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*

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* 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).

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.

Keywords:

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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, Gagliardo, & Vallortigara, 2011; Pecchia & Vallortigara, 2010).

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' 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 et al., 1997; Spetch, Cheng, & MacDonald, 1996). 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 et al., 2011; Pecchia & Vallortigara, 2010), 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 percieved 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 landmark-to-goal vectors, as birds are typically thought to do, then they should hover around locations in which the distances and/or directions of one or both landmarks are maintained, even if the view of the landmarks is different to that previously experienced.

<H1>METHODS

<H2>Subjects and Experimental Site

The subjects used in this experiment were eight wild male rufous hummingbirds, *Selasphorus rufus*. These territory-defending birds were individually distinguishable by a nontoxic ink mark on their chest. The mark lasted for the 6 weeks of the field season.

We conducted the experiment along the Westcastle Valley, located within the eastern range of the Canadian Rockies in southwestern Alberta (49°29’N, 114°25’W) where we hung feeders containing 20% sucrose solution in early May 2013. By late May male rufous

hummingbirds had arrived from their overwintering grounds in Mexico and established exclusive territories around individual feeders. Training and testing continued until early July, when the males began migrating south.

<H2>Ethical Note

All work was approved by the University of St Andrews' School of Biology Ethical Committee and the University of Lethbridge Animal Welfare Committee under protocol number 1207, and was carried out under permits from Alberta Sustainable Resource Development and Environment Canada. As the hummingbirds used in this study were free-living, participation in the experiment was voluntary and all birds had access to natural sources of food at all times, including when the training flower was removed during tests. Birds were only handled once during the field season, and then only by qualified personnel. Handling time was kept to a minimum and all birds were released within 5 min of being caught. Following release, birds were left for a minimum of 2 days before experiments began.

<H2>Training

We trained the hummingbirds to feed from an artificial flower made from a 0.6 ml microcentrifuge tube taped to the top of a 0.3 m wooden stake, which contained 25% sucrose. We placed the experimental flower in a 0.3 m equilateral triangle with a pair of plastic landmarks, such that the flower was the southern point of the triangle made from the landmarks and flowers. The orientation of the array never changed during training. The landmarks were two plastic pipes, one covered in blue duct tape, the other in grey duct tape. Both landmarks were 0.05 m in diameter and 0.39 m in height. During the experiment, we

moved the array of landmarks and flower 0.25 m in one of eight directions (N, NE, E, SE, S, SW, W, NW) on a 2 × 2 m experimental 'pitch' following every visit by the bird. We moved the array 0.25 m to ensure that the hummingbirds learned that the landmarks were the best predictor for the location of the flower (Pritchard et al., 2015). The direction in which we moved the array was pseudorandomized such that the flower stayed on the pitch and the flower was never in exactly the same location twice. Birds were trained for nine trials, followed by a 'pre-test' on the 10th trial. We intended this 10th trial to test whether the hummingbirds had learned the location of the flower. For this 'pre-test' the array was moved to the next position as in training, except the flower was not present. All test trials were recorded at 25 frames/s by two Sony Handicam HDR-CX115 cameras placed at 90° to each other and each 6 m from the centre of the experimental pitch (Fig. 2a).

While hovering, hummingbirds will hold their head still in space for at least 0.06 s. This behaviour is easy to distinguish from nonhovering flight, and we used the location of the first two such 'stops' by the birds as a measure of the locations in which the birds searched. Training continued for 40 trials with the 20th, 30th and 40th trials serving as test trials, described below. Flowers were never present during test trials and the order of test trials was pseudorandomized between birds.

<H2>Test Trials

For the 20th, 30th and 40th visits to the landmarks, we removed the flower and presented the bird with one of three tests: a View-consistent expansion test, a View-inconsistent expansion test or a Rotation test. The order of these tests was balanced across birds, and all eight birds received all tests. These tests were inspired by classic insect experiments (e.g. Brunnert, Kelber & Zeil, 1994; Cartwright & Collett, 1979, 1983; Durier,

Graham, & Collett, 2003; Wehner & Räber, 1979; Zeil, 1993) and were designed to put panoramic information based on matching retinal angles in conflict with landmark-to-flower vectors based on learned distances and direction. We used the rotation test to test whether the landmarks alone were used by themselves to guide search, or whether they were used in combination with other information, such as a sun or magnetic compass, or as part of an entire panorama.

<H3>View-consistent expansion

In this test the landmarks were placed 0.6 m apart, double the training distance. These landmarks were also roughly doubled in size (0.11 × 0.9 m), which resulted in view-based cues, such as the angular size of the landmarks and angular distance between them, remaining similar to that during training (Fig. 2b, Fig. 4), while the actual size of the landmarks and the absolute inter-landmark distance differed to the training array. This test shared some features with tests used with navigating insects, in particular, the experiments on desert ants from Wehner and Räber (1979). If, as observed for desert ants, hummingbirds match the view of the panorama seen from the flower, they should readily transfer to this View-consistent landmark array and search at the distance in which the retinal angular size of the landmarks matches that seen during training (0.6 m) and in the same direction from the landmarks in which they had previously found flower. If hummingbirds use vectors of distances and direction from each landmark to the flower, then they should either become disoriented because they do not recognize the landmarks, or they should search at the absolute distance at which the flower had been (0.3 m) from one of the enlarged landmarks.

<H3>View-inconsistent expansion

In this test we doubled the distance between the landmarks but kept the size of the

landmarks the same as in training. As a result, while the absolute distance between the landmarks was the same as in the View-consistent expansion, there was no location at which the birds could search where both the angular size of the landmarks and the angular distance between them was the same as during training (Fig. 2b). As in the View-consistent expansion, this test shared some features with experiments that demonstrated the use of angular size in desert ants (Wehner & Räber, 1979). But, in contrast to Wehner and Räber's experiments, in which they trained desert ants to search between the landmarks, the flower in this experiment was placed at the apex of a triangle formed together with the landmarks. As a result, if the birds matched the angular distance between the landmarks, the landmarks would appear too small. Whereas, if the hummingbirds matched the angular size of one of the landmarks, the angular size of the other landmark and the angular distance between the landmarks would be different than those they remembered. If the hummingbirds matched both cues as part of a remembered panoramic view, then we expected that they would be less likely to show a clear searching location in the View-inconsistent expansion than in the View-consistent expansion, as in the former, a good match would be impossible. If, on the other hand, they extracted and used actual distances and directions as vectors from each landmark, there should have been no difference in performance between the View-consistent and View-inconsistent expansions as the positions of the landmarks were identical in both tests. If the hummingbirds searched further from the landmarks in the View-consistent test because they used angular size to estimate distance as part of a landmark-to-goal vector, we would still have expected them to search on the correct side of the landmarks and to show a clear preferred distance in both of the expansion tests. If anything, the presence of the training landmarks in the View-inconsistent expansion should result in birds being better able to recognize the landmarks and thus search closer to the flower's perceived location. In this case we might expect hummingbirds to show a clearer preferred searching location in the

View-inconsistent compared to the View-consistent expansion.

<H3>Rotation

In this test we removed the flower and rotated the landmarks 90˚clockwise or anticlockwise around the predicted location of the flower. We did this to test whether hummingbirds determined direction using the configuration of the experimental landmarks, a bearing from one landmark, or used a combination of the panorama and landmarks. If the birds relied entirely on the landmarks when returning to search for the flower, using a view of only the landmarks or relative bearings from each landmark, then they should have followed the rotation. If the birds used a bearing from a sun or magnetic compass, or by matching the position of each landmark individually against the panorama, then they should have continued to search in the trained direction from one of the landmarks, but not show a preference for one landmark over the other. Birds would also have searched in the trained direction if they matched a remembered view of the entire panorama seen from the flower. Although the apparent sizes of the experimental landmarks themselves would be most similar if the birds followed the rotation (L1 + L2 in Fig. 3), the panorama behind the landmarks would be incorrect, resulting in a poorer overall match. Instead, if birds did search using a remembered view, the best match would be in the trained direction from the southernmost landmark as it would match the size and position of that one landmark in the panoramic backdrop, while minimizing the size of the other landmark (L2 in Fig. 3).

<H2>Data Extraction and Analysis

<H3>Extraction

To analyse where the hummingbirds searched relative to the landmarks, we went

through each video frame by frame (resolution 1920 × 1080 pixels) and recorded the first two locations on the *x* axis of the image where the hummingbirds stopped and hovered around the landmarks. Stop-and-hovers (hereafter referred to as 'stops') were defined as instances when the hummingbird did not move through the air for more than two frames (0.08 s). As hummingbirds usually fly very quickly, particularly on approach to the experimental pitch from a perch, it was easy to identify each instance in which they stopped.

To extract *x*,*y* locations for the stops by the hummingbirds, the landmarks and the flower, as viewed from above, we used position and field of view of the camera to triangulate the location of the key features in each shot, applying the reconstruction method detailed in Pritchard et al. (2015). We also transformed the orientation of the anticlockwise rotations, such that all the rotations were in the same direction for analysis. As we did not correct for lens distortions, we also reconstructed the position of the flower relative to the landmarks prior to testing. By reconstructing the position of features for which we know the true position, we were able to test how robustly our method captured the distance and direction of locations relative to the landmarks.

<H3>Analyses

Before analysis, we excluded as outliers any first or second stop more than two standard distances away from the respective first or second stop mean locations in each test (Pritchard et al., 2015). As a result we excluded a single data point, which was a second stop in the Rotation test.

All analyses were carried out in R (R Development Core Team, 2012), with circular statistics, including bootstrapped tests of specific mean directions and confidence intervals, using methods described in Pewsey, Neuhauser and Ruxton (2013) and bootstrapped Kolmogorov–Smirnov test using ks.boot in the 'Matching' R package (Sekhon, 2011). All

bootstrapped tests used 10 000 samples.

In addition to the circular statistics, for the View-consistent and View-inconsistent expansions, we were also interested in with the degree to which the birds searched in the direction of the flower and at the distance of the flower from the landmarks in the two kinds of expansion. In all cases, we first tested whether the values to be compared were normally distributed using a Shapiro–Wilk test and used a log transformation, or failing that a square-root transformation, for data which were significantly different to normal. If the data were normal, either before or following transformation, we then used paired *t* tests to compare different treatments. If the data were still not normally distributed despite the transformations, we compared treatments using a paired Wilcoxon signed-ranks test. These tests were either one tailed or two tailed depending on whether we had a directional prediction.

<H1>RESULTS

<H2>Reconstruction Accuracy

To test how accurately we could determine the locations of the hummingbirds' stops around the landmarks, we reconstructed the positions of the flower and the landmarks in the trial before each test. We could then compare the reconstructed flower position to the predicted true flower position relative to the landmarks. The mean distance of the reconstructed flower position from the predicted true flower position was 0.035 ± 0.004 m, less than half the body length of an adult male rufous hummingbird. These errors could be due to lens distortions or small differences in camera orientation, but these are smaller than the size of our predicted effects.

<H2>Pre-test

To determine whether the hummingbirds had learned the location of the flower after nine visits, for the 10th visit we removed the flower and reconstructed where the hummingbirds stopped and hovered around the landmarks. The birds did not stop at the location in which the flower should have been found. Four of the eight birds stopped on the opposite side of the landmarks to where the flower had been, while the other four stopped either close to the landmarks or to the southwest of the landmarks. As a result, the birds did not search significantly in any consistent direction around either landmark (Rayleigh tests: first stops: right landmark: $r = 0.0.39$, $N = 8$, $P = 0.31$; left landmark: $r = 0.0.097$, $N = 8$, $P = 0.93$; second stops: right landmark: $r = 0.46$, $N = 8$, $P = 0.19$; left landmark: $r = 0.11$, $N = 8$, $P = 0.88$).

<H2>Expansion Tests

If the hummingbirds used a remembered view of the landmarks, rather than having extracted actual distances and directions, they should have searched closer to the perceived location of the flower in the View-consistent expansion than in the View-inconsistent expansion, more closely matching the direction and the distance of the flower from the landmarks. Alternatively, if the birds extracted actual metric information about the location of the flower from the landmarks, they should have searched in similar locations in both tests, which conserved either the distances or directions learned during training.

To test whether hummingbirds concentrated their search in particular areas around the landmarks in the expansion tests, we placed a hexagonal grid over the stop locations and counted the number of stops in each hexagon. The edges of the hexagons were 0.2 m and

each hexagon covered 0.104 m^2. Because of differences in the distribution of stops in the two tests, there were 52 hexagons in the grid for the View-consistent expansion, and 53 for the View-inconsistent expansion.

To compare the concentration of stops in the two expansion tests visually, we coloured each hexagonal cell based on the number of stops it contained, creating a heatmap in which darker cells had concentrations (Fig. 4). The heatmap showed clear differences in the locations in which the hummingbirds concentrated their stops. Regions with the highest densities of stops in the View-consistent expansion were either 0.6 m from both landmarks, or 0.3 m from the right landmark. In the View-inconsistent expansion, however, the regions with the highest densities of stops were closer to the landmarks and were on the opposite side of the left landmark to location the flower had previously occupied (Fig. 4).

To test statistically whether hummingbirds stops were significantly clustered in the two expansion tests, we compared the observed distribution of stop densities to an 'even' distribution in which each stop inhabited a different hexagonal cell (16 ones, with the rest of the values at zero) using a one-way Kolmogorov–Smirnov test. This test was one way, as there could not be fewer than one stop in any cell, and was bootstrapped because the data contained ties. Hummingbird stops were significantly more clustered than expected from an even distribution in the View-consistent expansion test (bootstrapped one-tailed Kolmogorov–Smirnov test with 10 000 bootstraps: $D_{\text{one-tailed}} = 0.15$, $P = 0.036$), but not in the View-inconsistent expansion test ($D_{\text{one-tailed}} = 0.11$, $P = 0.11$). In addition, in the View-consistent expansion, hummingbirds were significantly more likely to stop on the side of the landmarks where the flower had been than on the other side (binomial test, 14/16 on flower-side with probability of 0.5: observed probability of success = 0.86 ± 0.26, $P = 0.004$). This was not the case in the View-inconsistent expansion, in which hummingbirds were just as likely to stop on either side of the landmark (binomial test, 8/16 on flower-side with

probability of 0.5: observed probability of success = 0.5 ± 0.25, $P > 0.99$). Comparing the two tests, hummingbirds tended to search on the flower's side of the landmarks more in the View-consistent expansion compared to the View-inconsistent expansion, although this was not significant (Fisher's exact test comparing stops on each side of the landmarks in each test: $P = 0.054$).

To compare how closely the hummingbirds searched in the direction of the flower, we calculated the difference between the direction each hummingbird stopped from the closer landmark and the direction of the flower from that landmark. If hummingbirds match the direction of the flower more accurately when the view of the landmarks is conserved between training and testing, we expected that difference between the predicted and observed directions should be smaller in the View-consistent expansion relative to the View-inconsistent expansion. Using a paired, one-tailed Wilcoxon signed-ranks test, we found that the first stops by hummingbirds tended to be closer to the direction of the flower in the View-consistent expansion than in the View-inconsistent expansion, but this was not significant ($V = 8$, $N = 8$, $P = 0.097$), possibly due to two birds in the View-consistent expansion stopping on the other side of the landmarks to the flower. On their second stop, however, the hummingbirds searched significantly closer to the flower's direction in the View-consistent expansion than in the View-inconsistent expansion ($V = 4$, $N = 8$, $P = 0.027$).

The difference between the observed stop direction and the direction of the flower could be due to hummingbirds always searching around the direction of the flower but being more variable in the View-inconsistent expansion, or due to hummingbirds in the View-inconsistent expansion searching in a different direction altogether. To test whether the hummingbirds searched in the direction of the flower in the View-consistent and View-inconsistent expansions, we calculated the confidence intervals around the mean search direction from the closer landmark. In the View-consistent expansion, the mean search

direction was very close to the direction of the flower, which always fell within the 95% confidence interval (mean direction ± 95% confidence interval, with flower direction normalized to 0°: first stops: -25.02 ± 61.2°, $N = 8$; second stops: -3.43 ± 18.19°, $N = 8$; Fig. 5b). The mean direction in which the hummingbirds searched in the View-consistent expansion was, therefore, not significantly different to the direction of the flower. This result was substantiated with a bootstrap test using the null hypothesis that the mean search direction was in the direction of the flower (specific mean bootstrap test: first stops: $N = 8$, $P = 0.29$; second stops: $N = 8$, $P = 0.75$). In the View-inconsistent expansion, however, the mean search direction was further from the direction of the flower, which always fell outside of the 95% confidence interval (first stops: 114.04 ± 73.22°, $N = 8$; second stops: 69.36 ± 54.27°, $N = 8$; Fig. 5b). The mean direction in which the hummingbirds searched in the View-inconsistent expansion was, therefore, significantly different to the direction of the flower. Again, the data for the first stops, if not the second, confirm this effect (specific mean bootstrap test: first stops: $N = 8$, $P = 0.0082$; second stops: $N = 8$, $N = 0.16$).

As well as looking at the direction from the landmarks in which the birds searched, we also measured the angle between the landmarks from where a bird stopped and hovered. Both ants (Durier, Graham, & Collett, 2003) and bees (Cartwright & Collett, 1983) preferentially match the retinal angle between landmarks rather than the angular size of any individual landmark when both are put in conflict. During training the inter-landmark angle was 60°, and using the bootstrap test we found that the mean inter-landmark angles in both the View-consistent and View-inconsistent expansion tests did not differ from the mean inter-landmark angle that the birds experienced during training (specific mean bootstrap test: View-consistent: first stops: $N = 8$, $P = 0.07$; second stops: $N = 8$, $P = 0.34$; View-inconsistent: first stops: $N = 8$, $P = 0.29$; second stops: $N = 8$, $P = 0.34$). Visual inspection of the data, as well as examining the range of the 95% confidence intervals, suggests that the

inter-landmark angle during the View-consistent expansion was more similar to training than it was in the View-inconsistent expansion, even though the training angle fell just outside the confidence interval for the first stops in the View-consistent expansion (mean inter-landmark angle ± 95% confidence interval: View-consistent: first stops: 48.13 ± 9.98°, $N = 8$; second stops: 68.10 ± 15.99°, $N = 8$; View-inconsistent: first stops: 43.64 ± 26.13°, $N = 8$; second stops: 73.79 ± 27.44°, $N = 8$; Fig. 5c).

In the expansion tests, hummingbirds could have estimated their distance from the landmarks using either absolute distance (0.3 m in both tests), the distance at which the angular size of the landmarks matched training (0.3 m in the View-inconsistent expansion, 0.6 m in the View-consistent expansion), or the distance where the angle between the landmarks matched that seen during training (0.6 m in both tests). Based on this, we compared the distance that the hummingbirds searched from the closer of the two landmarks to both 0.3 m and 0.6 m from the landmarks. In the View-consistent expansion, the distances that the hummingbirds hovered from the landmarks on their first stop were significantly different to 0.3 m, which fell outside the 95% confidence interval, but not significantly different to 0.6 m, which did not (mean distance of first stops in View-consistent expansion ± 95% confidence interval: 0.61 ± 0.24 m, $N = 8$). The distance of the second stops by the hummingbirds in the View-consistent expansion test showed the opposite pattern, being significantly different to 0.6 m, but not 0.3 m (mean distance of second stops in View-consistent expansion ± 95% confidence interval: 0.42 ± 0.14 m, $N = 8$). In the View-inconsistent expansion, both the first and second stops were significantly different to 0.6 m from the landmarks, but not 0.3 m (mean distance of stops in View-inconsistent expansion ± 95% confidence interval: first: 0.34 ± 0.21 m, $N = 8$; second: 0.23 ± 0.11 m, $N = 8$). To look at this difference in the distances that hummingbirds searched from the landmarks in the different expansion tests more closely, as well as to directly compare the behaviour of the

birds in the different tests, we calculated the absolute difference between the distance that the hummingbirds hovered from the landmarks and both 0.3 m and 0.6 m. Using a paired *t* test, we found that the hummingbirds tended to search closer to 0.6 m in the View-consistent expansion compared to the View-inconsistent expansion (paired *t* test of difference between observed hovering distance and 0.6 m: first stops: $t_7 = -2.87$, $P = 0.024$; second stops: $t_7 = -2.34$, $P = 0.052$). Hummingbirds did not, however, search significantly closer to or further from 0.3 m in the View-inconsistent or View-consistent expansion (paired *t* test of logged difference between observed hovering distance and 0.6 m: first stops: $t_7 = 0.41$, $P = 0.70$; second stops: $t_7 = 0.34$, $P = 0.74$). Looking at the distribution of stopping distances in the two expansion tests, we can see that this result could be due to hummingbirds in the View-consistent expansion using different strategies: half of the hummingbirds searched around 0.6 m, consistent with using angular size, while the other half searched around 0.3 m consistent with using absolute distance (Fig. 5a). In contrast, in the View-inconsistent expansion, there was no evidence of hummingbirds searching around 0.6 m but rather birds searched 0.3 m or closer to the landmarks. Furthermore, the hummingbirds were consistent in the distance at which they searched in the View-consistent expansion. Six of the eight birds tested stopped at similar distances on both their first and second stops, while the remaining two birds searched farther than expected on their first stop, but then stopped at either around 0.3 m or 0.6 m. The correlation between first and second stop distances was not significant due to the data for the first stops of these two birds (Spearman rank correlation: $r_S = 0.62$, $N = 8$, $P = 0.115$), but the pattern for the other six birds can be seen in Fig. 6a.

Given that hummingbirds searched more in the direction of the flower in the View-consistent expansion than in the View-inconsistent expansion, they might also have estimated the distance at which they preferred searching more precisely when the view of the landmarks was more similar to that seen during training. To test this, we took whichever value was

smaller for each bird between the difference from 0.6 m and from 0.3 m, and used a paired one-tailed *t* test to test whether hummingbirds searched closer to one of these predicted distances in the View-consistent expansion than in the View-inconsistent expansion. We found that there was no significant difference between the first stops by the birds in the two expansion tests (one-tailed paired *t* test of logged difference between observed and predicted hovering distances: first stops: $t_7 = -0.79$, $P = 0.23$), but the second stops in the View-consistent expansion were significantly closer to 0.3 m or 0.6 m than the second stops in the View-inconsistent expansion (second stops: $t_7 = -2.13$, $P = 0.035$). The lack of an effect for the first stops could be due to two birds stopping quite far from the landmarks on their first stop in the View-consistent expansion (Fig. 4), as the difference between the median distances of the first stops from 0.3 m or 0.6 m in both expansions (View-consistent: 0.05 m, $N = 8$; View-inconsistent: 0.11 m, $N = 8$) was similar to the difference between the median distances of the second stops (View-consistent: 0.03 m, $N = 8$; View-inconsistent: 0.09 m, $N = 8$). Just as hummingbirds searched more in the flower's direction when the view of the landmarks better matched that seen during training, these data tend to support hummingbirds stopping and hovering closer to either the absolute distance or the angular size of the landmark in the View-consistent expansion than in the View-inconsistent expansion.

The hummingbirds that appeared to match the angular size of the landmarks in the View-consistent test also tended to match the retinal angle between the landmarks. The stops of the hummingbirds that searched around 0.6 m from the landmarks in the View-consistent expansion appeared to be less scattered, with the mean never too far from the 60° experienced during training (inter-landmark angle of birds that stopped 0.6 m from landmarks: first stops: mean ± SD = 48.68 ± 9.37°, $N = 4$; second stops: mean ± SD = 58.55 ± 4.312°, $N = 4$; Fig. 6b). The stops of the birds that stopped 0.3 m from one of the landmarks in the View-consistent expansion, on the other hand, were more scattered. On their second stop, these

birds were further from the 60° experienced during training (inter-landmark angle of birds that stopped 0.3 m from landmarks: first stops: mean ± SD = 47.55 ± 17.94°, *N* = 4; second stops: mean = 81.17 ± 27.94°, *N* = 4; Fig. 6b). In the View-inconsistent expansion test, there was no such pattern (Fig. 6b). The strategies adopted by hummingbirds in the View-consistent test, therefore, not only included the distance at which they searched, but also how likely they were to have used the inter-landmark angle. Hummingbirds that searched at 0.6 m, where the angular size of the landmarks would best match that seen during training, were also more likely to have matched the retinal angle between the landmarks, whereas hummingbirds that searched at the absolute distance of the flower from the landmarks, 0.3 m, were less likely to have matched the inter-landmark angle.

<H2>Rotation Test

If the birds relied on the configuration of the landmarks to estimate direction, they should have followed the 90° rotation of the landmark array and searched 90° from the direction in which they had learned to find the flower. Alternatively, if birds used an absolute bearing from each landmark using, for example, a compass, they should have searched in the trained direction from one of the two landmarks. Finally, if birds used a remembered view of the entire panorama and not just of the landmarks, they should have searched in the trained direction from the southern landmark in particular because that location best matched the visual panorama they had seen during training. Although the angular size and relative positions of the landmarks would have been most similar if the hummingbirds had followed the rotation (L1 + L2 in Fig. 3), everything else in the panorama would have been different to the panorama they had seen during training. Of the two trained directions, the panorama seen in the trained direction from the southern landmark (L2 in Fig. 3) was the least different to

the training panorama because it maintained its position in the panorama while, because it was further away, the change in panoramic position of the northern landmark was reduced by this landmark occupying less of the panoramic view (Fig. 3).

As with the expansion tests, we examined whether hummingbirds concentrated their stops around the rotated landmarks by overlaying a grid of 53 hexagons each covering an area of 0.104 m^2. The density of the stops by the birds was not significantly different to an even distribution with each stop in a different hexagonal cell (bootstrapped one-tailed Kolmogorov–Smirnov test with 10 000 bootstraps: $D_{\text{one-tailed}} = 0.11$, $P = 0.104$). We did, however, observe that the highest density of stops was in the region around the trained direction from the southern landmark. When the area around the southern landmark was divided into quadrants (Fig. 4), hummingbirds stopped significantly more than expected by chance in the bottom left quadrant (binomial test, 8/15 in bottom left with probability of 0.25: observed probability of success = 0.53 ± 0.27, $P = 0.017$), and significantly less in the top right quadrant (0/15: observed probability of success = 0 ± 0.21, $P = 0.03$). The number of stops in the other quadrants, top-left and bottom-right of the southern landmark, were not different to chance (top-left: 6/15: observed probability of success = 0.4 ± 0.24, $P = 0.23$; bottom-right: 1/15: observed probability of success = 0.06 ± 0.26, $P = 0.14$).

When we standardized all rotation tests to a clockwise rotation, we found that the mean direction the birds searched from the southern landmark was not significantly different to the absolute direction and tended to be significantly different from the rotated direction (specific mean bootstrap test: southern landmark: rotated: first: $N = 8$, $P = 0.030$; second: $N = 7$, $P = 0.068$; absolute: first: $N = 8$, $P = 0.15$; second: $N = 7$, $P = 0.34$; Fig. 4). The mean direction hummingbirds searched from the northern landmark, however, was significantly different to the absolute direction but not the rotated direction (specific mean bootstrap test: northern landmark: rotated: first: $N = 8$, $P = 0.098$; second: $N = 7$, $P = 0.071$; absolute: first: N

= 8, $P = 0.0032$; second: $N = 7$, $P = 0.016$; Fig. 4). Both of these results are consistent with the birds searching southwest of the landmark. Searching in the rotated direction from the northern landmark did not mean, however, that the hummingbirds followed the rotation. Looking at the 95% confidence intervals around the mean search directions, the rotated direction fell outside the confidence intervals for first and second stops from both landmarks, while the absolute direction fell outside the confidence interval only from the northern landmark (mean search direction from northern landmark ± 95% confidence interval, with rotated direction at 210° and absolute direction at 300°: first stops: 234.84 ± 23.13°, $N = 8$; second stops: 240.76 ± 21.56°, $N = 7$; mean search direction from southern landmark ± 95% confidence interval, with rotated direction at 150° and absolute direction at 240°: first stops: 209.21 ± 32.24°, $N = 8$; second stops: 214.76 ± 37.72°, $N = 7$). These data are most consistent with the explanation that the hummingbirds searched in the previously trained absolute direction, but only from the southern landmark (Fig. 4).

<H1>DISCUSSION

When the landmarks were doubled in size and moved twice as far apart, the birds searched in the direction of the flower's previous location and at either the absolute distance of the flower's previous location from the landmarks or where the retinal angle of the landmarks and the angle between the landmarks matched that seen during training. When the landmarks were moved twice as far apart but remained the same size, however, there was no pattern to the birds' search: they searched all around the landmarks. In addition, when we rotated the landmarks 90˚ either clockwise or anticlockwise, the hummingbirds mostly searched in the direction of the flower's previous location, but only from one of the landmarks (Fig. 4).

Across the three tests, hummingbirds did not perform as would have been expected of birds tested in the laboratory. Although the hummingbirds tended to search in the trained absolute direction in the Rotation test as do nutcrackers tested with large rotations in the laboratory (Jones & Kamil, 2001; Kamil & Jones, 1997, 2000), the hummingbirds typically searched in a location that was in the absolute direction from only one of the landmarks. Nutcrackers, in contrast, searched relative to both landmarks (Jones & Kamil, 2001; Kamil & Jones, 1997, 2000). In the expansion tests, hummingbirds appeared to require both the size and position of landmarks in the panorama to be consistent with those experienced during training, a requirement that is not seen in either pigeons or nutcrackers (Kamil & Jones, 2000; Kelly et al., 2008; Spetch et al., 1997). Rather than searching at the absolute distance and direction from one of the landmarks (Kelly et al., 2008; Spetch et al., 1997; Spetch et al., 1996), averaging the vectors from both landmarks (Cheng, 1994), or using a vector of angular size and compass direction to search in the distance or direction from one of the landmarks, the hummingbirds in the View-inconsistent expansion appeared disoriented and searched in a scattered fashion around the landmarks. Hummingbirds searching in the direction of the flower in the View-consistent but not in the View-inconsistent expansion is consistent with the results of a previous study on landmark use in hummingbirds. In Pritchard et al. (2015), hummingbirds searched at a flower's distance from landmarks, but not in the direction of the flower when the landmarks and flower were moved 3–4 m between visits, but they did search in the flower's direction when the landmarks and flower were moved 0.25 m between visits. Although the landmarks and flower in this experiment were also moved 0.25 m between training visits, the hummingbirds' search direction changed when other aspects of the view changed during the different expansion tests. It could be, therefore, that the hummingbirds in Pritchard et al. (2015) searched closer to the flower's direction when the landmarks moved 0.25 m, because the panoramic view from the flower was more similar between visits. This

need for a consistent view in both Pritchard et al. (2015) and the expansion tests reported here could be seen as evidence that hummingbirds use a view-matching strategy to relocate their flowers.

Half of the birds did, however, search at the same absolute distance that the flower had been from the landmarks in the View-consistent expansion rather than match the apparent size of the landmarks and, in the pre-test, which we had intended as confirmation that the hummingbirds had learned the location of the flower, the hummingbirds appeared disoriented and did not search in either the flower's direction or at the distance the flower had been from the landmarks. Because it was clear by the 20th visit that all hummingbirds had learned both the distance and direction of the flower from the landmarks (data from the View-consistent and Rotation tests), we suspect that the scatter in the search locations on the 10th trial was due to the first removal of the flower, which led to the birds stopping to hover prematurely. In addition, while most hummingbirds in the Rotation test searched where the view was most consistent between training and testing, it is also possible that hummingbirds chose this location because the total error in the bearings from the landmarks (0° from the southern landmark, L2, ~45° from the northern landmark, L1) was smaller than the total bearing error would have been if the birds had searched relative to the northern landmark (0° from the northern landmark, L1, ~105° from the southern landmark, L2). This does not, however, explain why birds used such bearings in the View-consistent test but not in the View-inconsistent test. Overall, the hummingbirds' poor performance in the pre-test, their searching at the flower's absolute distance in the View-consistent expansion, and possibly minimizing their total bearing error, could all be seen as evidence that the hummingbirds did not always rely on a view-matching strategy to relocate the rewarded flower.

These data can be reconciled with the vector-navigation strategy thought to be used by birds in the laboratory, by considering that hummingbirds may use a remembered view

only to recognize the landmarks and not to relocate the goal itself. Spetch et al. (1997) suggested that landmark navigation occurred in two stages: first, birds recognize landmarks via 'landmark matching', then use these landmarks to locate a goal via 'search place matching'. For Spetch et al.'s pigeons, landmark matching was based on the appearance of individual landmarks or, for landmarks that were moved, the landmark configuration. If, however, hummingbirds use a remembered view to recognize the landmarks, then landmark matching would be more successful in the View-consistent expansion than in the View-inconsistent expansion. There would have been no need for the hummingbirds to locate the goal by matching a remembered view. This interpretation can explain at least some of the data. In the View-consistent expansion and the Rotation tests, both the size and position of the landmarks in the panorama were the same as during training, which may have allowed the birds to recognize the landmarks and so search appropriately. In the View-inconsistent expansion, on the other hand, it was impossible for the birds to match both the size and panoramic position of both landmarks to those seen during training. The birds' appropriate searching may have occurred because they did not recognize the landmarks.

Although this 'landmark matching/search place matching' account reconciles our data with data from birds tested in the laboratory, such that hummingbirds only differ from pigeons in how they 'recognize' landmarks, we are cautious in accepting this interpretation of the hummingbirds' search behaviour. First, according to this interpretation, the hummingbirds would have recognized landmarks on the basis of a remembered view rather than learning each individual landmark's appearance, as pigeons in the laboratory appear to do. It is not clear why they would have done this. In addition, the landmark matching/search place matching explanation as to why birds were oriented in the View-consistent expansion, but not in the View-inconsistent expansion, does not hold up to scrutiny. If hummingbirds only searched accurately having recognized the view of the landmarks, it is unclear why they

would then use vectors or bearings from individual landmarks as pigeons and nutcrackers are thought to do. If an individual landmark can be used for search place matching, it is not clear why it is not recognized during the previous landmark-matching stage. Similarly, this interpretation does not help to explain why some birds appeared to use apparent size to estimate distance while others used absolute distance, or why in the Rotation test the hummingbirds predominantly searched relative to the southern landmark.

View matching of the whole panoramic scene, rather than landmark matching, seems to explain more of the hummingbirds' search behaviour. For example, the better performance of hummingbirds in the View-consistent expansion than in the View-inconsistent expansion is akin to the better performance of ants tested under similar experimental manipulations (Narendra et al., 2007; Wehner & Räber, 1979) and to the results of several insect-derived models of view matching (Möller, 2001; Nicholson, Judd, Cartwright, & Collett, 1999). Requiring the landmarks to fit the same size and position in the panorama is consistent with hummingbirds using the entire panorama, rather than just the experimental landmarks, to relocate the flower. This was compellingly demonstrated in the Rotation test, where most of the birds searched at a location in which the landmark that did not match the training view was further away and so appeared smaller (L2 in Fig. 3). This behaviour can be explained if the birds matched the whole panorama, whereby they incorporated not only the size and position of the landmarks but the rest of the visual panorama as well. As bees and wasps can estimate absolute distances during view matching by matching patterns of optic flow, even the hummingbirds searching at the absolute distance that the flower had been from the landmarks is consistent with view matching (Brunnert, Kelber & Zeil, 1994; Cartwright & Collett, 1979; Dittmar et al., 2010; Lehrer et al., 1988; Zeil, 1993). The differences between birds could therefore be seen as individuals differing in which aspect of a remembered view to match. It is possible that some hummingbirds prioritized matching optic flow or used

stereopsis to encode depth information and searched at the absolute distance of the flower, while others prioritized apparent size and searched further away.

View matching thus appears to explain more of the hummingbirds' search behaviour than does landmark matching, but a definitive test of the two explanations is required. Importantly, and regardless of what information the hummingbirds used to relocate the flower, they did not behave like birds trained and tested in the laboratory. Rather, the hummingbirds were sensitive to the angular size and distance between landmarks, cues more commonly associated with maintaining stable flight than pinpointing a location relative to landmarks. This difference could be because most of the work on goal relocation in birds has been on birds walking to goals in the laboratory (e.g. Jones, Antoniadis, Shettleworth, & Kamil, 2002; Kelly, Kamil, & Cheng, 2010; Spetch et al., 1997). The use of view-based cues by goldfish (Douglas, 1996), suggest that what animals learn about landmarks could depend on whether an animal is navigating through two or three dimensions (Flores-Abreu, Hurly, Ainge, & Healy, 2014).

There are at least two possible causes for the disparity between the ways in which hummingbirds and other birds tested in the laboratory search for goals: (1) differences in panoramic stability between the laboratory and field, and (2) differences in locomotion between walking and flying birds. To understand how animals learn about locations in all environments, not just the walled testing rooms of the laboratory, it will be necessary to clarify how these factors influence what is learned about visual landmarks. This will involve testing a wider range of species, across a wider range of environments, and considering in more detail the visual information available to an animal as it moves and learns. Unravelling the influence of these causes will not only help to reconcile data from the laboratory and the field, but also provide an opportunity to better understand how ecology, behaviour and cognition come together to influence how animals find their way through the world.

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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.

Figure 2. (a) The experimental pitch, filmed by two cameras 6 m away and at 90° to each other. The landmarks (filled black circles) and flower (open circle) are shown in the upper-half of the pitch. (b) The angular size of the landmarks and the angular distance between landmarks in extracts from panoramic photographs of the training, View-consistent expansion and View-inconsistent expansion arrays. Diagrams to the left of photographs show the position (×) in which the photograph was taken, while the black and grey bars below the images show the angular size and angular distance, respectively. The combination of angular size and angular distance was most similar between the training array and the View-consistent expansion. In the View-inconsistent expansion, either the angular size of the landmarks was too small relative to the angular distance, or when the angular size of one landmark was the same, the angular distance was too large, while the angular size of the other landmark was too small.

Figure 3. Comparing panoramic images between the flower's position in training and

different locations in the rotation test. The top panels show the set-up of the landmarks during training and a panoramic photograph of the surroundings from the flower location. The bottom panels show the predicted locations and accompanying panoramic images, when the hummingbird followed the clockwise rotation and searched relative to both landmarks (L1 + L2), searched relative to only landmark 1 (L1, left pre-rotation, north post-rotation), or searched relative to only landmark 2 (L2, right pre-rotation, south post-rotation). When following the rotation (L1 + L2), the apparent size of the landmarks matched training and the landmarks were in the same positions relative to one another as in training, but the position of the rest of the panorama (seen in the background) was very different to training. In the trained direction from landmark 1 (L1), the panoramic background was the same as in training as was the size and position of one of the landmarks. The other landmark, however, appeared very large. In the trained direction from landmark 2 (L2), the panoramic background and the size and position of one landmark in the panorama was, again, conserved, but the other landmark was further away and took up less of the view. In terms of which panorama, as a whole, looked least different to training, the panorama from L2 could be considered the closest match to the panoramic view from the flower.

Figure 4. Predicted locations (left), results (centre) and heatmaps of stop density (right) for the three different transformation tests, with closed symbols in the results representing first stop locations and open symbols in the results representing second stop locations.

Figure 5. (a) Stacked histogram comparing the distance birds stopped from closest landmark in the View-consistent and View-inconsistent expansions across first stops (dark grey bars, total = 8) and second stops (light grey bars, total = 8). Dotted lines show 0.3 m (trained distance) and 0.6 m (double trained distance), and the black bar on the left-hand side

represents the landmark. (b) Stacked circular histograms comparing the directions the hummingbirds searched from the closest landmark in the View-consistent (top) and View-inconsistent (bottom) expansion tests across first stops (dark grey) and second stops (light grey), with the flower direction normalized to 0° (F). Solid arrows and arcs show mean and 95% confidence interval for first stops, dashed arrows and arcs for second stops. (c) Stacked circular histograms comparing the retinal angle between the landmarks at each hovering location in the View-consistent (top) and View-inconsistent (bottom) expansion tests and across first stops (dark grey) and second stops (light grey). During training the angle between the landmarks was 60° (dashed line). Solid arrows and arcs shows mean and 95% confidence interval for first stops, dashed arrows and arcs for second stops.

Figure 6. (a) Distances that hummingbirds stopped from the closest landmark on their first (*x* axis) and second (*y* axis) stops in the View-consistent (top) and View-inconsistent (bottom) expansions. The grey dashed lines show 0.3 m (trained distance) and 0.6 m (double trained distance), whereas the black dashed line represents perfect matching between first and second stops. Hummingbirds not only clustered around one of these distances, but were largely consistent across their first and second stops. (b) The inter-landmark angle plotted against the distance that hummingbirds searched from the closest landmark in the View-consistent (top) and View-inconsistent (bottom) expansions on their first (closed circles) and second (open circles) stops. The grey dashed lines show 0.3 m (trained distance) and 0.6 m (double trained distance), whereas the black dashed line represents the inter-landmark angle experienced during training. In the View-consistent expansion, hummingbirds that searched 0.6 m from the landmarks tended to closer match the inter-landmark angle experienced during training, compared to the birds which searched 0.3 m away. In the View-inconsistent expansion, there was no clear pattern.

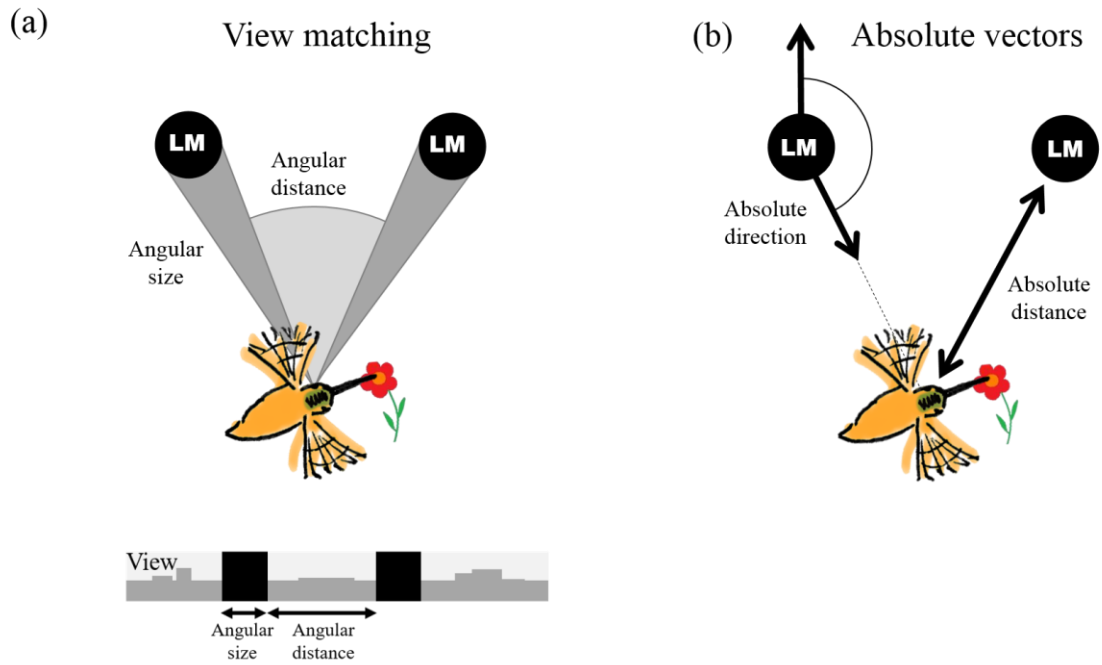
(a)
View matching
LM
LM
Angular distance
Angular size
View
Angular size
Angular distance
(b)
Absolute vectors
LM
LM
Absolute direction
Absolute distance

Figure 1

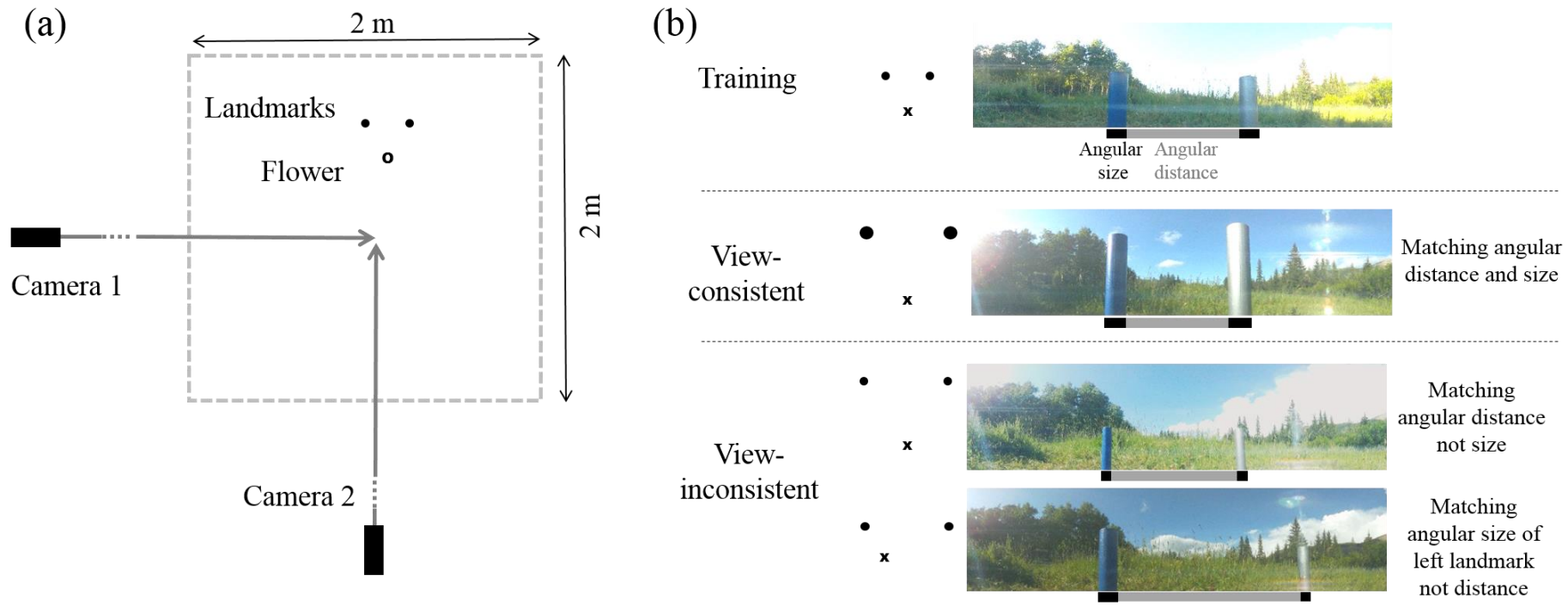
(a)
2 m
Landmarks
Flower
2 m
Camera 1
Camera 2
(b)
Training
Angular size
Angular distance
View-consistent
Matching angular distance and size
View-inconsistent
Matching angular distance not size
Matching angular size of left landmark not distance

Figure 2

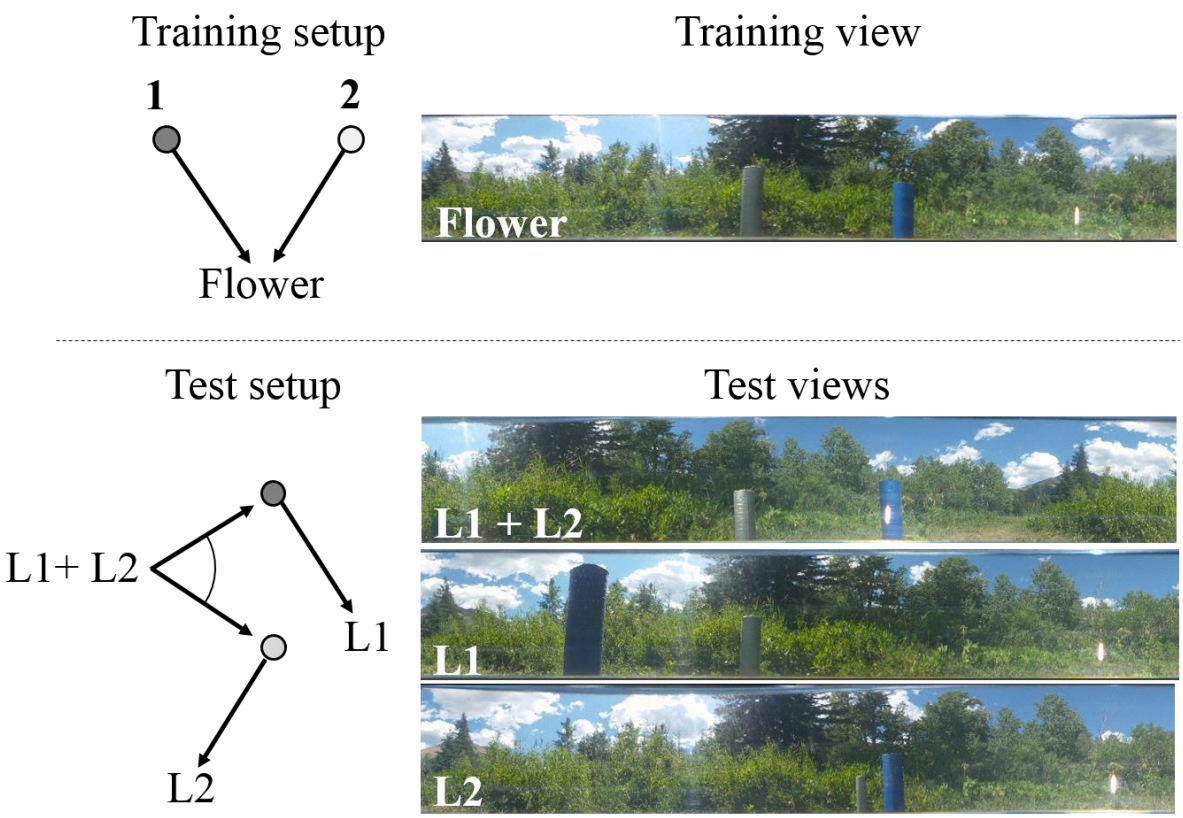
Training setup
Training view
1
2
Flower
Flower
Test setup
Test views
L1+ L2
L1
L2
L1 + L2
L1
L2

Figure 3

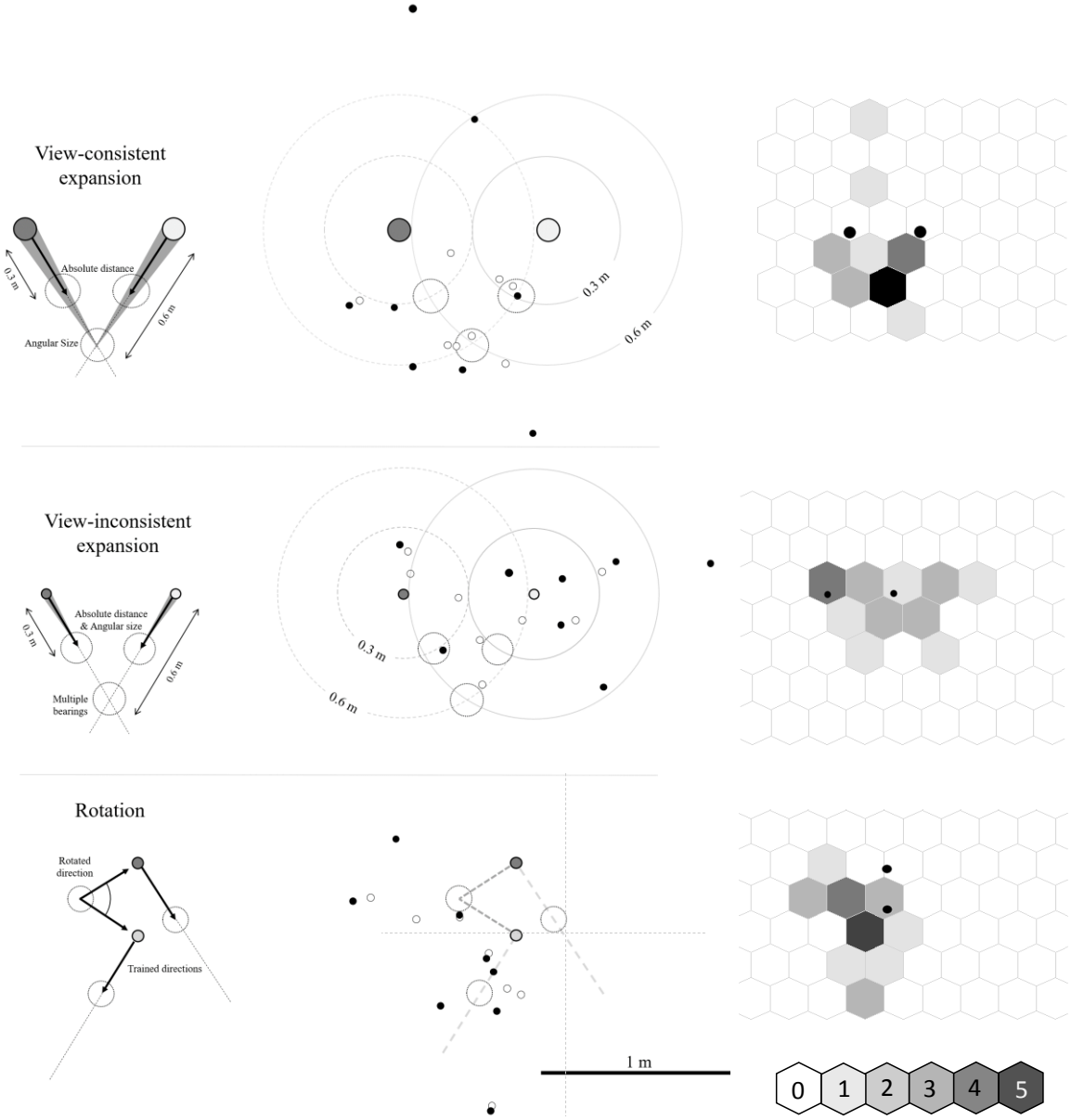
View-consistent expansion
Absolute distance
0.3 m
0.6 m
Angular Size
0.3 m
0.6 m
View-inconsistent expansion
Absolute distance & Angular size
0.3 m
0.6 m
Multiple bearings
0.3 m
0.6 m
Rotation
Rotated direction
Trained directions
1 m
0
1
2
3
4
5

Figure 4

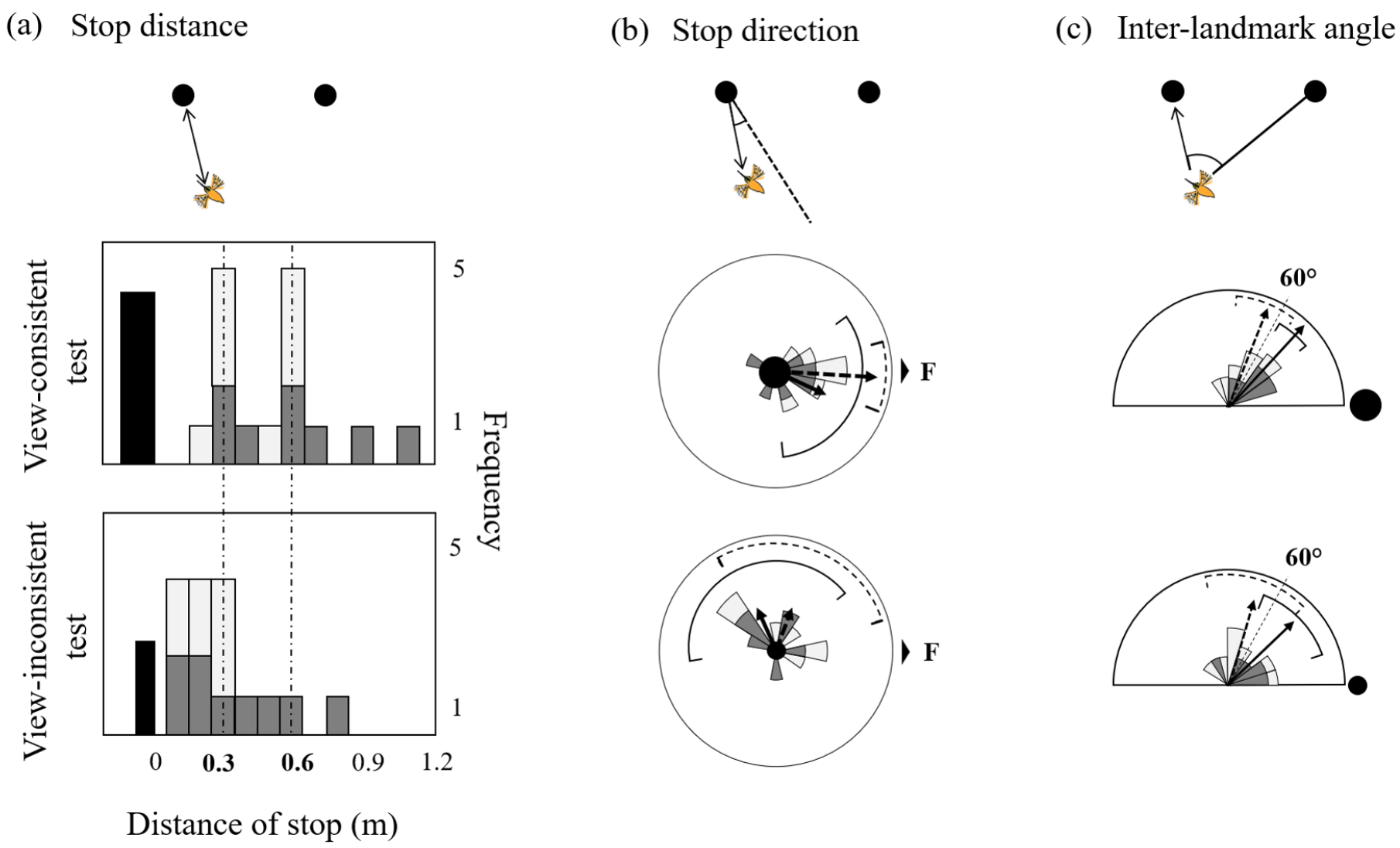
(a) Stop distance
(b) Stop direction
(c) Inter-landmark angle
View-consistent test
View-inconsistent test
5
1
5
1
Frequency
0
0.3
0.6
0.9
1.2
Distance of stop (m)
F
F
60°
60°

Figure 5

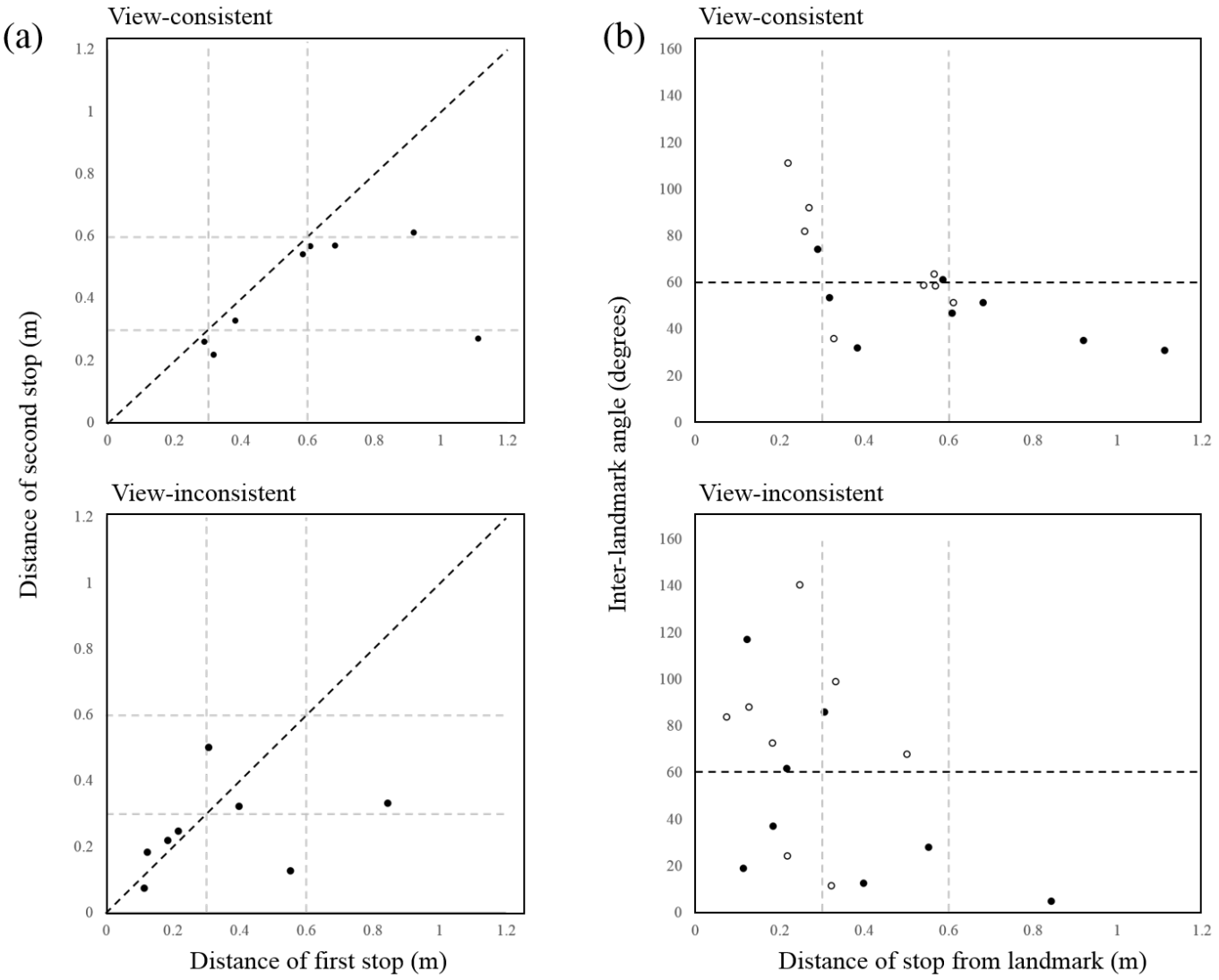
(a)
View-consistent
View-inconsistent
Distance of second stop (m)
Distance of first stop (m)
(b)
View-consistent
View-inconsistent
Inter-landmark angle (degrees)
Distance of stop from landmark (m)

Figure 6