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Alan C. Kamil

University of Nebraska-Lincoln

Ken Cheng

Macquarie University

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WAY-FINDING AND LANDMARKS: THE MULTIPLE-BEARINGS HYPOTHESIS

ALAN C. KAMIL^{1,*} AND KEN CHENG²

¹*Departments of Biological Sciences and Psychology, University of Nebraska-Lincoln, Lincoln, NE 68588-0118, USA*
and ²*Department of Psychology, Macquarie University, Sydney, NSW 2109, Australia*

*e-mail: akamil@unlserve.unl.edu

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Summary

Clark's nutcrackers (*Nucifraga columbiana*) are capable of very precise searching using the metric relationships between a goal and multiple landmarks to relocate the goal location. They can judge the direction more accurately than the distance to a landmark when the landmark is distant from the goal. On the basis of these findings, we propose that nutcrackers use a set of bearings, each a measure of the direction from the goal to a different landmark, when searching for that goal. The results of a simulation demonstrate that increasing the number of

landmarks used results in increasingly precise searching. This multiple-bearings hypothesis makes a series of detailed predictions about how the distribution of searches will vary as a function of the geometry of the locations of the relevant landmarks and the goal. It also suggests an explanation for inconsistencies in the literature on the effects of clock-shifts on searching and on homing.

Key words: navigation, Clark's nutcracker, *Nucifraga columbiana*, landmark, way-finding.

Introduction

Many animals navigate. Some perform incredible navigational feats. Foraging desert ants of the genus *Cataglyphis* can keep track of the home vector (the straight-line distance and direction to their nest) while wandering tens of meters (Müller and Wehner, 1988; Wehner and Wehner 1990). This process is called dead reckoning or path integration, and much is known about its mechanisms in *Cataglyphis* spp. (for reviews, see Wehner, 1994; Wehner et al., 1996). Many birds migrate long distances with great fidelity from year to year (for a review, see Berthold, 1993). The wandering albatross (*Diomedea exulans*) is aptly named because it flies hundreds, even thousands, of kilometers over the ocean before returning to its nest (Jouventin and Weimerskirch, 1990). Homing pigeons are famous for being able to find their lofts following release from very distant locations they have never before encountered (Keeton, 1974). The mechanisms by which animals navigate have been widely studied (for reviews, see Gallistel, 1990; Healy, 1998; Shettleworth, 1998). Remarkable mechanisms that have been discovered include sun, astral and magnetic compasses (Wiltschko and Wiltschko, 1998), the use of local landmarks (e.g. Tinbergen, 1951), the use of large-scale landmarks (e.g. Dyer and Gould, 1983) and path integration (Wehner, 1994). Many of these mechanisms have been discovered by detailed studies of organisms for which spatial navigation is of particular biological significance (e.g. migration, Emlen, 1970; Weindler et al., 1996). One excellent example of a navigational system that has been well characterized is that of foraging honeybees. Honeybees follow a sequence of

place-finding servomechanisms (Cheng, 2000), following a vector to the vicinity of the target, homing on a landmark located near the target and then flying in a stereotypical direction to match the image they see to a remembered image. In this study, we examine another biologically significant situation in which spatial navigation plays a central role, the recovery of stored food by birds, especially Clark's nutcrackers (*Nucifraga columbiana*). We develop a novel hypothesis about landmark-based navigation and explore its implications.

Characteristics of nutcracker seed-storing and recovery

The biological significance of cached food

The caching and recovery of pine seeds by Clark's nutcrackers have been studied extensively both in the field and in the laboratory (for a review, see Vander Wall, 1990). This is an extreme example of scatter-hoarding and recovery of stored food. Large numbers of cache sites are created, and the nutcrackers are highly dependent on this stored food for survival and reproduction. In an autumn with a good pine seed crop, an individual nutcracker will cache tens of thousands of seeds in the ground in thousands of locations, subsequently returning to them throughout winter and spring (Tomback, 1977; Vander Wall and Balda, 1977). These cached pine seeds are vitally important to the nutcrackers, serving as a primary food source for adults and for their young, which hatch the following spring. In years in which the pine cone crop fails, the nutcrackers leave the high elevations at which they

normally live, often not even attempting to breed (Vander Wall and Balda, 1977, 1981).

The accuracy and precision of cache recovery

A variety of studies have demonstrated that, when nutcrackers recover their seeds in the field, they are very accurate. That is, the probability of a nutcracker recovering a seed when it digs in the ground is very high. Tomback (1980) took advantage of the fact that nutcrackers usually husk recovered seeds immediately after digging them up. She recorded the presence of seed husks near excavations that appeared to have been made by nutcrackers and reported that as many as 72% had broken seed husks nearby in early spring, but that this number dropped to 32–44% in the summer. This decline could have been caused by increased cache losses to competitors, by previous recovery by the bird that created the cache or by forgetting. Vander Wall and Hutchins (1983) obtained similar data from direct observations of nutcrackers recovering seeds in the spring. In the laboratory, accuracy can be as high as 90% after 30 days (Balda and Turek, 1984) and is still far above chance after 270 days (Balda and Kamil, 1992).

Nutcrackers recover their caches with great precision. A cache of a few pine seeds is a small target and a beak is a very small shovel. To locate a cache site successfully, the bird must dig within a few centimeters of the center of the cache. This logic is reinforced by observations of the topography of digging behavior during cache recovery. Both in the field (Tomback, 1977; Vander Wall and Hutchins, 1983) and in the laboratory (Balda and Turek, 1984), nutcrackers have been observed to use three different types of digging. Bednekoff and Balda (1997) have termed these plunge (direct up-and-down movement of the head), sweep (side-to-side movement) and excavation (repeated digging motions in the same area). They found large differences in the success rates that accompanied these different types of digging. Approximately 2% of excavations, 20% of sweeps and 90% of plunges resulted in successful recovery of stored food. Thus, the topography that was most specifically oriented to a particular spot was the topography that was most likely to result in the correct re-location of a cache.

Nutcrackers have memories of cache sites

Many mechanisms could produce these levels of accuracy, including olfaction, path learning and memory. However, field conditions do not lend themselves to decisive tests among alternative hypotheses. A number of investigators have therefore turned to aviary and laboratory settings to perform experiments on the mechanisms of cache recovery. The results of these experiments have clearly established that memory for the location of cache sites plays an essential role in accurate cache recovery. The first such experiment (Balda, 1980) was with a single Eurasian nutcracker (*N. caryocatactes*). Balda found that the bird would cache and recover seeds in a dirt-floored room, digging very accurately at cache sites even when the seeds had been removed by the experimenter and the soil

surface smoothed. Vander Wall (1982) allowed two nutcrackers to cache seeds at different times in an outdoor aviary with a number of landmarks in it. He found that each bird recovered its own seeds very accurately, but not the seeds cached by the other bird. These two studies strongly support the cache-site-memory hypothesis for the accurate cache recovery of nutcrackers. However, the results do not make clear just what kind of memory is involved.

In particular, it is unclear whether the birds have a separate memory for each cache site or use some more general type of memory. For example, each bird could prefer to dig in certain kinds of locations such as south of rocks or north of trees. Then, if it tended to dig in those places during both caching and recovery, high levels of accuracy could be attained without any site-specific memory. To distinguish between these alternatives, Kamil and Balda (1985) devised a method of testing cache recovery in which the experimenters could control access to potential cache sites. In a long series of experiments (for a review, see Kamil and Balda, 1990a), results obtained with this method clearly established that nutcrackers could accurately recover cache sites when cache site location (e.g. Kamil and Balda, 1985) and/or order of recovery (e.g. Kamil and Balda, 1990b; Kamil et al., 1993) was controlled by the experimenters. These findings rule out any sort of general preference or movement pattern and strongly support the hypothesis that the nutcrackers have a distinct memory for each individual cache site that they have created. In other words, the nutcrackers must possess a representation (Gallistel, 1990) of the spatial location of each cache site.

What do nutcrackers encode about cache sites?

In many situations in various species, the last stages of re-locating a particular place are accomplished using a beacon, landmark or cue located at or near the goal. The loft of a homing pigeon or the nest of a bird would be examples. Nutcrackers, however, frequently cache in the middle of fairly open meadows with few local features (Tomback, 1977, 1980; Vander Wall and Balda, 1981). This may be a defense against cache-robbing by rodents (Vander Wall and Balda, 1981; Mattes, 1978). As a result, many caches are located relatively far from landmarks, particularly large landmarks. Small objects or ground markings may be present, but a great deal of evidence shows that nutcrackers largely ignore such markings or objects near cache sites. This may be due to changes in the surface of the ground between caching and recovery with the change of seasons. The most dramatic such change would be snow. There are a number of reports of nutcrackers accurately digging through an amount of snow sufficient to hide any surface features completely (e.g. Crocq, 1977; Mattes, 1978). Laboratory studies that have either obliterated surface cues (Balda, 1980) or provided them (Kamil et al., 1986) have found no effects of such surface signals.

What do we know about the representations nutcrackers form of their cache sites? A variety of evidence indicates that they are based upon information about the location of landmarks in the cache/recovery environment. After his birds

had finished caching, Vander Wall (1982) shifted the landmarks in one part of his experimental arena 20 cm in one direction, leaving the seeds where they were. Search behavior in that part of the aviary shifted in the same direction. Balda and Turek (1984) found that recovery accuracy declined substantially when many of the landmarks present during caching were removed during recovery. Little is known, however, about just what information about landmarks is encoded by the birds and then used to re-locate cache sites.

These representations appear to contain information about multiple landmarks. When Vander Wall (1982) shifted some of the landmarks in his aviary, the birds appeared to compromise between the shifted and the non-shifted locations in the area of the aviary on the edge of the shift. As Vander Wall (1982, 1990) has pointed out, this implies the use of at least two landmarks. Kamil et al. (1999) videotaped nutcrackers during caching and recovery and compared their body orientation during caching with that during recovery. Like Bossema and Pot (1974), they found that the birds tended to use the same orientation during caching as during recovery more than would be expected by chance. During recovery, however, the nutcrackers often approached and began probing at a cache site from a completely different direction from that used during caching. More critically, consistency of direction was completely unrelated to the accuracy of cache recovery. The nutcrackers recovered caches just as accurately when using a different direction during recovery from that during caching as when they used the same direction during both caching and recovery. This shows that nutcrackers can use any of a number of different views of a cache site to re-locate it, which in turn implies the use of multiple landmarks.

Evidence for the use of multiple landmarks also come from situations other than cache recovery. A number of studies have trained birds to find food buried in a location defined by its geometric relationship to a set of two or more landmarks and then found that the birds could locate the hidden seeds when only a small subset of the landmarks present during training was present during test trials (e.g. Bossema, 1979). The most extreme case was the study by Basil (1993). She trained nutcrackers to find a goal location defined by an array of eight landmarks arranged around the goal. The landmarks varied in height from 30 to 75 cm and were located 7.5–75 cm from the goal. The array was presented in different positions and orientations within the experimental room across trials. After the birds learned to solve this problem, they were tested for the ability to find the goal with various sets of three landmarks. Although the birds performed better with some arrays than others, they searched at least fairly accurately with all of the three-landmark arrays. Clearly, they had learned more than one small set of the available goal–landmark relationships.

The phenomenon of overshadowing appears to contradict the multi-landmark argument. A landmark very close to the goal location may ‘overshadow’ other landmarks and largely or completely control search behavior by itself (e.g. Morris, 1981; Cheng et al., 1987; Spetch, 1995). This may explain the discrepancy in results between the studies of Bennett (1993)

and Basil (1993), although their experiments appear to be very similar (albeit with different species). While Basil (1993) found that virtually all her landmarks had some effect on searching, Bennett (1993) found that only two landmarks had large effects. However, these two large landmarks were located very close to the goal, only 30 cm away, whereas many of Basil’s landmarks were located farther from the goal location. It seems likely that overshadowing is not a factor when the nearest landmark is not very close to the goal.

The importance of goal–landmark proximity to overshadowing in nutcrackers was confirmed (Gould-Beierle and Kamil, 1999) using procedures similar to those developed by Cheng and Sherry (1992). A seed was always buried at a fixed spot in a room in which there was an edge and a landmark on the floor as well as global cues. Gould-Beierle and Kamil (1999) varied the distance between the goal and the edge/landmark array for different groups. When they were 8–10 cm away from the goal, searching was completely controlled by the edge and landmark. For example, when the edge and landmark were removed on probe trials, searching by this group was very inaccurate. In contrast, when the edge and landmark were 24–30 cm away, the nutcrackers were able to dig fairly accurately when the edge and landmark were removed, using the global cues in the room (posters, lights, etc.). Clearly, nutcrackers often use multiple landmarks to re-locate a position in space.

This presents a puzzle. A spatial location can be defined by a single landmark in terms of distance and direction from that landmark. The results of spatial overshadowing experiments demonstrate that the information provided by a single landmark is sufficient for an animal to locate a goal, at least under some conditions. Yet some birds appear to include multiple landmarks in their representation of goal locations. Why should this redundancy exist? Would it not be more efficient to use just a single landmark? If nothing else, less information would need to be remembered. It has been suggested that this redundancy can be advantageous. Natural selection can be expected to favor redundancy when environmental variation is likely to interfere with the completion of an important task (Vander Wall, 1990). In the present case, the redundancy in using multiple landmarks could function as an adaptation against change in landmark availability. While this is a sensible hypothesis, it is difficult to test, and we do not find it convincing or compelling.

Do nutcrackers encode distance, directional information or both?

A location can usually be defined in more than one way (Gallistel, 1990). For example, consider a cache site located in a meadow within 6 m of three big rocks and 30–40 m from four large pine trees. The cache location could be defined in terms of its distance and direction from any one landmark, in terms of its directional relationship to any two landmarks, in terms of its distance from one landmark and direction from another, and so forth. Much evidence indicates that animals encode and use metric properties of distance and direction (for a review,

see Cheng and Spetch, 1998). For example, Cartwright and Collett (1982, 1983) worked with honeybees in an environment with just a few landmarks. They found that, when the distance between landmarks were changed, the bees tended to search in locations that preserved compass directions to the landmarks. Cheng and Spetch (1998, p.5) concluded that ‘... we cannot make sense of the data without assuming that the animals have encoded metric relations between the goal and surrounding landmarks’.

Clark’s nutcrackers also use metric relationships. Vander Wall (1982, 1990) suggested that his results with shifted landmarks, where the birds dug between the shifted and nonshifted loci, might be due to the use of some sort of triangulation. However, a similar result would also be obtained if the birds were using distances from two or more landmarks. Kamil and Jones (2000) have demonstrated that nutcrackers can learn to use directional relationships between a goal and two landmarks. They tested nutcrackers in a rectangular room in which the walls were oriented north–south and east–west. In one of the conditions of their experiment, birds were presented with two landmarks with varying distances between the landmarks. There was always a seed buried at a third point. The distance between the goal and the landmarks varied with the interlandmark distance so as to maintain constant directional relationships: the goal was always northwest of one landmark and southwest of the other. The birds learned this task easily, demonstrating an ability to use directional relationships.

Other results suggest that directional information is more valuable when the distance between goal and landmark is relatively large. For example, finding the point half-way between two landmarks logically involves two processes: finding the line connecting the landmarks, then finding the correct point along that line. While the first process is a judgement about direction, the second is about distance. When Kamil and Jones (1997) partitioned search error into directional and distance components, they found that the distance error increased much more rapidly than the direction error as distance from the landmarks increased. Thus, at longer goal–landmark distances, the error in estimating distance was considerably greater than the error in estimating direction.

Kamil and Jones (2000) obtained additional evidence that the direction from a goal to a landmark is a more potent cue than the distance from the goal to the landmark. They trained two groups of nutcrackers to find the third point of a triangle. The goal location was defined by two landmarks whose interlandmark distance varied from trial to trial. For one group, the third point of the triangle was defined by bearings. The goal was always buried at the intersection of two fixed bearings whose value was constant (requiring the goal–landmark distance to vary). For the second group, the goal was always buried at the same distance from each landmark (requiring the goal–landmark bearings to vary). The constant-bearing group learned to solve this problem much more rapidly and accurately than the constant-distance group. Under these conditions, bearings provided a more useful cue to location than did distance.

To summarize, research with nutcrackers shows that they use spatial memory to retrieve their caches with remarkable accuracy and precision. Nutcrackers form representations of the locations of cache sites, each based upon the relationship between the goal and the spatial location of multiple landmarks, usually landmarks at some distance. The one exception to this may be if the cache is very close to a distinctive landmark, in which case overshadowing may take place. These representations appear to entail encoding of the metric relationships between the goal and surrounding landmarks. Directional information may be more salient than distance information. Some features of this cognitive system are particularly impressive. Nutcrackers appear to remember separate representations of a very large number of individual cache sites, which may account for the relatively large size of their hippocampus (Basil et al., 1996). The memories can be maintained for many months, with significant retention for as long as 9 months after caching (Balda and Kamil, 1992). And these representations are maintained dynamically, being either checked off or forgotten once a cache has been emptied (Kamil et al., 1993).

The model

This body of knowledge about cache recovery in nutcrackers poses a major puzzle for the student of animal spatial navigation. How can the nutcracker possibly achieve the precision required to re-locate a small cache while digging with its relatively small-diameter beak? This is especially puzzling when we think about the effects of error in estimating distance or direction when the nearest landmark is located far from the goal. Consider an animal using a compass to determine the directional relationship between a goal and a landmark. There is evidence indicating that a sun compass may play a role in cache recovery by nutcrackers and other seed-caching birds (e.g. Wiltschko and Balda, 1989; Wiltschko et al., 1999). If the compass has an error of measurement of just $\pm 1\%$ ($\pm 3.6^\circ$), this will induce an error of ± 6.3 cm in search location when the goal is 1 m from the landmark and an additional ± 6.3 cm for each additional meter. And the estimation of the distance from a goal to a landmark is probably subject to even greater error than the judgement of direction (Kamil and Jones, 1997, 2000). This seems incompatible with the precise re-location of many caches in the midst of meadows or on isolated rocky ridges, more than a few meters from landmarks.

It is also interesting that the nutcrackers encode information about multiple landmarks in their representations of cache locations. All that is logically required to define a spatial position is two pieces of information: distance and direction from one landmark, or direction or distance from each of two, or distance from one and direction from the other. Using information from many landmarks appears redundant. Given the large number of cache locations that nutcrackers remember in the field (Vander Wall, 1990), such redundancy is perhaps surprising. We propose that the apparent redundancy is an

indicator of the mechanism by which high accuracy is achieved. Three points characterize our formulation.

(1) We hypothesize that nutcrackers represent the location of goals, including cache locations, in terms of the spatial relationship between the goal and multiple landmarks. This is consistent with the evidence both from nutcrackers and from many studies of spatial navigation in other species (e.g. see reviews in Healy, 1998).

(2) Although both distance and direction are probably encoded, we propose that directional information is primary in this system, at least when the landmarks are some distance from the goal location. As reviewed above, when the distance between the landmark and goal is relatively great, nutcrackers are more accurate in determining their direction from a landmark than their distance from it in several experiments (Kamil and Jones, 1997, 2000). They also learn directional relationships more easily than distance relationships (Kamil and Jones, 2000).

(3) We also propose that such encoding of information relative to multiple landmarks functions to increase dramatically the precision of searching in the face of errors in the estimation of distance or direction. We will address this last issue, the effects of using multiple landmarks on search accuracy, in a series of simulations.

Other models have incorporated directions to multiple landmarks. There have been a number of general discussions of the possible use of multiple bearings to landmarks (e.g. chapter 3 in Gallistel, 1990). Wiltschko and Wiltschko (1978, 1987) suggested that homing pigeons use a mosaic map of the territory with which they are familiar. This mosaic map was hypothesized to contain the compass directions between all possible pairs of salient landmarks. Our model differs from the mosaic map in its emphasis on directions from the goal location to landmarks rather than on directional relationships among landmarks. The model closest in spirit to ours was proposed by Baker (1982, Fig. 10.6). In this model, location-based navigation is based on a set of compass directions from a target to a number of salient landmarks. However, as far as we are aware, the implications and detailed predictions that follow from hypothesizing the use of goal-landmark bearings have not been fully explored. In the remainder of this paper, we begin this process.

Multiple landmarks and search accuracy

For theoretical purposes, let us suppose that only one bearing and one distance measurement can be made from each landmark. This rules out measuring bearings and/or distances to two different aspects of a landmark, which would be the equivalent of using each aspect as a separate landmark.

Whenever more than one landmark is used, there are many ways to define the goal location. It can be defined as the intersection of two bearings, each from the goal to a single landmark (except in the special case in which just two landmarks are present and the goal lies on the line connecting the landmarks). It can be defined as the intersection of an absolute bearing from one landmark with a circle whose radius

equals the appropriate goal-landmark distance drawn around either that or another landmark. Or it could be defined as the intersection of two circles, each around a different landmark. (In these latter two cases, however, some additional directional information is often needed because there are usually two intersection points.) Each of these different definitions of the location of a goal defines a potential encoding scheme the animal may use, and the different schemes are not mutually exclusive. We are proposing, however, that bearings provide the primary measure rather than distances when the landmarks are not in close proximity to the goal. This is based upon the evidence (reviewed above) that estimation of a bearing is more accurate than estimation of a distance under those circumstances.

In addition, we propose that using bearings to multiple landmarks reduces the error arising from estimating compass directions, especially when there are more than three landmarks to use. In this context, there are two types of bearings that can be used. With two or more bearings, the compass direction from target to landmark may be used; we call this the absolute bearing. With three or more bearings, the angle subtended by two landmarks when viewed from the target location may be used; we call this the relative bearing. We now consider the consequences of errors in directional estimates, how they relate to the number of landmarks that are used and how these affect the accuracy with which the target location can be found. The situations are somewhat different for absolute and relative bearings, and we first consider absolute bearings.

Absolute bearings

The absolute bearing between points X and Y is the compass direction from X to Y . When using absolute bearings, the target location is encoded in terms of the intersection of two or more such bearings, each originating at the target location. The general logic that follows from this perspective is illustrated in Fig. 1. Errors in measuring bearings from a goal to a landmark will certainly lead to errors in localization. Consider the case when only two goal-landmark bearings are used to represent a location. If there are errors in the bearings, there will still usually be an intersection of the bearings, but it will not be at the goal location (Fig. 1A). Furthermore, there will be no information available about the probable size of the error or the actual goal location. However, the situation changes dramatically if bearings from the goal to three or more landmarks are encoded.

When three or more goal-landmark bearings are encoded, there may be a constant error in measuring all the bearings (e.g. using a compass with a constant error in its output). This will result in a zone of uncertainty (Fig. 1B,C). The bearings to the landmarks do not yield a unique solution because they do not intersect at a single point. This failure to intersect is, in and of itself, informative. It indicates that there is error in the estimate of the location of the goal. Furthermore, these lines describe a polygon that does contain the goal. In the case of equal error in each of the bearings, the goal will be located near the center

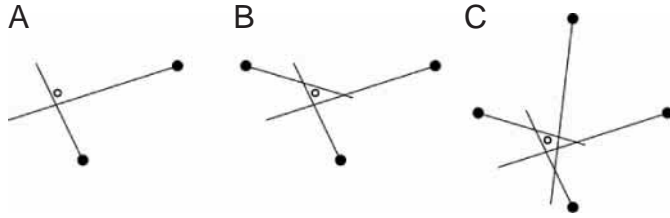


Fig. 1. An illustration of how increasing the number of landmarks can increase searching accuracy when there is compass error. Filled circles, landmarks; open circles, goal location; solid lines, goal-landmark bearings with error. (A) With only two landmarks, the goal is not at the intersection of the bearings. (B) With three landmarks, the bearings define a triangle that includes the goal. (C) With additional landmarks, the size of the polygon including the goal location decreases.

of the polygon. Presumably, an animal using this strategy could search in the middle of this polygon, by some definition of middle, e.g. the centroid. It is evident in the case of four landmarks (Fig. 1C), that the centroid is quite close to the location of the target.

In addition to errors common to all measurements, errors unique to each bearing may also be found (e.g. from using a compass with random error in its output). The use of multiple landmarks also reduces the deleterious effects of these errors. Fig. 2 shows how these errors affect localization in two particular situations with 2–4 landmarks. In general, four landmarks make for better localization than two. To evaluate the case more exhaustively, we conducted a Monte Carlo simulation on a standard spreadsheet (Excel 5). We placed four point-sized landmarks at four corners of a square: $(-5, -5)$, $(-5, 5)$, $(5, 5)$, $(5, -5)$. The target was a random location in a square ranging from $-2.5, -2.5$ on each axis. The measurement of the bearing to each landmark was given a random error of $\pm 2\%$ ($\pm 7.2^\circ$) in one series of runs and a random error of $\pm 1\%$ ($\pm 3.6^\circ$) in another. For all possible pairs of landmarks, we calculated a search point based on the intersection of the two faulty bearings, in the manner of Fig. 1. For measurements based on two landmarks, we took the distance from the search point of each pair of landmarks and calculated the average distance from search point to target. With a triplet of landmarks, three intersections of lines are generated from three possible pairs of landmarks. We took the average x and y coordinates of these intersection points as the search point. The average search-point-to-target distance of the four possible triplets was calculated. With all four landmarks, we first calculated all the intersection points based on pairs of landmarks. Then we averaged all the x and y coordinates to find the search point, and obtained the distance from the search point to the target. Distances were expressed as a proportion of the average landmark-to-target distance (they were scaled by dividing by $5\sqrt{2}$).

Each run of the model consisted of 1000 trials with random target and errors in measuring bearing. From each run, we obtained both mean and median error. They showed a similar pattern, but the mean was higher because it was distorted by a

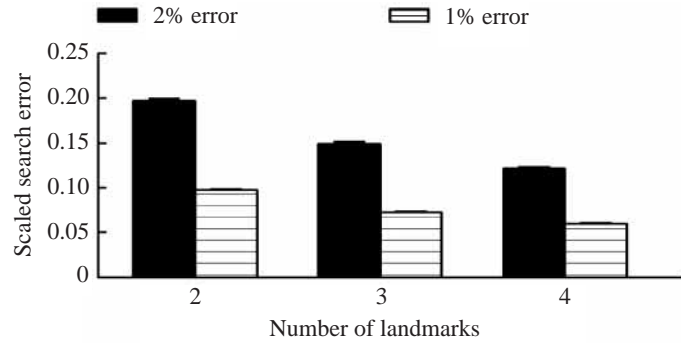


Fig. 2. Mean simulated search error (+ s.e.m.) as a function of the number of landmarks used. The effects of using a compass with 2% and 1% random error in its output are shown. $N=10$ runs at each level of compass error.

small number of huge errors. Fig. 2 shows the results of 10 runs at each level of compass error. The variability from run to run was tiny, and a mixed analysis of variance (ANOVA) showed all the effects to be highly significant: size of compass error ($F_{1,18}=2663.81$, $P<0.0001$), number of landmarks ($F_{2,18}=4586.52$, $P<0.0001$) and their interaction ($F_{2,18}=511.28$, $P<0.0001$). The interaction effect has a ready explanation. It comes about because error reduction with additional landmarks is proportional, whereas an ANOVA tests for additive effects. The error with three landmarks is 0.755 and 0.752 of the error with two landmarks, for $\pm 2\%$ and $\pm 1\%$ compass error, respectively. The error with four landmarks is 0.620 and 0.617 of the error with two landmarks, for $\pm 2\%$ and $\pm 1\%$ compass error, respectively. Proportionally then, error reduction with additional landmarks is virtually identical at both levels of compass error. Our simulation shows conclusively that the more absolute bearings to landmarks are used to pinpoint a target, the more accurate the localization.

Relative bearings

Although our argument up to this point has emphasized absolute bearings, similar arguments apply to the use of relative bearings. One useful way to define a relative bearing is as the difference between two absolute bearings. For example, if one landmark is north of the goal and another east of the goal, the relative bearing between the landmarks is 90° . Although relative bearings need not be estimated by comparing absolute bearings, we find this definition useful in conceptualizing how relative bearings might be used.

With just two landmarks, only one relative bearing is available and it cannot be used by itself to define the location of a goal. That relative bearing will define a curve of uncertainty. Every point on that curve will be characterized by the correct relative bearing to the two landmarks. If the two landmarks are located as points on a Cartesian plane so that they have the same ordinal value, then the curve of uncertainty is a quadratic function that runs through the two landmarks. Supplemented by absolute bearings or by distance measurements, however, relative bearings may be used to pinpoint a location using just two landmarks. With three or

more landmarks, the argument relating the number of landmarks used to accuracy is the same as the argument for absolute bearings, with one exception. A potential advantage of relative bearings is that they may not be sensitive to a constant error in the measurement of bearings. For example, if there is a $+5^\circ$ error in estimating the bearing from a point to each of two landmarks, the landmarks will still have the same relative bearing because they still subtend the same angle.

Although the role of relative bearings is not well-known, the results of Jones (1998) and J. E. Jones and A. C. Kamil (in preparation) demonstrate that nutcrackers can use relative bearings to find a target location. In her experiment, Jones trained nutcrackers to find the third point of a triangle. On each trial, they were presented with two landmarks, and the distance between the landmarks varied. The goal was always located at the third point of the triangle, such that the line drawn from the goal to either landmark always described the same angle with the line connecting the landmarks, regardless of interlandmark distance. For the control group, the landmarks were always presented in the same orientation to each other. For the second group, the orientation varied across trials. Thus, for the first (control) group, the goal location always had the same relationship to the landmarks in terms of both absolute and relative bearings. However, for the second group, only relative bearings were constant across all training trials. The relative-bearing group learned the task almost as rapidly as the control group and generalized well to new landmark orientations during probe test trials. These results strongly suggest that nutcrackers can use relative bearings.

Benhamou (1998) has developed a configuration-based model in which each location is represented as a kind of circular bar code that embodies the apparent sizes of and relative bearings to a set of multiple landmarks. The size of the bars in such a representation would be a function of the relative size and distance of each landmark. The distance between adjacent bars would be directly analogous to the relative bearing between the landmarks being represented.

Predictions

This theoretical view makes many specific predictions about the effects of different landmarks on searching when the landmarks are far enough away from the goal to prevent overshadowing.

(1) The distinction between directional error and distance error leads to a specific prediction about searching for a goal with only a single landmark. When the target location is defined by a single landmark, there is only one way to define, and therefore to encode, the location of the target. The searcher must measure the absolute bearing and distance to the landmark. The error in measurement under these circumstances has two components, error in measuring the bearing and error in measuring the distance. These two types of error can be assessed independently by dividing search error into two independent components. Error along an axis defined by the

hypothetical line from the landmark to the goal will estimate error in distance judgement. Error perpendicular to that line will be error in directional judgement. Thus, performance during single-landmark situations can be used to assess the accuracy of distance *versus* directional estimation. We predict that, as the distance between the goal and the landmark increases, the error in distance estimation will increase faster than the error in directional estimation. We also predict that, across a wide range of landmark–goal distances, the sine of the directional error will be constant because directional error should be constant when measured in angular terms. Finally, distance and directional error can be correlated across trials (within each animal) in such a study. A positive correlation could result from many factors. But an absence of correlation would be strong evidence that the two judgements, distance and direction, involve different mechanisms, as suggested by Cheng (1994).

(2) Adding landmarks to an array will improve search accuracy. This strikes us as relatively uninteresting because we suspect that virtually any model of multiple landmark use would make the same prediction. However, its confirmation would provide further evidence of simultaneous use of multiple landmarks, and this test might provide a good assay for determining whether the use of multiple landmarks needs to be considered for a particular species and situation. A more interesting variant on this prediction is that the amount of search error induced by error in measuring bearings should produce smaller effects when more landmarks have been used to encode the goal location.

Jones and Bingman (1996) tested a neural network model of navigational learning with several different landmark arrays. They found that the performance of the network improved when the number of landmarks was increased from two to four, but then decreased with a further increase in the number of landmarks to six. Our model suggests that this decrease in accuracy with more than four landmarks may not be characteristic of navigating animals.

(3) The geometric relationships of the goal–landmark configuration will determine the extent to which an additional landmark will improve accuracy. For example, consider comparing accuracy with a single landmark *versus* accuracy with two landmarks. Suppose that the second landmark is at least as far away from the goal as the first. If the second landmark is located so that the goal lies on the line connecting the landmarks, we predict it will have little effect on searching in the axis parallel to the line connecting the landmarks because searching along that axis will still depend on a distance judgement. This prediction is limited to the parallel axis, however. Directional error, error in the axis perpendicular to the line connecting the landmarks, might decrease because having the second landmark could provide relative bearings, reducing directional error. We also predict that the effects of a second landmark on overall search accuracy will be greatest when it is located so that the lines drawn from each landmark to the goal meet at 90° . This configuration is the only two-landmark array with which search in each axis is independent

of search in the other axis, leading to the greatest overall accuracy when using only directional information.

(4) The logic leading to prediction 3 also leads to some very specific predictions about the distribution of searching when two landmarks are present. Consider a goal–landmark array with two landmarks that are equidistant from the goal, one located directly east and the other directly north of the goal, and with a goal–landmark distance set so that directional error is distinctly smaller than distance error. Three trial types are conducted: only the east landmark present, only the north landmark present and both landmarks present. When only the east landmark is present, error will be greater in the east–west axis than in the north–south axis. The opposite will be true when only the north landmark is present. When both landmarks are present, however, east–west and north–south error should be equal and should also be equal to the directional estimates obtained from the single-landmark trials. (It should be noted that, if relative bearings are important, the increase in search accuracy may be even greater than predicted.)

(5) Animals using relative bearings should be less sensitive to constant error in their estimate of absolute directions than animals using absolute bearings. This leads to several predictions about animals trained to use relative bearings compared with those trained with absolute bearings (as in Jones, 1998; see above). For example, suppose that birds were trained to use relative bearings in an outdoor aviary and then clock-shifted during probe test trials. If the birds were using a sun compass, the clock-shift would induce an absolute error in the compass. This should have little effect on animals using relative bearings, but a strong effect on a control group trained with absolute bearings.

Implications

The multiple-landmark view we have proposed provides new perspectives on how information from landmarks and from a compass might interact. In many instances, compass information may be used independently of landmarks. A migrating bird coming to the end of summer in the northern hemisphere only needs to go south. It does not need to reference that southern movement to a landmark. However, compass information may need to be integrated with landmark location to find a specific spot. For example, the migrating bird might need to go south from a particular mountain or river to re-locate its wintering grounds.

The combined use of compass information with landmarks seems particularly likely for seed-caching birds searching for caches whose location has been defined by directional relationships between the cache site and a set of landmarks. Several studies have demonstrated clock-shift effects with seed-caching birds by showing that the direction within an aviary at which a bird searches changes systematically as a result of clock-shifting (Wiltschko and Balda, 1989; Balda and Wiltschko, 1991; Duff et al., 1998; Wiltschko et al., 1999). The multiple-bearings hypothesis suggests that clock-shifting induces error in the sun compass, which may then place

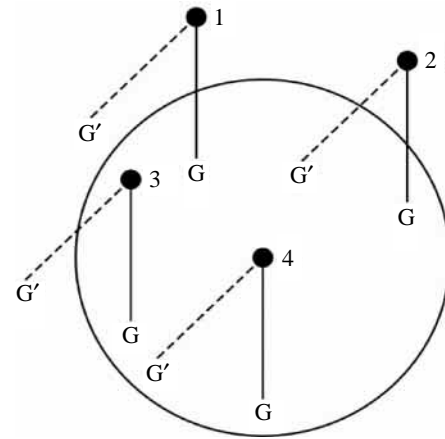


Fig. 3. An illustration of how a clock-shift may move the apparent location of the goal to a position outside the test arena, depending on landmark location. Solid lines, original goal–landmark bearings; broken lines, clock-shifted bearings. Only clock-shifted locations 2 and 4 remain inside the test arena after clock-shift. G, goal; G', position of goal after clock-shifting; 1–4, landmark positions. Landmark 4 is the central pole of the aviary.

different pieces of information such as the bearings from the goal to different landmarks into conflict. We hypothesize that this factor may explain some of the puzzles in the literature on the effects of clock-shifts on the recovery of stored food.

The effects of clock-shifts on seed-caching birds are sometimes inconsistent. For example, Duff et al. (1998) and Wiltschko et al. (1999) obtained clock-shift effects in only some of their experiments, and the effects were often much smaller than predicted (e.g. experiments 1 and 5 of Duff et al., 1998). These inconsistencies may be the result of how clock-shifts affected the apparent orientation of the landmarks. The arenas or aviaries used all had a central pole. Imagine that a bird remembers the goal location as being 150 cm east of a landmark, and that it has been clock-shifted so that its compass has been shifted 45° clockwise. If the landmark in the representation is the central pole, there will always be a location in the arena that matches the representation. But, if the landmark is either in the arena but not at its center or is outside the arena, the location that matches the representation may or may not be inside the arena (Fig. 3).

An additional argument about integration of compass and landmark information is based on the possibility that the birds in these experiments may have been using multiple landmarks to remember some goal locations. Suppose that the birds in these experiments represented spatial locations in terms of the bearings from the goal to each of three or more different landmarks. What effect will a clock-shift have? The answer depends on details such as goal–landmark and landmark–landmark distances and relative goal–landmark bearings. But, under many circumstances, a clock-shift will present the subject with an insoluble problem. Shifting the orientation of a compass but leaving the relevant landmarks in place can make it impossible to find a location that satisfies the original

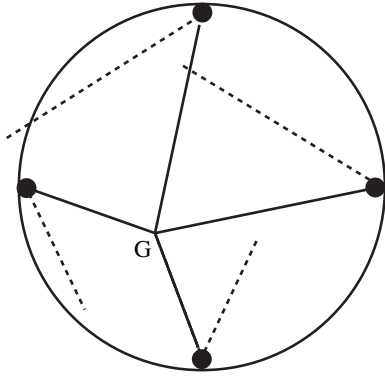


Fig. 4. An illustration of how a clock-shift can make a location impossible to find if encoded by multiple bearings. If the goal, G, was coded by the four bearings indicated by the four solid lines then, after a clock-shift, the new bearings would be oriented as shown by the dashed lines; there is no point at which more than two of the clock-shifted bearings intersect.

representation. Thus, in Fig. 4, the goal location (G) satisfies several directional relationships to landmarks, but after a clock-shift the new bearings from the landmarks no longer intersect (dashed lines).

This logic is not limited to clock-shifts with seed-caching birds. When homing pigeons (*Columba livia*) are clock-shifted and then released from a familiar site, the information from the sun compass and from landmark-based information will come into conflict. As would be expected from this perspective, inconsistencies are often found in studies of the effects of clock-shifts on homing pigeons (Chappell, 1997). Some of these inconsistencies may be due to the influence of landmarks on clock-shifted birds being released from a familiar site. For example, imagine that the route home from the site is north and takes the bird over a big church steeple near the release site. When clock-shifted, the bird flies in the direction that it now incorrectly judges to be north, but sees that it is not going over the steeple. This could easily affect the route that the bird flies.

Experiments in which pigeons are released from familiar sites have provided confusing and contradictory results. For example, Fuller et al. (1983) showed that pigeons that were very familiar with a release site still oriented in the clock-shifted direction when tested. Bingman and Ioyalé (1989), in contrast, found that clock-shifted pigeons released from familiar sites had a mean vanishing bearing intermediate between the clock-shifted and home directions, a result also obtained by Wallraff et al. (1994). It is not clear how to interpret flight in a direction that is intermediate between the home and the clock-shift directions, but a global analysis has shown that this is a common result (Chappell, 1997). This result could be due to the bird compromising between the home and the clock-shift direction, i.e. averaging the dictates of the two cues. It could also result if some birds are using a sun-compass-based mechanism while others use a mechanism independent of the sun compass, such as directional information from landmarks. Recent experiments (Holland et

al., 2000; Bonadona et al., 2000) in which clock-shifted birds were tracked from familiar release sites found that some birds had straight tracks while others had deflected tracks consistent with the use of a sun compass. This suggests that two different homing mechanisms are being expressed by different animals, an implication supported by the finding that hippocampal lesions disrupt navigation by local landmarks but not navigation using a sun compass (Gagliardo et al., 1999).

When this problem of variable results from clock-shifted homing pigeons released from familiar sites is considered from the point of view of landmark use, two additional points emerge. It seems quite likely that different release sites with different characteristics might produce different patterns of dependence on landmarks. A site without any nearby, highly conspicuous landmarks may be more likely to produce results consistent with the clock-shift, a suggestion also made by Gagliardo et al. (1999). In addition, if the birds use relative bearings based on a local landmark array to determine direction, clock-shifts would have no effect on their direction of flight. A constant error in a compass does not affect relative bearings.

Concluding remarks

Animals use many different mechanisms to orient and navigate. Our knowledge of many of these mechanisms has come from careful study of species for whom some aspect of their natural history makes spatial navigation particularly important for biological success. One such situation is the recovery of cached food. While this has been extensively studied, little attention has been given to just how the search for the stored food is guided. A review of what is known about spatial searching by one important seed-caching species, the Clark's nutcracker, has led us to propose a new model for the use of landmarks. We suggest that the birds use directional bearings to multiple landmarks. The use of multiple landmarks is not mere redundancy. It is essential for counteracting the deleterious effects of even small amounts of compass error. Without using multiple bearings, the precision that nutcrackers have shown in recovering caches is impossible to achieve short of using biologically unrealistically accurate compasses. This hypothesis makes specific qualitative and quantitative predictions and is eminently testable. It should also be applicable to many other situations in which searching must be precise and cannot be guided by landmarks located very close to the goal location.

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