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# The effect of proximity on landmark use in Clark's nutcrackers

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## Abstract

Clark's nutcrackers, *Nucifraga columbiana*, store thousands of pine seeds during the autumn and retrieve them throughout the winter. It has been shown that these birds are able to use visual cues to relocate hidden food in the laboratory. In this set of experiments, we trained three groups of Clark's nutcrackers to find a hidden food goal that was placed in the same spatial location relative to the testing room. During training, the location of two local cues in relation to the goal differed between the three groups. Group 1 learned the task with the cues closest to the goal, group 2 with the cues further from the goal, and group 3 with the cues furthest from the goal. To test whether the proximity of these two local cues to the goal affected how spatial information was used, we manipulated local and global information in a series of experiments. Results indicated that local cues were more important sources of spatial information for group 1, whereas global cues seemed to be used more by birds in groups 2 and 3. These findings suggest that the proximity of visual cues lead to overshadowing of other sources of spatial information surrounding the goal.

An individual Clark's nutcracker, *Nucifraga columbiana*, stores up to 33 000 pine seeds in thousands of cache sites during the autumn months. These seeds constitute the bulk of their winter diet and are also fed to nestlings in the spring (Vander Wall 1990). In the laboratory, it has been demonstrated that nutcrackers are able to remember the spatial location of each cache they make (Kamil & Balda 1985) and are able to use spatial information from landmarks in locating a cache or hidden goal (Vander Wall 1982; Balda & Turek 1984; Basil 1993). Therefore, the use of landmarks is thought to be the critical means by which these birds are able to code spatial information about a cache site and retrieve this information at a later time for accurate recovery of the cache in the field.

We have previously investigated how Clark's nutcrackers use two different types of landmarks while searching for a hidden goal: local and global cues (Gould-Beierle & Kamil 1996). In our laboratory setting, a local cue is defined as any landmark that is relatively close to the hidden goal (0–100 cm) and, generally, is part of the configuration on the floor of the room that is deliberately placed around the goal. A global cue is defined either as any landmark remote from the hidden goal (100 cm and beyond), or as a landmark that is part of the configuration of the room's walls and geometric shape. Previously, we carried out a set of experiments in a room in which we placed an experimental tray filled with wood chips. Local cues were located within the tray and global cues were external to the tray. The results from that study suggested that nutcrackers could learn to use local cues to find a hidden goal when those cues were in a predictable

spatial relationship with global cues. When a local cue was moved out of alignment with other cues, a shift parallel to the edge of the tray resulted in a significant shift in searching while a shift perpendicular to the edge did not. The birds were also able to maintain a high degree of accuracy in the absence of reliable global or local information.

Two other important ideas emerged from the results of Gould-Beierle & Kamil (1996). First, a local cylindrical cue within the tray seemed to be more salient in the task of locating the goal than cues derived from the tray itself (e.g. the edges, corners, etc.). However, the nearest edge of the tray may have had some influence when both local and global cues were available. Second, these birds can use information from global cues with a high degree of accuracy, even when they are initially trained with local information close to the goal. The experimental design of Gould-Beierle & Kamil (1996) did not allow the importance of edge cues versus other local cues to be tested directly, nor did it investigate how the location of local landmarks during training affects the use of global information. To expand on these two ideas, we designed the current set of experiments to investigate the importance of local landmarks, edges and global cues in more detail without the confinement of an experimental tray. More importantly, the experiments were designed to investigate how proximity of local cues to a goal affects searching behaviour.

The idea that the distance of a local cue from a goal location could influence the importance of that cue is supported by a number of experimental studies. First, we carried out a comparative landmark study that

replicated almost every aspect of Gould-Beierle & Kamil (1996). We compared the performance of the Clark's nutcracker to that of two other food-storing corvids, the pinyon jay, *Gymnorhinus cyanocephalus*, and scrub jay, *Aphelocoma coerulescens* (Gould-Beierle & Kamil 1998). The major difference in the training procedure of the comparative study was the location of the goal relative to the edge of the experimental tray. This distance was increased by 10 cm compared with that used in the training procedures of the original nutcracker study. When we compared the performance of the nutcrackers in Gould-Beierle & Kamil (1996) qualitatively to that of the nutcrackers in the comparative study (Gould-Beierle & Kamil 1998), differences in searching behaviour emerged. In the comparative experiment, the local landmark seemed to be a more salient cue than either the edge of the tray or global cues. During landmark displacement, the birds tended to shift their searching in response to all shifts of the local landmark. When local landmarks were removed, the birds did not maintain searching behaviour as accurately as the nutcrackers did in the original study. These results suggest there was a difference in how the available spatial information was used by these two sets of birds and that this difference might be due to the location of the goal relative to local cues during training.

There are other experiments suggesting that the proximity of cues may affect searching behaviour. Spetch & Wilkie (1994) trained two groups of pigeons to find a hidden goal within an array of three landmarks. The landmark closest to the goal differed between the two groups. During testing, the nearest landmark had the most control over searching behaviour for both groups. They concluded that the close association of one cue with a goal leads to the overshadowing of information from the other cues. This phenomenon has also been shown in humans (Spetch 1995). Cook & Tauro (1999) showed that rats trained to find food with landmarks proximal to baited poles learned to locate them much quicker than rats trained with landmarks distal to the baited poles. They also showed that when these landmarks were moved, the proximal group tended to follow landmark shifts while the distal group did not. Cheng (1989) found that pigeons searching for a hidden goal were controlled more by landmarks near to the goal than further from it, and Basil (1993) showed that Clark's nutcrackers made more errors searching for a hidden goal when proximal landmarks (7.5–40 cm from the goal) were removed from an array than when distal landmarks (50–75 cm from the goal) were removed. These studies, along with the qualitative difference in searching by nutcrackers in our previous two experiments, suggest that the closer a local landmark is to the goal, the more it influences searching behaviour. However, the role that different kinds of proximal cues play and the effect that their proximity has on the information gained from more global cues has not been addressed in detail.

The experiments we report here incorporated three important features in their design. First, we systematically altered the distance of local landmarks from a hidden goal for different groups of Clark's nutcrackers during training and then we manipulated the landmarks to test for displacement in searching behaviour. This method allows searching behaviour during both acquisition of the task and testing to be compared in a between-groups design. Second, the effect of the proximity of local cues on the processing of global cue information was addressed explicitly. All three groups of birds were trained to find food at the same globally defined goal location within the room. This allowed us to look at the use of global information based on differences in local cue proximity. Finally, two very different types of local cues were provided to define the goal: a cylinder and a flat edge. In our previous work (Gould-Beierle & Kamil 1996, 1998), the landmark was a cylinder located on a four-sided tray, and the results suggested that the edge nearest the goal may provide important spatial information. Therefore, the current experiments were designed so that the effects of an edge without all of the various other cues associated with an actual tray could be determined.

### Experiment 1: Movement of Each Individual Local Cue

#### Methods

##### Subjects

Three groups of four Clark's nutcrackers each were used. One bird in each group was naïve to any experimental procedures while the other three birds in each group had previous experience in various tasks. However, all birds were naïve with respect to finding hidden seeds in an experimental room. All birds were individually housed in a colony room maintained at 22°C on a 14:10 h light:dark cycle. They were kept at approximately 90% of their free-feeding weight and maintained on a diet of turkey starter, sunflower seeds, parrot pellets, mealworms, pine seeds and a vitamin supplement. They had free access to grit and water.

##### Experimental room

All experiments took place in an observation room, 440 X 270 cm, with three centrally located fluorescent lights. Within the room, we constructed a platform, 380 X 270 cm, which extended to the north, south and west walls of the room. The platform was elevated 4.5 cm from the floor and completely covered with wood chip bedding approximately 2 cm thick. We attached a board, 14 X 4 cm, to the east edge of the platform that extended 9.5 cm from the end of the platform. This acted as a barrier so that the wood chips stayed within the platform. A smoked-glass observation window, a small sliding trap door and a full-sized door were located on the east wall. A Panasonic

WV-BL200 black-and-white video camera was situated above the false ceiling with a hole cut into the centre ceiling tile as an opening for the lens. We observed the birds through the observation window and on the video monitor connected to the camera. We placed posters, 97.5#68 cm, on the north, south and west walls of the room. We used a green piece of PVC tubing, 9.6 cm in diameter and 12.9 cm high, as one landmark (the cylinder). As a second landmark (the edge), we used a board painted black, and measuring 120#3.5 cm. The board was placed parallel to the east and west walls of the room (see Fig. 1).

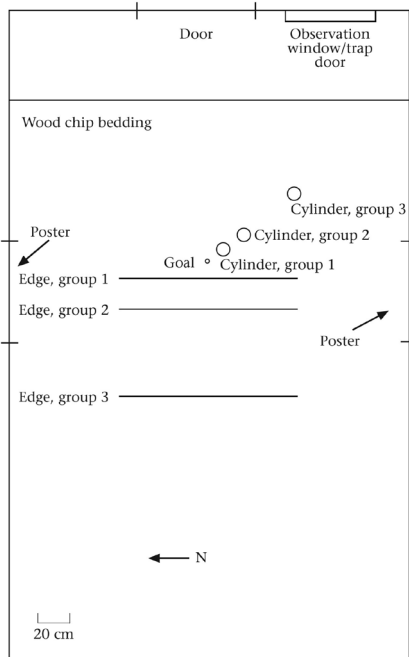


Figure 1. The training position of the cylinder and edge landmarks within the experimental room.

### Groups

The three groups of birds all learned to find two shelled pine seeds buried beneath the wood chip bedding on a plastic film canister lid. The location of this hidden goal relative to the room was the same for all three groups: 110 cm from the east edge of the platform, 270 cm from the west wall and 135 cm from both the south and north walls. Each group learned this task with the cylinder and edge at different distances from the goal location. The cylinder was always located on a diagonal line from the goal to the corner nearest the observation window (see Fig. 1). Group 1 learned the task with the cylinder 8 cm away from the goal and the edge 10 cm away from the goal at its middle point. For group 2, the cylinder was 24 cm and the edge 30 cm away from the goal. Group 3 learned the task with the cylinder 72 cm and the edge 90 cm away from the goal. An imaginary X-Y coordinate system was applied to the room to facilitate data collection and discussion of the results. The origin was at the goal location with positive values on the X axis towards the right and positive values on the Y axis towards the top (Fig. 1).

### Habituation

We used habituation procedures similar to those of Gould-Beierle & Kamil (1996, 1998). We began each habituation trial by carrying the bird from its home cage to a holding cage situated just outside the observation room. The bird entered the room from the holding cage through the sliding trap door located underneath the observation window. After the bird found the seeds or 30 min had elapsed, the observation room lights were shut off and the lights outside the room were turned on. We opened the sliding door and the bird flew into the holding cage. We returned each bird to its home cage after each trial. We ran each group as a squad and randomized the order in which the birds were tested each day within each group.

We carried out habituation in several stages over a number of trials depending on the bird. The cylinder and edge landmarks were in the appropriate training position for each group throughout habituation. During the first stage, we placed four shelled pine seeds in the film lid at the goal location on top of the wood chips. Stage 1 continued for each bird until it had eaten the seeds within 10 min on 3 consecutive days. The next stage consisted of reducing the number of seeds to two. This was done for one trial only. The final part of habituation consisted of gradually burying the film lid and the two seeds over the course of a number of trials. The criterion for ending this stage of habituation was finding the partially or fully buried seeds for three consecutive trials. Once this was met, we began training trials.

### Training and testing

During training, each bird received one to three trials per day, and in each trial the seeds and film lid were buried beneath the wood chips and the cylinder and edge landmarks were in their appropriate training positions for each group. A trial ended after the bird found the seeds or 10 min had elapsed. We recorded the number of digs each bird took to find the seeds. The criteria we used to end the training phase for a bird was that at least 30 trials had been completed and the bird found the buried seeds for 10 consecutive trials in under 15 digs. When a bird met the criteria, it was run only once a day to maintain training.

During the testing stage, each bird was run three times per day. The trials consisted of two rewarded training trials (cylinder and edge landmarks in training position for that group and two seeds available) and one unrewarded test trial (cylinder and edge landmarks in testing position for that group and no seeds available) per day. We randomly assigned the test trial as one of the first two daily trials. Each trial continued until 20 s had elapsed from the first probe of the wood chips. We defined a probe as the bird bringing its bill into contact with the wood chips. Once the 20 s had elapsed, the lights were turned off and the bird flew back into the holding cage.



**Table 1.** Mean (SE) of X and Y search locations for each group for the five test conditions in experiment 1

Group	Control		C+10 cm X		C+10 cm Y		E+10 cm X		E-10 cm Y	
	X	Y	X	Y	X	Y	X	Y	X	Y
1	-2.21 (1.53)	0.50 (1.51)	8.00 (1.71)	-0.02 (1.13)	-1.84 (1.64)	2.54 (1.40)	0.31 (2.01)	0.42 (1.00)	-3.92 (2.08)	-4.56 (1.18)
2	1.69 (2.40)	-0.06 (1.37)	8.86 (1.94)	-0.19 (1.22)	2.44 (2.03)	4.75 (1.28)	3.09 (2.63)	-0.25 (0.85)	-1.56 (0.65)	-2.73 (1.23)
3	-1.79 (3.77)	-0.11 (3.49)	5.31 (5.77)	2.58 (5.21)	-4.36 (1.72)	2.08 (1.71)	-0.32 (4.29)	2.44 (2.44)	-1.10 (5.00)	0.96 (2.23)

C: Cylinder; E: edge. Each search location is defined in centimeters away from the training position of the goal.

For each group we tested five experimental conditions, each consisting of a different location of the cylinder and edge landmarks with respect to the goal location: (1) control: cylinder and edge in the same position as during training; (2) cylinder+10 cm X: cylinder moved 10 cm along the X axis in a positive direction; (3) cylinder+10 cm Y: cylinder moved 10 cm along the Y axis in a positive direction; (4) edge+10 cm X: edge moved 10 cm along the X axis in a positive direction; (5) edge-10 cm Y: edge moved 10 cm west along the Y axis in a negative direction. These tests were carried out during the no-seed trial each day. We assigned the five test conditions so that each bird was tested four times under each test condition in random order. We videotaped each test trial on a JVC BR-32U video cassette recorder. From the videotaped trials, we recorded the location of each of the first 10 digs of each test session using a computer. The videotapes were played back using a Hitachi F372 video cassette recorder connected to a TARGA video board and displayed on a 14-inch monitor. When the bird probed the substrate, we used a SummaSketch mouse system to mark the location of the probe on the monitor screen, and we recorded the X, Y coordinates.

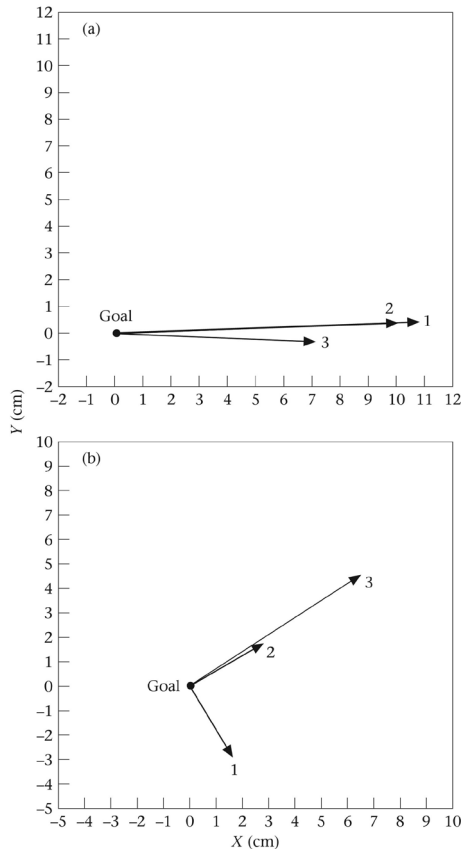
The results are presented in two forms for the following experiments. First, we present the mean search locations and standard errors for the X and Y axes for all test conditions, including the control condition (e.g. Table 1). The data in Table 1 show where the birds searched relative to the fixed location of the seeds. Second, we present the distance and direction each bird searched from their mean search location during the control test condition (e.g. Fig. 2) for specified test conditions. The graph in Fig. 2 shows where the birds searched relative to their mean estimation of the goal location when the landmarks were not manipulated. By using both formats, means and standard errors can be shown, including that of the control condition for each experiment, and we can also show the total distance each group of birds moved from their perceived goal location in response to a cue manipulation

## Results

All statistical analyses were carried out using repeated measures mixed ANOVAs. Subsequent tests were done only after significant results were obtained in the overall analysis. All birds in group 1 and one bird in group 2 met the criteria to end the training period within 30 trials. The remaining birds in group 2 met the criteria in 35 trials. However, none of the birds in group 3 met the criteria, even after 95 trials. Two birds in group 3 found the seeds in under 20 digs for 10 consecutive trials after 95 trials, but the other two birds were still taking a substantial number of digs. We decided to begin test trials for all birds at this point.

The results of test conditions for all three groups are shown in Table 1. All birds moved their searching in the appropriate direction in response to shifts of the cylinder landmark. Qualitatively, this did not appear to be the case when the edge was moved. When the edge was shifted 10 cm along the X axis, birds in group 2 moved their searching in the appropriate direction, although much less than 10 cm. Birds in groups 1 and 3 maintained their searching near the goal on the X axis. When the edge was shifted 10 cm along the Y axis, birds in group 1 and 2 searched in the appropriate direction, whereas birds in group 3 did not, but continued to search near the original goal location.

We statistically analyzed the data separately for the X and Y axes. We calculated the average X and Y coordinates of the first 10 probes for each bird for each condition across test trials. There was a significant main effect of condition for both the X ( $F_{4,36}=20.50$ ,  $P<0.001$ ) and Y axes ( $F_{4,36}=4.57$ ,  $P<0.004$ ). There was no main effect of group (X:  $F_{2,36}=0.46$ ,  $P=0.643$ ; Y:  $F_{2,36}=0.32$ ,  $P=0.733$ ) and no group by condition interactions (X:  $F_{8,36}=1.05$ ,  $P=0.418$ ; Y:  $F_{8,36}=1.09$ ,  $P=0.392$ ). To determine which test conditions produced significant changes in searching behaviour, we conducted planned contrasts for each condition and axis. Each test that involved moving the landmark was compared



**Figure 2.** Mean distance and direction each group of birds moved from their mean search location during the control test for two test conditions of experiment 2. The goal (0,0) is defined as the combined search location during the control tests of experiment 2 for all birds and represents the distance each group moved from this location when cues were manipulated. The mean distance each group moved from their respective control search point was calculated by subtracting their shifted search location from their control search location. Each group is labelled by its corresponding number and each unit equals 1 cm. (a) Distance and direction that each group shifted during movement of the cylinder in the X dimension and (b) during movement of the cylinder and edge in opposite directions along the Y dimension.

to the control test condition using a *t* test. There was a significant difference between the control condition and the cylinder+10 cm X condition for the X axis ( $t_{36}=6.80$ ,  $P<0.001$ ). There was also a significant difference between the control condition and the cylinder+10 cm Y condition for the Y axis ( $t_{36}=2.43$ ,  $P<0.02$ ; Table 1).

To determine how far the birds moved from the goal, we converted the data to distance measurements that incorporated both X and Y axes into one data point. With this information, we investigated whether the birds shifted their searching more overall when there was movement of the cylinder landmark in either the X or Y dimension. Because there was no group by condition interaction in the original ANOVA, we performed a two sample *t* test over all groups. There was a significant difference between X and Y displacement of the cylinder landmark in total distance displaced during

searching ( $t_{22}=3.19$ ,  $P<0.005$ ). Birds shifted more during displacement of the cylinder landmark along the X axis.

## Discussion

During training, there were significant differences in the acquisition of the task. The birds in group 1 and 2 met our criteria much sooner than birds in group 3. Birds in group 3 never reached the criteria determined at the beginning of the experiment and took over twice as long even to approach the criteria. They always located the goal during training trials, but took many more digs to do so than the other two groups. It appears that the distance of the local cues from the goal location during training had a significant effect on digging accuracy, thus making the acquisition of the task more difficult for birds in group 3.

During the testing phase of experiment 1, there were no significant differences between the groups. All birds followed the movement of the cylinder both in the X and Y direction. However, they did not displace their searching significantly from the control position when the edge landmark was moved. This indicates that searching behaviour for all three groups was controlled more by the position of the cylinder landmark than by that of the edge landmark, and suggests that the edge was not as salient a cue as the cylinder. There was a trend indicating that group 1 shifted more in the direction of the edge landmark than group 3, with group 1 shifting on average 5.06 cm along the negative Y axis from its average control searching position, and group 3 shifting on average 1.05 cm along the positive Y axis from its average control searching position. However, the variation around the mean for each group was great enough to render this difference nonsignificant.

Displaced searching behaviour was different for movement of the cylinder along the X versus Y axis. All birds shifted their digging further from the goal location during movement of the cylinder along the X axis than during movement along the Y axis. This is consistent with the results of previous landmark studies (Cheng & Sherry 1992; Gould-Beierle & Kamil 1996, 1998). However, the present results refute one idea brought up in our 1996 paper that could explain our previous results in terms of the two local landmarks being used in conjunction. The distance of the cylinder from the edge is more important as a spatial reference to the goal than the position of the cylinder along the edge. In the present experiment, negative movement of the edge along the Y axis should have been perceived in the same way as a positive movement of the landmark along the Y axis, if the birds were only using these two local cues to find the goal. The difference in searching behaviour between these two test conditions is most likely due to the birds gaining spatial information through use of the cylinder's position in space relative to the global cues. When the cylinder is displaced, a conflict may arise between its location and the global cues.

**Table 2.** Mean (SE) of X and Y search locations for each group for the four test conditions in experiment 2

Group	Control		CE+10 cm X		CE-10 cm Y		CE opposite Y	
	X	Y	X	Y	X	Y	X	Y
1	-3.38 (1.83)	1.18 (0.82)	7.10 (2.54)	2.02 (0.66)	-3.78 (2.41)	-6.82 (0.93)	-1.86 (1.72)	-1.66 (1.74)
2	-1.92 (1.98)	3.01 (0.75)	8.44 (1.93)	3.77 (0.99)	0.53 (1.78)	-4.60 (0.92)	1.10 (0.60)	4.42 (1.28)
3	-5.75 (4.79)	2.20 (1.42)	1.44 (3.36)	2.12 (1.91)	-1.19 (3.81)	-2.78 (1.94)	0.61 (1.70)	6.21 (2.51)

C: Cylinder; E: edge. Each search location is defined in centimeters away from the training position of the goal.

### Experiment 2: Movement of Both Local Cues Simultaneously

This experiment determined whether simultaneous movement of the cylinder and the edge landmarks had a significant effect on searching behaviour. Local cues were moved in the same (positive or negative) direction both in the X and Y dimensions, as well as in opposite directions along the Y axis.

### Methods

The same procedures and birds were used as in experiment 1. Experiment 2 began 3 days after experiment 1 ended, with no additional training. There were four test conditions, each presented four times in random order: (1) control: the landmark was presented in the training position of experiment 1; (2) both cues+10 cm X: the cylinder and the edge were simultaneously moved 10 cm in a positive direction along the X axis; (3) both cues-10 cm Y: the cylinder and the edge were simultaneously moved 10 cm in a negative direction along the Y axis; (4) both cues opposite Y: the cylinder was moved 10 cm in a positive direction along the Y axis and the edge was moved 10 cm in a negative direction along the Y axis.

### Results

As in experiment 1, all statistical analyses were carried out using repeated measures mixed ANOVAs and subsequent tests were done only after significant results were obtained in the overall analysis. We analysed the data separately for each axis and calculated the average X and Y coordinates of the first 10 probes, as in experiment 1 (Table 2). All groups followed the simultaneous movement of the cylinder and edge landmarks in the same direction by shifting their searching behaviour in

the appropriate direction. However, when the cylinder and edge were moved in opposite directions along the Y dimension, birds in group 1 followed the edge, while birds in groups 2 and 3 followed the cylinder (Fig. 2b).

A significant main effect of condition was found for the X ( $F_{3,37}=30.83$ ,  $P<0.001$ ) and Y axes ( $F_{3,27}=23.64$ ,  $P<0.001$ ). We used planned contrasts to compare the test conditions for each axis across groups. On the X axis, there was a significant difference between the control condition and the movement of both cues in a positive direction along the X axis ( $t_{27}=9.20$ ,  $P<0.001$ ). This was also the case for the control condition and the movement of both cues in opposite directions along the Y axis ( $t_{27}=3.57$ ,  $P<0.001$ ). On the Y axis, there was a significant difference between the control condition and the movement of both cues in a negative direction along the Y axis ( $t_{27}=6.42$ ,  $P<0.001$ ).

A significant group by condition interaction was found for the X axis ( $F_{6,27}=2.82$ ,  $P<0.02$ ), but not the Y axis ( $F_{6,27}=1.93$ ,  $P=0.112$ ). We used Bonferroni multiple comparison tests to compare all conditions between groups for both axes. A significant difference was found for the X axis between the search behaviour of birds in group 2 and group 3 when both cues were moved in a positive direction along the X axis. Birds in group 2 shifted an average of 10.36 cm from their average control searching position, while those in group 3 shifted an average of 7.18 cm from their control searching position along the positive X axis (Fig. 2a). A significant difference was also found for the Y axis between the search behaviour of birds in group 1 and group 3 when both cues were moved in opposite directions along the Y axis. Birds in group 1 shifted an average of 2.84 cm from their control searching position along the negative Y axis, while those in group 3 shifted an average of 4.01 cm from their control searching condition along the positive Y axis (Fig. 2b).

**Table 3.** Mean (SE) of X and Y search locations for each group for the four test conditions in experiment 3

Group	Control		C removed		E removed		CE removed	
	X	Y	X	Y	X	Y	X	Y
1	-2.87 (2.25)	1.31 (1.67)	1.26 (3.64)	1.82 (1.06)	-2.09 (1.82)	2.80 (1.19)	-8.92 (0.93)	-18.09 (8.13)
2	-1.29 (2.15)	4.02 (0.33)	3.12 (4.35)	1.93 (1.70)	0.55 (1.59)	4.09 (1.75)	-3.54 (2.95)	2.9 (0.63)
3	-1.13 (3.09)	-0.31 (3.52)	2.56 (1.86)	1.69 (1.36)	1.66 (1.71)	2.28 (1.10)	1.29 (2.24)	2.75 (1.30)

C: Cylinder; E: edge. Each search location is defined in centimeters away from the training position of the goal.

## Discussion

All birds followed the X and Y shifts of both the cylinder and the edge landmarks together. However, there were significant differences between the groups during movement along the X axis. Birds in group 2 shifted their searching more in both directions than birds in group 3. Birds in group 1 searched in a manner similar to those in group 2. This suggests that birds in group 3 were relying less on the local cues to gain spatial information than were the other two groups, which makes sense because birds in group 3 learned the task with the two local landmarks the furthest from the goal. They may have used other sources of spatial information, such as global cues, when the two local cues were shifted from the training position.

There were also differences between groups during movement of both cues in opposite directions. Birds in group 1 tended to shift their searching in the direction that the edge was moved by approximately 3 cm, while birds in group 3 shifted their searching in the direction that the cylinder was moved by approximately 4 cm. Birds in group 2 shifted on average 1.41 cm from their average control searching position along the positive Y axis, which was in the direction that the cylinder was moved. However, this shift did not differ statistically from the other two groups and suggests that this group searched near the goal location during this test. The difference between birds in groups 1 and 3 during movement of both cues in opposite directions cannot be easily explained. It is possible that birds in group 1 may have been affected by movement of the edge away from the goal more than the birds in the other two groups during this condition. In experiment 1, none of the birds in the three groups was significantly affected by the edge when it was moved independent of the cylinder along the Y axis. However, there was a nonsignificant trend, indicating that birds in group 1 shifted more in response to movement of the edge than those in group

3. This may have occurred in experiment 2 as well. The edge may have been a more salient cue for birds in group 1 because the edge was closer to the goal location for group 1 than it was for the other two groups.

## Experiment 2: Removal of the Local Cues

This experiment tested the influence of local cues by removing them. We examined the searching behaviour of the birds in the absence of either the cylinder landmark, the edge landmark, or both landmarks.

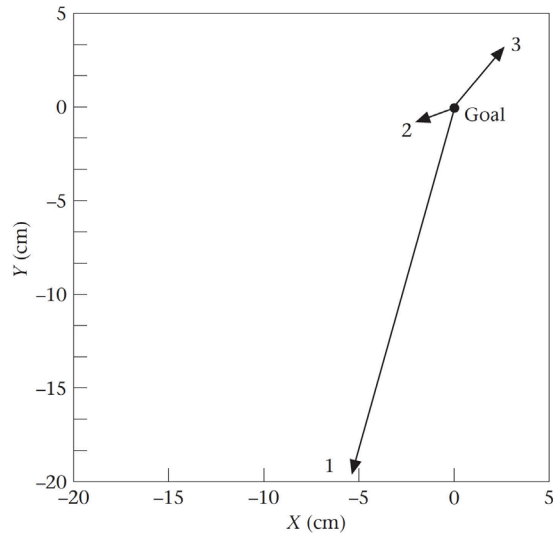
## Methods

The same procedures and birds were used as in the previous two experiments. Experiment 3 began 1 day after experiment 2 ended, with no additional training. There were four test conditions, each presented four times in random order: (1) control: the cylinder and edge in the same position as during training; (2) cylinder removed: the cylinder was removed and the edge left in the training position; (3) edge removed: the edge was removed and the cylinder left in the training position; (4) both removed: the cylinder and the edge were both removed.

## Results

Again, all statistical analyses were carried out using repeated measures mixed ANOVAs and subsequent tests were done only after significant results were obtained in the overall analysis. We analysed the data separately for each axis and calculated the average X and Y coordinates of the first 10 probes, as in the previous two experiments (Table 3). When the cylinder was removed, all birds shifted in a positive direction along the X axis. When the edge was removed, their searching did not seem to be as displaced. When both the edge and cylinder were removed, the searching behaviour of the birds in group 1 shifted





**Figure 3.** Mean distance and direction each group of birds moved from their mean search location during the control test when both the cylinder and edge were removed during experiment 3. The goal (0,0) is defined as the combined search location during the control tests of experiment 3 for all birds and represents the distance each group moved from this location when cues were manipulated. The mean distance each group moved from their respective control search point was calculated by subtracting their shifted search location from their control search location. Each group is labelled by its corresponding number and each unit equals 1 cm.

away from the goal area completely, while birds in groups 2 and 3 still searched in the general area of the goal (Fig. 3).

A significant main effect of condition was found for the X ( $F_{3,26}=6.49$ ,  $P<0.002$ ) and Y axes ( $F_{3,26}=3.72$ ,  $P<0.02$ ). We used planned contrasts to compare the test conditions for each axis across groups. For the X axis, a significant difference was found between the control condition and the cylinder-removed condition ( $t_{26}=2.92$ ,  $P<0.007$ ). The birds in all three groups shifted in a positive direction along the X axis relative to their control search locations when the cylinder was removed. For the Y axis, a significant difference was found between the control condition and the both-removed condition ( $t_{26}=2.50$ ,  $P<0.01$ ). All searching by the birds deviated from their control search locations when both cues were removed.

A significant group by condition interaction was found for the Y axis ( $F_{6,26}=4.56$ ,  $P<0.002$ ), but not the X axis ( $F_{6,26}=1.46$ ,  $P=0.330$ ). We used Bonferroni multiple comparison tests to compare all conditions between groups for both axes. The searching behaviour of birds in group 1 differed significantly from that of birds in groups 2 and 3 for the both-removed test condition. Birds in group 1 shifted an average of 19.39 cm in a negative direction, those in group 2 shifted an average of 1.12 cm in a negative direction, and those in group 3 shifted an average of 3.06 cm in a positive direction along the Y axis when both the cylinder and edge were removed (Fig. 3). All of these distances were calculated from the average control searching position for each group.

## Discussion

When the edge was removed and the cylinder maintained in the training position, the birds searched as if nothing had been changed. There was no significant difference between the control condition and the edgeremoved condition. This indicates again, as in experiment 1, that the edge was not used as a primary cue in finding the goal location by any of the birds in the three groups. When the cylinder was removed and the edge maintained, all birds shifted their searching in a positive direction along the X dimension by an average of 4 cm. The reason for this shift to the right of the goal is not easily explained, but it does indicate that the cylinder was an important cue for maintaining accuracy when finding the hidden goal. It is interesting to note that in previous studies with an experimental tray (Gould-Beierle & Kamil 1996, 1998), the same phenomenon was observed. Birds tended to move their searching in a positive direction along the X axis when the cylinder was removed from the tray.

When both the cylinder and the edge were removed, the searching behaviour of birds in group 1 differed significantly from that of birds in groups 2 and 3. Birds in group 1 shifted in a negative direction along the Y axis by a considerable amount (approximately 19 cm). Birds in groups 2 and 3 stayed relatively closer to the goal location (approximately 1 cm and 3 cm). This major difference indicates that birds in group 1 were more dependent on the local cue information to locate the goal accurately. Birds in groups 2 and 3 were less dependent on this information and able to use the global cues to maintain their searching accuracy. Previous studies indicate that nutcrackers can use global cue information in certain situations to locate a goal (Gould-Beierle & Kamil 1996). The current data suggest that the birds in group 1 did not learn the relationship between this global information and the goal because the proximity of the local cues to the goal during training caused the local information to become more salient. This result could be explained through an overshadowing effect. Because the local cues were closer to the goal for this group, they may have overshadowed any information that could be obtained through the global cues during training.

## Experiment 4: Movement and Removal of Local and Global Cues

This experiment investigated the effect of manipulating two prominent global cues in the presence or absence of local cues in order to determine the salience of global information. Manipulations of the global cues included moving or removing two prominent posters on the walls of the room.

## Methods

The same procedures and birds were used. Experiment 4 began 60 days after experiment 3 ended. During this time, training trials (cylinder and edge landmarks in the

**Table 4.** Mean (SE) of X and Y search locations for each group for the five test conditions in experiment 4

Group	Control		P+20 cm Y		P removed		P+20 cm Y/ L removed		PL removed	
	X	Y	X	Y	X	Y	X	Y	X	Y
1	-1.30 (2.21)	2.56 (1.32)	-1.28 (1.69)	-7.87 (11.16)	-1.36 (2.36)	2.82 (1.24)	-13.55 (5.78)	-3.17 (7.73)	-20.66 (8.09)	-4.57 (3.87)
2	1.62 (2.10)	2.97 (0.66)	1.23 (1.48)	3.48 (0.39)	1.23 (2.46)	3.36 (0.61)	15.09 (6.64)	0.34 (6.33)	9.93 (1.11)	-5.60 (9.18)
3	3.67 (1.97)	-7.15 (6.98)	1.13 (1.07)	-19.47 (12.95)	-7.46 (2.51)	1.85 (1.03)	2.18 (2.68)	0.83 (11.51)	-5.50 (5.43)	-4.50 (8.21)

P: Posters; L: local landmarks. Each search location is defined in centimeters away from the training position of the goal.

appropriate training position for each group with two seeds buried at the goal location) were done once a day between two and five times a week. During test conditions, the cylinder and edge could be manipulated as well as two of the three posters in the room. These two posters included a picture of a beach with a palm tree on the north wall and a picture of a castle on the south wall. A poster of a sunset on the west wall remained stationary. There were five test conditions, each presented four times in random order: (1) control: the cylinder and edge in the same position as during training; (2) posters+20 cm Y: the two posters were moved 20 cm in a positive direction along the Y axis, while the cylinder and edge remained in the training position; (3) posters removed: the two posters were removed while the cylinder and edge remained in the training position; (4) posters+20 cm Y/local cues removed: the two posters were moved 20 cm in a positive direction along the Y axis while the cylinder and edge were removed; (5) posters and local cues removed: the two posters, cylinder and edge were removed.

## Results

All statistical analyses were carried out using repeated measures mixed ANOVAs, and subsequent tests were done only after significant results were obtained in the overall analysis. We analysed the data separately for each axis and calculated the average X and Y coordinates of the first 10 probes, as in the previous three experiments (Table 4). When the posters were moved, the birds in groups 1 and 3 shifted their searching in the opposite direction of the poster shift, although the individual responses of birds in each group were highly variable. Birds in group 2 did not seem to be as affected by this test condition. When the posters were removed, birds in group 3 shifted somewhat along the negative X axis, while the birds in groups 1 and 2 stayed near the goal. When the posters were moved or removed in the absence of the local landmarks, birds in group 3

tended to search closer to the goal location than birds in the other two groups. Birds in group 1 shifted in a negative direction and those in group 2 shifted in a positive direction along the X axis. During these two test conditions, however, the variability in searching behaviour for each group increased (see Table 4).

A significant main effect of condition was found for the X axis ( $F_{4,32}=3.32$ ,  $P<0.02$ ), but not the Y axis ( $F_{4,32}=1.87$ ,  $P=0.140$ ). We used planned contrasts to compare the test conditions for each axis across groups. A significant difference was found between the control condition and the posters and local cues-removed condition on the X axis ( $t_{32}=3.04$ ,  $P<0.004$ ). During this test condition, all birds searched away from the control search location.

A significant group by condition interaction was also found for the X axis ( $F_{8,32}=7.67$ ,  $P<0.001$ ), but not the Y axis ( $F_{8,32}=1.03$ ,  $P=0.435$ ). We used Bonferroni multiple comparison tests to compare all conditions between groups for both axes. There was a significant difference in the searching behaviour of the birds during the posters+20 cm Y/local cues-removed condition between group 1 and group 2, as well as between group 1 and group 3 (Fig. 4a). Birds in group 1 shifted in a negative direction on average 12.25 cm from the average control searching position, those in group 2 shifted 13.47 cm from the control searching position in a positive direction, and those in group 3 shifted 1.49 cm from the control searching position in a negative direction along the X axis. There was also a significant difference in searching behaviour during the posters and local cues-removed condition (Fig. 4b) between birds in groups 1 and 2 and between those in groups 2 and 3. Birds in group 1 shifted in a negative direction on average 19.36 cm from the average control searching position, those in group 2 shifted 8.31 cm in a positive direction from the control searching position, and those in group 3 shifted 9.16 cm in a negative direction along the X axis from the control searching position.

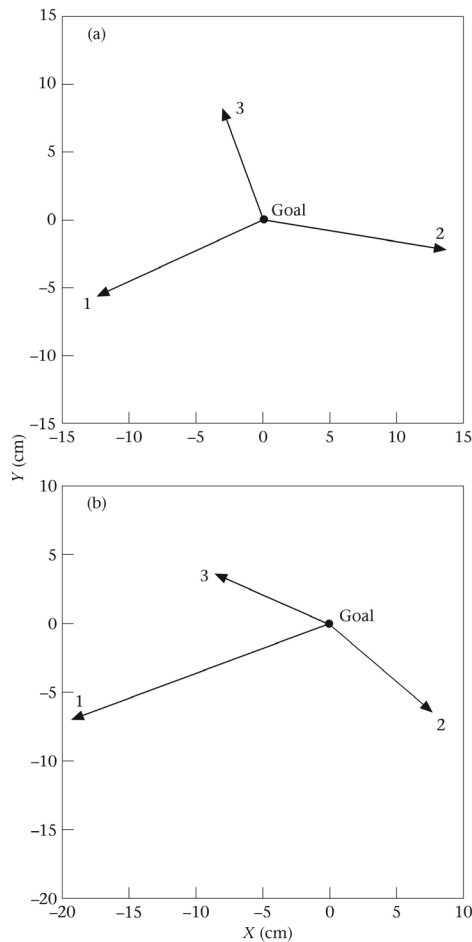


Figure 4. Mean distance and direction each group of birds moved from their mean search location during the control test for two test conditions of experiment 4. The goal (0,0) is defined as the combined search location during the control tests of experiment 4 for all birds and represents the distance each group moved from this location when cues were manipulated. The mean distance each group moved from their respective control search point was calculated by subtracting their shifted search location from their control search location. Each group is labelled by its corresponding number and each unit equals 1 cm. (a) Distance and direction that each group shifted when the posters were moved and both local cues were removed and (b) when both the posters and local cues were removed.

## Discussion

When the posters were moved or removed, there was no significant difference in searching patterns. The birds must have been able to obtain enough information from the local cues themselves or from other nonmanipulated global cues in the room to maintain searching behaviour. When the local cues were removed and the posters manipulated, a significant difference in searching behavior emerged between groups. Birds in group 1 shifted in a negative direction from the goal and those in group 2 shifted in a positive direction from the goal along the X axis. In contrast, birds in group 3 searched very close to

the goal location along the X axis, shifting approximately 1.5 cm in a negative direction. Thus, birds in group 3 were able to maintain a fair degree of accuracy on the X axis even with the local landmarks removed and the posters shifted on the walls. This suggests, along with the results in experiment 3, that birds in group 3 were able to use global information to maintain accuracy in the absence of local cues. However, birds in group 2 were also fairly accurate during experiment 3 when the local cues were removed. In the present experiment, the shift by birds in group 2 during the posters+20 cm Y/local cues-removed condition might simply be because the 20-cm shift of the posters was large enough to be detected by this group.

There was also a significant difference between groups when the posters and local cues were removed. Again, birds in group 1 shifted much more than the other groups, shifting along the X axis in a negative direction by approximately 19 cm. The difference in searching behaviour for birds in group 3 when the posters were moved versus removed along with removal of the local cues indicates that these birds were most likely using the two manipulated posters to some extent to gain spatial information during training. Moving the posters by 20 cm must not have been a large enough shift to cause the birds in group 3 to move their searching very far from the goal, but removing the posters altogether had a significant effect on their searching.

## General Discussion

The results from all four experiments show that the proximity of local cues to a goal influence how those cues and other available cues are used by Clark's nutcrackers. This was evident from the beginning of training. The group that learned the task with the cylinder and the edge landmarks furthest from the goal took over twice as long even to approach criteria and were less accurate at the end of training. This makes intuitive sense if one considers that the further away spatial information is from a goal, the harder it would be to pinpoint the goal location. This has been shown experimentally for pigeons (Cheng 1990; Spetch & Wilkie 1994) and Clark's nutcrackers (Kamil & Jones 1997). In the nutcracker's natural environment, there are many cues available. The distance of these cues from a cache location must vary depending on the placement of the cache. It may take more digs to relocate a cache that is further from landmarks than one that is in proximity to them.

During testing, all groups seemed to be affected by movement of the cylinder along the X axis. This implies that the cylinder was an important source of spatial information for all birds, regardless of the location of the cylinder during training. However, the birds must use more information to locate a position in space than just the location of a single landmark. It appears that the group with the local cues in clos-

est proximity to the goal during training might have been using the edge as another source of information. When the edge was shifted in the Y dimension during experiments 1 and 2, this group of birds tended to follow that shift. The other two groups of birds did not, indicating that the more distant edge landmark was not as likely to be used as a source of spatial information.

The results of experiments 3 and 4 suggest the two groups that learned the task with the local cues further from the goal may have used global cues as another source of spatial information. When the local cues were removed and the global cues remained stationary, these birds remained fairly accurate in their searching behaviour, staying within 3 cm of the goal location. When the local cues were removed and two of the closest global cues were moved, the group with the furthest local cues still remained accurate by staying within 1.5 cm of the goal along the X axis. However, when these two global cues and the local cues were removed, the accuracy of this group deteriorated. The two posters were indeed important sources of global information for these two groups.

It seems that the cylinder was a more salient local cue than the edge for all groups. This may be because the cylinder is taller than the flat edge. A taller landmark may be a better source of spatial information because it can be seen at greater distances and is less likely to be covered by debris or snow. Basil (1993) and Bennett (1993) have both found that birds were less accurate in finding a hidden goal when tall landmarks were removed from an array than when short ones were removed.

It appears that global cues can be used as a source of information if they are not diminished in importance by proximal cues. If global cues were learned, but not used in the presence of proximate local information, a different pattern of results would be expected during experiment 3 for the birds in group 1. They should have shown some ability to use global information when it was the only information available, but instead their searching was very inaccurate. The proximity of local landmarks to the goal influenced how spatial information was encoded and remembered. Birds in group 1 used the local cues to find the hidden goal, whereas those in the other two groups used a combination of local and global information. This combination could be hierarchical, with global information indicating where to search in general and local information providing a detailed spatial location of the goal.

The idea that the proximity of local information to a goal influences how that information is perceived and used by Clark's nutcrackers can therefore be confirmed. One result of this proximity effect that could explain our results would be overshadowing, in which the predictiveness of a stimulus relative to other stimuli affects the amount of control that stimulus has over behaviour. Simply put, the closer a landmark is to a target, the more control it seems to have on searching. This control may be due to a difference in relative

predictiveness; the more proximal landmark is more predictive of the goal location. Other forms of information that are further away from the target become irrelevant and are therefore not learned. In these terms, our results can be thought of as another example of the general psychological phenomenon of overshadowing that has been shown in both birds and mammals (March et al. 1992; Spetch & Wilkie 1994; Spetch 1995).

Proximity does not always have to lead to overshadowing. A case for more distant information overshadowing local information can be found in maze learning in rats (Diez-Chamizo et al. 1985; March et al. 1992). These set of experiments looked at the interactions between intra- and extramaze cues (which could be roughly compared to local and global cues in our current study). The results suggested that extramaze cues could overshadow intramaze cues. However, intramaze cues can overshadow extramaze cues in the same maze-learning task (March et al. 1992). Which type of cue becomes overshadowed is dependent upon a number of factors including the training procedure used and the competition for association with reinforcement among cues.

Our set of experiments shows that proximity of local cues leads to the overshadowing of global information in Clark's nutcrackers. However, the search behaviour of birds in groups 2 and 3 demonstrates that local cues do not always overshadow global cues. Below some distance threshold, the spatial location of the local cues in relation to the goal must create the overshadowing effect. It would be interesting to determine whether global cues could ever overshadow local cues in our procedure. The birds in groups 2 and 3 had learned, to some extent, the spatial relationship between the goal and more global cues. Different training procedures or goal placement may influence how these cues are used and could lead to differences in overshadowing.

Why does proximity lead to overshadowing in certain cases? One reason is that close landmarks permit higher accuracy in relocation. In the presence of permanent, salient local cues, more distant cues become redundant sources of information that cause a greater degree of error when used alone. Indeed, Weber's law would predict that the variation in estimating a spatial location would be proportional to the distance of the nearest landmark. In other words, the further a landmark is from the goal, the more errors will be found in searching for the goal. Nutcrackers trained to find the seeds with local landmarks closer to the goal made fewer searching errors and learned the task faster than those trained with landmarks further away. So, overshadowing may be beneficial by reducing the amount of 'unnecessary' information that is encoded and thus decreasing the memory load. However, when proximate local cues are not salient enough to provide accurate relocation of a goal, or are temporary in their spatial location across time, more information must be encoded to increase the chances of relocation of the target.



Why would overshadowing be important for Clark's nutcrackers? As stated earlier, these birds store tens of thousands of seeds in a wide variety of habitats with many potential spatial cues available. The closer a set of stable, local cues are to a cache, the more likely they are to increase the accuracy of finding it. With each cache being such a small, spatial location to accurately pinpoint (approximately 3 cm in diameter), it would be much easier to find if the bird used the closest available cues. Overshadowing could also be an inherent characteristic of a general learning mechanism associated with learning the spatial location of caches.

The use of close, local cues would seem important based on an increase in accuracy. However, as we have demonstrated in the past (Gould-Beierle & Kamil 1996) and in the current set of experiments, these birds can also use global room cues in the laboratory to a high degree of accuracy under certain conditions. Also, many local cues that are close to a cache site may be less spatially stable over time or as stated earlier, easily covered by debris and snow because of their size. Observational data have shown that these birds often make caches on the open and exposed part of south-facing slopes (Tomback 1977) and in open meadows above treeline (Vander Wall & Hutchins 1983). However, other observational data suggests that they place many caches near rocks, trees and logs (Tomback 1977; Vander Wall & Balda 1977). More detailed field work describing the habitat and available cues surrounding a nutcracker's cache site need to be done quantifying where each cache is placed in relation to potential cues. We know how these birds use cues in certain laboratory situations (Gould-Beierle & Kamil 1996, 1998; Kamil & Jones 1997), but we do not know how these results compare to what the birds are actually doing in their natural environment.

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