Wild hummingbirds require a consistent view of landmarks to pinpoint a goal location

David J. Pritchard [a, *], T. Andrew Hurly [b], Susan D. Healy [a]

[a] School of Biology, University of St Andrews, Fife, U.K.
[b] Department of Biological Sciences, University of Lethbridge, AB, Canada

One outcome of the extensive work on the ways that birds and insects use visual landmarks to return to a rewarded location is that they use landmarks differently. But this conclusion may have been reached because the almost exclusive training and testing of birds in small laboratory environments may prevent birds from using the view-matching strategies seen in insects. To test how birds use landmarks in an open-field environment, we trained free-living hummingbirds to search for a reward near two experimental landmarks. When the angular size and panoramic position of the landmarks were kept consistent, the hummingbirds searched in the direction of the flower and matched either the retinal angle of the landmarks or the absolute distance of the flower during training, even when the actual size and distance between landmarks changed. These data are more similar to data from view-matching ants solving a similar problem than they are to data from birds trained to use landmarks in the laboratory. This suggests that hummingbirds may also use a remembered view to relocate a rewarded site. Regardless of whether hummingbirds use a remembered view for navigation or just to recognize landmarks, data on landmark use collected from birds tested in the laboratory may not fully reflect how birds return to locations in the wild.
© 2018 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Animals often use configurations of surrounding visual landmarks to return accurately to the locations of important resources, such as a nectar- or pollen-providing flower or a hidden cache (Chamizo, 2003; Collett, Chittka, & Collett, 2013; Gould, Kelly, & Kamil, 2010; Pritchard & Healy, 2017). Although using landmarks requires learning, the information animals actually learn and how they use that information to navigate remains contentious. For example, 'using landmarks' does not necessarily require an animal to learn about individual landmarks because, for all animals, landmarks are initially experienced as part of a wider visual panorama. This panoramic view contains information about the distances and relative directions of surrounding landmarks in the form of perceived angular sizes and relative angular positions (Cartwright & Collett, 1983; Zeil, Hofmann, & Chahl, 2003). Animals can, then, perceive these properties 'directly' without having to compute absolute distances, compass bearings, or even separate landmarks from the background (Fig. 1a). Insects use such 'implicit' spatial information to return to a remembered location by matching their current view to a visual 'snapshot' of the panorama viewed from the goal location (e.g. Cartwright & Collett, 1983; Durier, Graham, & Collett, 2003; Narendra, Si, Sulikowski, & Cheng, 2007; Stürzl, Zeil, Boeddeker, & Hemmi, 2016; Wehner & Räber, 1979; Zeil, 2012). Despite some theoretical support for view-based navigation (Benhamou, 1998; Cheung, Stürzl, Zeil, & Cheng, 2008; Sheynikhovich, Chavarriaga, Strösslin, Arleo, & Gerstner, 2009; Stürzl, Cheung, Cheng, & Zeil, 2008), vertebrates are not thought to use landmarks in this way. Over the many years of work on vertebrate landmark use in the laboratory, only a few experiments have suggested vertebrates navigate by matching remembered views (Douglas, 1996; Pecchia & Vallortigara, 2010; Pecchia, Gagliardo, & Vallortigara, 2011).

Rather than view matching, vertebrates tested in the laboratory are thought to compute the location of the goal by extracting information about the actual distance and/or direction of the goal from one or more landmarks (Fig. 1b; Cheng, Spetch, Kelly, & Bingman, 2006; Gould et al., 2010). Most of this work has been conducted with pigeons or food-storing birds, who use visual landmarks to search for a reward. The places in which birds search when the dimensions of a learned landmark array are changed suggest that the birds learn the absolute position of the goal from each landmark: the birds either continue to search at the 'correct'

* Correspondence: D. J. Pritchard, School of Biology, University of St Andrews, Fife, KY16 9TH, U.K.
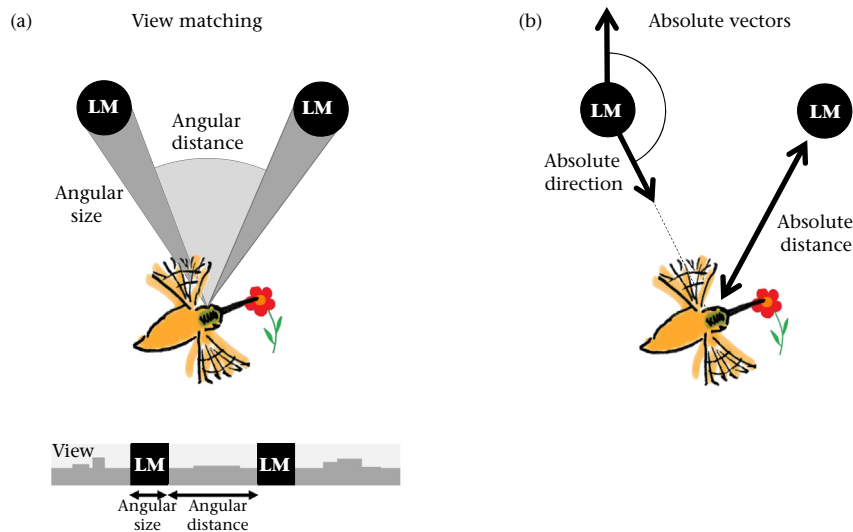*E-mail address:* djp4@st-andrews.ac.uk (D. J. Pritchard).

Figure 1. View-based versus absolute spatial information. A hummingbird could remember the position of a flower relative to landmarks (LM) in terms of either: (a) a remembered view containing the unique pattern of angles subtended on the retina when viewing landmarks from the goal location (including the 'angular size' of the landmarks on the retina (dark grey), the 'angular distance' separating landmarks (light grey) and patterns of optic flow), or, (b) in terms of absolute distances (e.g. solid arrow from right landmark) and directions (e.g. arrow from left landmark), akin to metres and compass bearings. While view-matching insects learn the view from a location and navigate by matching this remembered view, birds and mammals are thought to use more abstract absolute information to compute the location of the goal.

absolute distance and/or direction from one of the landmarks, e.g. '10 cm south of the red landmark', or to search at the location that represents the average of the 'correct' distances and directions from multiple landmarks (e.g. Cheng, 1988; Kelly, Kippenbrock, Templeton, & Kamil, 2008; Spetch, Cheng, & MacDonald, 1996; Spetch et al., 1997). Landmark use in birds is therefore often seen as a matter of extracting and using metric vectors between each landmark and the goal. From this perspective, even if birds were to learn and encode angular size, it would be as part of a landmark-to-goal vector, rather than as part of a panoramic view. Because landmark use is rarely examined in vertebrates outside the laboratory environment, it is not clear whether these search patterns reflect similar information use by birds both in the laboratory and the wild (Pritchard, Hurly, Tello-Ramos, & Healy, 2016).

The most obvious difference between test conditions in the laboratory and the field is that many information sources present in the wild are not found in the laboratory, such as the sun or atmospheric odours (e.g. Jacobs & Menzel, 2014), but the visual environment of the laboratory may also have a significant effect on what animals tested in that environment learn. The training and testing environment might prevent an animal from learning a view and/or using a remembered view to relocate a goal if, in that environment, the panoramic view from the goal changes every trial. By 'panoramic view' here, we mean everything that falls within an animal's field of view, including not only any experimental landmarks, but also any walls, edges, or 'extramaze' cues visible from the testing area. Landmark use experiments with birds typically involve the movement of both the landmarks and goal between training trials (Gould-Beierle & Kamil, 1996; Jones & Kamil, 2001; Kamil & Jones, 1997; Kelly et al., 2008; Spetch et al., 1997). This movement is intended to ensure that the birds attend to the intended landmarks and not to 'global' cues such as the walls of the room (Gould-Beierle & Kamil, 1996). As these experiments occur in walled rooms no more than a few metres across, however, moving the landmarks and goal also causes the visual panorama at the goal's location to change with every experience of the goal. If the landmarks and goal remained in the same location across trials, the visual panorama would remain stable both across training trials and between training and testing. This would give birds the

opportunity to learn and to use a familiar view of the surroundings and may be more likely to result in the use of a view-matching strategy. Indeed, when birds have been trained without this kind of intertrial movement and with access to a stable panorama, they relied less on a single landmark to remember a location and more on the 'global' room cues, as might be expected if birds matched an entire visual panorama (Gould-Beierle & Kamil, 1996). In addition, domestic chicks, *Gallus gallus domesticus*, and pigeons, *Columba livia*, can use environmental shape to reorient only when trained with a stable view of the environment (Pecchia & Vallortigara, 2010; Pecchia et al., 2011), which suggests that they might learn the shape of the environment as a view rather than by computing the distances and directions of landmarks in their surroundings (see Stürzl et al., 2008). Given these findings, it seems plausible that the reason birds do not seem to use view matching to relocate goals is due to the combination of the training methods used and the environment in which they are tested.

If training in a small enclosed space does bias animals against using a view-matching strategy, training in an open-field environment should not. To test whether birds trained under such conditions use a remembered view to pinpoint a goal's location, we trained and tested wild free-living hummingbirds to use a pair of landmarks to relocate an artificial flower. In tests, we manipulated the landmarks near the location of the flower, putting view-based information and absolute spatial information in conflict, and recorded how these manipulations affected where these birds searched for the flower. Hummingbirds will fly directly to a flower when it is available, but will hover around the location in which they last experienced a flower that has since been removed (Flores-Abreu, Hurly, & Healy, 2012; Hurly, Franz, & Healy, 2010). Hummingbirds can learn this location in reference to a pair of landmarks, and will search at the distance and direction from each landmark in which they had found the flower previously (Pritchard, Hurly, & Healy, 2015; Pritchard, Scott, Healy, & Hurly, 2016). If the hummingbirds, like insects, use a remembered view, then they should hover closest to the perceived location of the flower when the appearance of the visual panorama is most similar to that seen during training, even if the metric information from the landmarks is different. Alternatively, if the hummingbirds extract and use