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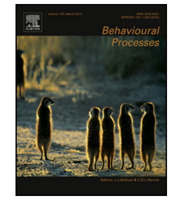

Wild rufous hummingbirds use local landmarks to return to rewarded locations

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ABSTRACT

Animals may remember an important location with reference to one or more visual landmarks. In the laboratory, birds and mammals often preferentially use landmarks near a goal ("local landmarks") to return to that location at a later date. Although we know very little about how animals in the wild use landmarks to remember locations, mammals in the wild appear to prefer to use distant landmarks to return to rewarded locations. To examine what cues wild birds use when returning to a goal, we trained free-living hummingbirds to search for a reward at a location that was specified by three nearby visual landmarks. Following training we expanded the landmark array to test the extent that the birds relied on the local landmarks to return to the reward. During the test the hummingbirds' search was best explained by the birds having used the experimental landmarks to remember the reward location. How the birds used the landmarks was not clear and seemed to change over the course of each test. These wild hummingbirds, then, can learn locations in reference to nearby visual landmarks.

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1. Introduction

Many species rely on visual information in the environment to return to important locations (Collett et al., 2013; Gould et al., 2010). They may use this information by matching their entire current view with a previously experienced visual panorama (Zeil, 2012) or by extracting prominent visual features and encoding the position of a location relative to such "landmarks" (Wiener et al., 2011). In theory, any visual feature at any distance could act as a landmark, however, animals tested in the laboratory generally show a preference for landmarks closer to the goal, rather than for alternatives further away (Bennett, 1993; Chamizo et al., 2006; Gould-Beierle and Kamil, 1996; Spetch, 1995).

Despite decades of work elucidating how vertebrates, primarily birds and rodents, use landmarks to return to locations in the laboratory, it is unclear how relevant those results are for such species living in the wild. In laboratory-like tests of spatial memory, wild, free-living birds appear to perform similarly to laboratory species (e.g. Healy and Hurly, 1995; Hurly et al., 2014; Hurly and Healy, 2002; Hurly, 1996). With the significant exception of homing pigeons (e.g. Biro et al., 2003; Guilford and Biro, 2014; Schiffner and Wiltschko, 2013), however, there are few data concerning the cues that vertebrates in the wild use to remember locations. This stands in stark contrast to the wealth of knowledge about small-scale navigation, especially landmark use, by birds in the laboratory (Cheng et al., 2006; Gould et al., 2010).

Thus far, in fact, there is very little evidence that birds in the wild even use local landmarks to remember locations. Most of the experiments examining small-scale navigation in the wild have been focused on wild rodents, such as ground squirrels *Spermophilus columbianus* and fox squirrels *Sciurus niger*, which do not preferentially use landmarks nearby the goal, and in some cases actively prefer more distant cues (Lavenex et al., 1998; Vlasak, 2006a). The best evidence for local landmark use in wild birds comes from field experiments with hummingbirds. Wild hummingbirds can be readily worked with in the wild (Healy and Hurly, 2013) and primarily remember flowers in their territory in terms of their spatial location (Hurly and Healy, 1996, 2002). There is some evidence that this spatial memory is based on visual landmarks close to the flower's location as hummingbirds will choose which of an array of four flowers to visit based on the presence of a landmark close to that flower (Hurly et al., 2014) and these birds can learn to search for a flower at the correct distance and in the correct direction from a pair of landmarks (Pritchard et al., 2015). What is still unknown, however, is whether wild hummingbirds will spontaneously acquire and/or weight distance and direction information from closer land-

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Fig. 1. (a) A diagram of the experimental apparatus, showing the position of the landmarks during training, and the relative size of the hummingbirds. The birds were trained to a Plexiglas™ board, with wells 52.4 mm apart drilled in a hexagonal pattern, attached to a tripod 60 cm above the ground at an angle of 45°. The location of a rewarded well, containing 120 μL of 20% sucrose, was in a constant position relative to three individually coloured bottle tops acting as landmarks.

marks over other sources of spatial information, without being trained to use local landmarks. Rather than moving landmarks between flowers, as was done by Hurly et al. (2014), we trained rufous hummingbirds *Selasphorus rufus* in the wild to visit one of three locations on a board in which many different wells had been drilled. The rewarded locations were presented within an array of three nearby landmarks (all on the board). To test the degree to which the birds relied on these landmarks, which were in very close proximity to the goal, we presented the trained birds with a test in which we expanded the landmark array (Figs. 1 and 2a). If the birds used the local landmarks to remember the rewarded location, they should shift the location in which they searched for the reward accordingly.

In addition to investigating whether the birds used local landmarks at all, we also examined whether the birds weighted the local landmarks by proximity to the rewarded location or whether they attended to the shape of the entire array of landmarks. To do this we investigated how the birds responded to the expansion of the landmark array when trained to each of the different rewarded locations. The three rewarded locations differed in the proximity of the three landmarks to the goal: (A) the rewarded location was closest to one landmark and equally far from the other two; (B) each of the three landmarks was at different distances to the goal; and (C) two landmarks were equally close the reward while the third was further away. If the hummingbirds weighted local landmarks by their proximity to the goal, they should specifically shift their search in the direction of the closest landmark or landmarks.

2. Methods

2.1. Subjects and experimental site

The subjects of this experiment were seven male rufous hummingbirds and the work was carried out in meadows along a valley in the Rocky Mountains, southwest of Beaver Mines, Alberta, Canada. Here, male rufous hummingbirds establish and defend feeding territories from mid-May to mid-July. Trials were conducted between 0730 and 1930 h Mountain Standard Time.

The work was conducted with approval by the University of Lethbridge Animal Welfare Committee and under permits from Alberta Environmental Protection and the Canadian Wildlife Service.

2.2. Initial training

Artificial feeders containing 14% sucrose solution were hung at several meadow sites along the valley in early-May. By mid- to late-May, males had established territories around the artificial feeders. Once it was evident that a male was successfully defending a feeder, it was marked with a coloured, non-toxic ink patch on its pale chest feathers to allow for identification. The ink was applied via a spray attached to a perch on the feeder, which meant that we did not have to catch or handle birds in order to mark them. All males resumed feeding within 15 min and we saw no diminution in territorial holding ability as a result of the mark, which remained visible for the duration of the field season (about six weeks).

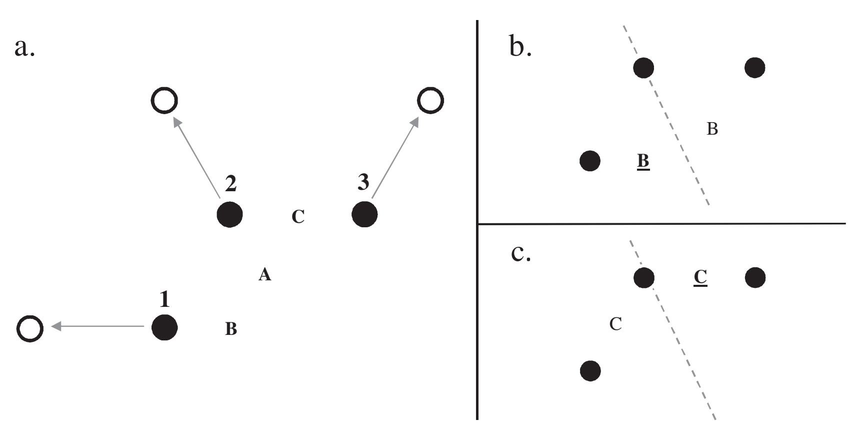

Fig. 2. (a) The location of the landmarks and rewarded well in each treatment. The closed, black circles show the locations of the three landmarks before the expansion, the open, white circles show the locations of the landmarks following the expansion. The landmarks are numbered as they are referred to in the text. In treatment A, the birds were trained to a well halfway between Landmarks 1 and 3. In treatment B, the birds were trained to a well east of Landmark 1, and south of Landmark 2. In treatment C, the birds were trained to a well halfway between landmarks 2 and 3. (b) The locations of B during the experiment. B was at one of two locations that were bilateral reflections of each other. For analysis, the data for B were all integrated into a single location for analysis (in bold and underlined). (c) The two locations of C, bilateral reflections of one another, that were integrated into a single location (in bold and underlined) for analysis.

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