

Spatial cues for cache retrieval by black-capped chickadees

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Abstract. Food-storing birds relocate scattered caches of food using surrounding features and objects as visual cues to the location of caches. Black-capped chickadees, *Parus atricapillus*, were observed storing food in an enclosure in which the visual cues available to the birds could be controlled. In the first experiment, distal objects on the walls of the enclosure and proximal objects at cache sites were both present when chickadees stored sunflower seeds in artificial trees. Removal of distal objects prior to cache recovery significantly reduced search accuracy, while removal of proximal objects had no significant effect on accuracy. In a second experiment, birds stored seeds with only distal objects present. Rotation of these objects around the walls of the chamber significantly reduced search accuracy. Birds searched for stored food at sites that were correct with respect to the distal objects, rather than at the original cache sites. These results show that black-capped chickadees remember the position of caches with respect to prominent global features of the environment.

Food-storing birds can relocate their scattered caches with remarkable accuracy. Experimental studies of a number of species indicate that memory for the spatial locations of caches is the principle means of cache recovery (for reviews see Kamil & Balda 1990; Shettleworth 1990; Sherry 1992a). The role of visual landmarks in cache recovery has been well documented for corvids (Bossema 1979; Vander Wall 1982). It has been shown, for example, that Clark's nutcrackers, *Nucifraga columbiana*, use prominent objects as landmarks to relocate seeds cached in the ground. Soil microtopography and other features near cache sites appear to be relatively unimportant for accurate cache recovery by nutcrackers (Vander Wall 1982). Similarly, Bossema (1979), found that European jays, *Garrulus glandarius*, use conspicuous objects in the vicinity of caches, rather than local features at cache sites, to relocate stored food. For grey jays, *Perisoreus canadensis*, the addition of prominent landmarks near cache sites

increases recovery accuracy (Bunch & Tomback 1986), while for Clark's nutcrackers, removal of such objects disrupts accurate cache retrieval (Balda & Turek 1984).

An experiment with marsh tits, *Parus palustris*, has shown that vision is the primary source of information for cache retrieval in parids. There is no interocular transfer for some kinds of visual information in many species of birds. For marsh tits, this has the result that birds that store food with one of their eyes covered are unable to find their caches 3 h later when using only the eye that had been covered during storing (Sherry et al. 1981). This result shows that visual information acquired during storing is critical for accurate cache recovery.

Black-capped chickadees, *Parus atricapillus*, scatter-hoarded food, placing each food item in a different cache (Sherry 1984). The present experiments were designed to determine what kind of visual information black-capped chickadees use to relocate hidden food caches. In particular, the relative importance of cues at a distance from cache sites and cues near cache sites were examined. Distal cues were operationally defined as objects about 0.5 m in size and up to 2 m away from cache sites, while proximal cues were defined as objects 5 cm in size and 4–12 cm away from caches. In the first experiment, birds stored seeds in an enclosed chamber designed to eliminate, as

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much as possible, all visual cues to cache locations except for the distal and proximal objects provided. We assessed the use of distal and proximal cues by allowing birds to make caches in the presence of distal and proximal objects, then selectively removing distal, proximal, or both kinds of object prior to cache recovery. In the second experiment, we assessed the chickadees' use of distal cues by rotating distal objects within the test chamber and determining the effect on search accuracy.

EXPERIMENT 1

Methods

Subjects

Eight wild-caught adult black-capped chickadees served as subjects. Birds were individually housed in home cages measuring $80 \times 80 \times 100$ cm, under a 10:14 h light-dark cycle (light onset 0800 hours). Food and water were available ad libitum in the home cage, except as noted below.

Apparatus

Behaviour was observed in a chamber measuring $2 \times 2 \times 2$ m, containing four artificial trees (Fig. 1). The purpose of this chamber was to eliminate, as much as possible, any visual cues that could specify spatial locations within the chamber. The chamber was constructed of wire mesh on a wooden frame, with an access door in one wall. The ceiling and interior walls of the chamber were covered with black fabric. The observer could view the interior of the chamber through dark Plexiglas windows (60×70 cm) placed in the centre of each wall, 80 cm above the ground. Birds were introduced to the chamber through a 20×20 -cm opening in the bottom of each window, which could be covered with a sliding panel. The interior of the chamber was illuminated by four 60-W bulbs with reflectors, attached to the ceiling. One light was directly over each tree. The floor of the chamber was painted a uniform grey.

Four artificial trees 1.7 m in height stood in metal bases in the chamber. Each tree consisted of a straight 5×5 -cm wooden trunk and eight branches 33 cm in length and 0.7 cm in diameter.

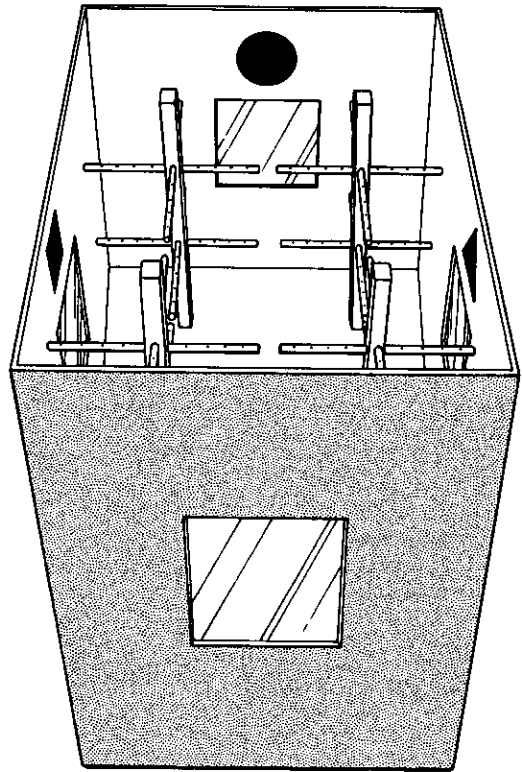


Figure 1. Schematic drawing of the observation chamber, viewed from above with the ceiling removed. Shown are the four observation windows, four artificial trees and three of the distal objects. See text for details. Reprinted with kind permission from the author and Lawrence Erlbaum Associates (Sherry 1992b).

Branches projected at right angles to the trunk and at right angles to each other in two groups of four branches, one 80 cm above the ground and another 140 cm above the ground (see Fig. 1). Four small holes measuring 0.5 cm in diameter and 0.5 cm deep, were drilled in the top of each branch 6.6 cm apart, for a total of 32 holes per tree. For convenience, the 128 holes on the four trees will be called 'sites' and holes in which food was stored on a given trial will be called 'cache sites'. Each tree was painted a uniform green. The trees were arranged in a 1-m square with its centre in the centre of the floor of the chamber. This arrangement had the effect that for each site there were three other sites, one on each of the other trees, in the same relative position on their trees and in the same position relative to nearby chamber walls as the original site.

A 'distal' object hung on each wall of the chamber just above the observation window. Three of these distal objects were cut from heavy cardboard: a yellow equilateral triangle 60 cm on a side, a red circle 80 cm in diameter, and a purple rectangle 40 × 60 cm. The fourth distal object was a 50 × 60-cm colour poster. A 'proximal' object was placed at each site. Proximal objects were 5-cm squares of red, yellow, brown or grey cardboard with a hole in the centre so they could be placed over the branch at each site. All proximal objects on a branch were the same colour and branches that were vertically in line on a tree had the same colour of proximal cue. Each tree had a different assignment of colours to branches, so that each tree was unique. Neighbouring branches on different trees had different colours of proximal objects.

Procedure

We exposed the birds to between one and four 30-min habituation trials in the chamber before experimental trials began with neither type of object nor any food present. An experimental trial consisted of a food-caching phase followed 4 h later by a cache-recovery phase. During the caching phase we deprived birds of food for 2–3 h and admitted them singly to the chamber. We placed a bowl of water and a bowl containing quarter pieces of husked sunflower seed in the centre of the chamber and recorded the bird's behaviour and the locations of all caches on a 24-key micro-computer event-recorder until 12 pieces of seed had been stored or 15 min had elapsed, whichever came first. All distal and proximal objects were present during the caching phase. Following caching, the observer returned the bird to its home cage, where food and water were available ad libitum. All cached and other food was removed from the chamber prior to the recovery phase, 4 h later, during which birds searched for 15 min for the caches they had made. Behaviour was again recorded, and search at a site was scored if the bird probed at the site with its bill or closely examined the site visually while standing beside it on the perch. During the recovery phase the chamber was in one of four states: all objects present; only distal objects present; only proximal objects present; neither kind of object present. Each bird was tested once in each recovery condition, on successive days, in a random order

determined independently for each bird. The windows through which the birds entered the chamber and the window through which the observer watched were chosen at random for the caching and recovery phases independently. Fans, room lights, and other equipment that might provide directional cues to a bird in the chamber were turned off during trials.

The number of searches at cache sites, expressed as a percentage of searches at all sites during a recovery trial, was taken as an index of cache-recovery accuracy. These percentage data were arcsin transformed for statistical analysis. The experiment was analysed as a two-factor randomized block analysis of variance design (Kirk 1982) with distal objects (present or absent), and proximal objects (present or absent) as the two factors. This design assumes no interaction between subjects and manipulated factors and this assumption was tested and confirmed for all of the results described below. All post-hoc multiple comparisons used the Student–Neuman–Keuls procedure, $\alpha=0.5$. Cache recovery accuracy expected by random search was calculated as the number of cache sites divided by 128, the total number of sites.

Results

The mean number of caches made per trial ranged from 1.8 to 6.8 for different subjects ($F_{7,21}=6.45$, $P<0.01$) but did not differ significantly between the four cache recovery conditions. The mean number of cache recovery attempts per trial ranged from 6.5 to 25.3 for different birds ($F_{7,21}=3.15$, $P<0.05$), but did not differ significantly between the four conditions.

Cache recovery accuracy (Table I) differed significantly between subjects ($F_{7,21}=4.71$, $P<0.01$) and was significantly affected by the removal of distal objects ($F_{1,21}=6.19$, $P<0.02$) but not by the removal of proximal objects ($F_{1,21}=3.14$, NS). There was no significant interaction between the removal of distal and proximal objects ($F_{1,21}=0.75$, NS).

Cache recovery accuracy was not high. In the most successful condition, with both types of object present, roughly 20% of searches occurred at cache sites. Cache recovery accuracy in previous studies with black-capped chickadees has been 50% or higher (Sherry 1984; Sherry & Vaccarino 1989; Shettleworth et al. 1990). Accuracy depends

Table 1. Search accuracy in experiment 1

Search accuracy relative to:	Objects present during testing			
	Distal and proximal	Distal	Proximal	None
Cache sites	19.19 ± 5.01	9.98 ± 3.48	8.35 ± 3.11	7.31 ± 2.36
Observer position	3.22 ± 1.32	7.22 ± 1.77	4.38 ± 0.92	3.25 ± 1.48
Entry window	1.99 ± 1.16 (3.19)	7.39 ± 2.22 (2.97)	19.72 ± 8.71 (3.03)	3.84 ± 1.35 (2.66)

The mean (\pm SE) number of searches at each kind of site is shown as a percentage of searches at all sites. Accuracy expected by random search is shown in parentheses.

on the number of sites available to search, which in the present experiment was 128, roughly twice that in previous studies. The low level of accuracy expected by random search in the present experiment, compared with roughly 10% in previous studies, reflects this. It is also likely that the deliberate reduction of cues in the design of the test chamber and the use of symmetrical, nearly identical, trees further reduced cache recovery accuracy compared with previous studies conducted in more complex cue-rich environments.

Birds may have been able to use the position of the observer as a cue to the location of caches. Although the position of the observer was randomized for the caching and recovery phases of each trial and provided no information about cache sites, birds may have treated the position of the observer as fixed and used it as a cue to cache locations. To test whether this was so, the location of each cache relative to the observer was determined for the caching phase of the trial. We then re-analysed recovery behaviour, treating as 'correct' those sites that occupied the same position, relative to the observer, that cache sites had during the caching phase. If birds were using the observer as a fixed landmark, their accuracy in this re-analysis would be expected to be greatest when distal and proximal objects were both absent, and so were not in conflict with the position of the observer. Analysis of these data showed no significant effect of subject, distal objects or proximal objects, but did show a significant interaction between distal and proximal objects ($F_{1,21} = 5.46$, $P < 0.05$). Post-hoc tests, however, showed no significant differences between the four recovery conditions. Accuracy in this re-analysis was no higher when distal and proximal objects were absent than when they were present (see Table I). Visits to sites in the same

relative position to the observer as cache sites had been during the caching phase ranged from 3.2 to 7.2%, close to the random search levels of 2.7 to 3.2%.

Similarly, birds may have searched for caches at sites that were in the same position relative to the entry window as the original cache sites had been during caching. An analysis similar to the preceding one showed no significant effect of subject, distal objects or proximal objects, but a significant interaction between distal and proximal objects ($F_{1,21} = 6.38$, $P < 0.05$). As with the previous analysis, post-hoc tests showed no significant differences between recovery conditions. Accuracy was high in this analysis when proximal objects were present but distal objects absent, although there was considerable variation around the mean (Table I). This condition did not differ significantly from the others according to post-hoc tests, but it may indicate some tendency for the birds to use the window through which they entered the chamber as a cue to cache location when distal objects were absent but proximal objects were still present. If this is the case, it also shows that conflicting proximal objects have little effect on birds that use the entry window for orientation.

Discussion

The results show that the removal of distal objects decreases the accuracy of cache recovery while the removal of proximal objects has no significant effect. There was a reduction in recovery accuracy when either kind of object was removed (Table I), but statistical analysis showed that the effect of removing proximal objects was no greater than expected by chance. Although this result probably depends a great deal on the nature of the objects themselves, the results do indicate

that at least under some conditions, black-capped chickadees depend more on global than on local features of the environment to relocate caches.

It is unlikely that the chamber and experimental procedures successfully eliminated all unintended cues that could be used to identify trees, walls or directions inside the chamber. Cache recovery accuracy was 7.3% when neither distal nor proximal objects were present, compared with a random search expectation of 2.7%. Cache recovery accuracy when both objects were present during recovery was 19.2%, however, indicating that the presence of additional objects considerably increased the search accuracy of the birds.

EXPERIMENT 2

If black-capped chickadees use distal cues to relocate cached food in the way suggested by the results of the previous experiment, then manipulation of distal cues should have predictable effects on the birds' search behaviour. In particular, when distal objects are rotated around the walls of the chamber after the birds have cached food, while maintaining the relation among the distal objects, then the birds should show low recovery accuracy at cache sites. They should search, instead, at sites bearing the same relation to distal objects as cache sites did before rotation. This was tested in the second experiment.

Methods

Subjects

Six additional wild-caught adult black-capped chickadees served as subjects. None had served as subjects in the previous experiment. Birds were housed in smaller home cages (60 × 36 × 36 cm) but were otherwise maintained as in the previous experiment.

Apparatus and procedure

The chamber was employed as in the first experiment except that no proximal objects were ever present. Instead, birds cached in the presence of the distal objects, then searched for their caches in one of four recovery conditions. The chamber was either left as it had been during caching, or the distal objects were rotated around the walls of

the chamber in a clockwise direction by 90°, 180° or 270°. Distal objects remained in the same relation to each other, but we changed their position relative to cache sites. For each rotation condition there was a new site in the same position relative to the rotated distal objects as the original cache site had been. Birds were habituated to the test chamber as in experiment 1, then tested twice in each recovery condition, in a random order determined independently for each bird. Tests occurred on successive days. One bird completed only a single trial in the 270° condition and another bird completed only a single trial in the unrotated and 90° conditions. Other procedures were as in the first experiment.

Results

The mean number of caches ranged from 1.6 to 4.8 per trial for different birds ($F_{5,15}=2.95$, $P<0.05$), and rotation conditions also differed significantly in the number of caches that had been made in the preceding caching phase ($F_{3,15}=3.64$, $P<0.05$). Post-hoc tests showed that fewer caches were made prior to 180° rotations than prior to 270° and 90° rotations. Other differences were non-significant. The number of recovery attempts made while searching for caches differed among birds, ranging from 12.3 to 79.1 attempts per trial ($F_{5,15}=5.53$, $P<0.01$). Recovery condition also affected the number of recovery attempts made ($F_{3,15}=3.93$, $P<0.05$). Post-hoc tests showed that significantly more recovery attempts were made in the 90° recovery condition than in the 180° and the unrotated conditions. Other differences were non-significant. It is not surprising that the number of recovery attempts would be affected by recovery condition. Rotation of the distal landmarks could have increased or decreased the amount of searching that birds exhibited in a particular trial. It is less clear why the number of caches made varied with recovery condition. Although recovery conditions were randomly ordered, it is possible that the preceding recovery condition had some effect on the amount of caching performed the following day. The foregoing results also show that the birds were highly variable in their caching and recovery behaviour in the chamber.

Recovery accuracy at original cache sites did not differ significantly between birds, but was significantly affected by recovery condition

Table II. Search accuracy in experiment 2

Search accuracy relative to:	Rotation condition			
	Unrotated	90°	180°	270°
Cache sites	10.92 ± 4.05	13.25 ± 3.15	1.67 ± 0.87	4.25 ± 2.50
Rotated cues	10.92 ± 4.05	10.42 ± 2.64	8.42 ± 3.63	14.67 ± 4.71
Observer position	6.58 ± 3.73	4.92 ± 2.35	2.25 ± 1.44	11.42 ± 4.73
Entry window	4.83 ± 2.85 (1.9)	7.92 ± 2.64 (2.9)	3.08 ± 1.96 (1.1)	8.25 ± 5.70 (2.9)

The mean (\pm SE) number of searches at each kind of site is shown as a percentage of searches at all sites. Accuracy expected by random search is shown in parentheses.

($F_{3,15}=4.46$, $P<0.05$, Table II). Post-hoc tests showed that accuracy was lower in the 180° rotation than in the 90° rotation. Recovery accuracy was unexpectedly high in the 90° condition, exceeding that in the unrotated condition, although post-hoc tests showed that the 90° condition did not differ significantly from the unrotated condition. Because there were no other significant differences among recovery conditions, we pooled results for the 90° rotation and the 270° rotation and re-analysed the data. Rotations of 90° and 270° correspond to 90° rotations in clockwise and anti-clockwise directions, respectively. Re-analysis with three recovery conditions, 90°, 180° and unrotated, showed again that recovery accuracy was significantly affected by recovery condition ($F_{2,10}=3.99$, $P<0.053$). Post-hoc tests showed that accuracy was lower in the 180° condition than in the 90° rotation, and that other differences were non-significant. In this experiment, cache recovery accuracy in the unrotated condition should approximately equal the recovery condition with only distal objects present in experiment 1, and a comparison of Tables I and II shows this to be the case.

A further test was performed in which we computed search accuracy, taking as 'correct' those sites in the same position, relative to the rotated distal objects, as the original cache sites had been. Under these conditions there was no significant effect of rotation condition on accuracy ($F_{3,15}=0.44$, NS, Table II). Comparison shows that birds clearly searched more at sites that were in the correct position with respect to distal objects than they searched at the original cache sites (Table II), with the exception of the rather anomalous 90° condition. This result shows that the chickadees treated the rotated objects as

stable landmarks indicating the locations of cache sites.

As in experiment 1, the position of the observer and the entry window were chosen at random for the caching and recovery phases of each trial independently. We re-analysed cache recovery, treating as 'correct' those sites that were in the same position, relative to the observer or to the entry window, as cache sites had been during the caching phase (Table II). These analyses showed, for observer position, a significant effect of subject ($F_{5,15}=4.57$, $P<0.01$), but no significant effect of rotation condition ($F_{3,15}=1.85$, NS), and for entry window, a significant effect of subject ($F_{5,15}=3.30$, $P<0.05$), but no significant effect of rotation condition ($F_{3,15}=0.98$, NS).

Discussion

The second experiment showed that the birds attended to the position of distal objects while caching and used their position to relocate caches during subsequent recovery. Cache recovery was more disrupted in the 180° than in the 90° rotation condition, corresponding to the amount of rotation of the objects. The effects of object rotation on the accuracy of cache search, however, were highly variable. Although the purpose of the chamber was to eliminate, as much as possible, all cues not under experimental control, it is likely that some cues, such as unique features of trees or chamber walls, were available and used by the birds. It is also possible that the sites at which birds searched for caches were compromises between rotated and uncontrolled cues. Vander Wall (1982) found that when multiple cues were available, nutcrackers searched for caches in places that were intermediate between the

positions indicated by displaced and undisplaced cues. Cheng (1988) has also proposed that spatial search occurs at places that are compromises between locations indicated by the available cues and landmarks. In Cheng's model, the weighting of cues can change with experience. Cache sites were always empty during the recovery phase of the present experiment, and failure to successfully retrieve stored food may have caused birds to change the weights assigned to distal objects and to other cues. The level of accuracy at sites that were correct with respect to the rotated distal objects did not differ from the unrotated condition, however, showing that according to this criterion, the birds primarily used distal objects to direct their search.

GENERAL DISCUSSION

The results of the first experiment showed that removal of proximal objects at a cache site had a relatively less disruptive effect on cache recovery accuracy than did removal of distal objects a few metres distant from the cache. This outcome may depend on the exact nature of the proximal and distal objects used. Proximal objects were not unique to cache sites. All proximal objects on a branch were the same colour and this colour occurred on upper and lower branches on the same side of a tree. None the less, branches within a tree could be identified by their proximal-object colours, and trees could be distinguished by the arrangement of proximal objects on their branches, for example, by whether a branch with a particular colour pointed to a wall or into the centre of the chamber. There was, however, no significant reduction in cache recovery accuracy after removal of proximal objects that had been present during caching. Distal objects could also be used to identify trees and branches within trees in a unique way. Removal of these cues did significantly reduce cache-recovery accuracy.

The results of the second experiment showed that rotating distal objects around the walls of the chamber reduced the amount of searching at cache sites. Chickadees searched instead at sites that were in the same position, relative to the rotated distal objects, as the original cache sites had been. There was some indication that searching at original cache sites was more disrupted by the 180° rotation than by the 90° rotation. This

outcome was due in part to unexpectedly high search accuracy in the 90° condition. It is possible that cues within the chamber that we were unable to control allowed the birds to distinguish among trees and branches. Sites the birds chose to search may have been compromises between sites specified by rotated objects and other cues, and search may have been seriously disrupted only when distal objects were sufficiently at variance with these uncontrolled cues.

The finding that distal cues are especially important for spatial orientation is supported by previous research with a number of species (reviewed in Honig 1990). In experiments in a cue-limited environment similar to that used in present study, Suzuki et al. (1980) demonstrated that laboratory rats, *Rattus norvegicus*, trained with distinct distal cues performed better in a radial-arm maze than rats trained without these stimuli, and that the rats' ability to locate the baited arms of the maze was disrupted by re-arrangement of the distal cues. Rotation of the distal cues caused rats to search in arms of the maze that were in the correct position relative to the distal cues.

It has generally been found that rats on the radial-arm maze rely more on cues outside the maze, extra-maze cues, than on cues inside the maze, intra-maze cues, to avoid previously visited arms (Olton & Samuelson 1976). On a cue-preference test it was found that rats that had been trained with extra-maze cues, intra-maze cues or both, relied on the extra-maze cues alone to avoid revisiting arms when both cues were present simultaneously (Kraemer et al. 1983). Other data show that rats in a water maze used stable distal cues outside the maze to relocate a submerged platform that they could not see (Morris 1981).

Pigeons, *Columba livia*, trained to find food in a radial-arm maze with extra-maze and intra-maze cues demonstrated accuracy greater than chance only when the distal cues on the walls of the experimental room were present during testing (Roberts & Van Veldhuizen 1985). Similarly, pigeons' memory for food sites in an open field task was shown to depend on the stability of spatial landmark configurations across trials (Spetch & Honig 1988).

The spatial relations between landmarks in an open field are used by gerbils, *Meriones unguiculatus*, to plan trajectories to previously visited goal

locations (Collett et al. 1986) and it has been shown that honey bees, *Apis mellifera*, learn the site of a food reservoir by learning its relation to a distal landmark array (Cartwright & Collett 1983). In a classic experiment, Tinbergen (1932) demonstrated that visual cues around the nest of a wasp, *Philanthus triangulum*, were used for orientation and that disrupting these cues led to disruption and then termination of search behaviour.

The results of the present study do not directly address how distal objects were used by chickadees to identify cache sites. Distance and direction from a single distal cue can specify a location in space, and direction alone can specify a location when more than one distal cue is used. A number of models of the use of cue or landmark information in spatial orientation have been proposed and the present results provide data relevant to one of these models. Cheng (1986) has proposed that animals can orient using only the geometric properties of their environment, such as the size of surfaces and the angles formed between surfaces. Rats have been shown in some experiments to use geometric information alone and to ignore features of surfaces, such as colour (Cheng 1986). The results of experiment 2 show that chickadees attend to more than the geometric properties of their environment. Indeed, the design of the chamber was such that birds using only the geometric properties of the chamber would have been unable to orient at all. Their search was clearly influenced by such features as the shape or colour of distal objects.

In the field, the distinction between proximal and distal cues is not so clear as in the experimental chamber used in these experiments. Cues are only proximal or distal relative to the size of the area being searched. A chickadee traversing its territory may treat a tree as a proximal cue but treat the same tree as a distal cue when searching for a cache site. Indeed, it is an open question whether the same mechanisms of spatial orientation are used on different spatial scales, or whether different mechanisms are employed depending on the scale of the area searched and the movements involved. The present results do show, however, that in the immediate vicinity of cache sites, objects at a distance from the cache had a greater influence on search than did proximal objects at cache sites.

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