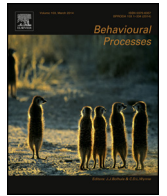




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# Wild hummingbirds can use the geometry of a flower array

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### 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, its use is not confined to the laboratory.

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## 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 natu-

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ral 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.

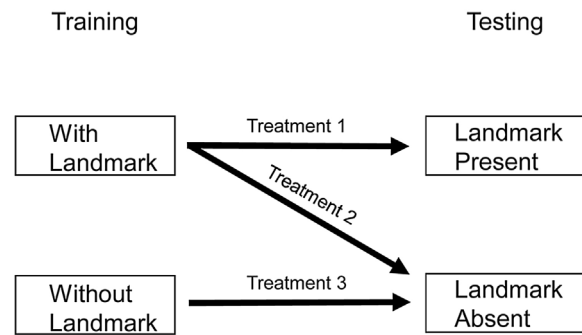
### 2.1. General training

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  $\times$  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 (Fig. 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).



**Fig. 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).

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 (Fig. 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,

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