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Review

What scatter-hoarding animals have taught us about small-scale navigation

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Many animals use cues for small-scale navigation, including beacons, landmarks, compasses and geometric properties. Scatter-hoarding animals are a unique system to study small-scale navigation. They have to remember and relocate many individual spatial locations, be fairly accurate in their searching and have to remember these locations for long stretches of time. In this article, we review what is known about cue use in both scatter-hoarding birds and rodents. We discuss the importance of local versus global cues, the encoding of bearings and geometric rules, the use of external compasses such as the Sun and the influence of the shape of experimental enclosures in relocating caches or hidden food. Scatter-hoarding animals are highly flexible in how and what they encode. There also appear to be differences in what scatter-hoarding birds and rodents encode, as well as what scatter-hoarding animals in general encode compared with other animals. Areas for future research with scatter-hoarding animals are discussed in light of what is currently known.

Keywords: scatter-hoarding; landmarks; cue use

1. INTRODUCTION

There is a large body of literature examining how animals use and encode cues for small-scale navigation. These cues can include the use of beacons, landmarks (both proximal/local and distal/global), external compasses and the geometric properties of objects, including geometric rules and the geometry of configurations. Much of this work has used traditional psychology laboratory animals such as rats and pigeons (for reviews, see Healy 1998; Shettleworth 1998; Cheng *et al.* 2006), but our understanding of small-scale navigation has also been furthered through studies using species such as gerbils, ants and bees (Cartwright & Collett 1982, 1983; Collett *et al.* 1986; Collett & Collett 2009). From this body of work, we have a much greater understanding of general cue use by animals. However, a growing body of research has investigated how scatter-hoarding animals use cues to relocate their caches. While scatter-hoarding animals and non-hoarding animals may have many similarities in how they encode and use cues, scatter-hoarding presents a unique situation. Scatter-hoarding animals have to remember and relocate many individual spatial locations in their environment. They have to be fairly precise in their searching in order to recover their caches. They also have to remember these locations for days, weeks and even months at a time. This makes

scatter-hoarding a unique system in which to study cue use for small-scale navigation. The goal of this paper is to review what we have learned about cue use in scatter-hoarding birds and rodents, and how this has contributed to our understanding of cue use in general. We will focus on how scatter-hoarding rodents and birds encode and use cues in ways that are similar to that found in non-hoarding animals and in ways that are potentially different, specifically in terms of learning and accuracy. Finally, we will also focus on a few important areas for future research.

The rat has had an important position in the history of psychological research, and certainly within the field of spatial learning and navigation. The development of the radial arm maze and the Morris water maze for studies of spatial memory has shown that the rat has an excellent ability to remember previously visited locations and accurately direct searches to new locations (Olton & Samuelson 1976; Morris 1981). This early research resulted in many important discoveries as to how spatial information is encoded (O'Keefe & Nadel 1978). By adopting and re-designing the traditional approaches used to study spatial abilities in rats, researchers began to examine the pigeon's use of spatial information for small-scale navigation (Spetch & Edwards 1986; Spetch & Honig 1988). One interesting result of these studies, using modified radial arm mazes, is the notion that pigeons, like rats, form a map-like representation of their spatial environment. Knowing that pigeons use relationships between locations to direct their search behaviour, researchers began to investigate the properties of this spatial representation. To do so, researchers

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One contribution of 10 to a Theme Issue 'Integrating ecology, psychology and neurobiology within a food-hoarding paradigm'.

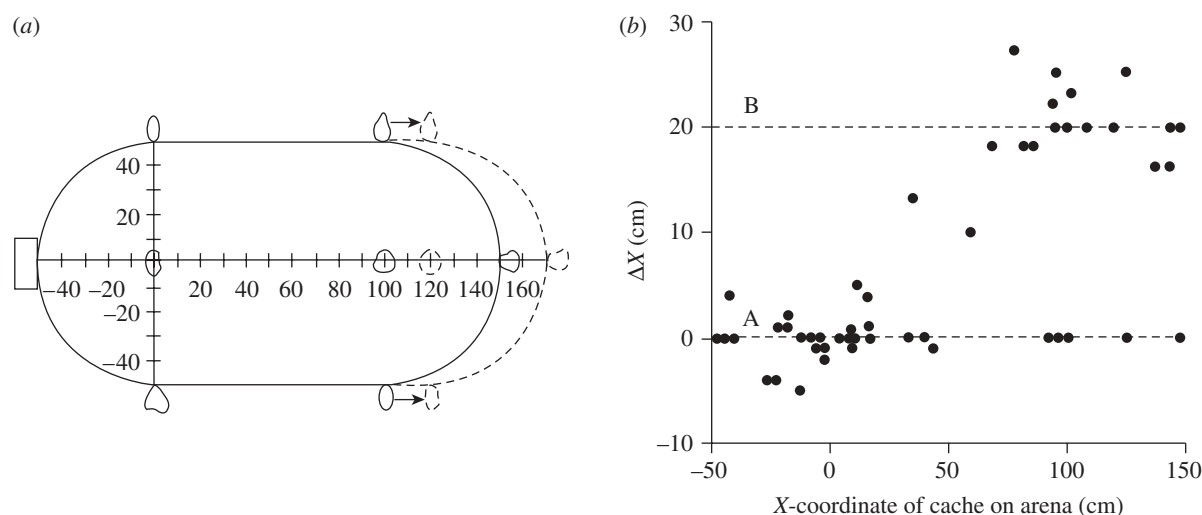


Figure 1. (a) The caching arena in Vander Wall (1982) during control (solid lines) and during landmark-shift (dashed lines) conditions. (b) The distance between a probe and the nearest cache on the y-axis as a function of the original position of the cache in the x-axis. Line A represents cache recovery and line B represents the expected ΔX if birds use the shifted objects as cues. Therefore, if the birds followed a shift, a ΔX score of 20 cm would be expected. Adapted from Vander Wall (1982).

had to develop spatial tasks that would allow one to examine how the particular location was being stored in memory; consequently, the novel tasks for the study of spatial learning and cognition in rats and pigeons were developed.

A collection of studies by Cheng and co-workers set out to better understand how pigeons were encoding landmarks within their environment (e.g. were the pigeons using retinal projections as Cartwright & Collett (1982, 1983) found with bees, and how was the relationship between a landmark and the surfaces of an arena encoded?). These studies showed that indeed pigeons encoded landmark information and that pigeons were encoding distance and direction information between landmarks and surfaces. The importance of these investigations was realized in the development of the vector sum model and subsequent revisions of this fundamental model (Cheng 1988, 1989, 1990, 1994; Cheng & Sherry 1992; Kamil & Cheng 2001). This model was central in defining how pigeons (and other animals) encode vectors, with distance and direction components, between two or more landmarks within an environment and a goal location.

Researchers have continued to build on these initial steps by examining issues such as how a landmark's location influences whether it is encoded, and if so, how particular landmarks are ranked in relation to other landmarks in a hierarchical fashion, how the metric relationships between landmarks are encoded, and how the search space itself is used to acquire spatial information (for a review, see Cheng *et al.* 2006).

Investigations into these questions have certainly built our understanding of the general mechanisms that are involved in spatial memory, and specifically how cues are used in navigation. However, research with scatter-hoarding animals has investigated cue use from a different angle. In scatter-hoarding animals, there is a very specific ecological adaptation that requires the use of spatial memory in a way that other animals may not have or need. Although most

animals have to use spatial navigation to some extent, including foraging for food, a scatter-hoarding animal has potentially more spatial information to remember, has to remember it simultaneously, more accurately, or for longer lengths of time (for further discussion on this issue, see Smulders *et al.* 2010). In order for scatter-hoarding to be a successful strategy, the animal that hoards has to have a good spatial memory and a mechanism for relocating its caches.

2. IMPORTANT STUDIES IMPLICATING THE USE OF LANDMARKS IN FOOD-HOARDING ANIMALS

Previous studies have demonstrated that both food-storing rodents and birds use spatial memory to relocate their caches (Balda 1980; Sherry *et al.* 1981; Shettleworth & Krebs 1982; Sherry 1984; Kamil & Balda 1985; Balda & Kamil 1989; Jacobs & Liman 1991; Jacobs 1992; Devenport *et al.* 2000). However, the mechanism used for remembering the spatial location of caches is a separate question, one that has been investigated for at least 30 years. Bossema (1979) was the first person to experimentally manipulate landmarks after a scatter-hoarding European jay learned to find a hidden food location in a laboratory setting. Bossema removed and moved two vertical landmarks that were present when jays learned to find the hidden food in a certain location relative to the landmarks. He found that the birds appeared to be using the distance between the cache site and the line created between the landmarks to relocate the cache.

Vander Wall (1982) also demonstrated that Clark's nutcrackers use landmarks to help relocate caches they have made. Nutcrackers cached seeds in an arena that contained an array of landmarks. The landmarks were then displaced in one half of the room 20 cm from their original location (figure 1a). When the birds recovered their caches, they consistently shifted their searching by approximately 20 cm in the

direction of the landmark shift in that part of the room. They did not, however, shift their searching at all in the other half of the room where the landmarks remained stationary. Interestingly, they shifted in an intermediate fashion when they searched for caches made in the middle of the arena, approximately 10 cm in the direction of the landmark shift (figure 1*b*). This suggests that they were using multiple cues as information in relocating the caches they made in the middle of the arena and modified their searching based on some kind of weighting or averaging of the individual landmarks and their locations.

In scatter-hoarding rodents, research with kangaroo rats indicates that they also use landmarks in retrieving caches. *Barkley & Jacobs (1998)* demonstrated that when Merriam's kangaroo rats cached seeds in an arena and had to retrieve them the next day, having landmarks present or absent did not make a difference in recovery. However, with a 10-day retention interval between hoarding and recovery, having an array of 16 landmarks improved the number of caches recovered as compared with having no landmarks present. They discussed that landmarks may help reduce proactive interference in memory for cache sites when the recovery time is long.

These three studies tell us that, in general, scatter-hoarding animals use spatial information from available landmarks to find the spatial location of food either they have cached or has been hidden by an experimenter. *Bossema's (1979)* study indicates that jays may be able to encode the distance of a spatial location in relation to a line or edge created by two landmarks. *Vander Wall's (1982)* study suggests that nutcrackers weight landmarks in accordance to their proximity to each cache location, averaging the information when some landmarks are moved and others remain stationary. *Barkley & Jacob's (1998)* study demonstrates that having landmarks present improves cache recovery in kangaroo rats over longer time spans, which implicates their use as a way to counter interference in memory over time.

Further research has explored exactly how landmarks are encoded by scatter-hoarding animals. It appears that there are some differences between scatter-hoarding and non-hoarding animals in the precision of searching that landmarks and other cues afford. It also appears that there may be some differences in the way scatter-hoarding rodents and birds use landmarks and other forms of spatial information. However, there does appear to be a great deal of flexibility in what kinds of spatial information can be used. The type of task, the form of training and the type of cues available all can affect how landmarks are used.

3. THE IMPORTANCE OF LOCAL (PROXIMAL) AND GLOBAL (DISTAL) CUES

(a) Scatter-hoarding birds

Landmarks are often categorized in terms of their distance from the goal. Within this framework, there are three different classes of landmarks. The first class is beacons, cues that are located at or very close to the target location. The use of beacons is sometimes described as a non-spatial strategy on the notion that

the animal simply needs to approach the beacon to 'automatically' locate the target. But the general spatial location of the beacon and its spatial relationship to the goal (e.g. on which side of the beacon the goal is located) has to be encoded and remembered.

The next two classes of landmarks are examples of what are thought of as more traditional examples of spatial strategies. They necessitate remembering the spatial position of a number of cues in relation to a target location when navigating towards the target. The second class of landmarks are local or proximal cues located within roughly 1 m or so from the target location, potentially necessitating use by the navigator of more than just the location of one landmark alone to find the target. Bearings, or directional information, as well as distance information can be encoded based on one such landmark, or a landmark with another global cue, or multiple local landmarks. The third class of landmarks is global or distal cues located further from the target. They could be located within a few metres from the target and thus be used in much the same way as mentioned before, gaining bearing and distance information from them. However, they could be large or continuous structures in the environment that create edges, natural geometric patterns, or are otherwise used for gaining bearings or reaching the general location of a target. One can imagine that an animal could use a global cue to get to the area near the target and then switch to rely more on local cues to pinpoint the exact target location. In any event, it is important to remember that the concepts of beacon, proximal and distal landmarks represent a continuum, not a trichotomy.

In scatter-hoarding birds, one-trial associative procedures have been used to demonstrate that these birds prefer to use spatial information in relocating hidden food when compared with birds that do not scatter-hoard (*Brodbeck 1994; Brodbeck & Shettleworth 1995*). In one such study, corvids (European jays) and parids (marsh tits) that store food were more likely to use spatial information in relocating a food source than corvids (jackdaws) and parids (blue tits) that do not store food (*Clayton & Krebs 1994*). From the way these tasks were designed, the non-spatial choice was to go to the same coloured feeder that contained food in the bird's first visit to the room, as opposed to choosing the location of the feeder relative to other feeders or cues in the room during the bird's first visit (figure 2*a* showing an example of the training set-up and figure 2*b* showing the dissociation test). Scatter-hoarding birds preferentially made the spatial choice that the dissociation test now contained a different featural cue, whereas non-storing birds made both choices (correct spatial location and correct featural cue) equally as often. This suggests that scatter-hoarding birds are primed to focus on the spatial location of food relative to local and/or global landmarks, as opposed to simply using a beacon (go to the red feeder). However, other studies have shown no preference for spatial information (*Healy & Krebs 1992; Healy 1995*) or an actual preference for non-spatial information (*LaDage et al. 2009*) by scatter-hoarding birds on such tasks. So, the use of local landmarks as true

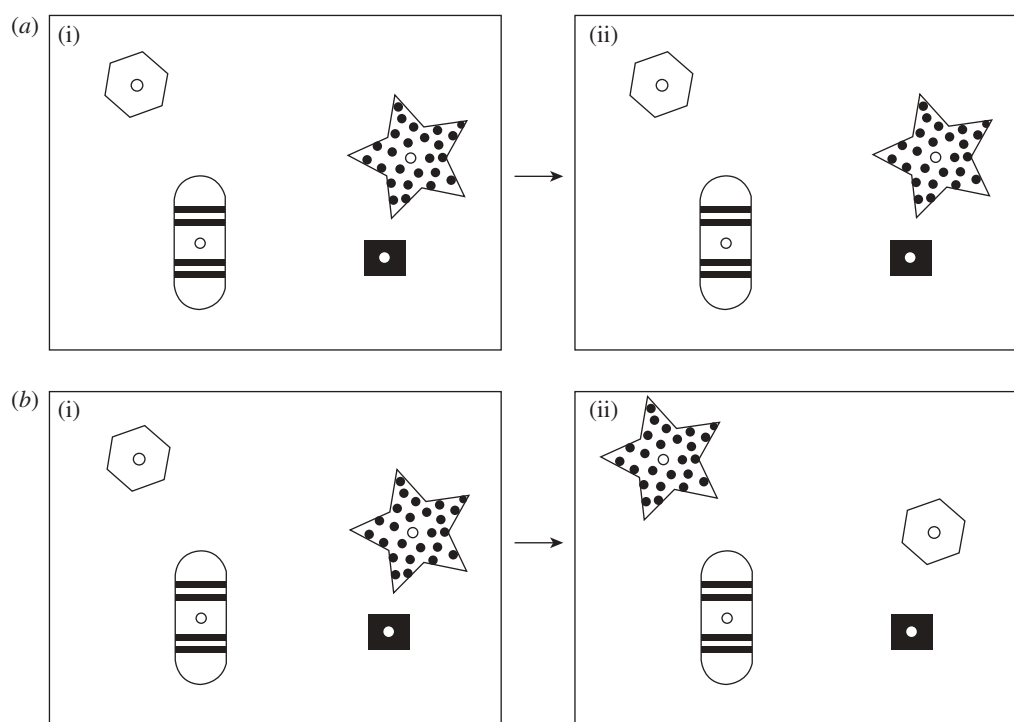


Figure 2. (a) Diagrammatic representation of the logic of one trial associative tasks. (i,ii) Figures showing training trials. One of the stimuli is randomly designated correct on each trial (with new, 'trial-unique' stimuli used for each trial). The bird is then rewarded when it chooses the correct stimulus (in this case the dot-filled star). The display then disappears for a retention interval, and the same display is presented for choice, and the bird is rewarded for choosing the same stimulus. (b) (i,ii) Once training is complete, the bird receives occasional dissociation test trials. These trials differ from training trials in that the spatial locations of two of the stimuli are switched. If the bird chooses the same visual stimulus (the dot-filled star, in this case), this indicates control by the stimulus. But if the bird chooses the old location (the hexagon), it suggests spatial control. Spatial location and visual stimulus have been dissociated.

beacons may or may not be important for scatter-hoarding birds in relocating caches depending on the experimental situation (but see Gray *et al.* 2005, discussed later).

Tasks that have looked at the use of proximal versus distal cues in scatter-hoarding corvids have shown that proximal information is more valuable. Bennett (1993) had Eurasian jays learn to find the position of hidden food among an array of landmarks that varied in height and distance from the target. In tests, subsets of the landmarks were removed. The birds were more accurate in their search when the proximate landmarks remained and when tall landmarks remained. J. A. Basil (1993, unpublished dissertation) found similar results with Clark's nutcracker. Using a different task but one that removed distal or proximal cues around a target location, Kelly (*in press*) also found that nutcrackers relied more on local cues compared with global cues. So in these cases, the birds relied more strongly on landmarks that were proximal to the target location and were taller.

In a study with a scatter-hoarding parid, the black-capped chickadee (Herz *et al.* 1994), birds were allowed to store food in artificial trees in a room. There were large, global cues on each wall and small, local colour cues located at each potential cache site. When local cues were removed, there was no effect on retrieval accuracy. However, when global cues were removed, retrieval accuracy decreased. Another group of birds were only given global cues during hoarding. When those cues were moved during

recovery, the birds displaced their searching in accordance to the shift. The results of Herz *et al.* (1994) indicate that global cues had more influence on spatial memory for caches than local cues did. However, when you compare this study with the three studies carried out with corvids, the way that local/proximal and global/distal cues were defined was different. Proximal landmarks in Bennett (1993) and J. A. Basil's (1993, unpublished dissertation) experiment were not directly at the target location of the food, whereas for Kelly and Herz *et al.*'s experiments, the local cues were at the exact location of the food, making them a beacon. As was demonstrated in some of the one-trial associative procedures described earlier (Brodbeck 1994; Clayton & Krebs 1994; Brodbeck & Shettleworth 1995), scatter-hoarding birds do not seem to rely on colour information in the form of a beacon to find the location of food under certain experimental conditions. It is possible that the chickadees were primed to gather spatial information in the form of non-beacon landmarks and that the 'global' cues were close enough to the cache sites to allow the birds to accurately retrieve them. Corvids in Bennett (1993) and J. A. Basil (1993, unpublished dissertation) were able to find the location of hidden food better with proximal cues, but those cues were 15–30 cm from the targets, not acting as beacons. Yet, in the Kelly study, the cues were directly in front of the target. These differing results suggest that the difference between parids and corvids may be an artefact of the methodological design used. Therefore, we are still not sure whether

parids share the corvid preference for proximal information encoding. Future research using a comparative approach with a similar methodology is certainly needed.

Watanabe (2005) demonstrated that in a scatter-hoarding corvid, the scrub jay, global spatial cues seemed to control searching behaviour more than cues specific to the searching tray. The birds preferred to rely on the spatial location of a tray when locating hidden food within the tray, rather than tray-specific cues. However, it was noted that when global spatial cues were made unreliable the birds could use the tray-specific cues to find the food. In this study, the searching tray was an ice-cube tray that had distinct Lego Duplo blocks attached to it. These cues were very close to the hidden food in the ice-cube trays, potentially acting as feature cues or beacons. Therefore, the fact that the birds' searching was more dependent upon global spatial information makes sense in the same way that the chickadees in the Herz *et al.* (1994) study ignored feature information. Feature cues and beacons may not be as reliable in terms of their ability to be used to retrieve caches.

Cheng & Sherry (1992) investigated the use of edges and landmarks as cues. Pigeons and black-capped chickadees were used to investigate the encoding of a landmark in relation to the edge of a tray filled with substrate in relocating hidden food. After being trained to find hidden food located 10 cm from the edge of the tray, the 13 cm high cylindrical landmark was shifted in one of three ways: 10 cm parallel to the edge of the tray, 10 cm perpendicular to the edge of the tray or a combination of 10 cm parallel and 10 cm perpendicular (diagonally) from the edge of the tray. Both groups of birds followed the shifting landmark more strongly when it was moved parallel to the edge during the parallel and diagonal shifts, shifting their searching approximately 10 cm in the parallel direction for both shifts. They did not demonstrate any perpendicular shifts in searching. The authors concluded that perpendicular distance to an edge can act as a cue for encoding spatial locations. This is similar to what Bossema (1979) showed with jays who seemed to be using the perpendicular distance from a line created between two landmarks as a cue.

The experimental design used by Cheng & Sherry (1992) was replicated with Clark's nutcrackers (Gould-Beierle & Kamil 1996) (figure 3). Results indicated that the nutcrackers responded in a similar way. However, in a second experiment when the landmark was removed and the tray was shifted in the room, the birds tended to search close to the original food location in relation to the room, not the tray. This suggested that they may have also been encoding information about the global cues in the room along with cues related to the cylindrical landmark. A third experiment made the global cues unreliable sources of information by rotating the tray within the room for each trial during training. When the same three displacements of the cylindrical landmark occurred as in experiment 1, the birds were more sensitive to perpendicular movement of the landmark, shifting their searching further along this dimension when

compared with the first experiment. Gould-Beierle & Kamil (1998) went on to show that two other species of scatter-hoarding corvids (pinyon jays and scrub jays) also reacted in a similar way to nutcrackers in the same experimental paradigm. The flexibility of encoding shown in these experiments suggests that multiple forms of information can be used, with preference based on the situation or training.

Investigating the encoding of local and global cues further, Gould-Beierle & Kamil (1999) trained three groups of nutcrackers to find a hidden food location in relation to two 'local' landmarks that were at three different distances from the target location in a room filled with substrate. The group that was trained with a cylindrical landmark and flat wooden 'edge' closest to the target location (cylinder 8 cm and edge 10 cm from target) relied on these cues more heavily, whereas the other two groups who were trained with these cues at further distances (group 2: cylinder 24 cm and edge 30 cm from target; group 3: cylinder 72 cm and edge 90 cm from target) relied more heavily on global cues in the room. More specifically, when the cylinder was displaced parallel to the edge, all three groups displaced their searching, indicating that they all encoded information about it. However, group 1 was the only group to shift its searching when the edge was displaced. This suggests that groups 2 and 3 must have been using a combination of the cylinder and global cues to accurately locate the food, whereas group 1 was using both forms of local information only. Interestingly, when the local cues (cylinder and edge) were removed, groups 2 and 3 were still fairly accurate in their searching, whereas group 1 searched randomly. Global information encoded by groups 2 and 3 could be used alone to come within 3 cm of the target location.

Another aspect of this study was that the third group of nutcrackers, which had the cylinder and the edge furthest from the target, took over twice as long to reach criteria during training. Research on landmark use has shown that the further away spatial information is from the goal, the harder it is to be accurate (Cheng 1990; Spetch & Wilkie 1994; Kamil & Jones 1997; Kelly *et al.* in press). It took longer to accurately learn to find the food in the third group, but amazingly they were within 3 cm of the target even when the local cues were removed.

Goodyear & Kamil (2004) demonstrated that Clark's nutcrackers do seem to weight landmarks that are close to the target location more heavily and that these landmarks can overshadow the potential information that could be used from other landmarks. Birds were trained with four landmarks, each a different distance from the target. Birds that had one landmark very close to the target were much more affected when that landmark was removed than birds that had longer distances between that same landmark and the target. They were also more accurate during testing when given only the landmark that was most proximate to the target location during training, as long as it was within 70 cm from the goal. The errors made by the birds suggest that both the distance from each landmark of an array to the target (absolute goal-landmark distance) and the distance of the array

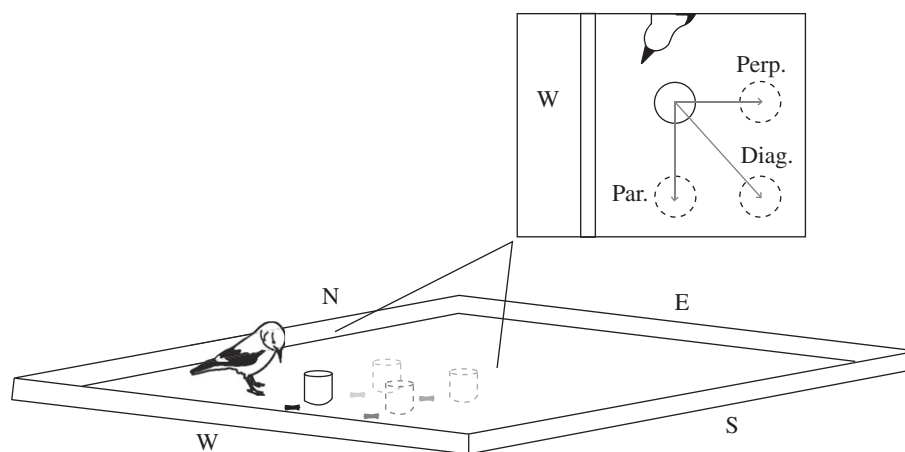


Figure 3. Typical set-up (not to scale) for experiments on landmark displacement with an edge and a single landmark present. The birds are initially trained with the cylinder in the location indicated by the solid circle (top right in the inset with perspective of looking down from above). They are then tested with occasional non-rewarded trials at each of the three test positions (dashed circles), representing displacements perpendicular, parallel and diagonal to the long axis of the nearest edge.

of landmarks to the target (relative goal–landmark distance) are important components in what the birds encode and how they use individual landmarks. These results also show that whether a landmark is encoded as local or global depends, in part, on the experimental situation.

So, in terms of local (proximal) and global (distal) cues, it appears that scatter-hoarding birds can encode information about both, but may rely more heavily on proximal cues when they are available, especially when they are closer to the target location. However, if beacons are available, they do not seem to be used to the same extent. The one-trial associative procedures (Brodbeck 1994; Clayton & Krebs 1994; Brodbeck & Shettleworth 1995) and the study with chickadees (Herz *et al.* 1994) suggest that they might not be encoded. More research on this topic is needed. One could argue that using a beacon is the simpler of the two options in terms of what needs to be remembered. However, if by placing caches directly next to a beacon increases the likelihood that the cache will be found by another animal due to the simplicity of the rule, then placing caches somewhat removed from landmarks, yet close enough to be accurate, might be the best strategy. This strategy has been proposed as a defence that nutcrackers use against cache-robbing by rodents (Vander Wall & Balda 1981) and field studies have shown that nutcrackers tend to cache in the middle of open meadows with few beacons available (Tomback 1977, 1980; Vander Wall & Balda 1981). On the other hand, beacons related to ground caches could also be highly variable in reliability, especially for many corvids who often are retrieving caches through the snow. Small cues have been found to not be important sources of spatial information for Clark's nutcrackers retrieving caches (Balda 1980; Kamil *et al.* 1986). It would make sense that landmarks a bit further from the cache site would be better sources of reliable spatial information.

(b) Scatter-hoarding rodents

Studies of scatter-hoarding rodents suggest that they may have a different strategy when it comes to

encoding information from cues in their environment. Although many scatter-hoarding rodents may use their keen sense of smell to locate cached food under certain circumstances, it has been demonstrated that they can and do use spatial memory strategies as well. Controlling for the possibility of olfactory-based strategies, many studies have shown that rodents have the ability to use spatial memory to relocate food (e.g. Jacobs 1992; Devenport *et al.* 2000). Lavenex *et al.* (1998) found that fox squirrels use distal environmental cues rather than proximal cues to find hidden food on a plastic board in a field experiment. Even when proximal cues were available in the form of arrays of objects on the plastic board, wild squirrels used cues outside of the board to find the location of peanuts hidden within the board. They most probably relied on directional information derived from these distal cues combined with remembering the spatial location of food on the previous trial, ignoring the proximal cues available on the board that predicted the position of the food. Jacobs & Shiflett (1999) also showed that wild fox squirrels in the field consistently used distal cues to find a peanut in a vertical maze, even when cues from the maze itself could be used. Columbian ground squirrels also seem to rely more on global cues in locating a baited platform within an array of nine identical platforms in the field (Vlasak 2006). Changing local landmarks did not affect accuracy but when global landmarks were changed, accuracy decreased.

More recent work suggests that scatter-hoarding rodents may be flexible in the kinds of cues they use to encode spatial locations. Gibbs *et al.* (2007) showed that flying squirrels do not have a single encoding strategy. Instead, they appear to average their searching based on different frames of reference (beacons, global cues or location of local landmarks within an array) when those cues are in conflict. The squirrels make a response that is consistent with the majority of frameworks available at the time of searching, meaning they choose the location predicted by the averaging of at least two of the three frames of reference. Waisman & Jacobs (2008) also showed that fox squirrels use a

flexible searching strategy, searching at locations predicted by the greatest number of cues. However, they do seem to prefer distal cues. One interesting result was that the squirrels seemed to use beacons over other cues when the feeders were very salient. It is possible then that the saliency of beacons can influence whether an organism encodes them.

So, in scatter-hoarding rodents, distal cues may be more important than proximal cues; however, recent work suggests a more flexible strategy. The experimental situation may contribute to the differences in encoding by rodents, in much the same way that is seen in the work with scatter-hoarding birds. The work conducted with scatter-hoarding birds suggests that proximal cues are more important, but that both proximal and distal cues can be encoded depending on the training procedure. More work with rodents is needed, potentially looking at how different training procedures influence the kinds of cues that are encoded.

Cheng *et al.* (2007) have hypothesized that a Bayesian model of cue weighting may be used by scatter-hoarding animals as a means of encoding and using landmarks. Bayesian psychophysical perception studies have shown that humans can combine multiple cues in a nearly optimal fashion to estimate spatial parameters. In this model, Cheng *et al.* predict that cue types that might be least preferred in a hierarchical sense might end up being weighted more heavily when they are combined when compared with the weight given to a preferred cue type. Landmarks would be weighted according to their variance and the prior experience the animal had with them. In other words, if there is a proximal cue located fairly close to a cache site, it might not be weighted as heavily as four distal cues that are more reliable and have been previously encoded. This idea may fit the work with scatter-hoarding squirrels demonstrating the flexibility of using a strategy where the majority of cues available predict the spatial location (Gibbs *et al.* 2007; Waisman & Jacobs 2008). It might also be an appropriate model for scatter-hoarding birds.

4. WHAT INFORMATION IS ACTUALLY ENCODED?

(a) *Bearings and geometric rules*

In a series of studies with Clark's nutcrackers, the ability to use geometric information in varying degrees was examined. In the first study, Kamil & Jones (1997) showed that the birds could learn to find a hidden food source that was always situated halfway between two tall landmarks. The position of the landmarks within the room and the distance between them varied from trial to trial during training. The birds acquired the task very rapidly and were extremely accurate when tested with probe trials with novel inter-landmark distances. Kamil & Jones (2000) also showed that nutcrackers could learn to search at a location one-fourth of the distance from one landmark and at the third point of a triangle created between the two landmarks and the target location based on constant bearings (directions) from the landmarks. A third group had more difficulty learning that the

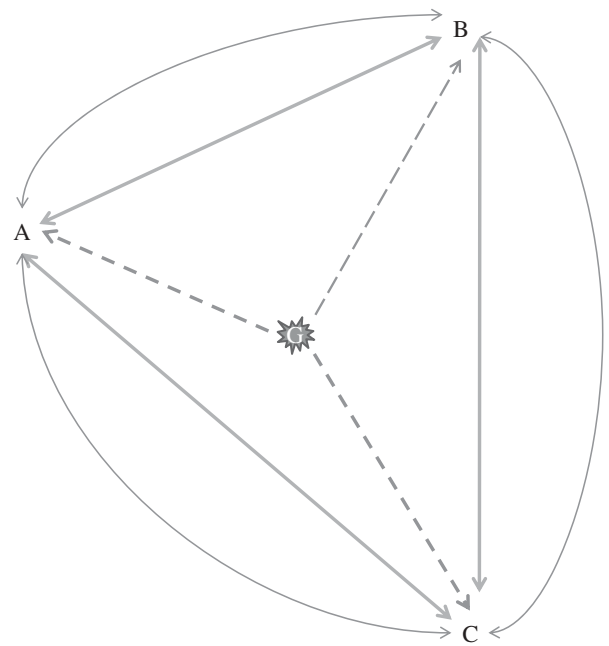


Figure 4. The star (G) is the goal location and A, B, and C are three landmarks. The direction from the goal to a landmark (e.g. GA) is an absolute bearing. The length of GA is the goal–landmark distance. The arcs between the landmarks (e.g. AB) represent relative bearings.

target location was at the third point of a triangle created between the two landmarks and a constant distance from the target to each landmark. When one of the landmarks was removed, this third group (constant distance group) did not search in the appropriate place, whereas the other groups did. This suggests that directional information may be weighted more heavily during encoding of spatial locations than distance information.

Kamil & Jones (2000) demonstrated that when absolute and relative bearings were put in conflict, the birds used absolute bearings to search for the target location. It is difficult to explain relative bearings. But consider the following example: suppose a target was always located south of one landmark and east of another and equidistant from both. Absolute bearings would be used by finding the spot that was simultaneously south of the first landmark and east of the second. To use relative bearings, one would have to find a spot from which the relative visual angle between the two landmarks was 90° . Furthermore, this relative angle rule, in and of itself, would describe a set of locations in an arc. So the use of relative bearings to define a unique location requires either three or more landmarks, or distance information. Another way to look at this is to imagine an animal at a goal location ('G' in figure 4). There are many ways that the location of G can be encoded, including the bearing and distance from any single landmark, the absolute bearings to any pair of landmarks and the relative bearings among landmarks.

Jones & Kamil (2001) found that nutcrackers can encode relative bearings from landmarks if trained in a specific way. In this study, the target location was defined by a constant angle from two landmarks whose distance between each other and position in

the room varied from trial to trial. One group's array was always in the same orientation with respect to the walls of the room, whereas the array rotated from trial to trial for the other group. The first group could then use either relative or absolute bearings to find the target, whereas the second group could only use relative bearings. Both groups learned the task and transferred to novel inter-landmark distances. Therefore, nutcrackers can use relative bearings if they are trained under conditions in which absolute bearings are unreliable. This flexibility is interesting and probably important in field settings where the environment is subject to change, with certain cues potentially being less stable or reliable. In most cases, the use of absolute bearings, along with distance information, is a reliable means of encoding locations. Stable global cues usually allow for this kind of encoding to be an adaptive strategy. However, in situations where absolute bearings are not possible or stable and there is a rich environment with many landmarks, relative bearing information can be encoded. It appears that the default means of encoding might be through absolute bearings, yet it is very difficult to manipulate relative bearings in the laboratory without also manipulating other important geometric dimensions or features.

One can also question whether there are species differences in the ability to learn geometric rules and bearings. Species differences in the ability to learn the geometric rule 'half-way' were reported by Jones *et al.* (2002). Scatter-hoarding corvids (Clark's nutcrackers), non-hoarding corvids (jackdaws) and non-hoarding non-corvids (pigeons) all learned the rule, but the jackdaws took much longer to learn it than the pigeons and nutcrackers. The nutcrackers were more accurate on this task than both the jackdaws and the pigeons. This indicates that although learning geometric rules may be something that many avian species can do, some learn it more quickly than others and some are much more accurate using the rule. It makes sense that the scatter-hoarding nutcracker might be able to learn this kind of task quickly and accurately, as finding individual spatial locations is more crucial to this species. Accuracy is also important in scatter-hoarding, as caches (especially those made in the ground) are small and a slight error in encoding their location might mean that a cache is never found. A bird's beak is quite small and hitting the target (cache) requires accuracy measured in millimetres (Kamil & Cheng 2001).

Spetch *et al.* (2003) compared the ability of pigeons to learn based on constant bearings or constant distances in a similar way to the nutcrackers in Kamil & Jones (2000). The results indicated that the pigeons could learn using both methods of encoding (as the nutcrackers did), but that the pigeons found both problems difficult to learn and were less accurate in both conditions. Nutcrackers learned the constant bearing problem fairly quickly and were much more accurate (both the constant-direction and constant-bearing groups) than the pigeons. The pigeons also could not transfer to novel extrapolated inter-landmark distances (those that were outside the range covered by the trained inter-landmark distances). Nutcrackers in the

constant-bearing group could, but those in the constant-direction group could not. The differences between pigeons and nutcrackers in this study also indicate that nutcrackers may be quicker and more accurate at learning the geometric relationships among landmarks, especially when using constant bearing information.

The results of these studies suggest that the geometric algorithm nutcrackers use depends on the conditions under which they were trained. This was shown in a different way by Kelly *et al.* (2008), who trained nutcrackers to find a hidden food location in the centre of a four landmark array that always remained stationary. When tested by expanding the landmark array in one direction only (east–west or north–south) or both directions simultaneously, the birds searched based on absolute distance and direction relationships between the target location and specific landmarks. They did not search in the middle. Similar results using fixed arrays of landmarks during training have been reported with pigeons (Spetch *et al.* 1997). The contrast between these studies with fixed landmark arrays and the results of Kamil & Jones (2000) and Jones & Kamil (2001) who used moving and/or rotating arrays suggest that training procedures influence how spatial information is encoded. When consistent, stable landmarks are present, nutcrackers (and pigeons) will encode locations using bearings and/or distances from landmarks rather than using more abstract rules such as halfway between landmarks.

One of the most interesting features of cache recovery in birds such as nutcrackers that cache small pieces of food (pine nuts) and then dig for those cached items with a very small shovel (their beak) is the degree of precision that successful cache recovery requires. Kamil & Cheng (2001) proposed the multiple bearings hypothesis as a way to understand how such accuracy could be attained by these birds. They noted that in the Kamil & Jones studies (i.e. Kamil & Jones 1997; Jones & Kamil 2001), there were indications that nutcrackers were more accurate when using directional information than distance information, especially when the goal location was located relatively far from the landmarks. This led them to consider the role of bearings, particularly the direction from the goal to each of several landmarks. A simple simulation model showed that the more bearings that were available, the more accurate searching should be. Since each landmark provides a bearing, additional landmarks in an array provide additional bearings and these additional bearings should increase search accuracy. This model is proposed for situations where the landmarks are not close enough to the target location to overshadow each other.

Kamil *et al.* (2001) tested a number of predictions made by the multiple bearings hypothesis with Clark's nutcrackers. As expected, accuracy improved as the number of landmarks present increased. In addition, as the target–landmark distance increased, direction error increased more slowly than distance error. This confirms that using bearing information might be more accurate than using distance information when locating a target in space. Finally,

direction error made by the birds was constant across increasing goal–landmark distances when measured in degrees, whereas distance error increased. This again supports the potential value in using bearing information for accurate search. Further analysis of the multiple bearings hypothesis would be beneficial, especially as it relates to scatter-hoarding mammals. It does appear, however, that encoding multiple bearings using multiple landmarks increases search accuracy and is an important mechanism used in food-hoarding birds.

(b) Use of sun compass for bearing information

The Sun is a prominent feature of the environment and therefore a potentially salient directional cue. Using it to gain bearing information necessitates the ability to compensate for its change in position in the sky throughout the course of the day. This ability has been shown to be important both in larger-scale navigation (e.g. homing in pigeons) and in smaller-scale navigation involving cache recovery. The Sun's position in the sky has to be converted to a compass direction from which the organism can gain a bearing. This is done by computing what is called the Sun's azimuth. An imaginary arc can be perceived that connects the Sun with the closest point on the horizon. If you measure the angle on the surface of the Earth between that point and north, you have calculated the azimuth. This bearing from the sun compass can be combined with bearings from landmarks on the Earth's surface to increase the accuracy of search.

When food-hoarding birds were allowed to hoard and retrieve in an outdoor aviary after being exposed to an artificial day-length in the laboratory that caused a shift in their internal clock relative to outdoors, pinyon jays (Wiltschko *et al.* 1999) and scrub jays (Wiltschko & Balda 1989) were more affected by a 6 h internal clock shift than Clark's nutcrackers were in relocating their caches (Wiltschko *et al.* 1999). The authors suggest that differences in the habitats of these birds may account for their ability to use a sun compass. Clark's nutcrackers live at high mountainous elevations where the coniferous forest canopy is usually complete, blocking the Sun from reaching the ground. Even in open areas where the Sun can be seen and where nutcrackers do hoard food, there is often considerable cloud cover during the autumn months when the birds are hoarding the most. Pinyon jays and scrub jays, on the other hand, live at lower elevations where there are more openings in the canopy and there are larger stretches of open areas. In the autumn at lower elevations, cloud cover is not as consistent as at higher elevations. Therefore, the two jay species may be more exposed to the Sun and thus be able to rely on a sun compass more readily than the nutcracker.

Black-capped chickadees, scatter-hoarding parids, also show shifts in searching based on internal clock shifts, but these shifts are smaller than those seen by the jays mentioned previously and the shifts only occur during certain testing situations (Duff *et al.* 1998). Chickadees will also not use a sun compass in the absence of familiar landmarks, suggesting the primary role of the sun compass is providing directional

information in combination with distance information from landmarks.

Although it is clear that clock shifts can disrupt cache recovery in outdoor aviaries, there is a conflict between these clock shift results and the multiple bearings hypothesis. Kamil & Cheng (2001) pointed out that if the animal has remembered bearings from a goal location to several landmarks, under many conditions, especially when the landmarks are scattered around the goal location, a clock shift should result in highly variable searching. This would be the result of the bearings no longer converging at a single location (see fig. 3 in Kamil & Cheng 2001).

These sun-compass studies demonstrate the importance of experimental methods conducted in semi-naturalistic settings, in these cases outdoor aviaries. Food-hoarding animals appear to have the capacity to encode spatial information from a number of sources within laboratory situations. However, much of this depends on how the animals are trained. In a more semi-naturalistic setting, the preference the animals have for certain kinds of cues may become more evident. Although there have been more semi-naturalistic field experiments done with mammals (Lavenex *et al.* 1998; Jacobs & Shiflett 1999; Vlasak 2006; Waisman & Jacobs 2008), the same cannot be said for birds. Now that we understand more detailed aspects of how scatter-hoarding birds use cues under certain conditions in the laboratory, it might be of interest to investigate what they are more likely to do in a more naturalistic setting.

(c) Geometric shape of enclosures versus feature cues

Another aspect of learning about geometry has to do with encoding shapes of enclosures in a laboratory setting versus encoding feature cues within the enclosure. Research with rats in rectangular enclosures has indicated that they seem to predominately encode spatial information about the geometric properties of the enclosure, ignoring features about other cues or landmarks that are available, when searching for hidden food in a working memory paradigm (the location of the hidden food varies from trial to trial), but when searching for hidden food in a reference memory paradigm (the location of the hidden food remains the same across trials), they seemed to encode both geometry and feature cue information. However, even in a reference memory task, rats continue to show a reliance on geometric cues when features and geometry are placed in conflict (Cheng 1986; see also Cheng 2005; Cheng & Newcombe 2005 for reviews and further discussion of this research area).

Pigeons also seem to encode both geometry and feature cue information in reference memory hidden food paradigms in rectangular enclosures. When trained with distinct features in the corners of a rectangular enclosure, birds simultaneously encoded the geometric shape of the enclosure (Kelly *et al.* 1998). But when the two kinds of information were placed in conflict, the way the birds were trained determined which cues were used. Birds trained with both features and geometry relied more on features during testing

and birds initially trained with only geometry divided their choices between features and geometry during testing. Therefore, it appears that pigeons usually encode both types of information, but rely more on feature information when it is present.

Kelly (*in press*) trained Clark's nutcrackers in an open-field task similar to that of rats and pigeons in rectangular arenas. Four landmarks were arranged in a rectangular configuration in a room. The birds either had (i) all four landmarks the same, thus requiring them to use the geometric configuration of the landmarks to figure out which one had the hidden food beside it, or (ii) had a unique landmark for each point of the rectangle, thus being able to use either the geometric configuration or the featural information. The first group had trouble learning the task, therefore demonstrating that they needed more information than just the geometric configuration of the array to effectively encode the location. The second group readily learned the task. When the second group of birds had the unique landmarks switched to identical landmarks in a testing phase, the birds could use the geometric configuration to find the food. Kelly concluded that learning feature information facilitated the learning of geometry.

Indeed, the facilitation of geometry by features has also been shown in rats (Pearce *et al.* 2001, 2006; Graham *et al.* 2006), humans (Kelly & Spetch 2004a) and pigeons (Kelly & Spetch 2004b), and an attempt to explain these findings has been modelled by Miller & Shettleworth (2007, 2008). In this model, it is assumed that the relative total associative strength of cues at a spatial location determines whether an organism will choose that location. Cues at the correct location become associated with a reward, and the cues present at the location can combine either to contribute to blocking through cue competition or contribute to feature enhancement, facilitating the learning of certain cues based on the saliency of the other available cues. However, Doeller and co-workers have proposed that learning the spatial relationships between landmarks and boundaries may elicit activation of separate brain systems, i.e. right dorsal striatal and right posterior hippocampal areas, respectively (see Doeller & Burgess 2008; Doeller *et al.* 2008).

Gray *et al.* (2005) used mountain chickadees in a rectangular enclosure and tested for differences in encoding feature and geometric cues in this setting. Feature cues were a unique colour on one wall. Geometric cues were the rectangular shape of the enclosure. Three groups of birds were trained. The first group could only use geometric information (all four walls the same colour). The second group had food hidden near the uniquely colored wall. The third group had food hidden distant from a uniquely colored wall. When tested, the birds in the first and third groups could both use geometry during testing. However, the birds in group 2 that were trained with a target located next to a uniquely colored wall could not. This is very different from studies with pigeons and nutcrackers in that the chickadees seemed to encode feature information when it was next to the target, but not also simultaneously encode geometric

information. The model of Miller & Shettleworth (2007, 2008), however, can accommodate both types of outcome, depending on the saliency and associative strength of the cues in question.

The previous studies investigating the encoding of the geometric shape of an enclosure versus feature cues are similar to studies examining the encoding of beacons versus spatial cues, either local or global. Feature cues can act as beacons in a rectangular enclosure. If an animal searches in the corner with a distinct cue in it or goes to the corner of the distinctly patterned or colored wall, it does not need to use spatial cues to find the food. Using geometric information obviously necessitates the encoding of the spatial layout of the environment. However, the main difference is that the geometric layout of experimental enclosures provides continuous surfaces (i.e. walls), whereas studies using discrete landmarks often may not be encoded in the same way, namely as contiguous geometric information.

The results of the Gray *et al.* (2005) study with mountain chickadees are interesting in two regards. First, they are in direct conflict with some previous studies with scatter-hoarding black-capped chickadees (Brodbeck 1994; Herz *et al.* 1994; Brodbeck & Shettleworth 1995). Unlike these previous studies, the mountain chickadees in this experiment seemed to be encoding featural cues to the exclusion of other sources of information when the features were very close to the target location and could act as a beacon. This example of overshadowing could be an artefact of the nature of this task, as opposed to the more semi-naturalistic nature of Herz *et al.* (1994) but it is also likely that training procedures may have influenced the differences between these two studies. However, LaDage *et al.* (2009), in a one-trial associative task, also found that mountain chickadees visited feeders more often based on their colour than on their spatial location. This could indicate a potential difference between the two species of chickadee (black-capped and mountain) in terms of their preference for spatial and non-spatial strategies. Why this might be the case is not clear, but warrants further exploration.

In Gray *et al.* (2005), feature cues and/or geometrical cues could potentially be used to solve the problem. One important aspect that is discussed is that animals raised in human-made environments with salient geometry in the forms of angles and edges may be more predisposed to encode information that way, whereas wild-caught animals, such as the mountain chickadees, may not. This might explain the differences found between chickadees and pigeons, but it does not explain why the nutcrackers in Kelly *et al.* (2008) encoded both geometry and feature information in much the same way that pigeons do. Furthermore, Batty *et al.* (2009) compared hand-reared and wild-caught black-capped chickadees in a food-finding task within a rectangular environment. They found that both groups encoded geometric information, so there were no differences based on rearing. They also found that only some of their wild-caught mountain chickadees encoded geometric information in the task, again indicating a potential difference in the way black-capped and mountain chickadees encode or use spatially based cues.

5. CONCLUSION

Scatter-hoarding animals have taught us a great deal about small-scale navigation. They can encode different types of information from multiple types of cues. They are highly flexible in how and what they encode, especially as a function of the details of the environment in which they are tested. It also appears that there may be some general differences in what scatter-hoarding birds and rodents encode, although further research is necessary to discern whether these differences are a reflection of true differences between the birds and rodents or differences based on experimental design.

For birds, proximal cues seem to be important because landmarks close to the goal are likely to overshadow other sources of spatial information. However, if such cues are located directly at the target in the form of a beacon, some studies using food-hoarding birds indicate that these cues are encoded, whereas other studies show that they are not encoded. Birds appear to use distance and directional information when landmarks are fairly close to a target location. However, birds can reliably use more distal landmarks, but perhaps in this case they rely more on directional information (bearings) taken from multiple landmarks. The more bearings birds encode, the more accurate their retrieval is likely to be when using more distal forms of landmarks. The scatter-hoarding Clark's nutcracker can learn abstract geometric rules if trained with other potential sources of spatial information made unreliable. However, if given a preference, these birds will most probably encode bearing and distance information from multiple landmarks. It appears that directional information is more important and that absolute bearings may be used over relative bearings, although there has yet to be solid experimental evidence to reliably demonstrate this latter issue. This implies that these birds are predisposed to encoding information from several sources, ranging from multiple proximal or distal landmarks, to global cues and potentially the use of a sun compass to gain bearings. However, the ability to use a sun compass may depend on its availability in the bird's natural environment and the types of landmarks present.

Comparative studies have shown differences between scatter-hoarding birds and non-scatter-hoarding birds. Using one-trial associative procedures, a number of studies have shown that scatter-hoarding birds preferentially encode and use spatial information to solve the task, whereas non-hoarding birds use spatial or feature information equally often (Brodbeck 1994; Clayton & Krebs 1994; Brodbeck & Shettleworth 1995). Although this predisposition to encode spatially may be more readily seen in scatter-hoarding birds, some studies have not found similar cue weighting (Healy & Krebs 1992; Healy 1995; LaDage *et al.* 2009). Whether or not scatter-hoarding birds are more attuned to spatial encoding, they have been shown to learn spatial tasks more quickly and to be more accurate at finding spatial locations. In Jones *et al.* (2002), scatter-hoarding Clark's nutcrackers learned to encode landmarks using a geometric rule more quickly than non-hoarding jackdaws. Nutcrackers were also more accurate at finding the hidden food location than either jackdaws or

pigeons. Although all three species could learn the task, their performance during the task differed. In studies looking at ability to find hidden food based on constant bearings or distances, Spetch *et al.* (2003) found that pigeons had more difficulty learning the task and were less accurate than the nutcrackers in Kamil & Jones (2000).

Scatter-hoarding and non-hoarding birds may share similar general abilities for encoding and using landmarks to find spatial locations within their environments. However, scatter-hoarding may have caused refinement in this general ability, as demonstrated through increased accuracy and learning. As was stated earlier, accuracy is a very important aspect of scatter-hoarding, since the to-be-located cache and the bird's beak are relatively small. Accurate retrieval of caches would save time and energy. One hypothesis based on Kamil & Cheng (2001) is that this need for increased accuracy may have driven the encoding of multiple landmarks when learning the spatial location of a target. The more bearings encoded, the more accurate retrieval will be. Although Kamil *et al.* (2001) demonstrated that Clark's nutcrackers' accuracy did indeed improve when the number of landmarks available to encode increased, what would be of interest is whether there might be differences in this in ability to encode multiple bearings in non-hoarding birds, such as the jackdaw or pigeon.

For rodents, the picture is not as clear. There have been fewer direct studies of landmark and cue use in scatter-hoarding rodents. However, research suggests that distal cues may be more important sources of spatial information. Why this would be the case is not clear, but it does warrant further investigation. The rodents that have been studied do appear to have some flexibility in encoding spatial information and may do so in ways that reflect the kinds of cues available and their salience. More research on this topic is needed.

For future research, how scatter-hoarding birds or rodents may differ in the details of encoding spatial information based on the kinds of caches they make or the length of time they need to remember the caches would be an interesting topic to investigate. This could include comparisons between families (i.e. parids and corvids) or within family comparisons based on differences in hoarding behaviour (for a similar analysis, see Smulders *et al.* 2010). Further analysis of when beacons may or may not be encoded would also be of interest. Questions to consider include whether the saliency of a beacon or other featural cues affects whether or not it is encoded, and if there are species differences in the hoarding and/or use of beacons in relocating food. The accuracy of retrieval under various encoding scenarios would also be interesting to examine. Just because an animal can learn to locate a spatial position using a particular strategy due to training procedures does not mean that it is the most accurate strategy for the situation. The multiple bearing hypothesis (Kamil & Cheng 2001) predicts that the more landmarks encoded, the more accurate searching will be. One could also assume that the preferred strategy for a given species would also provide the most accuracy, if accurate searching is of high importance.

Another interesting aspect that has not been investigated is the potential differences in performance between experiments allowing the birds and rodents to hoard their food versus experiments where the experimenter hides the food and the animal must learn the hidden location. When comparing hoarding and non-hoarding species, it is necessary to use the hidden food paradigm, but no one has investigated whether hoarding birds and rodents might encode or use cues differently when they learn to find food hidden by the experimenter versus food they have hidden themselves. This is an important question, considering that the hidden food paradigm has been used extensively to investigate cue use, especially in birds. Along these same lines, another aspect that has not been formally investigated is potential differences in encoding or using cues when retrieving caches the animal has made itself versus caches it has observed another animal make.

Finally, the combination of self-motion cues (dead reckoning or path integration) or celestial cues (magnetic or the sun compass) along with landmarks by Clark's nutcrackers has not received much investigation (but see Wiltschko *et al.* 1999; Gibson & Wilks 2008; Kelly *et al.* in press). These initial studies show that Clark's nutcrackers encode multiple cues and can rely on these in a weighted manner. Further work needs to be done looking at how these multiple sources of spatial information might be integrated in scatter-hoarding animals, as we know that many non-scatter-hoarding birds and rodents can encode multiple types of spatial cues (self-motion cues: Mittelstaedt & Mittelstaedt 1982; von Saint Paul 1982; Etienne *et al.* 1986; Etienne 1992; Etienne & Jeffery 2004; sun compass: Wiltschko & Balda 1989; Wiltschko *et al.* 1999).

Research on small-scale spatial navigation has grown substantially since early studies focusing on traditional laboratory species. However, these approaches have certainly provided a strong understanding as to the mechanisms underlying spatial navigation. This foundation has allowed researchers to address questions aimed at understanding whether scatter-hoarding animals use landmarks in different ways compared with non-hoarding species. As discussed in this review, these investigations have proven quite fruitful. They have shown that although many generalities can be seen in how hoarding and non-hoarding species use spatial information, there is significant support for a quantitative difference in how this information is used.

REFERENCES

- Balda, R. P. 1980 Recovery of cached seeds by captive *Nucifraga caryocatactes*. *Z. Tierpsychol. Beih.* **52**, 331–346.
- Balda, R. P. & Kamil, A. C. 1989 A comparative study of cache recovery by three corvid species. *Anim. Behav.* **38**, 486–495. (doi:10.1016/S0003-3472(89)80041-7)
- Barkley, C. L. & Jacobs, L. F. 1998 Visual environment and delay affect cache retrieval accuracy in a food-storing rodent. *Anim. Learn. Behav.* **26**, 439–447.
- Batty, E. R., Bloomfield, L. L., Spetch, M. L. & Sturdy, C. B. 2009 Comparing black-capped (*Poecile atricapillus*) and mountain chickadees (*Poecile gambeli*): use of geometric and featural information in a spatial orientation task. *Anim. Cognit.* **12**, 633–641. (doi:10.1007/s10071-009-0222-3)
- Bennett, A. T. D. 1993 Spatial memory in a food storing corvid. 1. Near tall landmarks are primarily used. *J. Comp. Physiol. Sensory Neural Behav. Physiol.* **173**, 193–207.
- Bossemma, I. 1979 Jays and oaks: an eco-ethological study of a symbiosis. *Behaviour* **70**, 1–117. (doi:10.1163/156853979X00016)
- Brodbeck, D. R. 1994 Memory for spatial and local cues: a comparison of a storing and a nonstoring species. *Anim. Learn. Behav.* **22**, 119–133.
- Brodbeck, D. R. & Shettleworth, S. J. 1995 Matching location and color of a compound stimulus: comparison of a food-storing and a nonstoring bird species. *J. Exp. Psychol. Anim. Behav. Process.* **21**, 64–77. (doi:10.1037/0097-7403.21.1.64)
- Cartwright, B. A. & Collett, T. S. 1982 How honey bees use landmarks to guide their return to a food source. *Nature* **295**, 560–564. (doi:10.1038/295560a0)
- Cartwright, B. A. & Collett, T. S. 1983 Landmark learning in bees. *J. Comp. Physiol. Sensory Neural Behav. Physiol.* **151**, 521–543. (doi:10.1007/BF00605469)
- Cheng, K. 1986 A purely geometric module in the rat's spatial representation. *Cognition* **23**, 149–178. (doi:10.1016/0010-0277(86)90041-7)
- Cheng, K. 1988 Some psychophysics of the pigeon's use of landmarks. *J. Comp. Physiol. Sensory Neural Behav. Physiol.* **162**, 815–826. (doi:10.1007/BF00610970)
- Cheng, K. 1989 The vector sum model of pigeon landmark use. *J. Exp. Psychol. Anim. Behav. Process.* **15**, 366–375. (doi:10.1037/0097-7403.15.4.366)
- Cheng, K. 1990 More psychophysics of the pigeon's use of landmarks. *J. Comp. Physiol. Sensory Neural Behav. Physiol.* **166**, 857–863.
- Cheng, K. 1994 The determination of direction in landmark-based spatial search in pigeons: a further test of the vector sum model. *Anim. Learn. Behav.* **22**, 291–301.
- Cheng, K. 2005 Reflections on geometry and navigation. *Connect. Sci.* **17**, 5–21. (doi:10.1080/09540090500138077)
- Cheng, K. & Newcombe, N. S. 2005 Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychon. Bull. Rev.* **12**, 1–23.
- Cheng, K. & Sherry, D. F. 1992 Landmark-based spatial memory in birds (*Parus atricapillus* and *Columba livia*): the use of edges and distances to represent spatial positions. *J. Comp. Psychol.* **106**, 331–341. (doi:10.1037/0735-7036.106.4.331)
- Cheng, K., Spetch, M. L., Kelly, D. M. & Bingman, V. P. 2006 Small-scale spatial cognition in pigeons. *Behav. Process.* **72**, 115–127. (doi:10.1016/j.beproc.2005.11.018)
- Cheng, K., Shettleworth, S. J., Huttenlocher, J. & Rieser, J. J. 2007 Bayesian integration of spatial information. *Psychol. Bull.* **133**, 625–637. (doi:10.1037/0033-2909.133.4.625)
- Clayton, N. S. & Krebs, J. R. 1994 One-trial associative memory: comparison of food-storing and nonstoring species of birds. *Anim. Learn. Behav.* **22**, 366–372.
- Collett, M. & Collett, T. S. 2009 The learning and maintenance of local vectors in desert ant navigation. *J. Exp. Biol.* **212**, 895–900. (doi:10.1242/jeb.024521)
- Collett, T. S., Cartwright, B. A. & Smith, B. A. 1986 Landmark learning and visuospatial memories in gerbils. *J. Comp. Physiol. Sensory Neural Behav. Physiol.* **158**, 835–851. (doi:10.1007/BF01324825)
- Devenport, J. A., Luna, L. D. & Devenport, L. D. 2000 Placement, retrieval, and memory for caches by thirteen-lined ground squirrels. *Ethology* **106**, 171–183. (doi:10.1046/j.1439-0310.2000.00522.x)

- Doeller, C. F. & Burgess, N. 2008 Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proc. Natl Acad. Sci. USA* **105**, 5909–5914. (doi:10.1073/pnas.0711433105)
- Doeller, C. F., King, J. A. & Burgess, N. 2008 Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proc. Natl Acad. Sci. USA* **105**, 5915–5920. (doi:10.1073/pnas.0801489105)
- Duff, S. J., Brownlie, L. A., Sherry, D. F. & Sangster, M. 1998 Sun compass and landmark orientation by black-capped chickadees (*Parus atricapillus*). *J. Exp. Psychol. Anim. Behav. Process.* **24**, 243–253. (doi:10.1037/0097-7403.24.3.243)
- Etienne, A. S. 1992 Navigation of a small mammal by dead reckoning and local cues. *Curr. Dir. Psychol. Sci.* **1**, 48–52. (doi:10.1111/1467-8721.ep11509737)
- Etienne, A. S. & Jeffery, K. J. 2004 Path integration in mammals. *Hippocampus* **14**, 180–192. (doi:10.1002/hipo.10173)
- Etienne, A. S., Maurer, R., Saucy, F. & Teroni, E. 1986 Short-distance homing in the golden hamster after a passive outward journey. *Anim. Behav.* **34**, 696–715. (doi:10.1016/S0003-3472(86)80054-9)
- Gibbs, S. E. B., Lea, S. E. G. & Jacobs, L. F. 2007 Flexible use of spatial cues in the southern flying squirrel (*Glaucomys volans*). *Anim. Cognit.* **10**, 203–209. (doi:10.1007/s10071-006-0059-y)
- Gibson, B. & Wilks, T. 2008 The use of self-motion cues and landmarks by Clark's nutcrackers (*Nucifraga columbiana*) during a small-scale search task. *Anim. Behav.* **76**, 1305–1317. (doi:10.1016/j.anbehav.2008.06.015)
- Goodyear, A. J. & Kamil, A. C. 2004 Clark's nutcrackers (*Nucifraga columbiana*) and the effects of goal-landmark distance on overshadowing. *J. Comp. Psychol.* **118**, 258–264. (doi:10.1037/0735-7036.118.3.258)
- Gould-Beierle, K. L. & Kamil, A. C. 1996 The use of local and global cues by Clark's nutcrackers, *Nucifraga columbiana*. *Anim. Behav.* **52**, 519–528. (doi:10.1006/anbe.1996.0194)
- Gould-Beierle, K. L. & Kamil, A. C. 1998 Use of landmarks in three species of food-storing corvids. *Ethology* **104**, 361–377.
- Gould-Beierle, K. L. & Kamil, A. C. 1999 The effect of proximity on landmark use in Clark's nutcrackers. *Anim. Behav.* **58**, 477–488. (doi:10.1006/anbe.1999.1185)
- Graham, M., Good, M. A., McGregor, A. & Pearce, J. M. 2006 Spatial learning based on the shape of the environment is influenced by properties of the objects forming the shape. *J. Exp. Psychol. Anim. Behav. Process.* **32**, 44–59. (doi:10.1037/0097-7403.32.1.44)
- Gray, E. R., Bloomfield, L. L., Ferrey, A., Spetch, M. L. & Sturdy, C. B. 2005 Spatial encoding in mountain chickadees: features overshadow geometry. *Biol. Lett.* **1**, 314–317. (doi:10.1098/rsbl.2005.0347)
- Healy, S. 1995 Memory for objects and positions: delayed non-matching-to-sample in storing and non-storing tits. *Q. J. Exp. Psychol. B* **48**, 179–191.
- Healy, S. 1998 *Spatial representation in animals*. New York, NY: Oxford University Press.
- Healy, S. & Krebs, J. R. 1992 Delayed-matching-to-sample by marsh tits and great tits. *Q. J. Exp. Psychol. B* **45**, 343–351.
- Herz, R. S., Zañette, L. & Sherry, D. F. 1994 Spatial cues for cache retrieval by black-capped chickadees. *Anim. Behav.* **48**, 343–351. (doi:10.1006/anbe.1994.1247)
- Jacobs, L. F. 1992 Memory for cache locations in Merriam's kangaroo rats. *Anim. Behav.* **43**, 585–593.
- Jacobs, L. F. & Liman, E. R. 1991 Grey squirrels remember the locations of buried nuts. *Anim. Behav.* **43**, 103–110. (doi:10.1016/S0003-3472(05)80506-8)
- Jacobs, L. F. & Shiflett, M. W. 1999 Spatial orientation on a vertical maze in free-ranging fox squirrels (*Sciurus niger*). *J. Comp. Psychol.* **113**, 116–127. (doi:10.1037/0735-7036.113.2.116)
- Jones, J. E. & Kamil, A. C. 2001 The use of relative and absolute bearings by Clark's nutcrackers, *Nucifraga columbiana*. *Anim. Learn. Behav.* **29**, 120–132.
- Jones, J. E., Antoniadis, E., Shettleworth, S. J. & Kamil, A. C. 2002 A comparative study of geometric rule learning by nutcrackers: (*Nucifraga columbiana*), pigeons (*Columba livia*), and jackdaws (*Corvus monedula*). *J. Comp. Psychol.* **116**, 350–356. (doi:10.1037/0735-7036.116.4.350)
- Kamil, A. C. & Balda, R. P. 1985 Cache recovery and spatial memory in Clark's nutcrackers *Nucifraga columbiana*. *J. Exp. Psychol. Anim. Behav. Process.* **11**, 95–111. (doi:10.1037/0097-7403.11.1.95)
- Kamil, A. C. & Cheng, K. 2001 Way-finding and landmarks: the multiple-bearings hypothesis. *J. Exp. Biol.* **204**, 103–113.
- Kamil, A. C. & Jones, J. E. 1997 The seed-storing corvid Clark's nutcracker learns geometric relationships among landmarks. *Nature* **390**, 276–279. (doi:10.1038/36840)
- Kamil, A. C. & Jones, J. E. 2000 Geometric rule learning by Clark's nutcrackers (*Nucifraga columbiana*). *J. Exp. Psychol. Anim. Behav. Process.* **26**, 439–453. (doi:10.1037/0097-7403.26.4.439)
- Kamil, A. C., Balda, R. P. & Grim, K. 1986 Revisits to emptied cache sites by Clark's nutcrackers (*Nucifraga columbiana*). *Anim. Behav.* **34**, 1289–1298. (doi:10.1016/S0003-3472(86)80200-7)
- Kamil, A. C., Goodyear, A. J. & Cheng, K. 2001 The use of landmarks by Clark's nutcrackers: first tests of a new model. *J. Navig.* **54**, 429–435. (doi:10.1017/S0373463301001436)
- Kelly, D. M. In press. Features enhance encoding of geometry. *Anim. Cognit.*
- Kelly, D. M. & Spetch, M. L. 2004a Reorientation in a two-dimensional environment: I. Do pigeons (*Columba livia*) encode the featural and geometric properties of a two-dimensional schematic of a room? *J. Comp. Psychol.* **118**, 384–395. (doi:10.1037/0735-7036.118.4.384)
- Kelly, D. M. & Spetch, M. L. 2004b Reorientation in a two-dimensional environment: II. Do adults encode the featural and geometric properties of a two-dimensional schematic of a room? *J. Comp. Psychol.* **118**, 82–94. (doi:10.1037/0735-7036.118.1.82)
- Kelly, D. M., Spetch, M. L. & Heth, C. D. 1998 Pigeons' (*Columba livia*) encoding of geometric and featural properties of a spatial environment. *J. Comp. Psychol.* **112**, 259–269. (doi:10.1037/0735-7036.112.3.259)
- Kelly, D. M., Kippenbrock, S., Templeton, J. & Kamil, A. C. 2008 Use of a geometric rule or absolute vectors: landmark use by Clark's nutcrackers (*Nucifraga columbiana*). *Brain Res. Bull.* **76**, 293–299. (doi:10.1016/j.brainresbull.2008.02.008)
- Kelly, D. M., Kamil, A. C. & Cheng, K. In press. Landmark use by Clark's nutcrackers (*Nucifraga columbiana*): influence of disorientation and cue rotation on distance and direction estimates. *Anim. Cognit.* (doi:10.1007/s10071-009-0256-6)
- LaDage, L. D., Roth II, T. C., Fox, R. A. & Pravosudov, V. V. 2009 Flexible cue use in food-caching birds. *Anim. Cognit.* **12**, 419–426. (doi:10.1007/s10071-008-0201-0)
- Lavenex, P., Shiflett, M. W., Lee, R. K. & Jacobs, L. F. 1998 Spatial versus nonspatial relational learning in free-ranging fox squirrels (*Sciurus niger*). *J. Comp. Psychol.* **112**, 127–136. (doi:10.1037/0735-7036.112.2.127)

- Miller, N. & Shettleworth, S. A. 2007 Learning about environmental geometry: an associative model. *J. Exp. Psychol. Anim. Behav. Process.* **33**, 191–212. (doi:10.1037/0097-7403.33.3.191)
- Miller, N. & Shettleworth, S. A. 2008 An associative model of geometry learning: a modified choice rule. *J. Exp. Psychol. Anim. Behav. Process.* **34**, 419–422. (doi:10.1037/0097-7403.34.3.419)
- Mittelstaedt, H. & Mittelstaedt, M. L. 1982 Homing by path integration. In *Avian navigation* (eds F. Papi & H. G. Wallraff), pp. 290–297. Berlin, Germany: Springer-Verlag.
- Morris, R. G. M. 1981 Spatial localization does not require the presence of local cues. *Learn. Motiv.* **12**, 239–260. (doi:10.1016/0023-9690(81)90020-5)
- O'Keefe, J. & Nadel, L. 1978 *The hippocampus as a cognitive map*. Oxford, UK: Clarendon Press.
- Olton, D. S. & Samuelson, R. J. 1976 Remembrance of places passed: spatial memory in rats. *J. Exp. Psychol. Anim. Behav. Process.* **2**, 97–116. (doi:10.1037/0097-7403.2.2.97)
- Pearce, J. M., Ward-Robinson, J., Good, M., Fisse, C. & Aydin, A. 2001 Influence of a beacon on spatial learning base on the shape of the test environment. *J. Exp. Psychol. Anim. Behav. Process.* **27**, 329–344. (doi:10.1037/0097-7403.27.4.329)
- Pearce, J. M., Graham, M., Good, M. A., Jones, P. M. & McGregor, A. 2006 Potentiation, overshadowing, and blocking of spatial learning based on the shape of the environment. *J. Exp. Psychol. Anim. Behav. Process.* **32**, 201–214. (doi:10.1037/0097-7403.32.3.201)
- Sherry, D. F. 1984 Food storage by black-capped chickadees: memory for the location and contents of caches. *Anim. Behav.* **32**, 451–464. (doi:10.1016/S0003-3472(84)80281-X)
- Sherry, D. F., Krebs, J. R. & Cowie, R. J. 1981 Memory for the location of stored food in marsh tits. *Anim. Behav.* **29**, 1260–1266. (doi:10.1016/S0003-3472(81)80078-4)
- Shettleworth, S. J. 1998 *Cognition, evolution, and behavior*. New York, NY: Oxford University Press.
- Shettleworth, S. J. & Krebs, J. R. 1982 How marsh tits find their hoards: the roles of site preference and spatial memory. *J. Exp. Psychol. Anim. Behav. Process.* **8**, 354–375. (doi:10.1037/0097-7403.8.4.354)
- Smulders, T. V., Gould, K. L. & Leaver, L. A. 2010 Using ecology to guide the study of cognitive and neural mechanisms of different aspects of spatial memory in food-hoarding animals. *Phil. Trans. R. Soc. B* **365**, 883–900. (doi:10.1098/rstb.2009.0211)
- Spetch, M. L. & Edwards, C. A. 1986 Spatial memory in pigeons (*Columba livia*) in an open-field feeding environment. *J. Comp. Psychol.* **100**, 266–278. (doi:10.1037/0735-7036.100.3.266)
- Spetch, M. L. & Honig, W. K. 1988 Characteristics of pigeons' spatial working memory in an open-field task. *Anim. Learn. Behav.* **16**, 123–131.
- Spetch, M. L. & Wilkie, D. M. 1994 Pigeons' use of landmarks presented in digitized images. *Learn. Motiv.* **25**, 245–275. (doi:10.1006/lmot.1994.1014)
- Spetch, M. L., Cheng, K., MacDonald, S. E., Linkenhoker, B. A., Kelly, D. M. & Doerkson, S. R. 1997 Use of landmark configuration in pigeons and humans: II. Generality across search tasks. *J. Comp. Psychol.* **111**, 14–24. (doi:10.1037/0735-7036.111.1.14)
- Spetch, M. L., Rust, T. B., Kamil, A. C. & Jones, J. E. 2003 Searching by rules: pigeons' (*Columba livia*) landmark-based search according to constant bearing or constant distance. *J. Comp. Psychol.* **117**, 123–132. (doi:10.1037/0735-7036.117.2.123)
- Tomback, D. F. 1977 Foraging strategies of Clark's nutcracker. *Living Bird* **16**, 123–161.
- Tomback, D. F. 1980 How nutcrackers find their seed stores. *Condor* **82**, 10–19. (doi:10.2307/1366779)
- Vander Wall, S. B. 1982 An experimental analysis of cache recovery in Clark's nutcracker. *Anim. Behav.* **30**, 84–94. (doi:10.1016/S0003-3472(82)80240-6)
- Vander Wall, S. B. & Balda, R. P. 1981 Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. *Z. Tierpsychol. Beih.* **56**, 217–242.
- Vlasak, A. N. 2006 Global and local spatial landmarks: their role during foraging by Columbian ground squirrels (*Spermophilus columbianus*). *Anim. Cognit.* **9**, 71–80. (doi:10.1007/s10071-005-0006-3)
- Von Saint Paul, U. 1982 Do geese use path integration for walking home? In *Avian navigation* (eds F. Papi & H. G. Wallraff), pp. 298–307. Berlin, Germany: Springer-Verlag.
- Waisman, A. S. & Jacobs, L. F. 2008 Flexibility of cue use in the fox squirrel (*Sciurus niger*). *Anim. Cognit.* **11**, 625–636. (doi:10.1007/s10071-008-0152-5)
- Watanabe, S. 2005 Strategies of spatial learning for food storing in scrub jays. *J. Ethol.* **23**, 181–187. (doi:10.1007/s10164-005-0150-x)
- Wiltschko, W. & Balda, R. P. 1989 Sun compass orientation in seed-caching scrub jays. *J. Comp. Physiol. Sensory Neural Behav. Physiol.* **164**, 717–721. (doi:10.1007/BF00616744)
- Wiltschko, W., Balda, R. P., Jahnel, M. & Wiltschko, R. 1999 Sun compass orientation in seed-caching corvids: its role in spatial memory. *Anim. Cognit.* **2**, 215–221. (doi:10.1007/s100710050042)