introduce a bias. In order to determine whether the absence of a seed affected performance, total error distance data collected during the introduction of no-seed trials period was subjected to an ANOVA in which seed/no seed and groups were the factors. Performance did not differ on buried-seed trials and probe trials [$F(1,7) < 1$]. Both groups performed at the same level of accuracy [$F(1,7) = 1.78, p > .05$], and there was no group × condition interaction [$F(1,7) = 4.64, p < .05$]. Since there was no difference between probe trials and buried-seed trials, we combined the data from all 32 trials during which the probe procedure was introduced for the following analyses.

An ANOVA was performed using the combined data on the effect of interlandmark distance and group on total error distance. As the interlandmark distance increased, total error distance also increased [$F(3,21) = 10.14, p < .05$]. The unrotated group performed with higher accuracy throughout the introduction of the probe trials phase, but this difference was not significant [$F(1,7) = 4.46, p > .05$]. Although increasing the interlandmark distance appeared to affect the performance of the rotated group more than that of the unrotated group, the group × interlandmark distance interaction was not significant [$F(3,21) = 2.04$, $p > .05$].

Next, error distance was broken down into two axis components. The first axis was parallel to the hypothetical line connecting the landmarks, and the second axis was perpendicular to that line. For the rotated group, the orientation of these lines changed, in global terms, as the orientation of the landmark array was rotated.
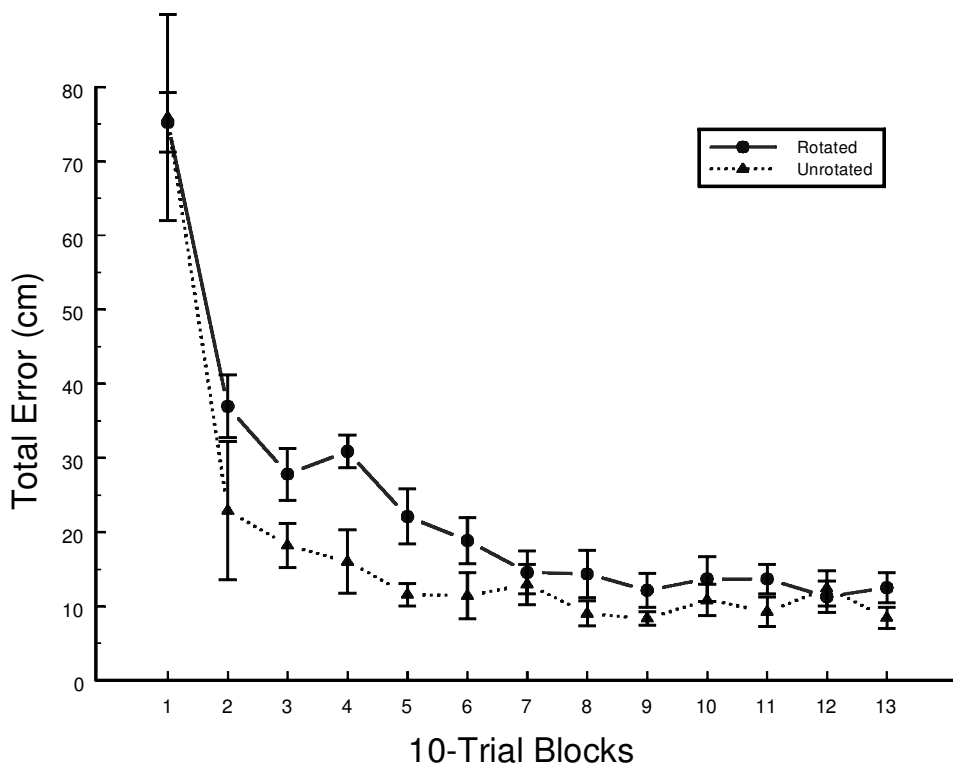

Figure 2. Mean distance ±SE between the location of the first five digs and the goal location on buried-seed trials throughout training. Each block contains 10 buried-seed trials.
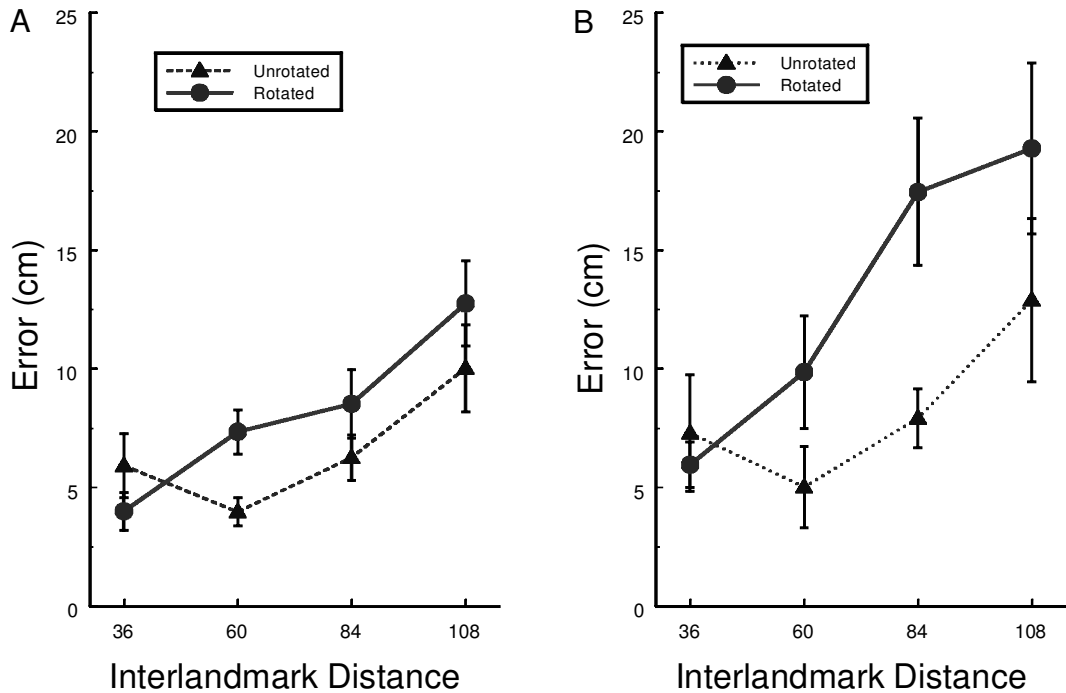
Figure 3. (A) Mean error distance ±*SE* between the location of the first two digs and the goal location in the parallel axis. (B) Mean error distance ±*SE* between the location of the first two digs and the goal location in the perpendicular axis.

Separate ANOVAs were performed on error distance in each axis, with group and interlandmark distance as factors. In the parallel axis, as interlandmark distance increased, error distance also increased [$F(3,21) = 8.32$, $p < .05$]. Both groups performed at approximately the same level of accuracy [$F(1,7) < 1$], and there was no group × interlandmark distance interaction [$F(3,21) = 1.41$, $p > .05$]. In the perpendicular axis, the unrotated group performed with higher accuracy than the rotated group [$F(1,7) = 6.80$, $p < .05$]. Again, as interlandmark distance increased, error distance also increased [$F(3,21) = 5.17$, $p < .05$], and there was no group × interlandmark distance interaction [$F(3,21) = 1.34$, $p > .05$; Figure 3].

Considering that the rotated group was tested at five different rotated positions, orientation of the landmark array could have affected search accuracy. The rotated group's total error distance was analyzed with a rotated position by interlandmark distance ANOVA. The orientation of the landmark array had no effect on accuracy [$F(4,16) < 1$]. As interlandmark distance increased, error distance increased [$F(3,12) = 5.76$, $p < .05$], and there was no interlandmark distance × rotated position interaction [$F(16,60) < 1$].

Discussion

These results have four implications. First, the accuracy of the rotated group demonstrates that nutcrackers can use relative bearings to find a hidden goal. For this group, the directional relationships of the goal–landmark array varied in absolute terms throughout acquisition, yet the nutcrackers appeared to learn as rapidly as the unrotated group. In fact, the results leave some doubt about whether or not learning relative bearings is more difficult than learning absolute bearings. Although the evidence is equivocal, we suspect that there is a small quantitative difference. Several statistical tests approached significance, and the unrotated group did perform significantly better than the rotated group in the perpendicular axis. However, this issue is not as important as the more basic finding that the birds were able to learn this problem about as readily as the birds that learned the problem when absolute bearings could be used.

Second, the fact that the rotated group performed worse than the unrotated group in the perpendicular but not the parallel axis suggests a particular hypothesis about how the groups may have differed. Suppose that the birds in both groups used two lines to locate the goal, one line along which all points were equidistant from the landmarks and the other line a bearing from one or both landmarks. The equidistant line is perpendicular to the line connecting the landmarks and can be found without the use of bearings. For example, apparent distance to the landmarks could be used. However, the other line must involve the use of bearings. This bearing could have been an absolute compass bearing for the unrotated group, but not the rotated group. Therefore, the finding that the group difference was limited to the perpendicular axis suggests either that relative bearings are less accurate than abso-

lute bearings or that two sources of information are more accurate than one.

Third, as interlandmark distance increased, error distance increased. This result is similar to findings from our two previous hidden goal studies (Kamil & Jones, 1997, 2000). The increasing error distance is probably due to increased difficulty judging distance and direction as distance from an object increases. While the increase in distance estimation error may be an instance of Weber's law (Cheng, 1989), the increase in error in directional estimation may not be. If the directional error is constant in angular terms (measured in degrees), this would lead to increased error when measured in centimeters.

Finally, the probe trial data indicate that the birds did not rely on olfactory cues to locate the buried seeds, replicating earlier cache recovery (Balda, 1980; Kamil, Balda, Olson, & Good, 1993) and hidden goal studies (Gould-Beierle & Kamil, 1996; Kamil & Jones, 1997, 2000). This allowed us to use probe trials without seeds to investigate effects of manipulations of the landmark array on search. The use of probe trials minimizes the problem of learning during manipulated trials.

EXPERIMENT 2

During Experiment 1, the birds in each group were trained with four specific interlandmark distances. Experiment 2 was designed to determine performance with novel interlandmark distances. Two types of novel inter-

landmark distances can be tested, those within the testing range (interpolated) and those outside the testing range (extrapolated). Results from our previous research have shown that birds trained either to find a goal located directly between two landmarks or to find a goal with a constant directional relationship to two landmarks (as in the control group of Experiment 1) generalized interpolated as well as extrapolated interlandmark distances. In contrast, nutcrackers trained to find a goal without a constant directional relationship to two landmarks generalized only to interpolated distances (Kamil & Jones, 2000). As Biegler et al. (1999) have pointed out, this failure to generalize to extrapolated distances suggests that these birds may have learned the problem by memorizing four vectors that correspond to the training interlandmark distances—as four separate problems rather than as a single problem. Therefore, it was of considerable interest to determine whether birds trained with relative bearings could generalize search to both interpolated and extrapolated interlandmark distances.

Method

Procedure. The second experiment began immediately following Experiment 1: The same subjects, assignments to groups, and materials and methods were used. Each day the birds received three buried seed trials and one probe trial. Training interlandmark distances (36, 60, 84, and 108 cm) were used for all buried-seed trials. For the entire training, interlandmark distances and five new interlandmark distances 24, 48, 72, 96, and 120 cm apart were used as probe trials. A probe trial was randomly assigned to Trial 2, three
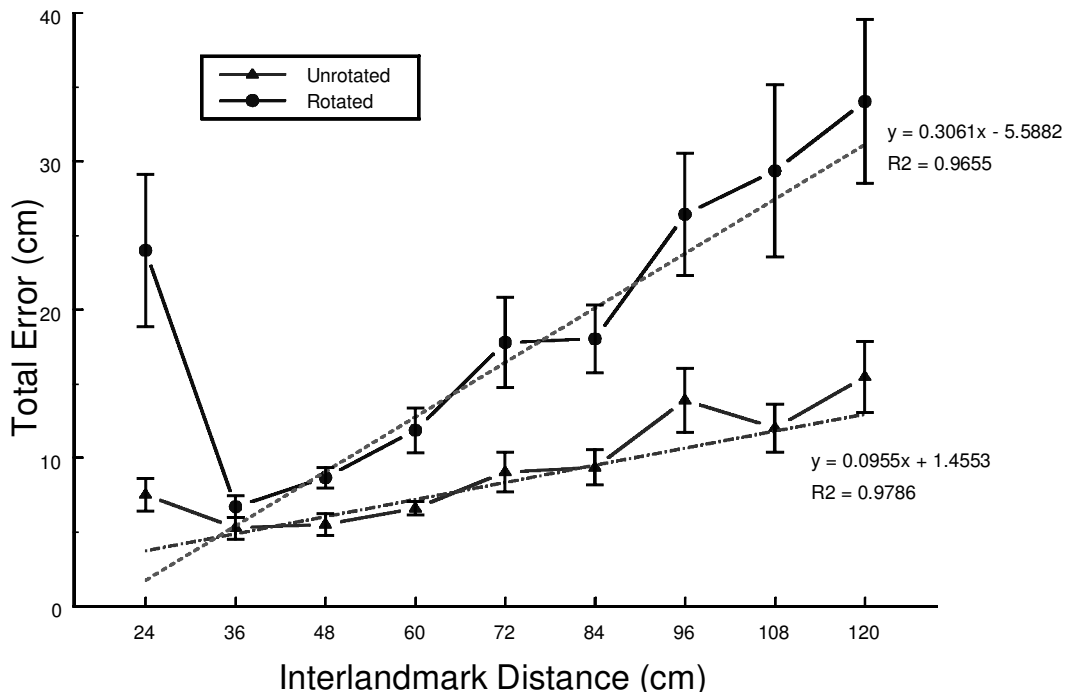

Figure 4. Mean total error distance between the location of the first five digs and the goal location on probe trials throughout transfer. Each interlandmark distance contains three probe trials for each bird. Dashed line: rotated group's predicted line. Broken dashed line: unrotated group's predicted line. Predicted lines were calculated using training interlandmark distance probe trials from Experiment 1.

or four each day. Across the 27-day experiment each bird received three probe trials at each of the nine interlandmark distances in a randomized block design. For the rotated group, interlandmark distance was counterbalanced across rotation position for the group.

Results

We analyzed error distance during transfer testing with a group × interlandmark distance mixed ANOVA. The unrotated group performed significantly better than the rotated group [$F(1,7) = 18.3, p < .05$]. As the interlandmark distance increased, the birds' accuracy decreased [$F(8,56) = 9.8, p < .05$], but there was no significant interaction [$F(8,56) = 1.45, p > .05$; Figure 4]. The rotated group was very inaccurate at the shortest interlandmark distance. Therefore, we ran independent ANOVAs on the effect of interlandmark distance for each group. For the rotated group, there was a significant effect of interlandmark distance [$F(8,32) = 6.81, p < .05$]. A subsequent Fisher's LSD test was carried out in which the total error at each interlandmark distance was compared with the total error with the next greater interlandmark distance. Only the difference between 24 and 36 cm was significant. There was also an effect of interlandmark distance for the unrotated group [$F(8,24) = 5.97, p < .05$]. A similar Fisher's LSD analysis revealed no differences in total error between any adjacent pairs of interlandmark distances.

It has been demonstrated in this experiment and previous experiments (Kamil & Jones, 1997, 2000) that as interlandmark distance increases, search accuracy decreases. In order to examine the magnitude of error with this general trend removed, we selected the data from Experiment 1, which consisted of the training interlandmark distances (36, 60, 84, and 108 cm), and calculated the linear equation for each group. The unrotated group's linear equation was $Y = 1.455 + 0.096X$ while the rotated group's linear equation was $Y = -5.588 + 0.306X$ (Figure 4). From the linear equations we calculated the predicted error distance for each new interlandmark distance (24, 48, 72, 96, and 120 cm) and analyzed the deviations from the predicted line with a two-way mixed ANOVA with group and condition as factors. Deviations were calculated as follows: Both training and transfer probe test data for each trial were subtracted from the predicted line at the appropriate interlandmark distance. This error term was used as the response variable in the ANOVA. The levels of condition were control (training), interpolated, and extrapolated interlandmark distances. The rotated group had more deviation from its predicted line than the unrotated group [$F(1,7) = 59.32, p < .05$]. When the landmarks were placed at the extrapolated interlandmark distances error distance was more deviant from the predicted line than on training or interpolated conditions [$F(2,14) = 14.62, p < .05$] and there was a group × condition interaction [$F(2,14) = 7.43, p < .05$]. A subsequent Fisher's LSD revealed that the effect of interlandmark distances was due to the decrease in accuracy for

the rotated group at the smallest interlandmark distance (which was an extrapolated distance).

Discussion

Our previous research with generalization to novel interlandmark distances suggests that one of two outcomes should have resulted. Either the birds should have generalized only to interpolated distances or they should have generalized to all novel distances. However, while both groups clearly generalized accurately to interpolated distances, the results from the extrapolated distances (24 and 120 cm) were more complicated. Search error and deviation from the predicted line increased when the 24-cm interlandmark distance was presented to the rotated group but not the unrotated group. However, for both groups there was no difference in performance measured at the 108-cm distance or an increase in deviation from the predicted line, even though such a difference might be expected on the basis of increasing interlandmark distance alone. Thus the results suggest that the birds transferred to the extrapolated interlandmark distance that was longer than any training distance, but not to the shorter extrapolated distance.

While it is possible that these results demonstrate a failure to generalize to extrapolated distances, it is also possible that the poor performance at the 24-cm interlandmark distance may have been a more specific effect. When the landmarks were 24 cm apart, the goal–landmark distance was only 16.97 cm and the birds appeared reluctant to search this close to the landmarks. If this hypothesis is correct, then birds trained with interlandmark distances of 48 to 144 cm would perform accurately when presented with an extrapolated interlandmark distance of 36 cm. Then the transfer shown by both groups during Experiment 2 would be due to the acquisition of a general principle based on bearings. In the case of the unrotated group, this principle could have been based on the use of either absolute or relative bearings, whereas the principle for the rotated group could have been based solely on relative bearings.

EXPERIMENT 3

It is apparent that the birds in both groups were able to generalize to new interlandmark distances; yet, the ability to generalize to novel orientations within the room has thus far not been tested. In previous experiments (Kamil & Jones, 1997, 2000), nutcrackers were trained with the landmark array in a fixed orientation, and probe tests were performed in which the array was rotated away from the training orientation from 22° to 180°. Results indicated that when the landmark array was slightly rotated (22°), the birds tended to follow the rotation, suggesting the use of relative bearings. However, when the landmark array rotation was greater than 45°, the birds tended to use absolute bearings. This leads to the prediction that the birds

in the rotated group would generalize to novel orientations because they have learned to use relative bearings. In contrast, the birds in the unrotated group should not generalize when novel orientations are presented because they tend to favor the use of absolute bearings. The purpose of Experiment 3 was to test this prediction.

Method

Procedure. The third experiment began immediately after Experiment 2 and the same subjects, assignments to groups, and materials and methods were used as those in Experiment 1. The birds received four trials a day with each interlandmark distance (36, 60, 84, and 108 cm) presented once, including one probe trial, randomly scheduled for Trial 2, 3, or 4.

There were three stages to this experiment. During the first stage (24 days), the landmarks were presented either in a control position or in a rotated position on each probe trial. There were six rotated test positions that were new to both groups. These positions were 15°, 45°, or 75°, both clockwise and counterclockwise from the 0° rotation orientation. The control position was 0° for the unrotated group. For the rotated group the control positions were the five orientations used during training. Each bird received a total of two probe trials at each new orientation at the interlandmark distance of 84 cm.

During the second stage (32 days), interlandmark distances of 60 and 84 cm were used for large rotation probe trials. The birds experienced control, 90° rotation (clockwise and counterclockwise) and a 180° rotation twice at each of the two interlandmark distances. In the third stage (8 days), each bird experienced two probe trials with the blue landmark removed and two probe trials with the red landmark removed. These probe trials were presented every other day, in random order. On the alternate days without a single-landmark probe trial, probe control trials at original training interlandmark distances were presented.

Results

Small rotation (15°, 45°, 75°). For the following set of analyses, we assumed that the birds were applying one of two strategies when presented with a novel orientation. The first assumption is based on the idea that the birds were applying absolute bearing information to the situation, whereas the second assumption is that the birds were utilizing relative bearings to locate the goal. For the following analysis, error was calculated from the relative rule location, which signifies the predicted placement of the goal determined by relative bearings. Thus, if the birds were applying the absolute bearing strategy, then error distance from the relative rule location should increase as degree of rotation increases. In order to test whether the direction of rotation had an effect on error distance, a group × direction of rotation ANOVA was performed on total error distance (as measured from the relative rule location), and there was no effect of direction of rotation (clockwise or counterclockwise) $[F(2,14) = 2.15, p > .05]$. Therefore we collapsed across direction of rotation for the remaining analyses.

The effect of rotation on total error distance from the relative rule location was analyzed with a group × degree of rotation (control, 15°, 45°, and 75°) ANOVA. Overall, the rotated group searched closer to the relative rule location than did the unrotated group $[F(1,21) = 50.3, p < .05]$. The rotated group's error distance from the relative rule location stayed consistent across newly presented rotated positions relative to the control trials. In contrast, the unrotated group's error distance increased as
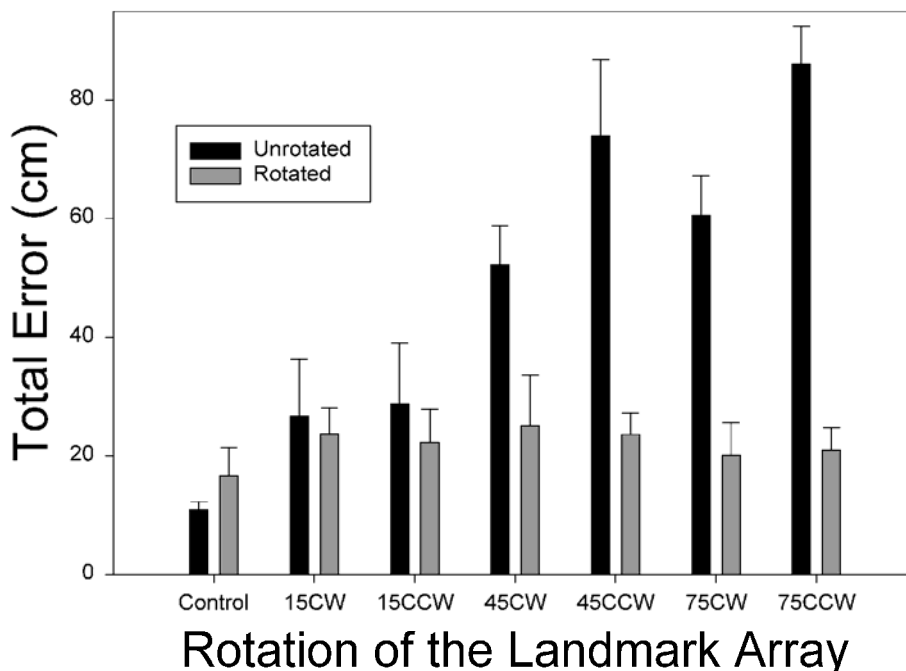

Figure 5. Mean total error distance ± *SE* from the correct location of search predicted by relative bearings. Black bars: unrotated group's total error distance. Gray bars: rotated group's total error distance.

the degree of rotation increased, resulting in both a significant main effect of rotation [$F(3,21) = 22.09, p < .05$] and a significant group $\times$ degree of rotation interaction [$F(3,21) = 18.88, p < .05$; Figure 5].

Large rotation (90º). We first analyzed the results of the large rotation experiment on total error distance from the relative rule location with a group $\times$ interlandmark distance $\times$ condition repeated measures ANOVA. The levels of condition were control and 90º rotated. The unrotated group searched further away from the relative rule location than did the rotated group [$F(1,7) = 14.59, p < .05$], and there was no effect of interlandmark distance [$F(1,7) = 1.94, p > .05$]. Both groups were more accurate on control trials than on trials during which novel orientations were presented [$F(1,7) = 190.25, p < .05$]. There was also a significant group $\times$ condition interaction [$F(1,7) = 18.5, p < .05$] and a significant landmark $\times$ condition interaction [$F(1,7) = 6.25, p < .05$].

The search patterns of the two groups appeared to differ qualitatively when the landmark array was rotated 90º either clockwise or counterclockwise. In particular, the search pattern of the unrotated group appeared to be oriented toward the west landmark (Figure 6). Therefore, we performed a separate analysis for the unrotated group. We calculated the error distance from two predicted absolute bearings, northwest and southwest from the west landmark, and selected the lower error distance (per dig) for analysis. A condition (control vs. 90º rotation) $\times$ interlandmark distance repeated measures ANOVA was performed on these error distances. The unrotated group was closer to the predicted absolute bearing on control trials than on rotated trials [$F(1,3) = 20.73, p < .05$], and there was no effect of interlandmark distance [$F(1,3) < 1$] nor any interaction [$F(1,3) < 1$].

Position reversal (180º). When the landmarks were rotated 180º there were two possible strategies that the nutcrackers could use. The first would be to use relative bearings, which would involve searching northeast from the red landmark and southeast from the blue landmark. The second would be to rely on absolute bearings, searching northwest from the red landmark and southwest from the blue landmark. The effect of the 180º rotation on search accuracy was analyzed with a group $\times$ interlandmark distance by predicted location (relative vs. absolute) ANOVA. Error distance was measured as the distance of search to the correct geometric location. The groups did not differ in error distance [$F(1,7) = 2.63, p > .05$]. The birds searched closer to the location predicted by the use of absolute rather than relative bearings [$F(1,7) = 123.72, p < .05$]. This pattern of search was not affected by interlandmark distance [$F(1,7) = 2.42, p < .05$; Figure 7]. None of the interactions were significant.
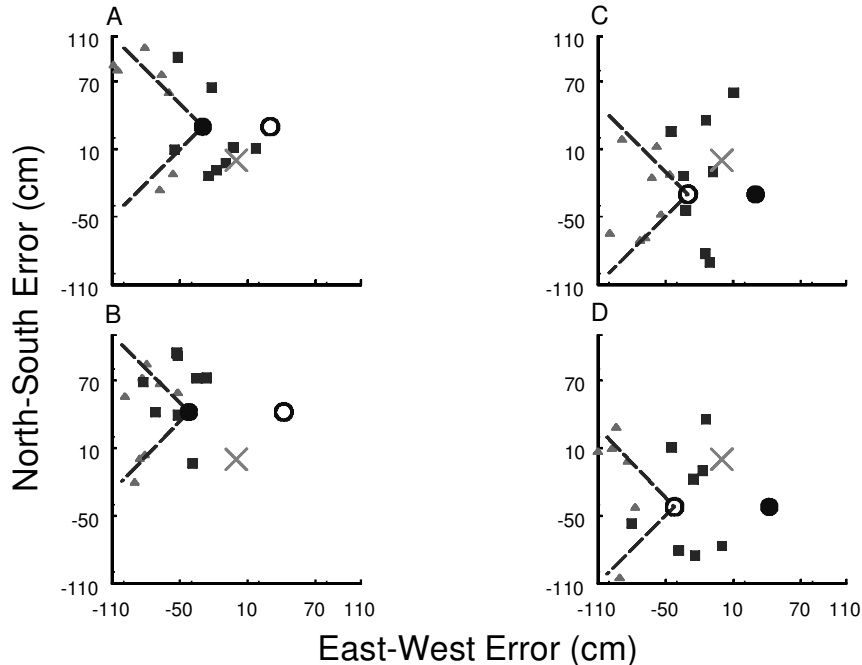

Figure 6. Maps of trial placement of search on 90º rotated (clockwise and counterclockwise) trials at the interlandmark distances of 60 and 84 cm apart. Filled circles: red landmark. Unfilled circles: blue landmark. Cross: goal location predicted by relative bearings. Squares: mean search location for each bird in the unrotated group. Triangle: mean search location for each bird in the rotated group. Dashed line: predicted absolute bearing. Interlandmark distance and orientation: (A) 90º rotated clockwise, 60 cm. (B) 90º rotated clockwise, 84 cm. (C) 90º rotated counterclockwise, 60 cm. (D) 90º rotated counterclockwise, 84 cm.
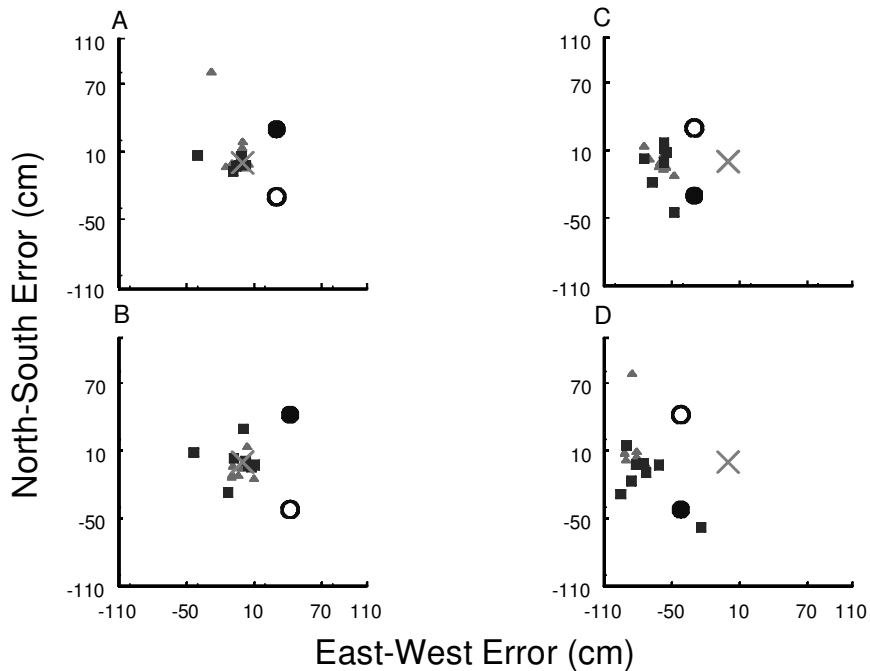
Figure 7. Maps of trial placement of search on control and 180° rotated trials at the interlandmark distances of 60 and 84 cm apart. Filled circle: red landmark. Unfilled circle: blue landmark. Cross: goal location predicted by relative bearings. Square: mean search location for each bird in the unrotated group. Triangle: mean search location for each bird in the rotated group. Interlandmark distance and orientation: (A) 0 rotated, 60 cm. (B) 0 rotated, 84 cm. (C) 180° rotated, 60 cm. (D) 180° rotated, 84 cm.

Since it appears that the animals did not follow the 180° rotation tests, we wanted to determine whether search accuracy (from the location where the seed would be buried if the landmark array was not rotated) changed between the 180° rotation and a control probe trial (in this case the landmarks were placed at 0° rotation). Thus, we compared total error distance (from the location predicted by the use of absolute bearings) from trials during which the landmark array was rotated 180° with the total error distance during control trials with a group × condition ANOVA. There was neither a significant difference between the groups $[F(1,7) = 3.92, p > .05]$ nor an effect of the rotation $[F(1,7) = 1.7, p > .05]$. There was also no group × condition interaction $[F(1,7) = 2.64, p > .05]$.

Single landmark. We analyzed the single landmark probe data by calculating the error distance between each dig and each of two predicted bearings: (1) the correct direction from the presented landmark (northwest from the blue landmark and southwest from the red landmark); and (2) the opposite bearing (southwest from the blue and northwest from the red landmark). Distance from both bearings was calculated, because if the birds did not use the color of the landmark as a cue, then search along either absolute bearing is a possibility. Thus, error distance to each bearing was calculated for each dig, and the lower error distance was used for analysis.

We carried out a similar calculation for control trials, on the basis of the distance from each dig to the absolute bearing. Data were analyzed with a group × condition (control vs. single landmark) ANOVA. The single landmark level was collapsed across landmark color, and the control trial level was collapsed across the interlandmark distances of 60 and 84 cm. The unrotated group searched with higher accuracy than the rotated group $[F(1,7) = 10.52, p < .05]$, and both groups searched closer to the predicted lines on control trials than on single landmark trials $[F(1,7) = 12.12, p < .05]$, but there was no group × condition interaction $[F(1,7) = 3.58, p > .05;$ Figure 8].

Discussion

It has been previously demonstrated that when nutcrackers are trained with two landmarks always presented north and south of each other and then tested with small rotations of the array, the birds use both relative and absolute bearings (Kamil & Jones, 1997, 2000). The search behavior of the unrotated group during small rotation probe trials was consistent with this pattern. In contrast, the rotated group appeared to use relative bearings when tested with novel orientations within 15° of training positions (Figure 5). However, the rotated group did not generalize search to new orientations greater than 15°. This suggests a limitation in the birds' ability to generalize rel-
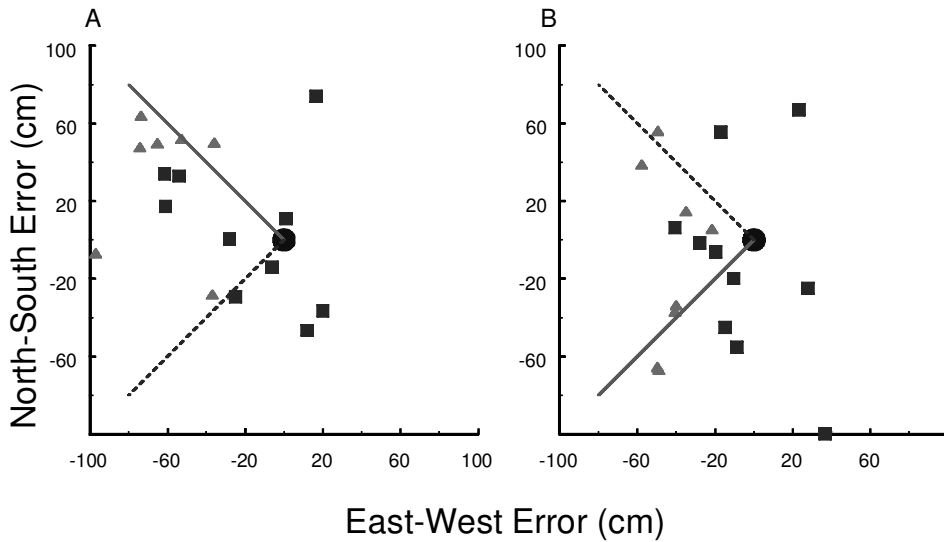
Figure 8. Maps of trial placement of search when one landmark was removed. Landmark: Circles. Unrotated group: Squares. Rotated group: Triangles. The solid line is the predicted location of search if using an absolute bearing and paying attention to the color of the landmark. The dotted line is the predicted location of search if using an absolute bearing and not paying attention to the color of the landmark. (A) Trials when the blue landmark was present. (B) Trials when the red landmark was present.

ative bearings to novel orientations that were drastically different from those to training orientations.

In order to show where birds were searching relative to the location of the landmarks and goal, we plotted the average location where each bird dug during each trial in Figures 6–8. These figures are laid out as overhead views of how the landmarks and goal were placed in the room. The triangles and squares represent the average location a bird was digging during one test trial. The porthole where the birds entered the room was at the west end of the room.

Results from the large rotation and the position reversal probe trials revealed three things. First, when the landmark array was rotated 90° or greater, the unrotated group searched in the location predicted by an absolute bearing from one landmark, but their accuracy to find this location was diminished when novel rotations were presented. One possible reason for this decrease in accuracy is that on control trials the birds could compare bearings from both landmarks, whereas during 90° and 180° rotations, the birds may have used only one bearing. Another possible reason is that when the landmark array was rotated 90°, the birds had to choose between using a relative bearing or an absolute bearing, thereby increasing variability of search.

Second, during the large rotation probe trials, the rotated group did not use relative bearings once the landmark array was rotated greater than 75°. It appears that three different search patterns arose when the landmark array was rotated 90° (Figure 6). Some birds used relative bearings and searched at the correct location; other birds searched opposite the goal location; and yet other birds searched west of the landmark in a random pattern.

Therefore, since the rotated group demonstrated no consistent pattern of search, it is difficult to draw a conclusion about the animals' search behavior or what cues and mechanisms the birds were applying to this situation.

Third, during the position reversal probe trials the nutcrackers ignored the color of the landmarks and searched southwest from the blue landmark and northwest from the red landmark. One possible reason for this behavior is that when the landmark array was rotated 180°, the configural orientation with respect to the room was unchanged. This suggests that the spatial configuration of the landmark array was more salient than the color of the individual landmarks. Even though the presence of color vision has not been studied in nutcrackers, nutcrackers have been shown to discriminate between two colors in an operant task (Olson, Kamil, Balda, & Nims, 1995), as do pigeons and other corvids (e.g., Wilson, Mackintosh, & Boakes, 1985). Nutcrackers have also been shown to respond differentially to differently colored landmarks during buried-seed tasks (Kamil & Jones, 2000). In addition, many related passerine species have four-peak photopic wavelength sensitivity (Chen & Goldsmith, 1986).

The final test to determine whether the birds were using absolute or relative bearings was the presentation of a single landmark. When just one landmark was present during probe trials, the unrotated group used absolute bearings, as did birds with similar training in Kamil and Jones (2000). However, the rotated group appeared to dig randomly (Figure 8). The difference between the error distance on control trials versus single landmark trials was 4 cm for the unrotated group but 15 cm for the rotated group. In addition, the birds in the rotated group showed

no clustering of search or common search pattern when a landmark was removed, nor was there a consistent search pattern between the two landmark colors. Whereas the rotated group learned a geometric principle based on relative bearings (which require two landmarks), the unrotated group learned a geometric principle based on absolute bearings (which can be applied to a single landmark).

GENERAL DISCUSSION

When Clark's nutcrackers store seeds, they must encode information about the location of the food in order to relocate the cache months later. The results of previous studies using cache recovery procedures (e.g., Kamil & Balda, 1995; Vander Wall, 1982) have suggested that nutcrackers use both global and local cues in order to locate buried seeds. However, because it is extremely difficult to control the geometric relationship between goal and landmarks when a bird chooses cache sites, buried-seed procedures in which the experimenter determines the goal location are also needed to study the mechanisms that nutcrackers use to find a specific location. Results from such studies (e.g., Gould-Beierle & Kamil, 1996) are consistent with the cache recovery studies, indicating that nutcrackers use both global and local cues.

The buried-seed studies have also demonstrated that nutcrackers relocate the goal by remembering relationships (distance and direction) between the goal location and one or more landmarks. In two previous studies (Kamil & Jones, 1997, 2000), Clark's nutcrackers demonstrated the ability to utilize absolute and relative bearings to learn a geometric relationship among two landmarks and a goal. In these studies, the orientation of the landmark array was fixed with respect to the walls, and the birds could have either focused on directional information that was consistent with global cues (absolute bearings) or focused on directional information that was taken solely from the landmark array (relative bearings). Results demonstrated that the birds utilized a geometric principle based on both absolute bearings and relative bearings, but when the two were put in conflict, the birds always chose to use absolute bearings. The main question posed in the present experiment was whether these birds could learn a geometric task that was dependent on the use of relative bearings.

The performance of the rotated group during the present experiments demonstrated that nutcrackers could learn a geometric principle based on relative bearings and generalize the principle to many new conditions during which the landmarks were presented at novel interlandmark distances or orientations. However, they did not generalize well when the landmarks were rotated 90° or more, and the reasons for this failure are not clear. When the landmarks were rotated 90°, some of the birds searched in locations other than that defined by relative bearings. This indicates that the birds learned some relationship between the location of the goal and landmarks in addition to relative bearings. One possibility is directional information. Although the landmark array was rotated over a range of 150°, during training the red landmark was always north of the blue landmark, and the goal location was always west of the hypothetical line between landmarks. If the birds depended on this type of directional rule, then these directional cues were invalid when the landmark array was rotated 90°. Thus, it appears that even the birds in the rotated group encoded some directional information due to the lack of training orientations. Hence, if the birds had been trained with a greater range of landmark orientations, then this might have forced the nutcrackers to rely exclusively on relative bearings. In addition to increasing the degree landmark array rotation during training, another possibility is using landmarks that are distinctly different in appearance. This might be beneficial because nutcrackers pay more attention to the spatial orientation of features in their environment than to the appearance of the landmarks. Another possibility would be to conduct the experiment in a room that had no directional cues. Therefore testing the effects of training with rotating landmark arrays might produce exclusive reliance on relative bearings.

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