

Do rufous hummingbirds (*Selasphorus rufus*) use visual beacons?

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Abstract Animals are often assumed to use highly conspicuous features of a goal to head directly to that goal ('beaconing'). In the field it is generally assumed that flowers serve as beacons to guide pollinators. Artificial hummingbird feeders are coloured red to serve a similar function. However, anecdotal reports suggest that hummingbirds return to feeder locations in the absence of the feeder (and thus the beacon). Here we test these reports for the first time in the field, using the natural territories of hummingbirds and manipulating flowers on a scale that is ecologically relevant to the birds. We compared the predictions from two distinct hypotheses as to how hummingbirds might use the visual features of rewards: the distant beacon hypothesis and the local cue hypothesis. In two field experiments, we found no evidence that rufous hummingbirds used a distant visual beacon to guide them to a rewarded location. In no case did birds abandon their approach to the goal location from a distance; rather they demonstrated remarkable accuracy of navigation by approaching to within about 70 cm of a rewarded flower's original location. Proximity varied depending on the size of the training flower: birds flew closer to a previously rewarded location if it had been previously signalled with a small beacon. Additionally, when provided with a beacon at a new location, birds did not fly directly to the new beacon. Taken together, we believe these data demonstrate that these hummingbirds depend little on visual

characteristics to beacon to rewarded locations, but rather that they encode surrounding landmarks in order to reach the goal and then use the visual features of the goal as confirmation that they have arrived at the correct location.

Keywords Beacon · Local cue · Landmark · Rufous hummingbirds

Introduction

Animals use visual landmarks in a hierarchical manner to approach a goal such as a familiar feeding location, a nest, burrow, etc. Large immobile landmarks are used when far from the goal with the animal switching to small less conspicuous landmarks near to the goal or to the visual aspects of the goal itself (beaconing: Collett and Zeil 1998; Shettleworth 1998). In many laboratory experiments, learning that a goal is localisable by the beacon appears to preclude the learning of other landmarks, perhaps due to overshadowing (e.g. Redhead et al. 1997; Shettleworth 1998). Conceptually, beaconing is such a simple and reliable method of goal location that it is tempting to assume that animals will always use this method when an appropriate beacon is present. Indeed, learning of routes or locations may be easier using beacons rather than associative learning (Cook and Tauro 1999; Waller and Lippa 2007). As a consequence of these observations and assumptions, most recent research has focused on how animals locate goals that are not localisable via a beacon (e.g. Gould-Beierle and Kamil 1998; Kamil et al. 2001; Spetch et al. 2003).

However, beacon use is not always as straightforward as it might appear. Large landmarks that are initially used in beacon-like fashion along a route, in wood ants at least, can

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act as a ‘scaffold’ for the memorisation of other nearby landmarks, so that when the beacon is removed, the animal’s trajectory along the now familiar route remains unaffected (e.g. Graham et al. 2003). Similarly, rats in mazes also move from total dependence on a beacon to a situation in which a stable goal can be located without the beacon (e.g. Pearce et al. 2001). If the goal is unstable and moved between trials, the beacon remains essential for continued accurate goal location (Hogarth et al. 2000).

Visual beacons may play a similar important role for vertebrates in the natural world as they learn a spatial location. For example, numerous anecdotes describe the return of migratory hummingbirds to locations of artificial sucrose feeders from which they fed the previous year: people are often prompted to replace the feeder each spring by the appearance of hummingbirds hovering at the appropriate window. Plant-pollinator systems such as hummingbirds and their flowers are excellent models with which to investigate the use of beacons by free-living animals because the floral displays of plants appear to be adaptations selected to attract avian or insect pollinators. To return to a flower, or a patch of flowers, a pollinator could use the distinctive visual features of the floral display as a beacon. A hummingbird, for example, capable of seeing a colourful flower from tens of metres away, might use the flower’s conspicuous display to fly directly to that flower to feed (distant beacon hypothesis). At the other extreme, the hummingbird could use other cues to return to the location of the flower, either choosing to ignore or recognizing the visual features of that particular flower only when it was close enough to insert its bill into the corolla (local cue hypothesis).

Here, we compared these two hypotheses in wild, free-living rufous hummingbirds *Selasphorus rufus*. In two different experiments we investigated whether, and how, birds might use distant beacons by training hummingbirds to return repeatedly to a single, visually distinctive artificial flower. In Experiment 1, the training was followed by test trials to determine (1) the accuracy with which hummingbirds could return to the reward location in the absence of the flower and, (2) at what point during the approach to the trained location hummingbirds re-oriented towards the flower when we had moved it to a new location. If the visual cues of the flower are used as a distant beacon, we predicted that the birds would fly directly to the flower’s new location. In Experiment 2, we trained birds with either a large or a small flower, predicting that when we removed the flower in a test trial, birds would approach the goal location more closely when trained on the small flower than when trained on the larger flower. The logic here is that with the smaller flower, more of the landmarks en route to the flower are required before the flower is employed as a visual cue.

Methods

Study site and subjects

The experiments were conducted along a valley in the Rocky Mountains 20 km southwest of Beaver Mines, Alberta, Canada. Rufous hummingbirds migrate to this valley to breed and males establish feeding territories around commercial hummingbird feeders filled with 14% sucrose solution. Experiment 1 was conducted in 2003 and Experiment 2 in 2004 with different males. Five male rufous hummingbirds were the subjects in each experiment and each bird was individually marked by the application of a small amount of non-toxic, coloured ink onto the breast feathers. Birds were not handled at any point during the experiments and all were trained and tested in their own territories. These free-living, wild birds chose when to visit the flowers we presented to them.

Training procedure

A male’s feeder was removed while he was trained to feed from an artificial ‘flower’. This consisted of a syringe cap inserted into a cork (3 cm × 2.5 cm), painted red, glued onto the top of a 60 cm wooden stake, which was then set into the ground. The syringe cap was filled with 600 µl of 25% sucrose solution, a quantity that was too great for a hummingbird to consume in a single visit. Once a bird had learned to feed from this flower, the flower was gradually moved to a distance of approximately 20 m from the feeder location and training specific to the experiment began (see below).

Two video cameras were used to record the bird flying to the flower to feed. Both these cameras captured 60 frames/s (60 Hz). The cameras were set up 2–3 m from the flower and approximately 90° from each other. The bird was allowed to feed from the flower 8–12 times with the last five feedings recorded as ‘training’ flights and then the flower was removed/moved. The subsequent flight to the vicinity of the flower’s previous location was recorded as the test flight.

Analysis of video recordings

We used the Peak Motus Motion Measurement System to synchronise the video input from the two cameras. Synchronisation of the video input was achieved firstly by recording the calibration device. This had eight tubular arms each with three small white spheres spaced at 52 cm intervals (centre to centre) along those arms. For the recording from each camera the positions of each of the 24 spheres were manually digitised in a specific order so that the spheres were matched across the two sets of videos.

This provided the basis for the 3-D calculations that the computer made when the video from each camera was subsequently digitised. The bird's flight path was manually digitised for each frame for each camera.

The combination of the small size of the hummingbirds (body length 9–10 cm) and the limited resolution of the video cameras restricted the field of view in which we could collect data. Thus, with the flower in the centre of the field of view we captured birds as far away as 3.21 ± 0.24 (SE) m from the goal flower. Interbout intervals were determined by the birds and did not differ among trials: 16.04 ± 0.59 min for training trials and 14.23 ± 0.92 for removed and moved flower test trials combined (paired t test: $t_4 = 1.624$, $P = 0.139$).

The minimum distance to which the birds approached the original flower location and the time at hovering were determined for the test flights. For the moved flower test flight we determined the distance from the moved flower when the bird was at its closest to the original flower location.

Experiment 1

The day after the bird had been trained, the flower was placed in the same location it had occupied the previous day. The bird fed from the flower 8–12 times (number determined by randomized schedule) and cameras were set up to record the last five of these training flights. The flower was then removed and the following test flight towards the flower location was recorded. Once the first removed flower test flight had been recorded, the flower was again replaced and the bird was allowed a further 8–12 training flights to the flower. The last five of these training flights were recorded and then a second removed flower test trial was recorded. This procedure was repeated a third time but instead of removing the flower, we moved it to a new location. The distance for each moved flower trial was randomly chosen within 1.30–1.70 m range, as was the direction in which it was moved. The flight to the flower in its new location was recorded.

Experiment 2

Following initial training, each bird was trained to feed from a large red cardboard cube (10 cm per side) at least 8 m from the feeder and location of initial training. The upper surface of this experimental 'flower' contained a syringe cap filled with 25% sucrose solution. The bird was then allowed to feed 20 times from this flower at this location and we set up the cameras to record the last five training flights. We then removed the cube flower and recorded the next flight that the bird made (large test 1).

Once the bird had flown off, the training flower was replaced at the original feeder location and the bird was then trained to a second location at least 8 m from the training location and at least 2 m from the first experimental location. This time the training flower was a small red cardboard cube (2 cm per side). The bird was allowed to feed 20 times (the last five of which were recorded), after which we removed the flower for the test flight (small test 1).

When the bird had flown off after this second test flight, the bird was trained to a third location (also at least 8 m from the feeder and 2 m from either of the two earlier locations), again with the large red cardboard cube. The bird was allowed to feed 20 times (the last five of which were recorded) after which the large cube was removed and the following flight recorded (large test 2).

When bad weather interrupted training to a particular location, a new location was chosen when the weather improved and training restarted.

Results

Experiment 1

Distance to original flower location

We calculated the closest distance the birds approached to the flower's original location for test flights during removed- and moved flower trials (Fig. 1). We measured distance in three ways: (1) the straight-line distance in three dimensions; (2) horizontal distance; and (3) vertical distance. These latter two were used to compare accuracy between the horizontal and vertical components.

When the flower was removed, or moved, the birds flew to within 0.68 ± 0.20 m of the original flower location (Fig. 2). There were no differences in closest distance reached by the birds between the two 'removed flower' trials or between those trials and the 'moved flower' trial (paired t tests, removed flower trials: $t_4 = 0.421$, $P = 0.695$; removed flower trials vs. moved flower trials: $t_4 = 0.074$, $P = 0.945$).

If the flower was used as a distant beacon, then moving the flower 1.3–1.7 m should attract the bird directly to it. Specifically, when a bird achieved its closest approach to the original goal location, it should actually be closer to the new test flower than to the original location. This was not the case: the birds flew no closer to the moved flower (0.76 ± 0.28 m) than to the original flower location (0.68 ± 0.20 m) (paired t tests, $t_4 = 0.089$, $P = 0.933$). Additionally, the birds reached their minimum distance to the location of the original flower in less time than it took to fly to the new flower ($t_4 = 3.00$, $P = 0.040$). It is

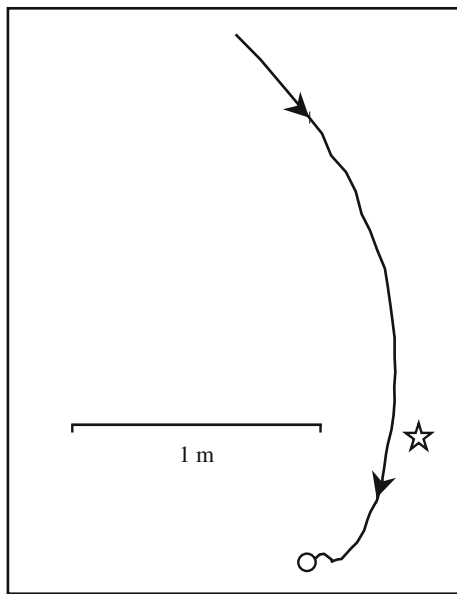


Fig. 1 An example of a two-dimensional plot of a bird's flight path on a test trial when the flower had been moved. The bird flew towards the original reward location (*star*), approaching to a distance of 28 cm, and then proceeded to the current location of the moved flower (*open circle*)

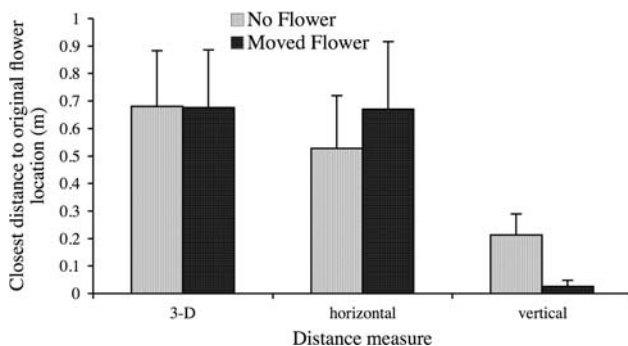


Fig. 2 Mean closest approach to the location of the original flower (\pm SE) achieved by hummingbirds in test trials in which the flower was removed (*light bars*) and the test trial in which the flower was moved (*dark bars*) 1.30–1.70 m from the flower's original location in Experiment 1. We present the closest distance to the flower's original location in three dimensions and in separate horizontal and vertical components

evident that the hummingbirds were capable of seeing the flower from at least 1.30 m away because all birds found the moved flower after they had achieved their minimal approach distance to the original goal location.

Accuracy was significantly better in the vertical component than the horizontal component: birds came closer to the flower's original height than to its original location in the horizontal plane (two-way repeated measures ANOVA: $F_{1,4} = 17.93$, $P = 0.013$; Fig. 2). Neither the trial type (removed vs. moved) nor the interaction (component \times trial type) were significant (all $F_{s,1,4} < 0.84$, $P_s > 0.40$).

Time taken to reach original flower location

If flowers were used as distant beacons, then flight time to the flower in the moved flower trial should not differ from flight time in training trials. Alternatively, if birds used the visual cues of the flower only when they had already arrived in the vicinity of the goal, then noticing that the flower had moved from its original training location should result in a slower approach to the new location. Although birds took longer to reach the flower on moved flower trials than they did on training trials, this difference was not significant (one-tailed t test; $t_4 = 1.602$, $P = 0.092$; training = 0.71 ± 0.07 s, test = 1.2 ± 0.36 s).

Experiment 2

Birds never aborted their approach from a distance during removed flower test trials (Fig. 3). On removed flower-large test trials birds flew to within 0.62 ± 0.15 m of the goal location, a distance very similar to that seen in Experiment 1 (0.68 ± 0.20 m). Additionally, birds flew closer to the original flower location in removed flower-small test trials (0.26 ± 0.10 m) than in the removed flower-large tests (one-tailed, paired t test: $t_4 = 2.507$, $P = 0.033$). Approach distances did not differ between the two removed flower-large test trials (two-tailed, paired t test; $t_4 = 0.049$, $P = 0.964$).

Decomposition of approach distance into horizontal and vertical components produced patterns similar to those from Experiment 1. Birds were significantly more accurate in the vertical component than in the horizontal component (two-way repeated measures ANOVA; vertical vs. horizontal: $F_{1,4} = 17.54$, $P = 0.014$). Birds approached more closely to the original flower location in the small flower trials than in the large flower trials ($F_{1,4} = 7.94$, $P = 0.048$). The

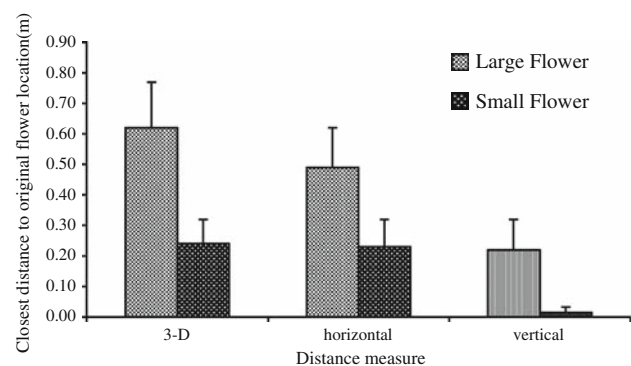


Fig. 3 Mean closest approach to the location of the original flower (\pm SE) achieved by hummingbirds in large flower trials (*light bars*) and small flower trials (*dark bars*) in Experiment 2. The data represent the closest distance to the flower's original location in three dimension, and in separate horizontal and vertical components

interaction was not significant (component \times flower size: $F_{1,4} = 3.11$, $P = 0.153$; Fig. 3).

Discussion

We trained wild, free-living rufous hummingbirds to feed from artificial flowers so that we could test the use of beacons. To our knowledge, this is the first time that beacon use by a vertebrate has been manipulated in the field. Furthermore, we tested the birds while they carried out their daily routines (foraging, territorial defence, courtship, etc.) and the experimental presentations were ecologically relevant both spatially and temporally. Finally, rather than manipulating an array of flowers and asking the birds to indicate which specific flower they remembered as the goal (e.g. Healy and Hurly 1998), we employed a single training flower that was removed or moved to prompt the birds to indicate where in the territory they remembered the goal to be. The data from our experiments fail to support the hypothesis that rufous hummingbirds employ conspicuous flowers as distant beacons. First, birds travelled from a considerable distance and never aborted approach during tests with the flower removed. Rather, they approached the goal location to within an average of 0.68 m, or closer, when the flower was absent. Second, when a flower was present (ca. 1.5 m from the training location) to act as a beacon, the birds did not approach the moved flower directly but rather flew just as close to the original training location as they had in removed flower tests with no flower present. Third, approach to the moved flower was slower, though not significantly, than approach to the training flower, indicating that birds did not regard the visually cued flower in the same way as they regarded the training flower. Fourth, training to a larger more conspicuous flower in Experiment 2 did not cause the birds to employ it as a distant beacon while the use of a smaller training flower caused the birds to approach even more closely to the goal location in the flower's absence.

Given that the hummingbirds in this study defended territories ca. 1 ha in size, the accuracy with which they returned to the goal location is noteworthy. That is, the area circumscribed by the average distance to the goal in Experiment 1 (0.68 m) represents ca. 0.02% of a bird's territory, the territory being considerably larger than what is typically available for testing in the lab (dimensions ca. 1–3 m). The closest return distance may simply represent where the birds abandoned their search for the missing flower, rather than a definitive measure of accuracy.

Unlike other studies in which animals were tested in a two-dimensional environment (e.g. Cheng and Sherry 1992; Gould-Beierle and Kamil 1996; Tse et al. 2007), we decomposed proximity into vertical and horizontal

components. The superior vertical accuracy may be because the vertical component is a linear dimension (distance only) that is relative to a fairly constant and reliable landmark (the surface of the earth), while precision in a horizontal plane is likely to be more difficult because both distance and direction must be encoded.

The accurate return to the goal location supports previous findings that hummingbirds encode and use spatial cues such as landmarks rather than cues intrinsic to the goal itself (Brown and Gass 1993; Healy and Hurly 1998; Hurly and Healy 1996). Hummingbirds learn spatial relationships between two artificial flowers, one of which was rewarded (Henderson et al. 2006). In arrays of five to ten flowers, when flowers were closely spaced (<50 cm) non-rewarded flowers were used as landmarks, whereas in widely spaced arrays (>70 cm) they were not (Healy and Hurly 1998). Data from past studies and the current experiment shed little light on the identity of extra-array landmarks or how they are adopted. Although the birds reach familiar goals without retracing flight paths, it is possible that the beacon training flower was used as a scaffold for developing a spatial representation as seen in wood ants (e.g. Graham et al. 2003). Possibilities as to how the birds might have encoded the goal's location include: with respect to the centre of the field (MacDonald et al. 2004; Tommasi and Vallortigara 2000), with respect to one conspicuous nearby landmark (Spetch 1995) or with respect to multiple landmarks (Cook and Tauro 1999; Kamil and Jones 2000). The territories of the birds we tested were large open fields surrounded by large trees with mountains as the backdrop. While these large-scale visual features are very conspicuous and may help the bird to find its territory on return from migration, or on return from chasing intruders, it seems unlikely that a bird could use them to pinpoint the location of a single flower in a field. The context in which we trained and tested our birds did not readily allow them to learn the location of the flower relative to nearby landmarks, or to use the geometry of the test arena to determine the goal location (e.g. Pearce et al. 2001) as is possible in laboratory experiments. We specifically chose training locations that were at least 10 m from visual landmarks that we considered conspicuous. The birds may have employed less conspicuous objects, local topography or patterns of vegetation patches as landmarks. Alternatively they may have used non-visual information, such as a sun or magnetic compass. Compass cues, alone or in combination with visual cues, have been demonstrated on spatial scales both larger and smaller than hummingbird territories (e.g. Freire et al. 2005; Sherry and Duff 1996; Wiltschko et al. 1999). Investigation of compass use with free-living rufous hummingbirds is not straightforward.

Moving or removing the goal flower did not seriously disrupt approach to the reward location and thus we

conclude that the hummingbirds did not employ the flower as a distant beacon, or if they did then such use was subordinate to other navigation cues. However, two lines of evidence suggest that the visual features of the flower were in some way relevant. First, in Experiment 1 when the flower was moved, the initial approach distance to the training location and the moved flower were similar. This similarity suggests that the new flower had been noticed and that there may have been a conflict in where the bird thought the goal was. Second, in Experiment 2 birds seemed to adjust their use of the visual cues according to cue prominence. They approached to within ca. 20 cm of the goal location when trained on the small flower as opposed to ca. 60 cm when trained on the large flower.

Our results are consistent with anecdotal reports that the bright colours of commercial hummingbird feeders are not necessary for guiding a bird to a rewarded location, once the bird has learned the location of that reward. Although this is at odds with the view that many hummingbird-pollinated flowers are coloured red so as to attract hummingbirds to feed, experiments have shown that rufous hummingbirds return to a rewarding location by using spatial cues rather than the colour of the flower (e.g. Brown and Gass 1993; Healy and Hurly 1995; Henderson et al. 2001; Miller et al. 1985). Indeed, it has proved difficult to show that hummingbirds pay much attention to the visual elements of a rewarded feeder/flower/goal, even having visited it only once (Hurly and Healy 1996, 2002). Visual cues are likely, however, to play a much larger role in locating new flowers. In laboratory studies, various species of birds seem to use different cues on different scales, attending first to global landmarks to determine location, next to local landmarks to determine relative position within an array of potential reward sites, and least of all to visual features of reward sites themselves (Brodbeck 1994; Sherry and Duff 1996). Wild rufous hummingbirds appear to employ spatial information in a similar fashion when they are foraging in their territories, using absolute locations, relative positions, and lastly, visual features of their goal flowers within the last ca. 70 cm of approach. Surprisingly, this occurs despite the lengthy evolutionary history of visiting plants with vivid floral displays, and despite the conditions of the current experiment encouraging the use of visual features as distant beacons. A recent study on pine siskins (*Carduelis pinus*) foraging at backyard feeders supports the use of spatial cues in preference to featural cues (Humber et al. 2009).

Although difficult to confirm definitively, either in the field or in the lab, we suggest that rufous hummingbirds use intrinsic visual cues of a flower to confirm that they have arrived at the correct place rather than as a long-distance beacons. Thus, it is entirely possible that a hummingbird might be able to relocate exactly the window outside of

which he fed the previous year. These data also fit with the striking accuracy of philopatry seen in songbirds, with males especially returning to their natal territory, often after journeys of 100 or 1,000 s of kilometres (Godard 1991). Confirmation in hummingbirds of the degree of accuracy, and frequency, of relocation of territories and specific feeders will require detailed examination of banding records.

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