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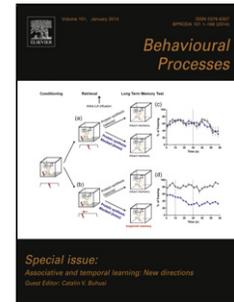
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## Wild hummingbirds can use the geometry of a flower array

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Running head: Geometry outside the box

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Highlights:

- 1) We trained birds to find a rewarded flower in a four-flower array
- 2) After rotation and translocation of the array, hummingbirds used geometric cues to choose a flower
- 3) Geometry is more than a robust laboratory artefact, but more research is required

**Abstract**

Animals use cues from their environment to orient in space and to navigate their surroundings.

Geometry is a cue whose informational content may originate from the metric properties of a given environment, and its use has been demonstrated in the laboratory in nearly every species of animal tested. However, it is not clear whether geometric information, used by animals typically tested in small, rectangular boxes, is directly relevant to animals in their natural environment.

Here we present the first data that confirm the use of geometric cues by a free-living animal in the wild. We trained rufous hummingbirds to visit a rectangular array of four artificial flowers, one of which was rewarded. In some trials a conspicuous landmark cued the reward. Following array translocation and rotation, we presented hummingbirds with three tests. When trained and tested with the landmark, or when trained and tested without it, hummingbirds failed to show geometric learning. However, when trained with a landmark but tested without it, hummingbirds produced the classic geometric response, showing that they had learned the geometric relationships (distance and direction) of several non-reward visual elements of the environment. While it remains that the use of geometry to relocate a reward may be an experimental artefact, it is one cue that is not confined to the laboratory.

Keywords: Geometry; *Selasphorus rufus*; hummingbirds; landmarks; spatial orientation; navigation

## 1. Introduction

Spatial orientation and navigation are crucial for mobile animals, and the information they derive from their environment to this end is often diverse (Healy 1998). Over the last three decades, much attention has been focused on the use of geometric relationships of enclosures for locating a goal (reviewed in Cheng et al. 2013). For example, when trained to locate a reward in one of the four corners inside a rectangular enclosure, an experimentally-disoriented animal typically chooses, with approximately equal probability, either the correct corner or the diagonally-opposing corner (the “geometric error”) during a test. The favoured explanation for these results is that both the correct corner and the geometric error share the same metric and visual information (e.g., a long wall to the left, and a short wall to the right; Sutton 2009).

This type of geometric cue use was first shown in rats: following disorientation, rats trained to receive reward in one corner of a rectangular enclosure systematically made geometric errors at about the same rate as they made correct choices (Cheng 1986). Furthermore, even when provided with visual or olfactory cues that differentiated the correct corner from the others, the rats continued to make geometric errors. Similar use of geometric relationships has been found in nearly every species tested since (Cheng et al. 2013), including humans (Hermer and Spelke 1994, 1996), cyprinid and cichlid fish (Sovrano et al. 2002, Brown et al. 2007), pigeons (Kelly et al. 1998), toads (Sotelo et al. 2015), ants (Wystrach and Beugnon 2009), bees (Sovrano et al. 2012) as well as three-day old domestic chicks (Chiandetti and Vallortigara 2008, 2010) that were naïve to any visually-derived geometric information prior to testing (Chiandetti et al. 2014).

If geometric relationships within an environment convey useful information for locating a goal, as demonstrated in the laboratory, then free-living animals should also use them. Because

rufous hummingbirds (*Selasphorus rufus*) learn locations of rewarding locations after a single visit but do not need to use the colour of the flower when they return to the location, they have been used as a model species with which to study spatial cognition in the wild (Healy and Hurly 2004, Henderson et al. 2001, Hurly and Healy 2002). These birds will also use the relative spatial positions between flowers in an array when choosing which flower to visit (Healy and Hurly 1998). However, when specifically tested for the use of geometric information, in a field analogue of laboratory tests, the hummingbirds did not make the characteristic pattern of correct choices and geometric errors. Rather, they relied on experimental and/or natural landmarks (Hurly et al. 2014) or on small, floral-specific visual features (Hornsby et al. 2014).

One explanation for these results is that it is difficult in the field to disorient test animals in a fashion similar to the way it is done in the laboratory (e.g., physically rotating an individual). Here, therefore, we attempted to disorient wild, free-living rufous hummingbirds that had been trained to feed from a stationary rectangular array of artificial flowers, with and without a prominent landmark that signalled which flower contained reward, by rotating and translocating the array during tests, rather than the birds. This is a procedure that has been used in laboratory tests, which has led to similar results as those produced when the birds are themselves rotated (Kelly et al. 2010).

## 2. Material and Methods

The subjects in this experiment were 10 wild, free-living, territorial male rufous hummingbirds. Each of these males was defending a territory centred on a commercial feeder, which contained 14% sucrose solution and which was within a ~5 km radius of the University of Lethbridge Westcastle Research Station (49°20.9'N, 114°24.6'W, 1400 m elevation). To identify

individuals, we trapped the birds using a wire-mesh cage and colour-marked them on the chest with coloured, non-toxic ink. The effects of trapping and handling were negligible as birds displayed routine behaviour shortly after release and did not then abandon their territory. All procedures were approved by the University of Lethbridge Animal Welfare Committee under the auspices of the Canadian Council on Animal Care.

### *2.1 General training*

We trained each male to feed from an artificial flower composed of a circular, yellow foam disk (5 cm diameter) with a syringe cap in the middle as a well. The flower was mounted on a wooden stake (60 cm tall) and, feeder removed, moved a few metres at a time until the bird flew directly to the artificial flower during subsequent foraging bouts. Throughout the duration of flower and experimental training (below), the syringe cap was filled with 600  $\mu$ L 25% sucrose solution. The feeder was returned at the end of each experimental session.

### *2.2 Experimental design*

We constructed a rectangular array (20 x 40 cm) composed of four identical, artificial flowers and wooden stakes not more than 10 m from the usual position of a male's feeder. We randomly determined whether the shorter or longer arm of the array was perpendicular to the position of the feeder. We also randomly determined which flower was to be rewarded and filled the other three flowers with water, which the birds find unpalatable. Following each foraging bout, during which a bird flew to the array and probed flowers until he found the sucrose solution, we haphazardly exchanged the flowers and stakes within the array. After every fourth bout, we exchanged all flowers and stakes for four new flowers and stakes. This was done to prevent the

birds learning that they could use minute visual features of each flower or stake to locate the reward (Hornsby et al. 2014). The position of the array as a whole remained stationary and did not change until we presented the birds with a test.

The experiments comprised three independent training and testing treatments (Figure 1), which were given to all 10 experimental subjects (i.e., a within-subject design): train with a landmark and test with a landmark (Treatment 1), train with a landmark and test without a landmark (Treatment 2), and train without a landmark and test without a landmark (Treatment 3).

For treatments that included a landmark, we constructed a red cube (cardboard and red duct tape; 5 cm per side) affixed to the top of a wooden stake, which we then placed between 5 cm and 45° from the rewarded flower. Because of the within-subject design and the use of three experimental treatments, we trained and tested each bird three times (Treatments 1-3), the order of which we selected from a randomized, unbiased schedule. We considered that a bird had made a correct choice when he visited the rewarded flower first on a visit to the array. For all treatments, we trained a bird until he reached a learning criterion of eight sequential correct choices. Once this criterion was met, the bird was tested.

For the tests, we translocated the array 2 m E or W and 1 m N or S from the training position and rotated it 90° clockwise or anticlockwise (all randomly determined; compass directions were in reference to the position of the feeder, which was taken to be north). Because re-trapping and then physically disorienting the hummingbirds was not practical, we disoriented the hummingbirds indirectly by using translocation and rotation of the array to dissociate the array from other visual cues in the local environment (Hornsby et al. 2014). We then exchanged all of the stakes and flowers for new stakes and flowers and filled all of the new flowers with water. When the birds had been trained with the red cube landmark they were presented with one

of two tests: (Test 1) array translocation and rotation with the landmark, where the association between landmark and rewarded flower remained, or (Test 2) array translocation and rotation without the landmark. When birds had been trained without the landmark they were presented with only one test: (Test 3) array translocation and rotation without the landmark (Figure 1).

Once a test was completed, we haphazardly shifted the experimental array more than 40 cm away from its previous position to minimize past associations with a particular rewarded location (Healy and Hurly 1998). We then randomly assigned each bird to a new experimental treatment until each bird had successfully completed Treatments 1-3.

### *2.3 Statistical analysis*

We recorded which flower the bird visited first when he came to the array during training, the inter-trial intervals between foraging bouts, and the number of trials taken to reach the learning criterion during training. To analyze training data, we used a Replicated  $G$ -test of Goodness of Fit (Sokal and Rohlf 1997, McDonald 2014), which allowed patterns to emerge from the data that were specific to each bird within a group (landmark trained or not) as well as for each group overall (a set of 10 landmark-trained birds, pooled, and a set of 10 birds trained without the landmark, pooled). Due to the small bin frequencies for some of the hummingbirds and their flower choice data (i.e., some hummingbirds never visited a particular flower; Table 1), the  $G$ -test could not produce  $G$  scores for affected hummingbirds due to the computation of  $\ln(0)$ . We therefore replaced all nil values (“0”) with “1”. This allowed the  $G$ -test to compute the necessary calculations, and additionally made each test more conservative by way of artificially reducing each affected bird’s performance. Although we could have replaced nil values with infinitesimally small ones (i.e., computing every  $G$  score as a flower choice’s value approached

0), the functional value of doing so readily became questionable. As we monotonically decreased the order of magnitude for the “nil” value, which began at 1 and which gave an average  $G$  score of 29.7 (already indicative of a strongly non-random event), a clear asymptote emerged after only a two-order reduction in magnitude (i.e., 0.01, which gave an average  $G$  score of 39.0; for reference, a three-order reduction in magnitude [i.e., 0.001] gave an average  $G$  score of 39.2) in relation to the maximum  $G$  score we might obtain for a given bird. Furthermore, since these data represent discrete flower choices, which is inherently binary (i.e., a hummingbird could not have made 0.5 of a choice), we opted to maintain the integrity of the dataset.

As we trained and tested each bird multiple times, and might expect that each individual bird might not show the same response as all other birds, we used a random slopes and intercepts linear mixed-effects model to determine whether array orientation and the presence or absence of the landmark influenced (1) the number of trials taken to reach the learning criterion or (2) the inter-trial intervals between foraging bouts. We used the results of likelihood ratio tests between the full model and the model with relevant effects removed to test for statistical significance, and report the resulting  $\chi^2$  and  $P$  values (Winter 2013, Zuur et al. 2009). Because the landmark may have acted as a feature enhancer, we predicted that hummingbirds trained with a landmark would reach criterion in fewer foraging bouts than when trained without a landmark.

For the test trials, our dataset contained small sample sizes (i.e., 10 test trial results split over 4 flower visitation options); therefore, we could not reliably use a  $G$ -test for analysis. Instead, we categorized the correct flower and its rotational error together as geometrically “correct” choices, and we categorized the other two flowers as “incorrect”, and thereafter used Sign tests. We therefore asked whether the observed number of successful trials (which, here, refers to a bird having visited either of the “correct” flowers), out of all trials performed (which,

here, was 10), was statistically significant when chance was set to 50%. For Test 1, we performed a similar analysis but also asked whether the observed number of visits to the flower associated with the landmark (i.e., the “featurally-correct” flower) was statistically significant if chance was 25%. All tests were performed in R version 3.1.2 (R Core Team 2013). All tests were two-tailed unless otherwise noted. Raw data for the number of trials taken before reaching criterion, and for the inter-trial intervals between foraging bouts, were log-transformed in order to achieve normality. The random slopes and intercepts linear mixed-effects model used the *lme4* statistical package (Bates et al. 2015) and we considered tests statistically significant when  $P < 0.05$ .

### 3. Results

#### 3.1 Training

Overall, hummingbirds took fewer trials to reach the learning criterion when trained with the landmark than when trained without it (random slopes and intercepts linear mixed-effects model with number of trials taken to reach criterion as the dependent variable:  $\chi^2(2) = 8.30$ ,  $P = 0.008$ , one-tailed; visits  $\pm$  SE., landmark present:  $11.2 \pm 0.83$ , landmark absent:  $14.7 \pm 1.35$ ), irrespective of the orientation of the array (orientation:  $\chi^2(2) = 3.89$ ,  $P = 0.14$ ; landmark x orientation:  $\chi^2(2) = 3.43$ ,  $P = 0.064$ ).

Birds returned to the array at similar intervals (combined mean:  $11.2 \pm 0.50$  min), irrespective of the presence or absence of the landmark or the array’s orientation (landmark:  $\chi^2(2) = 0.99$ ,  $P = 0.61$ ; orientation:  $\chi^2(2) = 0.66$ ,  $P = 0.72$ ; landmark x orientation:  $\chi^2(2) = 0.10$ ,  $P = 0.75$ ).

During training, all hummingbirds visited the rewarded flower first far more often than at chance (Table 1), and all birds within each group (i.e., trained with the landmark and trained without the landmark) showed similar responses (trained with the landmark:  $G(27) = 8.64$ ,  $P = 0.99$ ; trained without the landmark:  $G(27) = 6.43$ ,  $P = 1$ ). Collectively, then, each group also showed highly-directed search behaviour towards the rewarded flower (trained with the landmark:  $G(3) = 307.0$ ,  $P < 0.001$ ; trained without the landmark  $G(3) = 159.5$ ,  $P < 0.001$ ; Figure 2), which showed that training was effective for both treatments (trained with the landmark, “total”  $G(30) = 315.6$ ,  $P < 0.001$ ; trained without the landmark, “total”  $G(30) = 166.0$ ,  $P < 0.001$ ).

### 3.2 Test trials

In the test trials after they had been trained and tested with the landmark (Test 1), the hummingbirds did not choose to visit the flower at the landmark more often than they chose the other flowers (4 out of 10 visits directed to the “correct feature” flower; Sign Test,  $P = 0.28$ , 95% confidence interval [CI] for whether observed data are greater than 25% chance: 12% - 74%). Furthermore, the hummingbirds did not visit either of the “correct geometry” flowers more often than would be predicted by chance (7 visits out of 10; Sign Test,  $P = 0.34$ , CI for whether observed data were greater than 50% chance: 35% - 93%; Figure 3). However, when trained with, but tested without, the landmark (Test 2), birds chose to visit the “correct” flowers (9 “correct” visits out of 10;  $P = 0.02$ , 95% CI for whether observed data are greater than 50% chance: 55% - 99%) and did not discriminate between them ( $P = 0.51$ , 95% CI for whether observed data are greater than 50% chance: 7.5% - 70%; Figure 3).

When trained and tested without the landmark (Test 3), hummingbirds did not choose the “correct” flowers any more often than would be predicted by chance (3 “correct” visits out of 10;  $P = 0.34$ , 95% CI for whether observed data are greater than 50% chance: 6.7% - 67%; Figure 3).

#### 4. Discussion

Here we show that wild, free-living hummingbirds can encode geometric relationships between elements in their environment. Demonstrating this, however, required removal of a number of visual cues (the landmark, other, nearby environmental features and the panorama through the translocation and rotation of the experimental array) as only when birds had been trained with, but tested without, the landmark (Test 2), did they choose either the correct flower or its geometric equivalent (Figure 3). When hummingbirds were trained and tested with the landmark (Test 1), or trained and tested without the landmark (Test 3), they chose flowers at random in the test trial. Although animals in the laboratory often use geometric cues after disorientation, this is the first demonstration of this cue choice in the wild with free-living animals.

Rufous hummingbirds will learn the locations of rewarded flowers using a variety of cues, alone or together, including a conspicuous nearby landmark (Hurly et al. 2014), flowers within the same array when they are 40 cm or closer (Hurly and Healy 1998) and (to the human eye) inconspicuous visual features of the flower itself (Hornsby et al. 2014). They will also encode views of the panorama surrounding the flower (Pritchard et al. 2015, 2016) and perhaps local, natural landmarks (e.g., small bushes, ground squirrel holes; Nardi et al. 2015, Hurly et al. 2010). Now we can add geometric cues provided by the relationship among the four flowers to this list.

Demonstrating that the birds can use the geometric arrangement of the flowers, however, appears to require the removal of all of these visual cues, which themselves do not seem to be

used in isolation. If the red landmark, for example, had been sufficient, birds trained and tested with the red landmark should have chosen the flower closest to it in the test (see Hurly et al. 2014). While some birds (i.e., 4 of 10) did do this, the group of birds as a whole were no more likely to choose the flower closest to the red landmark than they were to choose any of the other flowers. Although we should be cautious in our interpretation given the small sample size, we think it more likely that the landmark may have scaffolded the learning of the reward's location as seen in previous tests of landmark use in this species (Hurly et al. 2010), but it was not sufficient to control the birds' test choice after the rotation and translocation of the array. Determining which of the visual cues (local natural cues, panorama) the birds used is difficult since a number of them will have been disrupted by the translocation/rotation of the array, and our sample size was not sufficient to provide a clearer pattern.

The red landmark was not needed for the birds to learn which flower was rewarded either: birds trained and tested without the red landmark learned which was the rewarded flower, although they did take more training than when they learned that the rewarded flower was that closest to the red landmark. When trained without the landmark, the birds could have learned the rewarded flower's location with respect to the other flowers in the array (e.g. 20 cm to the neighbouring flower on the left plus 40 cm to the flower on the right) and/or the location of the rewarded flower in the environment (either the panorama or local cues even closer to the rewarded flower than the other flowers). As the birds behaved at random in the test, it appears that the change in local environment (local natural cues and/or the panorama) was sufficient to disrupt the birds' search. Which cues the birds used in the test is not clear, as there was no pattern to their choice. We would require further experimentation with a larger sample size to identify those cues.

The birds did not choose at random, however, when they were trained with the landmark but tested without, as 9/10 hummingbirds chose one of the two “correct” flowers. We have a two-step explanation for this effect. Firstly, the red landmark led the birds to learn the geometry of the array because the red landmark allowed them to identify which of the two identical corners was rewarded. This must also have been the case in the trained and tested with the landmark condition. The second part of the explanation comes from the removal of this disambiguating cue in the test. Just as seen in Clark’s nutcrackers (Kelly 2010), without this cue in the test, the birds used the geometry of the array to choose which flower to visit. Rats tasked with finding a submerged platform in a triangular water maze enclosure also did something similar (Austen et al. 2013): when trained consistently with a landmark that disambiguated the platform, but tested without the landmark, rats relied on the geometry of the enclosure to guide their search behaviour. Although these data come from a small sample, collectively, they may suggest that the ability to learn and use geometric relationships in spatial orientation, at least when trained in the presence of a disambiguating landmark, and now, regardless of whether experiments were performed in the lab or the field, might stem from a similar mechanism that is independent of whether the geometrical information was gleaned from surfaces or discrete points (e.g., Cheng and Newcombe 2005). Additional experiments with a larger sample size would be required to confirm this suggestion.

That these hummingbirds can use the geometry of the elements of a rectangular array in an environment rich in local and global landmarks, with an array set in heterogeneous grassy fields, suggests that such a response is robust beyond the highly-artificial nature of the small testing enclosures typical of the laboratory (Cheng 2008, Hurly et al. 2014). The extent to which

geometry is used by animals in the wild, alone or in conjunction with other cues, is not yet clear, however, and it is still possible that the use of geometric cues is an experimental artefact.

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### **Competing Interests**

The authors declare that there are no competing interests.

**References**

- Austen JM, Kosaki Y, McGregor A (2013) Within-compound associations explain potentiation and failure to overshadow learning based on geometry by discrete landmarks. *J Exp Psychol Anim Beh* 39, 259-272.
- Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B (2015) Package ‘lme4’: Linear mixed-effects models using Eigen and S4. Version 1.1-7.
- 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 (2008) Whither geometry? Troubles of the geometric module. *Trends Cogn Sci* 12, 355-361.
- Cheng K, Newcombe NS (2005) Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychon B Rev* 12, 1-23.
- Cheng K, Huttenlocher J, Newcombe NS (2013) 25 years of research on the use of geometry in spatial reorientation: A current theoretical perspective. *Psychon B Rev* 20, 1033-1054.
- Chiandetti C, Vallortigara G (2008) Is there an innate geometric module? Effects of exposure with angular geometric cues on spatial re-orientation based on the shape of the environment. *Anim Cogn* 11, 139-146.
- Chiandetti C, Vallortigara G (2010) Experience and geometry: Controlled-rearing studies with chicks. *Anim Cogn* 13, 463-470.
- Chiandetti C, Spelke ES, Vallortigara G (2014) Inexperienced newborn chicks use geometry to spontaneously reorient to an artificial social partner. *Dev Sci*, doi: 10.1111/desc.12277.

- Healy S (1998) Spatial representation in animals. Oxford University Press, New York.
- Healy SD, Hurly TA (1998) Rufous hummingbirds' (*Selasphorus rufus*) memory for flowers: Patterns or actual spatial locations? *J Exp Psychol Anim Beh* 24, 396-404.
- Healy SD, Hurly TA (2004) Spatial learning and memory in birds. *Brain Behav Evol* 63, 211-220.
- Henderson J, Hurly TA, Healy SD (2001) Rufous hummingbirds' memory for flower location. *Anim Behav* 61, 981-986.
- Hermer L, Spelke ES (1994) A geometric process for spatial reorientation in young children. *Nature* 370, 57-59.
- Hermer L, Spelke ES (1996) Modularity and development: The case of spatial reorientation. *Cognition* 61, 195-232.
- Hornsby MAW, Hurly TA, Hamilton CE, Pritchard DJ, Healy SD (2014) Wild, free-living rufous hummingbirds do not use geometric cues in a spatial task. *Behav Proc* 108, 138-141.
- Hurly TA, Healy SD (1996) Memory for flowers in rufous hummingbirds: Location or local visual cues? *Anim Behav* 51, 1149-1157.
- Hurly TA, Healy SD (2002) Cue learning by rufous hummingbirds (*Selasphorus rufus*). *J Exp Psychol Anim Beh* 28, 209-223.
- Hurly TA, Franz S, Healy SD (2010) Do rufous hummingbirds (*Selasphorus rufus*) use visual beacons? *Anim Cogn* 13, 377-383.
- Hurly TA, Fox TAO, Zwueste DM, Healy SD (2014) Wild hummingbirds rely on landmarks not geometry when learning an array of flowers. *Anim Cogn* 17, 1157-1165.
- Kelly DM (2010) Features enhance the encoding of geometry. *Anim Cogn* 13, 453-462.

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

Kelly DM, Kamil AC, Cheng K (2010) Landmark use by Clark's nutcrackers (*Nucifraga columbiana*): Influence of disorientation and cue rotation on distance and direction estimates. *Anim Cogn* 13, 175-188.

McDonald JH (2014) Handbook of biological statistics, third ed. Sparky House Publishing, Baltimore.

Nardi D, Holmes CA, Newcombe NS, Weisberg SM (2015) Sex differences and errors in the use of slope for navigation. *Cogn Process* 16, S323-S326.

Pritchard DJ, Hurly TA, Healy SD (2015) Effects of landmark distance and stability on accuracy of reward relocation. *Anim Cogn* 18, 1285-1297.

Pritchard DJ, Scott RD, Healy SD, Hurly TA (2016) Wild rufous hummingbirds use local landmarks to return to rewarded locations. *Behav Proc* 122, 59-66.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

Sokal RR, Rohlf FJ (1997) Biometry: The principles and practices of statistics in biological research, third ed. Freeman and Company, New York.

Sotelo MI, Bingman VP, Muzio RN (2015) Goal orientation by geometric and feature cues: Spatial learning in the terrestrial toad *Rhinella arenarum*. *Anim Cogn* 18, 315-323.

Sovrano VS, Bisazza A, Vallortigara G (2002) Modularity and spatial reorientation in a simple mind: Encoding of geometric and nongeometric properties of a spatial environment by fish. *Cognition* 85, B51-B59.

Sovrano VS, Rigosi E, Vallortigara G (2012) Spatial reorientation by geometry in bumblebees.

PLoS ONE 7(5), e37449.

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

343.

Winter B (2013) Linear models and linear mixed effects models in R with linguistic applications.

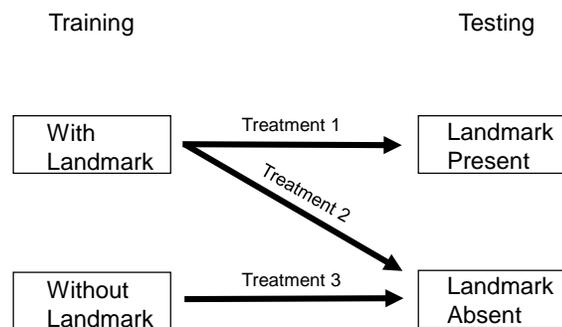
arXiv 1308.5499.

Wystrach A, Beugnon G (2009) Ants learn geometry and features. Curr Biol 19, 61-66.

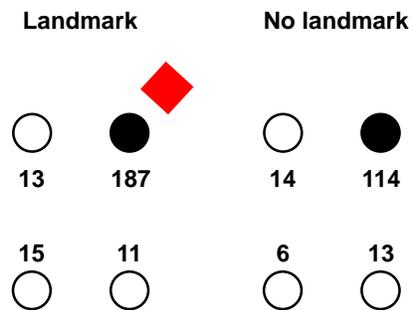
Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009). Mixed effects models and

extensions in ecology with R. New York: Springer Science + Business Media.

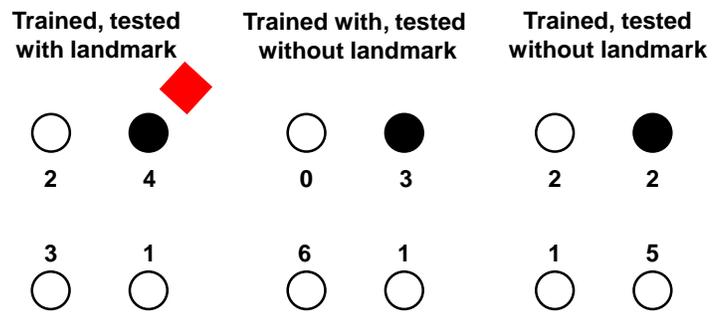
**Figure 1.** Experimental progression for all training and testing procedures, which all hummingbirds ( $n = 10$ ) received. Each hummingbird was first randomly assigned to train either with or without the landmark and was required to reach the learning criterion (8 sequential correct choices) before we presented him with a test. Hummingbirds that were trained with the landmark received two, independent tests: one that included the landmark (landmark present) and one that did not (landmark absent).



**Figure 2.** The first choices that the hummingbirds made during training on the three sets of training trials. The circles represent flowers (filled circles represent reward; open circles represent flowers that contained water), and the square represents the landmark. The numbers outside the circles represent the number of first visits that birds made to that particular flower. Note that the numbers for the landmark training trials come from two sets of training trials. The position of the rewarded flower was randomized for each trial, but the data are presented as if the reward always occurred in the upper-right flower.



**Figure 3.** The first choices that the hummingbirds made during test trials. Flower and landmark representations are the same as in Figure 2. The position of the rewarded flower was randomized for each trial but the data are presented as if the reward always occurred in the upper-right flower.



**Table 1.** Individual bird performance during training, adjusted such that Flower 2 is always represented as the rewarded flower (see also Figure 2). Note that birds trained with the landmark received two bouts of training as they received two tests (with and without a landmark), whereas birds trained without the landmark received were only trained once as they only received one test. Statistics associated with each bird form a portion of the Replicated  $G$ -test of Goodness of Fit (individual  $G$ -tests).

Landmark Present?	Bird	Flower 1	Flower 2	Flower 3	Flower 4	$G$	$P$
Yes	Bird 1	3	20	0	0	34.8	<0.001
	Bird 2	3	19	0	0	32.5	<0.001
	Bird 3	0	16	0	2	27.1	<0.001
	Bird 4	0	16	2	1	27.1	<0.001
	Bird 5	2	19	3	2	26.7	<0.001
	Bird 6	1	18	3	1	30.2	<0.001
	Bird 7	1	20	2	1	36.6	<0.001
	Bird 8	2	26	4	1	44.0	<0.001
	Bird 9	0	16	0	2	27.1	<0.001
	Bird 10	1	16	1	1	29.5	<0.001
No	Bird 1	0	12	2	0	18.0	<0.001
	Bird 2	2	12	1	0	18.0	<0.001
	Bird 3	2	17	0	5	23.6	<0.001
	Bird 4	1	8	0	1	11.0	0.012
	Bird 5	2	15	1	1	24.8	<0.001
	Bird 6	2	11	0	1	15.9	0.001
	Bird 7	2	8	0	0	9.68	0.022

Bird 8	1	8	1	1	11.0	0.012
Bird 9	1	12	0	2	18.0	<0.001
Bird 10	1	11	1	2	15.9	0.001

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