



Short report

Wild, free-living rufous hummingbirds do not use geometric cues in a spatial task



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ABSTRACT

In the laboratory, many species orient themselves using the geometric properties of an enclosure or array and geometric information is often preferred over visual cues. Whether animals use geometric cues when relocating rewarded locations in the wild, however, has rarely been investigated. We presented free-living rufous hummingbirds with a rectangular array of four artificial flowers to investigate learning of rewarded locations using geometric cues. In one treatment, we rewarded two of four flowers at diagonally opposite corners. In a second treatment, we provided a visual cue to the rewarded flower by connecting the flowers with “walls” consisting of four dowels (three white, one blue) laid on the ground connecting each of the flowers. Neither treatment elicited classical geometry results; instead, hummingbirds typically chose one particular flower over all others. When we exchanged that flower with another, hummingbirds tended to visit the original flower. These results suggest that (1) hummingbirds did not use geometric cues, but instead may have used a visually derived cue on the flowers themselves, and (2) using geometric cues may have been more difficult than using visual characteristics. Although hummingbirds typically prefer spatial over visual information, we hypothesize that they will not use geometric cues over stable visual features but that they make use of small, flower-specific visual cues. Such cues may play a more important role in foraging decisions than previously thought.

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1. Introduction

Animals use environmental cues to orient and navigate in space (reviewed in [Shettleworth, 2010](#)). The degree to which a given species is reliant on a cue is probably driven by its particular salience in the immediate environment, the quality of its informational content, and its utility to the species in question ([Hodgson and Healy, 2005](#)). In contrast, the geometric cues do not seem to be context-dependent (reviewed in [Tommasi et al., 2012](#)), and their use, until recently (i.e., [Hurlly et al., 2014](#)), has only been investigated in the laboratory.

[Cheng \(1986\)](#) first documented that animals encode and remember geometric relationships within an arena. He trained rats

to find food in one corner of a rectangular enclosure and, during tests, found that the animals divided their choices between the correct corner and the diagonally opposite corner. Cheng reasoned that rats used the geometric properties of the enclosure to guide their search for a reward (e.g., search where the long wall is to the left, and the short wall is to the right; see [Fig. 1a](#)) resulting in visits to rotationally symmetrical corners. Many laboratory-trained taxa have since demonstrated the same characteristic pattern of choices (reviewed in [Cheng et al., 2013](#)).

Increasingly, researchers have investigated how visual features conflate geometric learning to disentangle what cue is more often used and why, with results varying within and between taxa ([Sutton, 2009](#)). Laboratory results are typically discussed in terms of mechanisms, however, rather than their relevance to the evolutionary ecology of the species in question (but see, e.g., [Sovrano et al., 2007](#)). One species that is particularly amenable to this latter approach is the free-living rufous hummingbird *Selasphorus rufus*, which heavily relies on visually mediated spatial memory ([Healy and Hurlly, 2013](#)) but uses visual cues when spatial information is unreliable ([Hurlly and Healy, 2002](#)).

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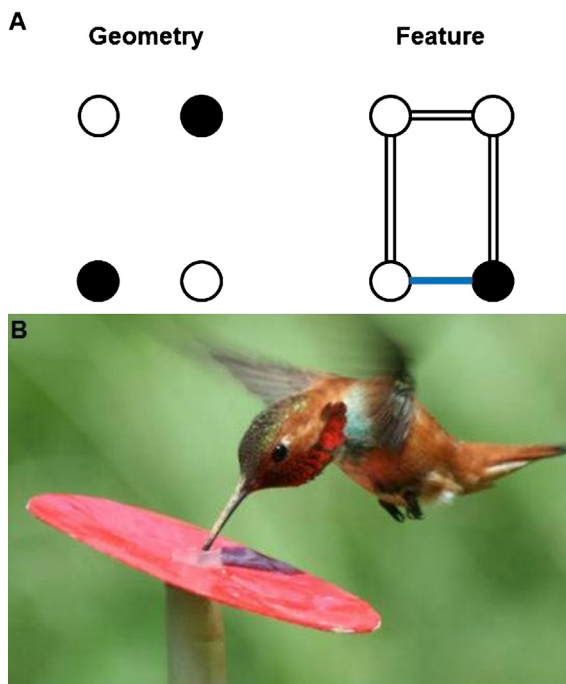


Fig. 1. Rectangular arrays of flowers used for geometry and feature training paradigms, and a floral exemplar. (A) In the geometry treatment (left), diagonally opposing flowers were both rewarded (filled circles). In the feature treatment (right), the rewarded flower (filled circle) was one of the previously unrewarded flowers in the geometry treatment. Additionally, a wooden dowel coloured either blue (the visual feature) or white was placed between each flower, thus emphasizing the rectangular nature of the array. If, relative to the rewarded flower, a bird chose the unrewarded flower (i) connected to the feature border, (ii) diagonally opposite from it, or (iii) perpendicular to it, the bird was said to have made a 'feature', 'geometry' or 'total' mistake, respectively. Following each foraging bout in both treatments we translocated the array no more than 2 m away from its previous location towards a randomly-determined compass location, and rotated between 90 and 180°. (B) Close-up photo of a typical flower used during experiments and tests. Note the distinct patterns on the flower that likely arose from spilled and dried sucrose, and the short distance between the bird and flower. Photo credit: C.E. Hamilton.

We therefore investigated whether free-living rufous hummingbirds encode the geometry of a rectangular array of flowers as do laboratory-trained animals encode the geometry of objects or enclosures. Previously, when hummingbirds in this population were presented with artificial landmarks and flowers, they did not appear to use the geometric cues of a rectangular array of four flowers (Hurly et al., 2014). As the flowers remained in the same location for the duration of the experiment, however, the hummingbirds might have used experimental and/or natural landmarks to guide their search patterns. Here, we attempted to facilitate the birds' use of geometry by using field-analogues of laboratory techniques. After every array visit, we translocated and rotated the array, making other spatial information (e.g., local landmarks, global orienting cues) unreliable indicators of the rewarded flower's location (Kelly, 2010; Pecchia and Vallortigara, 2010). In one treatment, we rewarded two geometrically identical flowers in the array (Pecchia and Vallortigara, 2012) and in a second, we enhanced the rectangular arrangement of the array flowers by providing "visual walls" (Lee et al., 2013) and a visually distinctive reward location (Sovrano et al., 2013).

2. Materials and methods

2.1. Experimental subjects

Nine free-living male rufous hummingbirds *S. rufus* in the West-castle River Valley (Alberta, Canada, 49°21' N, 114°25' W, 1400 m

elevation) were observed defending territories, each with a commercial feeder (14% sucrose) at its centre. These birds were trapped, colour-marked with non-toxic ink, and then released. Territorial males were then trained to feed from an artificial flower (6 cm diameter cardboard disc with a syringe cap in the middle, mounted to a 50 cm tall wooden stake) containing 600 μ L 25% sucrose. All procedures were approved by the University of Lethbridge Animal Welfare Committee under the auspices of the Canadian Council on Animal Care.

2.2. Experimental design

Birds were trained under two field-analogues of the laboratory geometry paradigm: with and without a prominent visual feature provided to aid subjects in learning the rewarded flowers. For both treatments, a rectangular array (40 cm \times 10 cm) composed of four, identically constructed artificial flowers (Fig. 1b) was constructed not far from a bird's feeder. All birds were first presented with the geometry task, followed by the feature task. Rewarded flowers were filled with 25% sucrose. The remaining flowers contained water, which the birds find unpalatable.

In the geometry treatment, we rewarded two of the four flowers during training. These flowers occupied corners that were diagonally opposing each other (Fig. 1a). Rewarded floral pairs were counter-balanced across birds, thus giving two non-transposable array configurations.

In the feature treatment we rewarded only one flower, which always occupied one of the flower positions in the array that had not been rewarded in the geometry treatment. Additionally, we attempted to emphasize the rectangular nature of the array by connecting the bases of the flowers with coloured wooden dowels (40 or 10 cm long, 1 cm diameter). Three of the dowels were white and one was blue, colours chosen to mirror laboratory studies wherein three enclosure walls are typically white and the fourth blue (e.g., Kelly et al., 1998; Sovrano et al., 2007). The location of the blue dowel, i.e., whether it was placed to the long or short arm of the rewarded flower, was counter-balanced across birds (Fig. 1a).

Regardless of treatment, the rectangular array was translocated and rotated after every visit to the array in an attempt to reduce reliance on other orientation cues (e.g., local, natural landmarks; see Fig. 1a) although flowers and stakes were not interchanged and remained in their relative spatial locations. Birds were trained independently and were required to reach a learning criterion of six consecutive correct choices (our a priori assumption that the birds had learned the association between a particular flower, its spatial location and/or its visual associations) before being presented with a test. A bird had made a correct choice when his first visit to the array was to a rewarded flower.

2.3. Tests

After reaching criterion in the geometry treatment, each bird received a single test where we recorded the first visit to the array, which typically required <10 s to complete before a bird flew away. In the test all flowers contained water and we again translocated and rotated the array. After reaching criterion in the feature treatment, we presented the birds with two tests, the first of which was randomly determined: a feature test, where the blue dowel was shifted to the opposite side of the rewarded flower, thus placing the feature in conflict with geometry, and a geometry test, where all dowels were white, thus leaving the birds able to use only geometric information when choosing a flower. Following the completion of the first test, a bird's training was reinforced with five additional trials, after which he received the second test. As a result of preliminary analyses, we implemented a third test on a small subsample ($n = 4$) of birds. Here, all dowels were white, and the flower that was

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