Wild hummingbirds rely on landmarks not geometry when learning an array of flowers

T. Andrew Hurly[1], Thomas A. O. Fox[1,3], Danielle M. Zwueste[1,4], Susan D. Healy[2]

Corresponding Author:

TA Hurly, hurly@uleth.ca, 403 329-2320, Fax 403 332-4039

[1] Department of Biological Sciences, University of Lethbridge, 4401 University Dr., Lethbridge, AB, Canada, T1K 3M4

[2] School of Biology, University of St. Andrews, St. Andrews, Fife, UK

[3] Current Address: Department of Geography, McGill University, 845 Sherbrooke St W, Montreal, QC, Canada, H3A 0G4

[4] Current Address: Veterinary Medical Teaching Hospital, University of California, Davis, CA.

Abstract Rats, birds or fish trained to find a reward in one corner of a small enclosure, tend to learn the location of the reward using both nearby visual features and the geometric relationships of corners and walls. Because these studies are conducted under laboratory and thereby unnatural conditions, we sought to determine whether wild, free-living rufous hummingbirds (*Selasphorus rufus*) learning a single reward location within a rectangular array of flowers would similarly employ both nearby visual landmarks and the geometric relationships of the array. Once subjects had learned the location of the reward we used test probes in which one or two experimental landmarks were moved or removed in order to reveal how the birds remembered the reward location. The hummingbirds showed no evidence that they used the geometry of the rectangular array of flowers to remember the reward. Rather, they used our experimental landmarks, and possibly nearby, natural landmarks, to orient and navigate to the reward. We believe this to be the first test of the use of rectangular geometry by wild animals and we recommend further studies be conducted in ecologically relevant conditions in order to help determine how and when animals form complex geometric representations of their local environments.

Key Words: hummingbird, orientation, navigation, spatial memory, landmark, geometry

Introduction

Orientation and navigation by vertebrates are often considered in the context of long distance migrations (Guilford et al. 2011, Fuxjager et al. 2011). However, orientation and navigation are common phenomena in animals' everyday lives as they defend territories, forage in their home ranges, return to nests or burrows, etc. In many ways this latter expression of orientation and navigation is more tractable and amenable to experimental manipulation than is the former and numerous studies employing rats or pigeons have revealed the use of cues such as global landmarks, local features and geometry of an enclosure for orientation. For example, Cheng (1986) demonstrated that rats learned the food-rewarded corner of a small arena by encoding both local visual features and the geometry of the arena.

Geometry in this context has a specific meaning. In Cheng's (1986) study, the rats remembered not just the location of food relative to one or more features of the arena. Significantly, they encoded and recalled aspexts of the arena relative to each other; this is considered a geometric representation of their environment. Specifically, the rewarded corner in the arena had a short wall on one side and a longer wall on the other. When tested, the rats demonstrated memory for this configuration by selecting the rotationally similar (diagonally opposite) corner as often as they selected the correct corner.

Subsequent to Cheng's (1986) first reporting the use of arena geometry by rats, there have been numerous studies investigating the extent to which animals use geometry vs. visual cues when they learn and remember a reward location (recent reviews: Tommasi et al 2012, Cheng et al. 2013). For example, Kelly and Spetch (2001) tested pigeons (*Columba liva*) in a small rectangular room with identical visual features in each corner. With only the geometric relationships between long and short walls available to indicate the rewarded corner, pigeons did indeed use the relative lengths of walls to find the reward. When mountain chickadees (*Poecile gambeli*) were tested in a similar rectangular arena with one wall painted blue (visual cue), birds trained with the reward close to the cue learned the cue and birds trained with the reward far from the visual cue learned arena geometry (Gray et al. 2005). In a follow-up experiment, wild-caught and hand-reared black-capped chickadees (*Poecile atricapillus*) tended to use geometry whereas wild-caught mountain chickadees tended to use the blue-wall cue (Batty et al. 2009). Kelly (2010), recognizing that geometry may be particularly salient when available only as the walls of a room, presented a rectangular array of four objects to Clark's nutcrackers (*Nucifraga columbiana*) in an arena with no reliable global landmarks. The birds learned the geometric relationships of the rectangular array only when a distinctive visual feature marked each object.

Although these laboratory studies are carefully controlled and provide valuable insights into the orientation capabilities of animals, they are also highly artificial and lack ecological relevance. One solution to this concern has been to use more naturalistic tasks such as caching and recovery of food items by birds flying freely in an aviary (corvids: Kamil et al. 1999, parids: Krebs et al. 1990), or foraging by bees in large enclosures (Ohashi et al. 2007). Increasing ecological relevance involves animals in the wild, such as ants (Collett 2012) or ground squirrels (Vlasak 2006). One particularly tractable system is that of free-living territorial rufous hummingbirds (*Selasphorus rufus*), which forage at both natural and experimental flowers (Healy and Hurly 2013; Waser and McRobert 1992). Experimental incorporation of foraging behaviours, interspersed with activities such as territorial defense, courtship and predator avoidance, provides a realistic and ecologically relevant context for studies of orientation and navigation.

Several studies of hummingbirds, rufous hummingbirds in particular, have demonstrated that they distinguish a rewarded flower from other nearby flowers primarily in terms of spatial location rather than the visual features of each flower (Hurly and Healy 2002, Miller et al. 1985). Spatial locations seem to be remembered relative to nearby objects (Healy and Hurly 1998, Hurly et al. 2010), a process that must, by definition, employ aspects of geometric representation. However, the identity and use of such natural landmarks remains elusive. One solution to this problem is to provide artificial flowers and conspicuous landmarks that can be systematically manipulated in order to assess how objects are combined and encoded to represent relevant information about the environment.

Here we ask how wild, free-living hummingbirds presented with a four-flower rectangular array employ nearby visual cues and array geometry, and whether their use of these cues parallels the results from laboratory experiments conducted on a similar spatial scale. After the birds learned the location of the rewarded flower, we manipulated conspicuous nearby landmarks to determine whether the birds had incorporated these landmarks into their memory for the reward and whether they had also learned the geometry of the array. The strongest evidence for geometry would be if, in a test, the birds were to choose frequently the flower diagonally opposite to the rewarded flower.

Materials and Methods

The study was performed during June and July, 2007 – 2009 at the University of Lethbridge Westcastle Research Station (49°20.9’N, 114°24.6’W, 1400m elevation) in the front ranges of the Rocky Mountains in southwestern Alberta, Canada. The subjects were male rufous hummingbirds, each defending a territory surrounding a commercial hummingbird feeder containing 14% sucrose solution. Individual birds were with non-toxic ink on the breast feathers. Six subjects were studied in 2007, eight in 2008 and ten in 2009.

Study sites were openings in the forest at least 200 m^2 in size and vegetated with green grass, forbs and shrubs less than 40 cm in height. Within the study sites were naturally occurring objects such as logs, rocks and soil disturbances, as well as clumps of vegetation of different shades of green. At medium distances were trees and forest edges, with ridges, mountains and sky visible at greater distances (Fig. 1). Experimental control of visual features on any of these scales was not possible.

Experiment 1

Initial Training

A subject's feeder was removed during training and testing but was available at all other times. First, a subject was trained to feed on 25% sucrose from an artificial flower consisting of a vial that was taped to the top of a 62cm wooden dowel that projected visibly above the surrounding vegetation. The flower was then moved a few metres at a time away from the original feeder location until the bird flew directly to the flower each time it came to feed.

Experimental Training

We presented an array of four identical flowers in a rectangular pattern. One flower was randomly selected as the reward and this was cued by a conspicuous artificial landmark consisting of a red cube, constructed of cardboard and duct tape, atop a 62cm dowel. The cube was positioned outside of the array at an angle of 45^{o} to the corner of the rectangle and at a distance of 5cm from the reward flower. Each of the remaining flowers was filled with water, which the hummingbirds find distasteful. A subject approached the array to feed and probed flowers until he found the reward, fed to satiation and then left. The flowers were then exchanged with each other to ensure that the bird could not learn the reward flower based upon its subtle visual features. The flower at the reward location was filled with sucrose and the others with water. Training occurred until the subject flew directly to the reward flower for 8 consecutive feeding visits and at this point we conducted a Test Probe to assess what information the subject was employing to return to the reward flower. In all cases a choice was defined as the bird inserting its bill into a flower. Following the Test Probe the array was moved to a new orientation and location that did not overlap spatially with the previous array and a new series of training trials began.

Test Probes

During a Test Probe the array remained in the same location but the flowers were exchanged, each was filled with water and no flower was rewarded. A probe involved manipulation of the landmark in one of three ways (Fig. 2a):

1) Diagonal – The landmark was moved to the diagonally opposite corner. A bird could use both landmark and geometric information to visit the flower now cued by the landmark.

2) Removal – The landmark was removed. A bird could use only geometric information about the long and short spacing of the flowers in the array and was expected to visit either the original location or the location diagonally opposite. It was also possible for the bird to use natural visual cues that were not under experimental control.

3) Conflict – the landmark was shifted along the adjacent short side of the array to create a conflict between geometric information and the landmark. The bird was expected either to follow the landmark or to go to one of the two geometrically-correct flowers.

As they were free-living, the hummingbirds were not under our direct control, hence they determined the time interval between feeding visits (presumably based on hunger). Further, we could not physically disorient the birds as is done in laboratory tests by using a rotating turntable (e.g. Kelly 2010). However, during the ca. 10 minutes between visits to the array birds engaged in multiple activities: vigilance, preening, territorial chases, courtship displays (see Hurly et al. 2001), hawking insects. Moreover, these multiple activities caused the birds to approach the array from different directions. Thus, the birds' natural behaviours in the wild considerably reduce the possibility that they found the reward through stereotypical approach paths, thus acting in a similar fashion to experimental disorientation used in the lab (e.g. by rotation, entering arena through different doors). Further, altering the experimental landmark by changing its normal relationship with other cues in the environment may also have acted as a surrogate for disorientation by creating conflicting information. A subject's choice during a Test Probe should reveal whether it was relying most on the experimental landmark, the geometry of the array, or other cues in the environment that were not under experimental control.

Experimental Training Treatments

In 2007, six subjects were trained with both Small Arrays (10x20cm) and Large Arrays (60x120cm) using a large landmark (see below) and for each array size they were tested with each Test Probe: Diagonal, Removal and Conflict. The order of Test Probes was selected randomly from an unbiased schedule. In 2008, eight subjects were trained under four conditions in which array size (Small vs. Large as above) was crossed with landmark size (Small: 5cm per side vs. Large: 10cm per side). The order of Test Probes was randomized as above.

Experiment 2

In 2009, we studied 10 territorial male rufous hummingbirds from the same population as Experiment 1. All training methods were the same, including the learning criterion of 8 first visits to the reward flower prior to Tests. The rectangular array was 50x100cm and the single reward flower was cued by two red cubes (10cm per side), one at 5cm (Near) and one at 100cm (Far) (Fig. 3a).

Test Probes

The Test Probes were: Remove Near, Remove Far, Remove Both, Conflict Near and Conflict Far (Fig. 3b). As with Experiment 1, each subject received each Test Probe only once, with the order of presentations selected randomly from an unbiased schedule.

Analyses

We analysed the choices birds made during Test Probes using G-tests (with William's correction G_{adj}), either comparing observed choices with the expectation of chance performance across the four flowers, or comparing choices between training treatments or Test Probes. When the sample size was smaller than 20 the expectation for any cell is less than the critical value of 5. In these cases we also employed randomization tests (R_p with 10,000 permutations) to determine the probability of occurrence of the observed and more extreme results, as recommended by Sokal and Rohlf (1995). We report the results of both G_{adj} and R_p. In every case the two tests were in agreement relative to the assessment of statistical significance (alpha = 0.05). We report data as mean ± SE.

Results

Experiment 1

Training

The birds achieved the criterion of eight consecutive visits to the rewarded flower within 10.8 ± 0.4 trials. Learning rate did not differ between years (2007, 11.2 ± 0.5 trials; 2008, 10.4 ± 0.5 trials; $t = 1.405$, $df = 12$, $p = 0.185$), nor was it affected by Array Size or Landmark Size (Array: $F_{1,5} = 1.874$, $p = 0.229$; Landmark: $F_{1,5} = 0.241$, $p = 0.883$, Interaction: $F_{1,5} = 0.678$, $p = 0.448$). The mean inter-trial interval (9.8 ± 0.3 min) did not vary by year ($F_{1,12} = 1.278$, $p = 0.280$). Inter-trial intervals were not influenced by trial type (Training vs. Test), nor by Array Size or Landmark Size (all $F_{1,7} < 0.247$, all $p > 0.163$). Given that we found no differences between years in task acquisition or inter-trial intervals, we felt confident in combining data from 2007 and 2008 in Experiment 1.

Test Probes

When we combined data across the different array and landmark sizes it was evident that the three different Test Probes elicited significantly different patterns of choices (G-test of independence, $G_{adj} = 82.48$, $N = 129$, $p < 0.001$, Fig. 2b). Furthermore, choices within each Test Probe were significantly different from chance. In the Diagonal tests the birds' choices were concentrated on the flower diagonally opposite the reward and thus were consistent with the use of the landmark or geometry ($G_{adj} = 26.40$, $N = 43$, $p < 0.001$). In the Removal tests the birds' choices were mostly to the rewarded location ($G_{adj} = 22.99$, N = 43, $p < 0.001$), with no evidence that they used geometry. If birds had relied upon geometry then choices should have been divided equally between the reward location and the flower diagonally opposite; instead they were biased to the reward location (Binomial test, $p<0.001$, N = 29, $R_p = 0.003$). Even examination of choices to the three less-preferred flowers showed no preference for the flower diagonally opposite the reward ($G_{adj} = 1.29$, N = 17, p = 0.26, $R_p = 0.27$). During the Conflict tests birds most frequently followed the landmark ($G_{adj} = 54.17$, N = 43, $p < 0.001$). Other choices were significantly in favour of the reward location with no evidence for geometry ($G_{adj} = 9.40$, N = 13, p = 0.002, $R_p = 0.001$).

The sample sizes were insufficient to consider the effects of array size and landmark size simultaneously so we examined each separately (Fig. 2c, d). Birds exhibited significant non-random choices in 11 of the 12 Test Probe conditions. In the Diagonal and Removal tests, birds chose the original reward location most often when the array was large (Diagonal: $G_{adj} = 12.53$, N = 43, $p < 0.001$; Removal: $G_{adj} = 8.31$, N = 43, $p < 0.001$) but they did not do this in the Conflict tests ($G_{adj} = 6.57E-02$, N = 43, p = 0.80). Landmark size had a significant effect on choices in Removal tests ($G_{adj} = 4.52$, N = 31, p = 0.033); birds returned to the reward location most often when the landmark was small. There was no effect of landmark size in the Diagonal ($G_{adj} = 2.52$, N = 31, p = 0.11) or Conflict ($G_{adj} = 1.48$, N = 31, p = 0.22) tests.

Experiment 2

Results from Experiment 1 indicated that birds followed the experimental landmark but that they also used other cues to return to the reward location when the experimental landmark had been removed. We introduced a second conspicuous experimental landmark in Experiment 2 as an attempt to increase their attention to the experimental landmarks and to decrease their attention to other, natural landmarks in the environment.

Training

The number of trials required to reach criterion in Experiment 2 (11.8 ± 0.4) did not differ from Experiment 1 (10.8±0.4, $t = 1.570$, $df = 22$, $p = 0.131$). The mean inter-trial interval was 9.8 ± 1.8 minutes.

Test Probes

When we removed only one landmark, the birds primarily chose the reward location in both Remove Near ($G_{adj} = 3.95$, $N = 10$, $p = 0.047$, $R_p = 0.019$) and Remove Far ($G_{adj} = 10.78$, $N = 10$, $p < 0.001$, $R_p < 0.001$) tests and these results did not differ from each other ($G_{adj} = 2.83$, $N = 20$, $p = 0.092$; Fig. 3b). However, removal of both landmarks seemed to disrupt orientation and choices did not differ from chance ($G_{adj} = 2.08$, $N = 10$, $p = 0.149$, $R_p = 0.236$). Choices differed significantly across the three types of removal tests ($G_{adj} = 6.73$, $N = 30$, $p = 0.009$) and in no test did birds prefer to use geometry.

In Near Conflict tests most of the birds followed the landmark ($G_{adj} = 9.39$, $N = 10$, $p = 0.002$, $R_p < 0.001$). In contrast, in the Far Conflict tests most of the birds chose the near landmark at the reward location ($G_{adj} = 9.39$, $N = 10$, $p = 0.002$, $R_p < 0.001$). These choice distributions differed significantly from each other ($G_{adj} = 7.23$, $N = 20$, $p = 0.007$; Fig. 3c). Birds never chose the flower diagonally opposite the reward location and thus we found no evidence for the use of geometry.

Discussion

In these experiments, wild, free-living male rufous hummingbirds learned the location of a single rewarded flower in a rectangular array of four flowers when one or two conspicuous experimental landmarks cued the reward. To determine what information the birds used to remember the location of the reward, we manipulated the landmarks in occasional Test Probes. In 18 of 20 comparisons the birds' first flower choices indicated significant patterns about where they expected the reward to be. It is clear that the birds attended to the experimental landmarks because they often followed the landmarks when they were moved to a different location in the array (Diagonal or Conflict). When we removed the landmarks the birds most often returned to the rewarded flower, which indicates that they also used cues from the environment over which we had no control. There was no evidence that the hummingbirds recognized or used the geometry of the rectangular array to remember the location of the rewarded flower. To our knowledge, this is the first test of the use of rectangular geometry by wild animals in the field and the results do not parallel those from numerous lab studies.

The Diagonal test aligned geometric and landmark information and thus acted as a positive control demonstrating that the birds both responded to Test Probes and paid attention to the experimental landmarks. This test cannot however, distinguish between the use of landmarks vs. geometry. The Removal test was the condition in which we could best detect the use of geometry with the expectation of equal choices to the reward and the flower diagonally opposite the reward. Surprisingly, the birds chose the diagonally opposite flower least frequently, soundly rejecting the exclusive use of array geometry in this task. Finally, in the traditional test that is used to determine whether the landmark or geometry has the greater influence on learning the reward location, the Conflict test, the birds also failed to choose the flower specified by geometric cues. Additional cues that may have been used in conjunction with the geometry of the array are discussed below.

Given the ubiquity of positive geometry results in the laboratory for various species, it is surprising and intriguing that we found no evidence that hummingbirds recognized the geometry of the rectangular array. To make sense of these results we must distinguish between two related but different questions, the first being whether hummingbirds can form geometric representations of our experimental flowers. The answer to this is yes: hummingbirds most certainly can learn and recognize the geometry of an array of artificial flowers. Healy and Hurly (1998) presented wild male rufous hummingbirds in this same population with an array of five artificial flowers arranged in a cross pattern and in which only the centre flower was rewarded. Once a bird learned which flower contained the reward, the array was translocated one flower-spacing unit such that upon return the bird's flower choice would indicate that it thought the reward should be in the flower currently in the actual spatial location previously occupied by the reward or that the reward should be in the centre of the array (relative position). When the arrays were composed of flowers with relatively wide spacing (80, 160, 320cm) the birds selected the flower in the absolute spatial location. In contrast, when flower spacing was relatively small (5, 10, 20 , 40cm) the birds selected the centre flower, indicating that they recognized geometric relationships between the flowers within the array. This effect of flower spacing on the use of geometric relationships between flowers was also obtained in more complex arrays of 16 flowers (Healy and Hurly 1998).

Because wild hummingbirds can indeed recognize and use at least some aspects of the geometry of an array of flowers, a second question attains relevance: under what circumstances do wild foraging hummingbirds employ geometry? Healy and Hurly (1998) speculated that when presented with compact arrays, hummingbirds use non-rewarded flowers as landmarks to remember the rewarded flowers but when presented with dispersed arrays they use natural, nearby landmarks. From the previous data it seems reasonable to infer that these natural landmarks were generally less than 80 cm from the reward. The results of the current experiment are consistent with this inference. First, during the Diagonal tests in Experiment 1 (Fig. 2c), the hummingbirds almost ignored the reward location when the array was small (10x20cm), but not when it was large (60x120cm), differences that are consistent with the 40 vs. 80 cm spacing threshold reported by Healy and Hurly (1998). Second, when landmark size was manipulated (Fig. 2d) and birds experienced Removal tests, they returned less often to the reward location when the landmark had been large than when it had been small, suggesting differential attention between the experimental and natural landmarks. Third, in Experiment 2 the birds were influenced more strongly by the near (5cm) than by the far (100cm) landmark (Fig. 3c). Thus it seems reasonable to hypothesize that wild hummingbirds remember the locations of one or more rewarded flowers in relation to the locations of nearby objects (landmarks) and that these landmarks can be other nearby flowers. It is notable that removal of both landmarks in Experiment 2 seriously disrupted choices, suggesting that the two experimental landmarks together played a significant role in memory for the reward location.

Such reliance upon landmarks (natural or experimental) is consistent with the results of past studies. Hummingbirds seem to remember rewards in terms of spatial locations (absolute or relative) rather than distinctive visual features of rewarded flowers but they will employ such visual features when spatial cues are made ineffective (Hurly and Healy 2002). Moreover, when Hurly et al. (2010) trained hummingbirds to feed from a single conspicuous rewarded flower and after several flights to the rewarded flower it was either removed or moved approximately 1.5m, birds returned to the original reward location. This demonstrated that they had not used the visual features of the flower as a distant beacon but rather as a visual cue only when they were very close to its location. It seems likely that the birds recognized the rewarded location using natural, nearby landmarks and recent evidence indicates that such learning of rewarded locations occurs with a single experience (Flores-Abreau et al. 2012).

The methods and scale of our field study paralleled the methods and scale of a host of laboratory studies testing whether animals encode the geometric properties of rectangular enclosures or arrays of objects and then later use this information to reorient and return to a goal. The hummingbirds may have encoded geometry but they showed no evidence of using it to find the goal, even when the conspicuous landmarks were removed. Aside from following the experimental landmark, the birds' most common choice was the flower location that had been rewarded in training, for which they must have used other spatial cues. One possibility is that they navigated to the absolute spatial location of the goal flower by using visual landmarks in the environment that were not under experimental control. Objects conspicuous to the human eye, such as logs, rocks, soil disturbances and shrubs are obvious candidates. Consistent with this idea, rats tested in small rectangular enclosures generally avoided diagonal errors when they were permitted views of the surrounding environment (Margules and Gallistel 1988). The other possibility was that the birds encoded the flowers in the array as a group and then used some sort of directional cues to represent which one of the flowers was the reward (e.g. the flower closest to a landmark, the flower farthest north). Candidate directional cues include magnetic (Freire et al. 2005) or sun compass (Wiltschko et al. 1999), asymmetry in the panoramic view of the landscape such as a distant mountain (Wystrach et al. 2011), or even the slope of the ground (Nardi et al. 2010). Using natural visual landmarks, in addition to our experimental landmarks, requires the encoding of geometric properties such as sense, direction and distance. Similarly, using directional cues requires the encoding of, at the very least, distance relationships between the array elements and a compass direction. Thus, we can conclude only that our tests did not show that the hummingbirds placed high priority on using the geometry of the rectangular array to orient to the reward and that they used other cues instead. We consider the use of idiothetic mechanisms in this case to be unlikely because the minimum flight distance to the array was more than 10 times the maximum length of the array (1.2m). One final consideration is that it may require severe disorientation of the subjects to get them to reveal their use of geometry and such disorientation was not possible in this field study with free-living birds. However, unlike laboratory experiments in which the subjects sit in a holding cage during intervals between trials and tests, the wild hummingbirds spent the 10-minute intervals engaged in vigilance, territorial chases, courtship flights, capturing insects, etc. Thus, birds frequently approached the array from different directions between trials. These activities are very likely to have provided some degree of disorientation or interference with learned information.

Cheng's (1986) original study demonstrating that rats encoded the geometry of a small room even when a distinctive visual feature, which could act as a beacon, cued the location of the reward, has spawned a substantial assortment of laboratory studies with other species that demonstrate similar results (e.g. fish: Brown et al. 2007, Sovrano et al. 2005; chicks: Chiandetti and Vallortigara 2008; pigeons: Kelly and Spetch 2001). These studies consistently show that the subjects can encode rectangular geometry but, unlike Cheng (1986), most indicate that when geometry and visual features are placed in conflict, features frequently play a greater role. Here we again face the issue of what specific question we are addressing; whether we wish to know that animals are capable of learning the geometry of small enclosures or whether we wish to know under what circumstances animals encode and rely upon geometry.

Some evidence suggests that use of visual features vs. geometry is related to proximity. In both mountain chickadees (Gray et al. 2005) and goldfish (*Carassius auratus*) (Vargas et al. 2011), visual features dominated geometry when subjects were trained with the feature proximal to the reward but no clear dominance of either cue occurred when subjects were trained with the feature distant from the reward. Thus, it is difficult to draw general conclusions about the overall influence of overshadowing or salience on the relative weighting of visual features and geometry because results seem specific to training conditions (Kelly et al. 1998, Brown et al. 2007).

Although most laboratory studies have examined whether animals learn the geometry of enclosures, several have examined whether they learn the geometry of a rectangular array of discrete objects. Gibson et al. (2007) tested rats and Kelly (2010) tested Clark’s nutcrackers. In both studies subjects did learn about the geometry of the array, but the array was moved between each training trial to make global cues in the room ineffective. Rats’ learning was dominated by the unique features of the objects and they learned geometry best when the objects were made identical. In contrast, nutcrackers did not learn the location of the reward unless features were individually distinctive, and in learning the task they also acquired the geometry of the array. As with this hummingbird study, when the reward feature was placed in conflict with the geometry of the array the nutcrackers followed the feature. A series of experiments with chicks (ca. 3-14 days of age) indicate that the geometry of enclosures is encoded much more readily than is the geometry of an array of objects (e.g. Pecchia and Vallortigara 2010). Conversely, chicks could encode the geometry of a rectangular array of objects but only when their view of the array was carefully controlled (Pecchia and Vallortigara 2012). This finding suggests that view-matching is very important for young chicks and it would be interesting to determine whether it is necessary for older birds that have greater experience navigating in a complex environment. The issue is further complicated by evidence that view-matching is acquired during training whereas spontaneous reorientation in chicks employs geometric 3-dimensional properties of the enclosure (Lee et al. 2012a). Similarly, fish may spontaneously reorient by the geometry of walls but favour landmarks following training (Lee et al. 2012b), and they did not encode the geometry of the corners of an enclosure that were emphasized as objects rather than as the intersections of walls (Lee et al. 2013).

As Kelly (2010) suggests, animals may regard the rectangular geometry of enclosures or edges differently than they regard the rectangular geometry of discrete objects (points). Certainly, animals in the laboratory frequently encode reward locations in terms of distance from a straight edge (Cheng and Sherry 1992, Gray et al. 2004). Alternatively, there may be something special about an animal being contained within an enclosure that makes the walls and corners particularly salient and which are then incorporated into a geometrical representation of the environment. Perhaps some of the objects within a rectangular array of discrete objects can be ignored or weighted less heavily than others, whereas the restrictive nature of a small enclosure forces animals to regard walls as extremely salient (Sutton 2009).

Finally, the degree to which animals attend to rectangular geometry may relate to the degree to which the learning task is ecologically relevant or natural. In the least natural situations, small laboratory enclosures, animals readily learn rectangular geometry but in the most natural situation, four artificial flowers in a rectangular array in the field, our hummingbirds showed no evidence of having done so. It is interesting to note that in an intermediate situation, four objects in a large arena, Clark's nutcrackers did learn about geometry of an array but only when the objects were visually distinctive (Kelly 2010). Using fish, Sovrano et al. (2005) showed that subjects trained in a small tank were slightly better at geometry and tended to make errors about visual cues, whereas fish trained a large tank were more likely to make errors about geometry, supporting the idea that some aspects of containment might influence which objects are included in a cognitive spatial representation of the environment. Although containing animals in small rooms is highly artificial, the spatial scale is ecologically realistic. Although the territories of rufous hummingbirds are on the order of 1 ha and they must orient and navigate on that spatial scale, they also experience flowers separated by only a few centimetres and experiments with artificial flowers indicate that they discriminate between flowers separated by 5 cm or less (Healy and Hurly 1998; Hurly and Healy 1996). Future research should focus on how and when animals form these complex spatial representations during their natural activities in the wild and what ontological and evolutionary conditions influence this process.

Acknowledgments

We thank Mark Hornsby, Ken Cheng and two anonymous reviewers for valuable discussion or helpful comments on the manuscript. Logistical support was provided by the University of Lethbridge and financial support by the Natural Sciences and Engineering Research Council of Canada (TAH, TAOF, DMZ) and the Association for the Study of Animal Behaviour (SDH).

Ethical Standards

This research was conducted with the approval of the University of Lethbridge Animal Welfare Committee, meeting the standards of the Canadian Council on Animal Care, and under permits from the Canadian Wildlife Service and Alberta Sustainable Resource Development.

Conflict of Interest

None of the authors have conflicting financial relationships with any of the funding or approval agencies associated with the research reported here.

References

Batty ER, Bloomfield LL, Spetch ML, Sturdy CB (2009) Comparing black-capped (*Poecile atricapillus*) and mountain chickadees (*Poecile gambeli*): use of geometric and featural information in a spatial orientation task. Anim Cognition 12:633-641.

Brown AA, Spetch ML, Hurd PL (2007) Growing in circles: rearing environment alters spatial navigation in fish. Psychol Sci 18:569-573.

Cheng K (1986) A purely geometric module in the rat's spatial representation. Cognition 23:149-178.

Cheng K, Sherry DF (1992) Landmark-based spatial memory in birds (*Parus atricapillus* and *Columba liva*): the use of edges and distances to represent spatial positions. J Comp Psychol 106: 331–341.

Cheng K, Huttenlocher, J, Newcombe, NS. (2013) 25 years of research on the use of geometry in spatial reorientation: a current theoretical perspective. Psychon Bull Rev 20:1033-1054.

Chiandetti C, Vallortigara G (2008) Is there an innate geometric module? Effects of experience with angular geometric cues on spatial re-orientation based on the shape of the environment. Anim Cognition 11:139-146.

Collett M (2012) How navigational guidance systems are combined in a desert ant. Curr Biol 22:927-932.

Flores-Abreau IN, Hurly TA, Healy SD (2012) One-trial spatial learning: wild hummingbirds relocate a rewarding location after a single visit. Anim Cognition 15:631-637.

Freire R, Munro U, Rogers LJ, Wiltschko R, Wiltschko W (2005) Chickens orient using the magnetic compass. Curr Biol 15:R620–R621.

Fuxjager MJ, Eastwood BS, Lohmann KJ (2011) Orientation of hatchling loggerhead sea turtles to regional magnetic fields along a transoceanic migratory pathway. J Experimental Biol 214:2504-2508.

Gibson BM, Wilks TJ, Kelly DM (2007) Rats (*Rattus norvegicus*) encode the shape of an array of discrete objects. J Comp Psychol 121:130-144.

Gray ER, Bloomfield, LL, Ferrey A, Spetch ML, Sturdy, CB (2005) Spatial encoding in mountain chickadees: features overshadow geometry. Biol Letters 1:314-317.

Gray ER, Spetch ML, Kelly DM, Nguyen A (2004) Searching in the center: pigeons (*Columba livia*) encode relative distance from walls of an enclosure. J Comp Psychol 118:113-117.

Guilford T, Akesson S, Gagliardo A, Holland R.A, Mouritsen H, Muheim R, Wiltschko R, Wiltschko W, Bingman VP (2011) Migratory navigation in birds: new opportunities in an era of fast-developing tracking technology. J Experimental Biol 214:3705-3712.

Healy SD, Hurly TA (1998) Rufous hummingbirds' (*Selasphorus rufus*) memory for flowers: patterns or actual spatial locations? J Experimental Psychol Anim Behav Processes 24:396-404.

Healy SD, Hurly TA (2013) What hummingbirds can tell us about cognition in the wild. Comp Cognition and Behav Rev 8:13-28.

Hurly TA, Scott RD, Healy SD (2001). The function of displays of male rufous hummingbirds. Condor 103:647-651.

Hurly TA, Franz S, Healy SD (2010). Do rufous hummingbirds (*Selasphorus rufus*) use visual beacons? Anim Cognition 13:377-383.

Hurly TA, Healy SD (1996) Memory for flowers in rufous hummingbirs: location or local visual cues? Anim Behav 51:1149-1157.

Hurly TA, Healy SD (2002) Cue use by rufous hummingbirds (*Selasphorus rufus*). J Experimental Psychol Anim Behav Processes 28:209-223.

Kamil AC, Balda RP, Good S (1999) Patterns of movement and orientation during caching and recovery by Clark’s nutcrackers, *Nucrifraga columbiana*. Anim Behav 57:1327-1335.

Kelly DM (2010) Features enhance encoding of geometry. Anim Cognition 13:453-462.

Kelly DM, Spetch ML (2001) Pigeons encode relative geometry. J Experimental Psychol Anim Behav Processes 27:417-422.

Kelly DM, Spetch ML, Heth CD (1998) Pigeons' encoding of geometric and featural properties of a spatial environment. J of Comp Psychol 112:259-269.

Krebs JR, Healy SD, Shettleworth SA (1990) Spatial memory of Paridae: comparison of a storing and a non-storing species, the coal tit, *Parus ater*, and the great tit, *P. major*. Anim Behav 39:1127-1137.

Lee SA, Spelke ES, Vallortigara G (2012a) Chicks, like children, spontaneously reorient by three-dimensional environmental geometry, not by image matching. Biol Lett 8:492-494.

Lee SA, Vallortigara G, Ruga V, Sovrano VA (2012b) Independent effects of geometry and landmark in a spontaneous reorientation task: a study of two species of fish. Anim Cogn 15:861-870.

Lee SA, Vallortigara G, Flore M, Spelke ES, Sovrano VA (2013) Navigation by environmental geometry: the use of zebrafish as a model. J Exp Biol 216:3693-3699.

Margules G, Gallistel CR (1988) Heading in the rat: Determination by environmental shape. Anim Learn Behav 16:404-410.

Miller RS, Tamm S, Sutherland GD, Gass CL (1985) Cues for orientation in hummingbird foraging: color and position. Can J Zool 63:18-21.

524 Nardi D, Nitsch KP, Bingman VP. (2010). Slope-driven goal location behavior in pigeons. J Experimental Psychol Anim Behav Processes 36:430-442.

526 Ohashi K, Thomson JD, D'Souza D (2006) Trapline foraging by bumble bees: IV. Optimization of route geometry in the absence of competition. Behav Ecol 18:1-11.

528 Pecchia T, Vallortigara G (2010) Reorienting strategies in a rectangular array of landmarks by domestic chicks (*Gallus gallus*). J Comp Psychol 124:147–158.

530 Pecchia T, Vallortigara G (2012) Spatial reorientation by geometry with freestanding objects and extended surfaces: a unifying view.Proc R Soc B 279:2228-2236.

532 Sokal RR, Rohlf FJ (1995) Biometry. 3rd ed. WH Freedman.

533 Sovrano VA, Bisazza A, Vallortigara G (2005) Animals' use of landmarks and metric information to reorient: effects of the size of the experimental space. Cognition 97:121-133.

535 Sutton JE (2009) What is geometric information and how do animals use it? Behav Proc 80:339-343.

537 Tommasi L, Chiandetti C, Pecchia T, Sovrano VA, Vallortigara G. (2012) From Natural geometry to spatial cognition. Neurosci Biobehav Rev 36:799-824.

539 Vargas JP, Quintero E, López JC (2011) Influence of distal and proximal cues in encoding geometric information. Anim Cognition 14:351-358.

541 Vlasak A (2006) Global and local spatial landmarks: their role during foraging by columbian ground squirrels (*Spermophilus columbianus*). Anim Cognition 9:71-80.

543 Waser NM, McRobert JA (1998) Hummingbird foraging at experimental patches of flowers: evidence for weak risk-aversion. J Avian Biol 29:205-313.

545 Wiltschko W, Balda RP, Jahnel M, Wiltschko R (1999) Sun compass orientation in seed-caching corvids: its role in spatial memory. Anim Cogn 2:215–221.

Wystrach A, Beugnon G, Cheng K. (2011) Landmarks or panoramas: what do navigating ants attend to for navigation? Frontiers in Zoology 8:21

Figure Captions

Fig. 1 An example of one of the study sites. Visual cues outside of experimental control were available in the immediate area of the experimental array (see foreground), in the intermediate distance (trees and forest edge), and in the far distance (ridges and mountains).

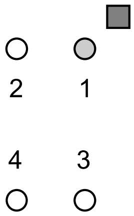
Fig. 2 Experiment 1. a) Positions of flowers and the landmark during training. Note that the relative position of the rewarded flower was assigned randomly. For convenience, the results are presented as if the rewarded flower was always flower number 1. b) Choices to flowers during the Test Probes for all data combined. c) Choices to flowers during Test Probes separated by array size. d) Choices to flowers during Test Probes separated by landmark size. Asterisks within an array identify significance levels for choices between flowers. Asterisks between arrays indicate significance levels for comparisons between arrays. ns not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Fig. 3 Experiment 2. a) Positions of flowers and the two landmarks during training. b) Choices to flowers during Test Probes in which landmarks were removed. c) Choices to flowers during Test Probes in which landmarks were moved into conflict positions. Asterisks within an array identify significance levels for choices between flowers. ns not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

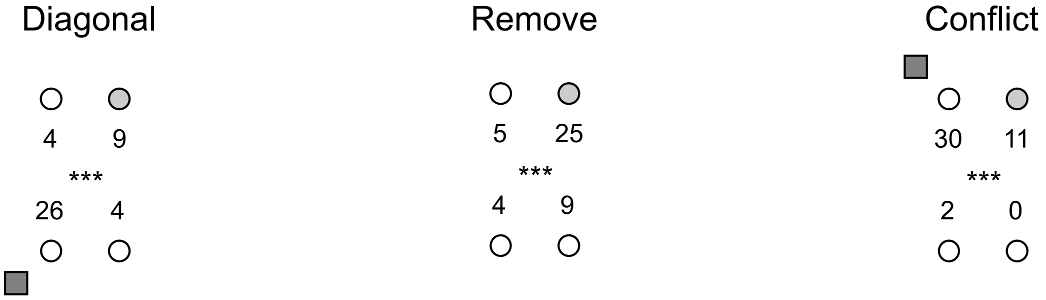
Figure

Figure

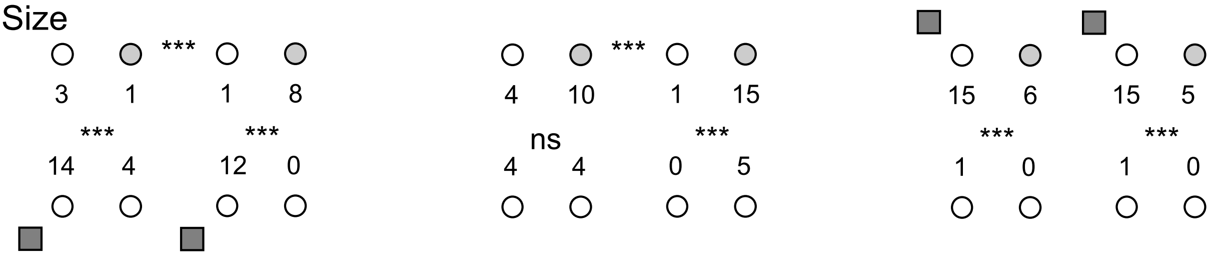
a. Training Array



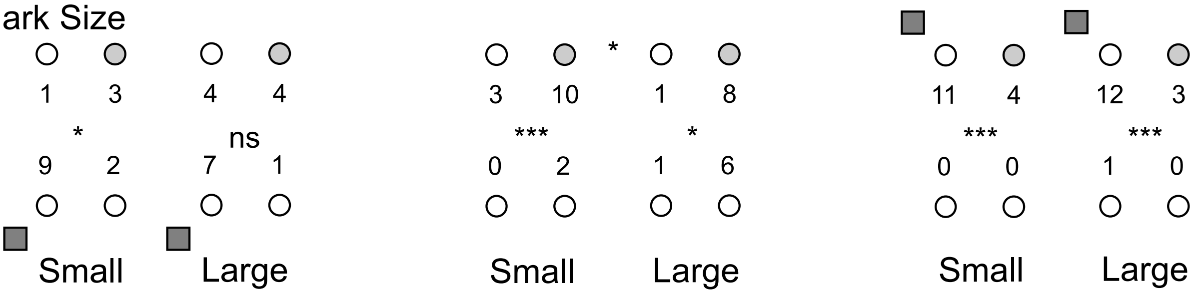
b. Combined Data



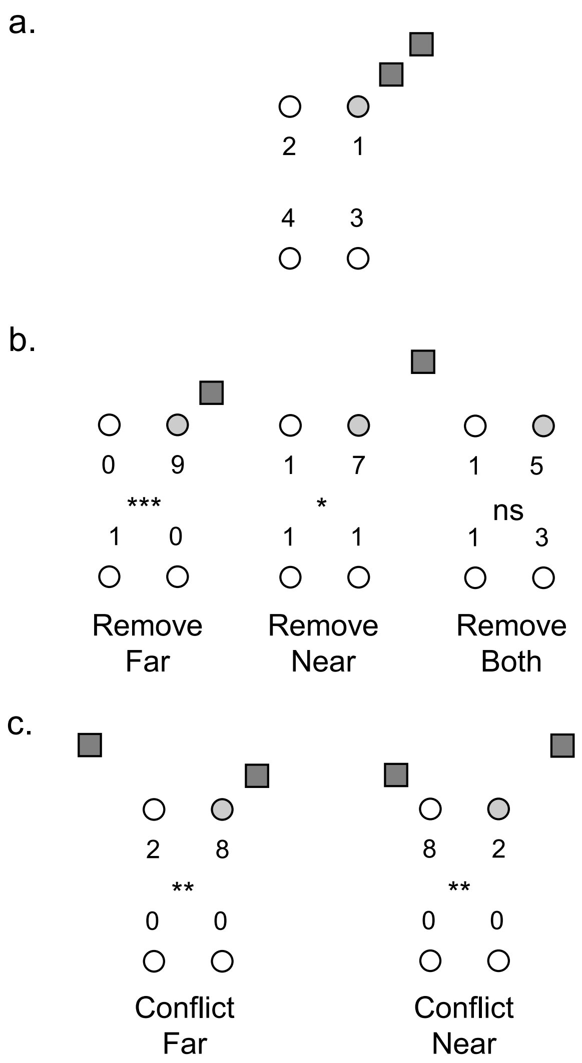
c. Array Size



d. Landmark Size



Figure


a.
2
1
4
3
b.
0
9
***
1
0
1
7
*
1
1
1
5
ns
1
3
Remove Far
Remove Near
Remove Both
c.
2
8
**
0
0
8
2
**
0
0
Conflict Far
Conflict Near