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Bumblebees strategically use ground-level linear features in navigation

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Abstract:

Extended ground-level structures like roads or field edges can be important cues for navigating animals, seen for example in road-following pigeons. In a landscape devoid of skyline cues but with a rectangular grid of pathways and roads, we used harmonic radar to track free-flying bumblebees. Individual bees consistently used ground-level linear features for navigation in a wide range of behavioural contexts. Bee exploration flights, search behaviour and foraging routes were shaped by linear features, with bees frequently flying along and parallel to pathways and roads. Comparisons of flight trajectories across these behavioural contexts show that individuals modulated their use of linear features strategically with respect to their individual goals and experience. Bees searching for a feeder used linear features to target their search, while foragers often followed pathways to return to their hive without overshooting. These findings on a major pollinator have important implications for the placements of bee colonies for agriculture and floral resources for conservation.

Keywords: Bee, *Bombus terrestris*, Exploration flight, Harmonic radar, Insect navigation, Orientation flight, Pollination, Road following, Route formation, Search flight

INTRODUCTION

Ground-level elongated linear structures, such as rivers, forest edges, paths and roads provide unique visual information which can affect animal dispersal and navigation (Billington, 2003; Gesicki et al., 2019; Schiffner and Wiltschko, 2014). For instance, pigeons follow roads (Guilford et al., 2004; Lipp et al., 2004), bats fly along hedgerows and tree-lines (Billington, 2003) and turtles follow coastlines (Luschi et al., 1996). Such features may be particularly relevant for pollinators that exploit agricultural terrains which often present sparse visual environments with prominent man-made linear features.

There is tentative evidence that bees use such linear structures for navigation. For example, von Frisch and Lindauer (1954) trained honeybees to fly along continuous forest edges, lake edges and roads and observed that they would prioritise this information over cues gained from their sun compass (von Frisch, 1967). Menzel *et al.* (2019) observed that some experimentally displaced honeybees tended to use gravel roads, field edges, hedgerows and irrigation channels to return to their hive. Collett and Graham (2015), reviewing other radar studies (Degen et al., 2016; Osborne et al., 2013; Wolf et al., 2014), further observed that displaced honeybee foragers seemed to follow a pathway then a hedgerow back to their hive, while honeybees performing their first exploration flights appeared in some cases to follow field edges.

These observations suggest that bees use ground-level linear features for some navigational tasks. However, none of the studies were designed to examine this question in a quantitative and experimental manner, so cannot address the likelihood or degree of use of these features, or the variety of contexts in which they are used. Interpreting these observations is made more difficult still because the landscapes in which the bees were tracked contained potential landmarks such as trees and buildings that bees could have used for navigation. Thus, important questions remain about the likelihood of bees using ground-level linear features, the contexts in which they are used and whether their use depends on a bee's experience with the local landscape. If bees consistently use

ground-level linear features for navigation, this may strongly affect the areas they are most likely to discover, pollinate and fly through.

Here we examined how and to what extent bees learn to use linear features during navigation using a harmonic radar to track free-flying bumblebees (*Bombus terrestris*) in a unique, visually sparse landscape, characterised by a ground-level rectangular grid of roads, pathways and field borders. While compass cues remained, the horizon provided no skyline cues that bumblebees could exploit to indicate location (including the farm which was too far from the hive, Fig 1a; for more detail see Appendix, Field site panorama). In the absence of skyline information, any influence of ground level cues can be isolated, allowing us to quantify bumblebees' use of linear features in exploration flights, searching flights, foraging flights and over route development.

METHODS

Bees and Field Site

Field work was carried out on a rice farm (Finca Casudis, La Puebla del Río; Latitude 37.13562305, Longitude: -6.080421855), South of Seville, Spain, between the 20 April and the 15 May 2018. The field site was composed of a series of unflooded rice paddies on flat terrain, with few to no above ground level features (Fig 1a; Appendix, Field site panorama). The rice paddies were all 420 m by 200 m, set out in a grid and separated by raised pathways of compacted earth (approximately 0.5 m higher than the fields). All pathways running WSW-ENE comprised two single-lane roads separated by a narrow irrigation channel. Every second pathway running WNW-ESE was a single lane road, while the others were narrow footpaths, approximately 1 m wide. A small packed earth runway ran along one of the WSW-ENE roads, from the main farm outward (thicker pale line, Fig 1b). To the north of this road is a footpath along which the hives were placed (Hive Location 1) for Experiments 1-4, while to the South, in a field were placed the hives (Hive Location 2) for an additional test (see Appendix, Experiment A3). All pathways (including roads, footpaths, field edges and the runway) are referred to as this environment's linear features.

85 Eight commercially bred bumblebee colonies (*Bombus terrestris*; colonies with 150-200 individuals
86 on average; Koppert Biological Systems, Spain) were used. Each colony was transferred to a custom
87 wooden hive box (30 × 21 × 16 cm high), with a Perspex tunnel (26 × 4 × 4 cm high) ending in a small
88 Perspex platform (4 × approx. 6 cm), through which the bees could access the outside world. Small
89 sliding barriers could be used to block the tunnel, allowing us to control which bees could go in and
90 out. Two hives (placed side by side) were used at a time to maximise the number of active foragers.
91 Bees were allowed to feed freely from experimental feeders in a flight tent (3 × 3 × 3 m) for 2-4 days
92 before the hive was transported to the field site. The flight tent was located more than 15 km from
93 the field site, in a very different visual environment (either a walled garden, or bordered by a wall on
94 one side and a dense grove of orange trees on all others. The horizon was not visible from either
95 location). Bees were only able to fly within the flight tent, so that their visual experience prior to the
96 field site was restricted to a small space walled with fine white mesh, while the fields and paths in
97 our field site were generally uniformly coloured (mostly brown) during data collection (Fig 1a).
98 Individual bees were thus familiar with the feeder design but naïve to the field site and their location
99 within it at the beginning of experiments. Feeders were made of a raised blue platform (20 × 20 cm),
100 approximately 1 m above ground level, identical to those used in Woodgate *et al.* (2017) supporting
101 a gravity feeder (described in Chap 2, section 5, von Frisch, 1967). A 1 m tall feeder could have been
102 visible to bees at a range of 25 m maximum (calculated from the smallest measured bee spatial
103 resolution of 2.3°; Dyer et al., 2008). This is a generous estimate, since in reality the feeders were
104 thin, and located on the lower-level field beside the footpath so that they appeared less than 1 m
105 above the horizon. We are therefore confident that feeders could not be used as landmarks for bee
106 orientation outside of this 25 m range.

107 Natural foraging sources were present along the river Guadalquivir (West of the farm, over 1200 m
108 from the hive site), but were largely absent within the rice paddies themselves. Experimental feeders
109 providing *ad libitum* 30% (by weight) unscented sucrose solution were placed 160-250 m from the

bumblebee hives, either along the linear features (Feeders F1, F2 and F3) or in the middle of a rice paddy (Feeder F4) (Fig 1b).

All tracked bees were given unique colour and letter identification using custom-made metal tags (Qualitech, March, Cambridgeshire, UK), attached to their thorax using superglue (Loctite Power Flex Gel, Henkel Ltd., Hemel Hempstead, UK). Bees were primarily tagged within the flight tent before the hive was transported to the field site, but this tagging process continued after experiments started so that newly emerged bees could also be tracked. What was known about individual experience was carefully noted for reference.

Harmonic Radar

Individual bees were tracked using a 32 mm harmonic radar described in previous studies (Riley et al., 1996), located approximately 310 m from the hive (Fig 1b). To allow radar tracking, a lightweight transponder (16 mm long, approximately 20 mg) was attached to the metal tag of a focal bee as it left the hive, using a small magnet at the base of the transponders. This allowed us to attach and remove it from the metal tags very quickly without capturing or handling the bee, thus minimizing stress due to manipulation.

The radar rotated constantly, scanning through 360° once every 3 seconds. When a bee with a transponder was within a line of sight of the radar up to approximately 1 km, the radar returned its distance and azimuth from the radar once every rotation. Flight path tracks were converted to GPS coordinates by triangulating the radar signals against two locations whose GPS coordinates were known, using a custom-written Matlab script (Mathworks Inc., Natick, USA). These tracks were visualised by plotting them on top of a satellite image of the field site. We tracked a total of 180 flights from 83 individuals (Appendix, Table A1).

Ethical note

Bees were kept outside (first in a distant location within a flight tent and then in the field site), covered with tarp to protect them from rain and sun. The hive boxes kept the bee colonies in a dark environment, comparable to their natural underground hives. Bees were frequently given full access to the field site (as in a natural setting), except in specific circumstances, for up to a day at most, for the purposes of the experiment. They were never locked in for long enough to cause stress or harm. Bumblebees store food (nectar and pollen) in their hive, and workers have intrinsic motivation to leave and forage for the colony. Supplementary pollen was provided every two days. Colonies were checked regularly for food stores and were provided with sugar solution if their stores were low. The bees were never starved. Handling was kept to a minimum. Individual foragers were tagged with metal tags, involving one short capture per individual, where tags were attached to the thorax using super glue. Metal tags allowed us to apply and remove our magnetised radar transponders without capturing them, involving only brief containment within the tunnel leading to their hive. This minimised stress and handling time to only a few seconds. Non-worker individuals were not manipulated. Radar transponders were small enough to allow for normal bumblebee flight. Bumblebees regularly carry heavier loads of nectar and pollen than the weight of the transponder. Eighty-three bees were tracked.

Once the colonies were no longer being used for experiments, they were humanely killed via freezing, so as to prevent commercially-bred bees from affecting local wild bumblebee populations.

The research described here aligns with the ASAB/ABS Guidelines for the use of animals in Research. No license or permits were required for these experiments.

Experiments

Details of dates, bumblebee colonies, number of tracks and individuals for each experiment can be found in Appendix, Table A1. In all cases described below, the colonies were placed at the first hive location 'Hive Location 1' (Fig 1b). Colonies were placed at location 'Hive Location 2' (Fig 1b) for an additional test (see appendix, Experiment A3).

Experiment 1

Do bees use ground-level features during exploration flights? The first flights of bees in a new environment focus on exploring the surrounding landscape and, in the case of bumblebees, also the food sources within it (Osborne et al., 2013; Woodgate et al., 2016). These ‘exploration flights’ usually consist of several loops in all directions around the hive, starting small and progressively widening (Osborne et al., 2013). Individuals with no previous flight experience in this environment were tracked on their first exploration flights in the field site. This was done using the sliding barriers in the hive tunnel to allow access to the outside for only the focal bee and no others. These first flights were primarily recorded on the 24 April, when there were no artificial feeders present in the field site. Three more first flights were recorded on the 4 May, when several feeders were present in the field.

We also recorded flights displaying typical looping behaviour around the hive, characteristic of exploration flights (Osborne et al., 2013; Woodgate et al., 2016), between the 30 April and the 8 May, from bees in colonies whose tunnels were kept open to allow free access to the field site. We could not be certain whether these bees had previously flown, and so we call these tracks ‘apparent exploration flights’. There were feeders present during these recordings (Appendix, Table A1).

Experiment 2

Do bees use linear features during repeated back and forth flights to forage locations? Once bees had completed their exploration flights, we opportunistically tracked foraging bumblebees while all individuals had free access to the field site. Two main feeder treatments were set up during this time. All colonies were given a day of exposure to the field before feeders were introduced, and different colonies were used for each treatment.

In the first treatment, we placed feeders in positions F1 and F2 (35 m apart) along linear features (Fig 1b). F1 was located next to a crossroads, connected to both the hive and F2 by linear features.

The hive and F2 were not placed on the same linear feature, so that the straightest path from the hive to F2 did not involve flight along a linear feature. The intention was to compare flights to F1 (where the most direct flight coincided with a flight over a linear feature) and to F2 (where the most direct flight crossed over open field). Since most of the foraging flights tracked in this condition (60%) involved individual bees visiting both F1 and F2 in the same foraging trip, we set up a second treatment.

In the second treatment, we placed feeders in positions F1 and F3 (168 m apart) along the same linear features. F1 remained next to the crossroads, connected to both the hive and F3, while F3 was located on the same path as F2 had been, but further from F1 to increase the cost of joint visits to F1 and F3. As with the previous condition, we aimed to compare tracks to F1, along a linear feature, with tracks to F3, where a flight following linear features would take the bee on a longer flight via the crossroads, and the most efficient flight would be across the field.

Some of the bees we tracked did not visit our experimental feeders but flew instead to distant locations, primarily in the direction of the river. Many of these bees returned with pollen. We therefore categorised non-looping flights to distant locations as *natural forage flights* (Appendix, Experiment A2). Unlike the flights to feeders, the final goals of these natural forage flights were out of range of the radar. This means that the flight we tracked was the portions of outbound and inbound flight within range of the radar, up to 1 km from the hive location. Outbound flight portions therefore stop before bees reached their destination, while inbound flights begin when the bees pass into the radar's range.

Experiment 3

Does bee reliance on linear features change with experience? One bee was repeatedly tracked while habitually foraging at feeder F3 (Fig 1b). Here, the most direct route from the hive to this feeder would involve no flight along linear features (238 m), while an alternative route continuously following linear features would be 41% longer (336 m). The inbound and outbound portions of flight

were manually categorised as follows: if the flight approaching the goal (feeder for outbound and hive for inbound portions of flight) followed the associated linear feature for at least the final 30 m, then it was labelled as 'using linear features' to reach the goal, while if the bee did not follow the associated linear feature on its way to the goal, it was labelled 'not using linear features'. Tracks in which the bee followed linear features after or not immediately before reaching the desired goal were classified as 'not using linear features'. We used 30 m as a cut-off point since it is larger than our generous calculated maximum range (25 m) at which bees might be able to discern a feeder and use it as a beacon. We assessed the frequency of each of these flight strategies as the bees gained experience.

Experiment 4

Do bees use linear features to search for a removed feeder? When a bee does not find a goal (e.g. hive or feeder) in its usual position, it searches using a distinctive flight pattern, performing looping flight in all directions around the goal's last known location (Reynolds et al., 2007). We identified focal bees from individuals who regularly visited a single feeder, either F1 or F3 (Fig 1b). When the focal bee returned from a flight to its preferred feeder, we used the tunnel dividers to confine all bees to the hive. All feeders were then removed from the field. The focal bee was released from the hive and then tracked until it returned to the hive. The focal bees tested searched either for F1 ($N = 3$ bees) or F3 ($N = 3$ bees).

Track Analyses

Proximity Score:

To quantify use of ground level linear features by bees, we analysed all tracks for the bees' proximity to linear features. All tracks were reduced to non-stationary data by excluding points that showed less than 1 m of motion since the previously recorded bee position.

230 We used a satellite image of the field site, acquired from Google Earth Pro (Google, Mountain View,
 231 California, USA), which we converted to a black and white image (1116 x 632 px) showing the
 232 positions of all linear features. The pixel coordinates for all linear features in the image were
 233 extracted using custom written Matlab script (Mathworks Inc., Natick, USA). The rest of the
 234 calculations were done using custom written C# code (Microsoft Visual Studio Community, 2017).

235 We translated all radar track coordinates into the same pixel coordinate system as the image, using
 236 the relative positions of the hive and feeder F1 for reference. We calculated the Euclidean distance
 237 between each bee track coordinate and the closest linear feature and rescaled it to real-world
 238 distance in meters. This allowed us to assess the minimum distance to any linear feature for every
 239 point in the bees' flight path. From this we calculated an 'initial score', the proportion of points in
 240 the track (excluding stationary points) which were less than 5 m from any linear feature.

241 Since flights were centred on the hive, which was positioned next to a linear feature for Experiments
 242 1-4, and since the field site was a regular grid of linear features, it is to be expected that bees would
 243 often approach or cross linear features even if they do not use them in any way for navigation. To
 244 ask whether bees spent a greater proportion of their time in close proximity to linear features than
 245 expected by chance, we calculated a track-specific 'control score'. This control represented the
 246 average expected proximity score from the same track rotated multiple times around the hive.

247 Specifically, we rotated every track around the hive position in 10° increments and calculated the
 248 initial score, as described above, for each rotated track. The control score is the average of all initial
 249 scores from the 35 rotations, and estimates the level of proximity we would expect by chance if the
 250 bee's flight path was independent of landscape features, while still centred on the same hive
 251 position.

252 We tested whether bees followed linear features more than expected by chance, during exploration
 253 flights, using a series of paired-samples t-tests (after testing each dataset for normality using a
 254 Kolmogorov-Smirnov test; a Wilcoxon matched-pair signed-rank test was used as a non-parametric

alternative if the data was not normally distributed), comparing the initial proximity scores to their paired control proximity scores. The null hypothesis was that there would be no significant difference between initial and control scores, suggesting that bees spent no more time in close proximity to linear features than they would by chance. The dependent variables for each test were the proximity scores (initial and control scores) from flights categorised as first flights or apparent exploration flights (Experiment 1). Our method of generating control scores assumes that flights have no specific destination, so is not suitable for assessing flights to feeders. We report initial proximity scores for foraging and search flight, but do not test them against a control.

In all cases, repeated measures of individuals were averaged before statistical tests so that all tests were performed on data representing one data point per individual. Flights where the individual was unknown were not included in analyses.

Flight bearings:

Flying along linear features is not the only way in which bees might use linear features in navigation. Bees might also fly parallel to linear features, or their internal representation of space may be influenced by the grid of features around them even when out of sight of linear features. We therefore calculated the bearings flown by bees in our experiments to determine whether they showed any biases matching the orientations of linear features.

Flight bearings were calculated as degrees anti-clockwise from East between every two consecutive points of non-stationary track. For each track, these angles were sorted into 10° bins, and the proportion of data points falling into each bin was calculated. This allowed tracks to be assessed together (with every track equally weighted) to explore group level effects. These data were plotted in circular bar charts, and the raw data were tested for uniformity for first and apparent exploration flights (Experiment 1) to assess initial biases in flight path; and for searching flights to removed feeders (Experiment 4), to assess biases during targeted searching. We tested whether the flight bearings in each experiment were uniformly distributed using Kuiper's test of uniformity, which is

sensitive to multimodal distributions (Birch, 2018; Landler et al., 2018), since flights parallel to linear features would be predicted to have four modes at 90° intervals. Kuiper's tests were performed using R (RStudio Team, 2016).

RESULTS

Experiment 1

Do bees use ground-level features during exploration flights? To examine if the structure of exploration flights was affected by linear features, we tracked bumblebees during their very first flights ($N = 14$ bees, $N = 17$ flight tracks; 3 of the flight tracks are portions of the 14 flights in which the precise bee identity is uncertain) and apparent exploration flights ($N = 18$, from 13 bees; see Appendix, Table A1). Exploration flights showed a visible bias for linear features, where bees frequently flew along and parallel to surrounding roads, field borders and pathways (see Fig 2a-d). Bees showed significantly higher proportions of their flight in proximity to linear features than expected by chance during first flights (paired-samples t-test, $t_{13} = 3.438$, $P = 0.004$; Fig 2e) and apparent exploration flights (paired-samples t-test, $t_{12} = 3.648$, $P = 0.003$; Fig 2e). The distribution of flight bearings was significantly non-uniform (Kuiper's test of uniformity, $V = 3.1921$, $N=35$, $P < 0.01$), showing more flight in the directions of linear features aligned with the one associated with the hive than in any other direction (Fig 2f). This corresponded not only to bees flying along the footpath associated with the hive, but also to bees flying parallel to that linear feature and along other identically-oriented linear features nearby (Fig 2). One bee showed extensive flight along a field border parallel to the footpath along which the hive was located, suggesting an aliasing error (where the bee mistook one linear feature for another, similar one; Fig 2a). These flights are distinctly different to previously published examples of bumblebee exploration flights, which showed quasi-circular loops in all directions (see Osborne et al. 2013; Woodgate et al. 2016).

A bias toward following linear features during exploration flights can predict where individual foragers discover food sources and so may lead to colony-level biases in exploitation of resources.

Some support for this is provided by a further experiment in which a feeder located along a linear feature received far more visits than an identical one in the middle of a field (Appendix, Experiment A1).

Experiment 2

Do bees use linear features during repeated back and forth flights to forage locations? In the first treatment, feeders F1 and F2 were presented together (Fig 3). Here, twelve bees out of 15 were observed flying to both feeders, for a total of 17 flights out of 28 to both feeders rather than only to F1 (5 flights from 5 bees) or only to F2 (6 flights from 5 bees). In the second treatment, feeder F1 remained in the same place, while F2 was removed and replaced by F3, 168 m from F1 along the same road as F2 had been. Only one bee visited both feeders in a single flight, compared to 28 flights of 3 bees to F3 only. No bee was recorded flying to F1 only during this time.

In both treatments, bees flying to feeders consistently spent a high proportion of flight within 5 m of linear features (flights to F1: Mean \pm SD = 0.88 ± 0.18 , $N=10$ bees; flights to F1 and F2: Mean \pm SD = 0.80 ± 0.11 , $N=8$ bees; flights to F2: Mean \pm SD = 0.71 ± 0.09 , $N=5$ bees; flights to F3: Mean \pm SD = 0.59 ± 0.11 , $N=3$ bees). When bees flew to feeders other than F1, where the shortest potential route would not follow linear features, they still frequently flew over linear features more than necessary (Fig 3a-d), particularly during their final approach to the feeder or hive. Some bees did not visit feeders and instead flew beyond the range of the radar, presumably to natural forage. The return portions of these flights almost always followed the hive's footpath on the final approach to the hive (see Appendix, Experiment A2). Nonetheless, even bees flying back and forth to feeders F2 and F3 never followed linear features for the entire route, instead cutting across the corner of the field, demonstrating that they were not entirely dependent on linear features. The use of linear features in the last approach then likely indicates a strategy to locate the exact hive position.

In a further experiment, where neither hive nor feeders were located on linear features, we still observed extensive flight along footpaths, field borders and roads, and more flight in close proximity

to linear features than expected by chance (Appendix, Experiment A3). Linear features were therefore not salient in these experiments only because the hive and feeders were located on them.

Experiment 3

Does bees' reliance on linear features change with experience? One bee was recorded on 21 foraging trips over 4 days to feeder F3. The most direct route from the hive to this feeder would involve no flight along linear features while an alternative route continuously following linear features would be 41% longer. As the bee gained experience, we observed a switch in flight strategy (Fig 4). In the first 10 foraging trips, 60% of outbound and inbound flights went directly over linear features for at least the last 30 m approaching the goal (the feeder for outbound flights; the hive for inbound flights; Figs 4a-h). By contrast, in the last 11 foraging trips of the bumblebee, only 14% of outbound and inbound flights went directly over linear features during the final approach to the goal (Fig. 4i-p). This suggests that linear features initially played an important role in helping the bee precisely locate the goal, but that with experience the bee was able to form a more efficient route and approach the goal without such a guide.

Experiment 4

Do bees use linear features to search for a removed feeder? We investigated whether bees would use information from linear features to search efficiently by identifying repeat visitors to individual feeders and tracking their flight after removing all feeders from the field. Feeders and the hive were all placed along linear features for this experiment. Search flights ($N=7$ flights from 6 bees) showed consistently very high proportions of flight within 5m of linear features (Mean \pm SD = 0.70 ± 0.17 ; Fig 5). These numbers are comparable to those from flights to feeders, despite the lack of looping behaviour in those cases, suggesting that searching bees largely restricted their search to linear features.

During their search, bees not only flew repeatedly over the stretch of road along which the feeder was usually found, but also along other linear features (Fig 5). Initially, bees returned to familiar locations such as the crossroads or even the hive itself before repeating their route to the feeder location. Later in their search, bees often scanned other parallel and perpendicular linear features (Fig 5a-d). This suggests that bees either widened their search space for the lost feeder or switched strategy and searched for novel feeders, while relying on their learnt association between the feeder and road to guide them.

Flight bearings of bees during searching flights were significantly non-uniformly distributed (Kuiper's test of uniformity, $V=4.9107$, $N=7$, $P < 0.01$), with more flight in directions associated with prevalent ground-level features (Fig 5e). These flights offer a striking contrast to the variety of azimuthal directions adopted by bees searching in landscapes less dominated by regular linear features (Reynolds et al., 2007).

In contrast, when searching for unpredictably located feeders within a field, where the hive and feeders were located away from linear features, bees largely restricted their flight within the field, often approaching field borders without crossing them (Appendix, Experiment A3). The structure of searching flights thus appears to be flexible, with bees using linear features strategically, based on individual experience.

DISCUSSION

Our experimental manipulation of hive and feeder location in a landscape with a featureless, flat horizon and a regular grid of ground-level linear features demonstrates that bees made extensive use of these features during their exploration flights, foraging flights and searching flights. Their utilisation of ground information was strikingly strategic, directly linked to each individual's goals and experience.

Exploration flights performed by bees in our field site were vastly different to those observed in environments with a variety of skyline and ground level cues (Osborne et al., 2013; Woodgate et al., 2016). Flights previously recorded in landscapes less dominated by linear features show distinct looping patterns in all directions (see Osborne et al., 2013, Fig 2A; Woodgate et al., 2016, Fig 2). Our flight tracks show, instead, high proportions of flight along and parallel to linear features (Fig 2), demonstrating that the shape of exploration flights is determined by the structure of the surrounding landscape. This could have important implications for bee spatial distribution, through potentially biasing the discoveries of suitable nest locations by new queens (Makinson et al., 2019). Moreover, since bumblebees use exploration flights to discover forage (Osborne et al., 2013; Woodgate et al., 2016), we predict that linear structures will bias floral resource discovery and pollination at a colony level. Support for this comes from our observations of bee visitation rates to feeders, where a huge majority of total visitations were to the feeder along a footpath rather than to the identical feeder in the centre of a field (Appendix, Experiment A1). This was all the more striking since bumblebees do not communicate forage locations with each other (Dornhaus and Chittka, 1999), so that this was the result of individual-level exploration and foraging decisions. Furthermore, after simulating a foraging source no longer being available (for example, flowers running dry or a tree being cut down) by removing the feeders (Experiment 4), bees used their previous experience of linear features to limit their search, making it likely that the first discoveries made may shape the next floral resources discovered and pollinated long-term.

Bees flying to experimental feeders often flew distinct, detouring routes along linear features (Experiment 2). This was reminiscent of previous observations by Chittka *et al.* (1995), where bees detoured via a salient landmark to reach a feeder. One bee, observed over many flights gradually refined her route from cutting across the corner of a field but still following linear features, to eventually bypassing linear features altogether (Experiment 3). Likewise, the formation of efficient routes between multiple food sources (termed trap-lines) are refined over time and experience (Woodgate et al., 2017). This suggests that while inexperienced, the bee relied on linear features for

accuracy, switching to using vector memories and/or more detailed visual memory once she was sufficiently experienced (Collett et al., 2013; Menzel et al., 1998). If bees rely more on linear features when they have less certainty about their position, this could explain previous observations in which displaced honeybees (Collett and Graham, 2015; Menzel et al., 2019; Wolf et al., 2014) and pigeons (Lipp et al., 2004) showed extensive detouring along linear features.

Why do bees preferentially follow pathways, field edges and roads? Experiments with humans and rats have suggested that beacon cues (that indicate a nearby target location) are preferentially used over more complex visual cues (for example, cues which inform on the next direction in a route, but do not directly indicate the goal) (Chan et al., 2012; Waller and Lippa, 2007). Following a linear feature to a desired goal may be similar to using a beacon cue, by providing an easier alternative to navigating directly to an otherwise isolated point, an example of ‘cognitive offloading’ (Risko and Gilbert, 2016). The last part of a bee’s return to the hive often relies on beacons and other landmarks (Turner, 1908), because path integration lacks small-scale accuracy (Collett and Collett, 2000; Menzel et al., 1998). In our experiments, bees may have implemented a strategy in which they switched to following linear features before they expected to reach their hive. This could allow them to compensate for errors and imprecisions in their path integration and avoid missing their goal.

Path integration is only possible with a combination of distance estimation and heading information (Collett and Collett, 2002). The latter is derived from compass cues within the environment, either from celestial information (eg. the sun) or from the geomagnetic field (Wajnberg et al., 2010; Wehner, 1984). Could linear features have had an effect on the use of compass cues and path integration? Bee distance estimation, derived from visual feedback, becomes more precise when paired with location-specific landmarks (Srinivasan, 2014). Linear features however often extend over long distances and might instead be more indicative of direction. When bees are unable to use their sun compass, they rely on the visual landscape to infer direction information (Dyer and Gould, 1981). When, experimentally, learnt celestial cues are put into conflict with the visual landscape,

bees appear to rely first on their visual memory, and not compass cues, to locate food sources (von Frisch and Lindauer 1954; von Frisch, 1967), similarly to what we suggest above. If our field site had not presented bees with a regular arrangement of linear features but instead given bees an irregular set of paths and roads, would this have caused bees to fly less efficient routes? Alternatively, if through experimental manipulation linear features could be added or removed, how would that affect bee orientation?

Bees rely primarily on celestial cues for compass information (Collett, 2008). However, Fleischmann et al. (2018) showed that *Cataglyphis nova* ants appear to use geomagnetic cues to control the 'pirouettes' during which they are thought to learn views of the nest, during their first learning walks around the nest. This raises the question of whether our use of a small magnet at the base of the radar transponder may have hindered the use of magnetic cues by our bees. Previous experiments on honeybees have suggested that they may be able to detect geomagnetic fields but that they rely on them only when no other cues are available, if at all (REFS & CHECK LIT TO CONFIRM IF THIS IS ACCURATE). It is unknown if bees also make use of magnetic cues when they first exit their nest. If so, our use of magnets may have made them more reliant on visual cues, affecting the structure of their first flights. Bumblebees combine learning about the immediate surroundings of the hive with more extensive explorations, during which they search for food sources (REFS: OSBORNE PAPER, WOODGATE 2016). It is these longer-range explorations that show the greatest influence of linear features in our study, but there is no evidence from any species for any effect of magnetic cues on such exploration flight. Our bees showed no evidence of any difficulty in returning to the hive after their exploration flights.

Insects are thought to use visual-familiarity-based mechanisms to navigate, where the heading is determined by a measure of similarity between the current view and a relevant subset of memories (Baddeley et al., 2012; Collett et al., 2013; Zeil, 2012). In this linear-feature-rich landscape, we might predict that footpaths and roads might all present very similar visual cues. When returning or

searching for a location on a linear feature, using familiarity to guide the bee's route might always direct the bee towards the closest linear features, causing the behaviours we observed. If this is the case, we would consequently also predict frequent aliasing errors, where one linear feature is mistaken for another. This was not the case: one single aliasing error was observed, from a bee on her first flight (Fig 2a), and experienced bees readily flew away from linear features, even reducing their flight along linear features with experience (Experiment 3, Fig 4). Instead, bees changed how they used linear features depending on their goal: following them to reach a feeder placed along a footpath (Experiment 2); relying on them more when inexperienced (Experiment 3); flying along them when searching for a feeder previously placed along a road (Experiment 4); using linear features as visual boundaries within which to focus their flight when searching for feeders within a field (Appendix, Experiment A3). This flexible, goal-dependent use of linear features strongly suggests that bees strategically use the information available to them for efficient navigation.

Bees and other insects are known to monitor their movements using visual feedback from their own motion, termed 'optic flow' (Srinivasan, 2011). For example, bees control their position within flight tunnels by maintaining the speed of optic flow from their left and their right (either matching left and right inputs to position themselves in the centre, Srinivasan et al., 1991; or keeping the optic flow input constant and following one surface, Serres et al., 2008). If linear features were less visually rich, and thus provided less optic flow, than the surrounding fields, bees might move closer to linear features in order to increase the visual input from that direction. However, when using ventral optic flow to control position (as they must in such flat terrain), bees have been shown to prefer to fly over surfaces with rich feedback (Linander et al., 2017). Furthermore, adjustments would only happen if there was extremely little visual feedback from linear features, since differences in frequency and visual contrast have no effect on bee position (Srinivasan et al., 1991). In our field site, the dirt paths and roads were visually rich, presenting an uneven surface full of visually contrasting elements (such as cracks and shadows; see Fig 1a). Moreover, this optic-flow driven positioning behaviour is characterised as a direct response to visual input (Lecoeur et al.,

2019; Srinivasan et al., 1991). If flying closer to linear features was caused by this mechanism, bee flight trajectories should drift until they reached a visually balanced position. We observe instead sudden detours (Appendix, Fig A2), loops into open fields (Fig 2), and a gradual reduction in flight along linear features with experience (Experiment 3). We thus believe flight along linear features is not caused by a response to optic flow but instead reflects an adaptive use of available landmarks. Ground-level linear features are of under-appreciated importance to animal navigation, especially flying insects. Understanding their utilisation by bees will have practical consequences of considerable importance for agriculture and conservation, in the context of the pollination crisis. Insect pollinators are responsible for 35% of global food production (Klein et al., 2007; Potts et al., 2016) and bee hives are routinely transported for pollination services in intensive agricultural terrains characterised by regular man-made linear features that could be used to direct pollination outcomes (Alger et al., 2018). We predict for example that placing a hive along a linear feature will predispose the bees to travelling along this particular linear feature whereas placing a hive in the centre of a field might instead predispose bees to concentrate their pollination efforts within the field's borders. Linear features could also be used for conservation purposes to influence the movements of bees in semi-urban and urban environments, and facilitate the localisation of suitable habitats or foraging areas by wild species.

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APPENDIX

FIELD SITE PANORAMA

The rice farm Finca Casudis was set in extremely level land, with an almost completely flat horizon and almost no above ground level landmarks. The highest point on the skyline was an installation with grain silos and grain elevator at the farm (dark shape to the right of the panoramic image, Fig 1a). We assessed whether this could provide a landmark for bees using a panoramic image from the location of Hive Location 1 (since Hive Location 1 was closer to the farm than Hive Location 2, see Methods, Fig 1b). A 360° panoramic photograph was taken using a Samsung Galaxy A3 mobile phone (Fig 1a). From this panorama, assuming pixels were square (so that the height of the image was scaled identically to the width), we calculated that the top of the grain silos was 1.86° above the adjacent ground level. The maximum resolution of bumblebees has been placed anywhere between 2.3° (Dyer et al., 2008) and 4.8° (Chakravarthi et al., 2016). Thus, it is unlikely that bumblebees could detect the grain silos or any other man-made structure from anywhere close to the hive. It is harder to determine whether there was enough variation around the skyline to provide useful cues, because there is some distortion in the panoramic image: the skyline was visibly flatter than it appears on the image. The maximum difference in horizon level on the panoramic image was 3.30°, but we believe this is an overestimation. We used heywhats-that.com (Kosowsky, 2021) to calculate the projected skyline as seen from 6ft above ground level at the hive's GPS position (Hive Location 1), and estimated the maximum variation to be 1.03°, suggesting that there was little or no variation detectable by bumblebees.

DETAILS OF DATA COLLECTED

ADDITIONAL EXPERIMENTS

Experiment A1

Do linear features affect feeder visitations? Between the 7 and 8 May 2018, we compared the visitation rates between two identical feeders by bees from two bumblebee colonies without prior

experience of the field site. Feeder F1 was located 168 m from the hive along a path, while feeder F4 was located 168 m from the hive in the middle of the adjacent field (100 m from the closest path; Fig 1b). Bees were allowed to come and go freely from the hive from 1735 to 2135 on the 7 May and from 1100 to 1740 on the 8 May 2018. Visitations at each feeder were filmed (Sony Handicam HDR-CX240, Sony Corporation, Tokyo, Japan) between those times, for a total of 10 hours and 45 min. The footage was analysed to record the timing of every visit by a bee.

Bees visited F1 far more often than F4 (F1: 341 visits over 10 hours 45 min; F4: 8 visits over the same period; F1 received 97.7% of all visits, Fig A1). The visitation frequency to F1 was on average 3.22 visits over a 5 min period, with a highest frequency of 10 visits in any consecutive 5 min period, while F4 received on average 0.06 visits per 5 min and never more than 1 visit in any consecutive 10 min period. The first visit to F1 occurred only 10 min after bees were allowed access to the field site, while the first visit to F4 was 35 minutes after that (45 minutes since the hives were opened).

Experiment A2

Do bees use linear features when flying to distant natural forage sources? During experiment 2, not all bees used our experimental feeders. Some were tracked flying to distant locations, out of range of the radar ($N = 39$ tracks, 29 bees; 4 were from unknown individuals and were excluded from statistical analysis). These locations were presumed to be natural forage, since these individuals frequently returned with pollen and tended to fly towards the river (along which were natural foraging sources).

Bees flying to distant locations spent significantly more flight in close proximity to linear features than expected by chance (Kolmogorov-Smirnov test of normality, $P = 0.009$ for initial scores, $P = 0.024$ for control scores; Wilcoxon related-samples signed-rank test, $P < 0.001$). Within these flights, those that included clear inbound and outbound portions of flight showed lower initial scores in their outbound journeys compared to the corresponding inbound journeys (paired sample t-test, $t_{19} = -2.391$, $P = 0.027$). During the final approach (last 30 m) to a feeder or their hive, bees very often

flew along the closest linear feature to reach their goal, suggesting that linear features play an important role in finding the precise location of a goal (Fig A2). We tracked a total of 39 flights to distant locations, from 29 bees, of which 22 flights were complete enough to examine the inbound portions of flight. Bees clearly followed the footpath adjacent to the hive during their final approach in 21 of these 22 flights ($N=20$ bees; Fig A2).

Experiment A3

Do bees use linear features when their hive is located in the centre of a field? We investigated whether linear features influenced feeder discovery when feeders were not associated with linear features. For this experiment, the hives were located in the centre of a field (Hive Location 2, Methods), 100 m from the closest linear features.

Bees were trained and tracked individually searching for an array of three feeders from a hive position in the centre of a field (Hive Location 2, Materials and Methods).

Pretraining: All bees were given free access to the field site and trained to feed from three feeders near the hive entrance, providing *ad libitum* 40% sucrose solution. Once bees were accustomed to this, the feeders were each placed 5 m from the hive in a triangle formation. Individual bees were then trained one by one on all three feeders, each containing 10 μ L 40% sucrose solution, refilled regularly using an electronic pipette (HandyStep, BrandTech Scientific Inc., Essex, CT, US). The average crop content (from 3 measures) was determined for each individual bee.

Experiment: The three feeders were then arranged in random arrays, where the feeder locations were determined by an algorithm, with the limitation that no two feeders could be closer than 5 m from each other, all feeders were located within the surrounding field and no new array positions used could be within 5 m of any previously used array. Individuals were then tracked searching for the three feeders, each containing one third of the focal bee's crop capacity of 40% sucrose solution. Every bee ($N=13$) was tracked during several foraging trips searching for such arrays. Some flights

723 were excluded from analysis due to missing data within the tracks, so that a total of 20 tracks from
724 13 bees were analysed.

725 *Results:* Even when searching for feeders placed randomly within a field from a hive located in the
726 centre of that same field, bees showed a higher proportion of flight within 5 m of linear features
727 than expected by chance (Kolmogorov-Smirnov test of normality, $P < 0.05$ for initial scores, $P = 0.061$
728 for control score; Wilcoxon matched-pair signed-rank test, $N=13$, $P = 0.006$; Fig A3a). The bees' flight
729 bearings were not uniformly distributed (Kuiper's test of uniformity, $V = 3.5925$, $N=20$, $P < 0.01$),
730 showing a bias in directions corresponding to ENE-WSW linear features (Fig A3b).

731 Out of 20 tracks, the bee left the field in half of them. Of these 10, 5 only made a single flight loop
732 outside the field borders while 3 showed extensive exploration beyond the field. Of the 10 tracks in
733 which the bee remained within the field, the bee flew up to but not beyond the field borders in 7,
734 suggesting that bees may have learned to use linear features to bound their search space and turned
735 back when they encountered one (Fig A3c-d). The last three tracks remained in close proximity to
736 the hive. Four of the 20 tracks (the 3 with extensive flight outside the field and 1 without flight
737 extending beyond the field borders) were long flights showing sustained periods following linear
738 features, suggesting that a learned association between the hive and a linear feature is not the sole
739 cause of line following behaviour.

Experiment	Hive location	Number of colonies used	Number of flight tracks	Details (<i>Dates carried out, number of individuals tracked in that time, presence or absence of feeders</i>)
Experiment 1: Exploration flights	1	2 (C3, C6)	35	<i>First flights:</i> 24 April 2018 ($N = 11$), no feeders 4 May 2018 ($N = 3$), feeders F1, F3, F4 <i>Apparent exploration flights:</i> 30 April 2018 ($N = 2$), feeders F1, F3 4 May 2018 ($N = 1$), feeders F1, F3, F4 7–8 May 2018 ($N = 10$), feeders F1, F4
Experiment 2: Foraging flights	1	6 (C1-C6)	79	20–23 April 2018 ($N = 12$), feeders F1, F2 26–30 April 2018 ($N = 3$), feeders F1, F3 5–8 May 2018 ($N = 6$), feeders F1, F4
Experiment 3: Route formation	1	1 (C3)	21	26, 27 and 30 April 2018 ($N = 1$), feeder F3
Experiment 4: Searching flights	1	4 (C3-C6)	7	27–30 April 2018 ($N = 3$), feeder F3 5–8 May 2018 ($N = 3$), feeder F1
Experiment A1: Visitation rates to feeders	1	2 (C5, C6)	N/A	5–8 May 2018, 349 visits recorded from video footage at feeders F1 and F4
Experiment A2: Foraging flights to natural forage	1	6 (C1-C6)	39	20–23 April 2018 ($N = 2$) 26–30 April 2018 ($N = 17$) 2 May 2018 ($N = 10$) 5–8 May 2018 ($N = 4$)
Experiment A3: Searching flights from hive in the centre of a field	2	2 (C7, C8)	20	9–17 May 2018 ($N = 13$), three feeders present within the field in random positions

Table A1: Details of experimental data. Hive locations ‘Hive Location 1’ was along a linear feature and ‘Hive Location 2’ was in the centre of a field, see Methods Fig 1b. Individual colonies used were labelled C1 to C8. The number of flights tracked indicate tracks used solely for that experiment, and for none other, except in the case of Experiment 3, where that data was also included in Experiment 2. N = Individual bees tracked during each time period for each experiment. Some individuals were tracked during several periods. All data from flights tracked were averaged per individual within relevant categories irrespective of date tracked before statistical analysis. Where relevant, the number and position of feeders is indicated for each time period.

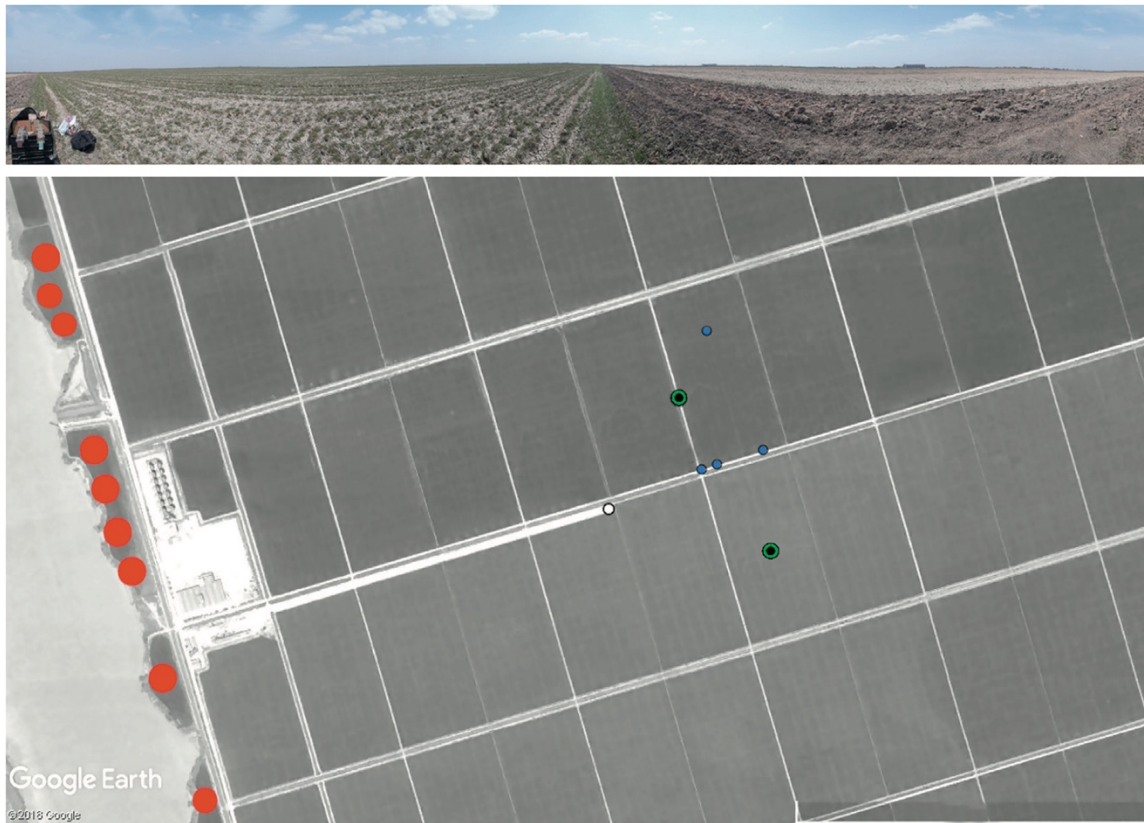


Figure 1: Panorama and satellite view of the field site. (a): 360° panorama of the field site from the hive position. The hive, with a black tarp covering, is visible on the left of the image. To the right are the grain silos at the farm, barely visible as a small dark grey building above the horizon. The landscape lacks skyline cues (see Appendix). **(b):** Satellite image with relevant locations. Bumblebees were tracked from two hive locations (Hive Location 1 and Hive Location 2, represented by green circles). Hives were located at Hive Location 1 for Experiments 1-4 and at Hive Location 2 for Experiment A3. Bees in our experiments foraged at experimental feeders (F1, F2, F3 and F4, represented by light blue dots). F1 and F4 were both 168 m from the hive, with F1 along the footpath directly connected to the hive and F4 NE from the hive in the centre of a field. F2 and F3 were along a dirt road perpendicular to the footpath where the hive was placed and directly connected to F1, 172 m and 238 m from the hive respectively. F1 and F2 were 35 m apart, while feeders F1 and F3 were 168 m apart. Different feeder treatments were used for experiments as follows: F1 and F2 from the 20 to the 23 April, F1 and F3 from the 26 to the 30 April, F1, F3 and F4 on the 4 May, and F1 and F4 from the 5 to the 8 May. Flight paths were tracked using harmonic radar (represented by a white dot), located at the end of a packed earth runway which ran East from the farm. The farm Finca Casudis is located to the West, next to the banks of the river Guadalquivir, where some natural forage sources (represented by red ellipses) could be found. The satellite image used is from Google Earth, ©2018 Google. Note that all rice paddies were dry (no vegetation, brown) at the time of the experiments.

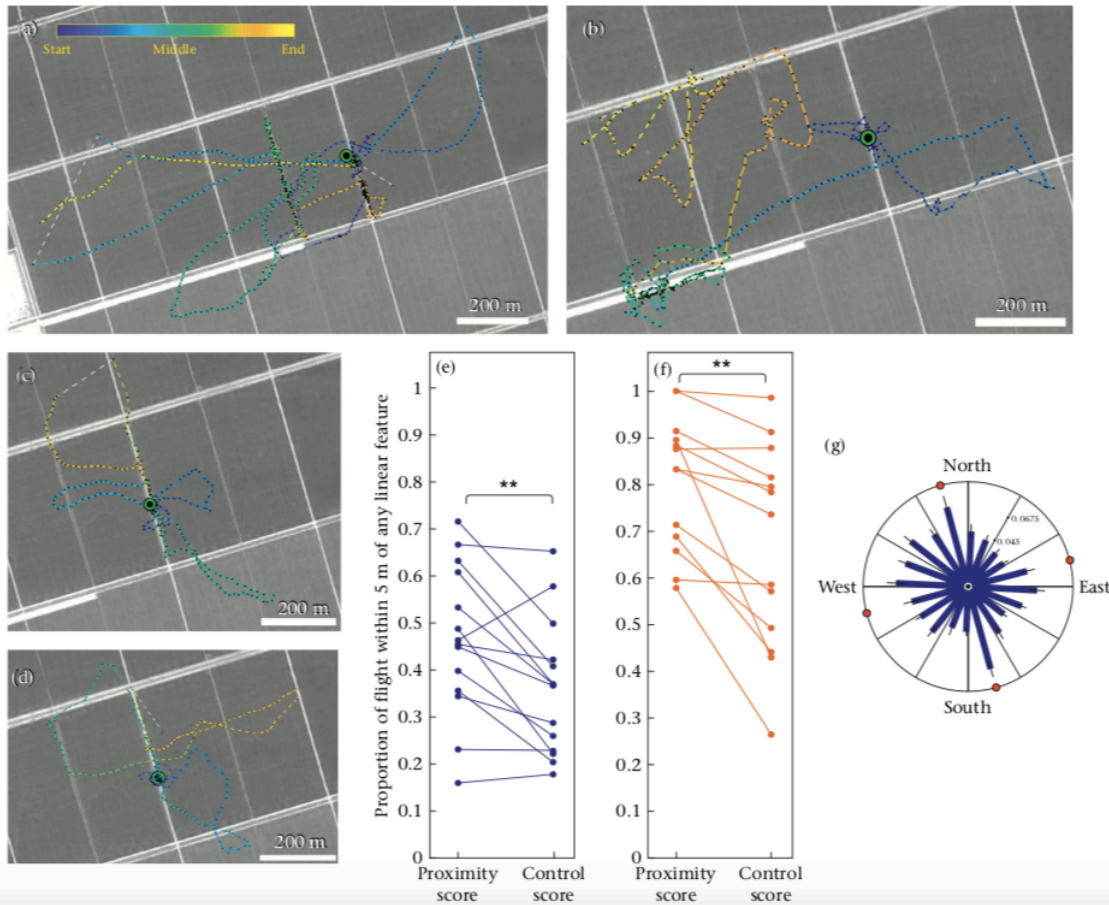


Figure 2: Bees biased their first exploration flights towards linear features. (a-d): Example first flights of individual bees. Tracks begin dark blue, turn green then yellow by the end of the recorded track. Grey dashed lines indicate a period where the bee's position was unknown. The hive is represented by a green circle. Initial portions of flight were close to the hive and frequently followed the associated footpath. Subsequent loops took the bee further afield, often in directions along or parallel to linear features, showing distinctive right angle turns that matched the surrounding grid (b, d). (a): Example of aliasing error. The bee started with flight along the footpath associated with the hive, performed several loops outward which also scanned along other linear features, and flew away to a distant location. On its return flight, this bee spent a long time flying back and forth along a field border parallel to the footpath associated with the hive, before it successfully re-joined the correct linear feature, found the hive, and returned to distant forage. The satellite image used is from Google Earth, ©2018 Google. (e): Proximity of bee to linear features (initial score) compared to the track-specific control proximity (control score) for first flights (left, in blue; $N = 14$) and apparent exploration flights (right, in orange; $N = 13$). Each set of two linked points represents a single individual's scores. Asterisks indicate p-values from paired-samples t-tests: $** P < 0.01$. (f): Circular bar chart representing the mean proportion of each first and apparent exploration flight spent flying in each direction ($N = 35$). Black lines represent standard error of the mean for each bar. Red dots on the perimeter show the orientations of linear features in the environment. Bees in first and apparent exploration flights showed a bias towards flying in directions matching the orientations of linear features, specifically those running WNW-ESE.

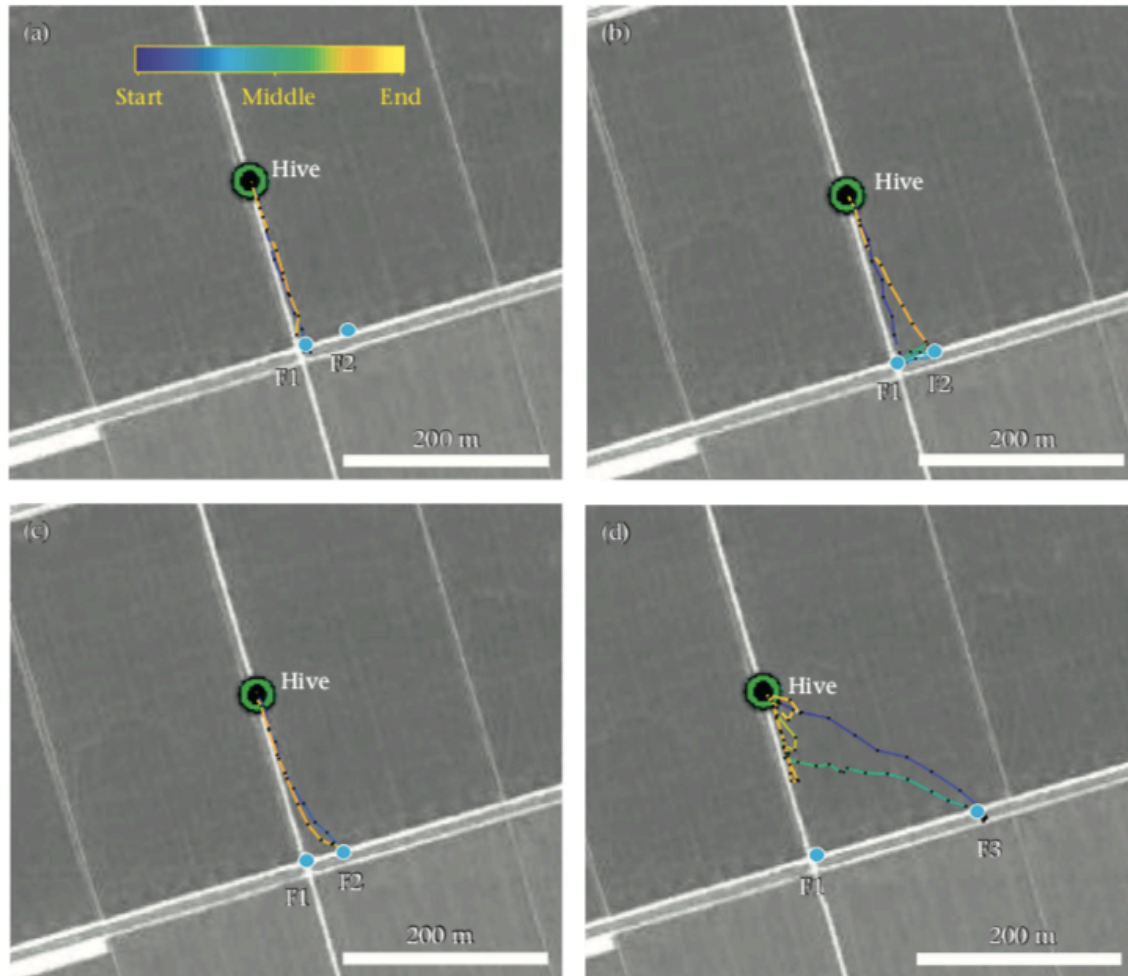


Figure 3: Bees followed linear features during foraging flights to feeders. (a-d): Example flights of bees to experimental feeders F1, F2 and/or F3. Tracks begin dark blue, turn green then yellow by the end of the recorded track. Grey dashed lines indicate a period where the bee's position was unknown. The hive is represented by a green circle, and feeders are represented by light blue dots. **(a):** Example flight to F1, showing a direct, straight route along the path. **(b):** Example flight to F1 and F2. The bee followed the footpath to F1, followed the dirt road at a right angle to reach F2, zigzagged between the feeders multiple times before cutting across the corner of the field from F2 to return to the hive. **(c):** Example flight to F2. The bee followed the footpath connected to the hive for about a third of the distance before crossing over the corner of the field to the feeder in a curved route. **(d):** Example flight to F3. The bee flew directly to the feeder from the hive. On the return flight the bee joined and followed the footpath connected to the hive until it reached its goal. The satellite image used is from Google Earth, ©2018 Google.

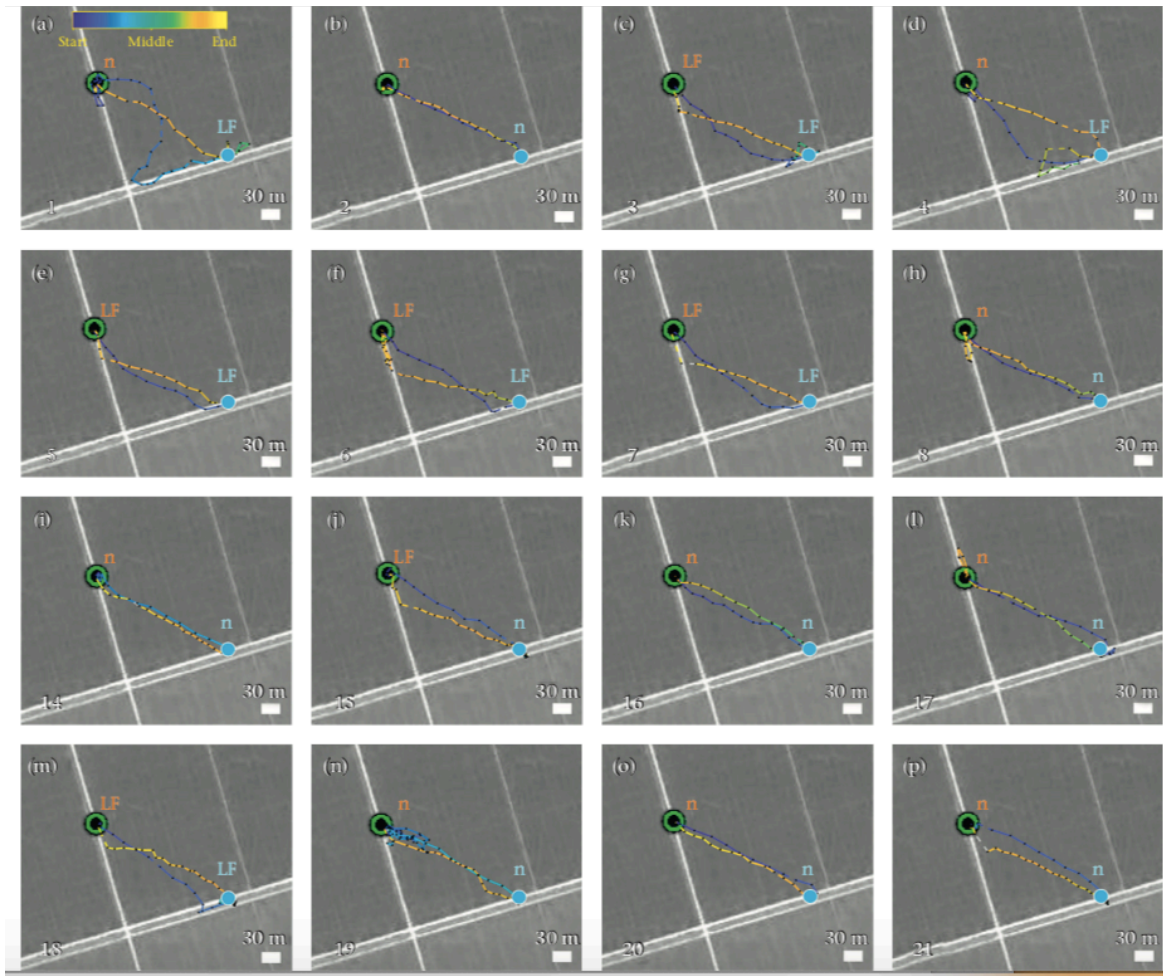


Figure 4: Development of direct route to feeders with experience. (a-p): Radar tracks of the first eight (a-h) and last eight (i-p) flights of a single bee foraging at F3. Flight bouts are indicated by white numbers at the bottom left of each track. Each flight is split into an outbound (blue to green) and inbound (green to yellow) portion of flight. Portions of flight are labelled 'LF' if the bee followed a linear feature for the last 30 m of flight approaching the goal (F3 or the hive); portions of flight without line following are marked 'n'. Outbound portions of flight are labelled in blue, next to the feeder. Inbound portions of flight are labelled in orange, next to the hive. The hive is represented by a green circle, and the feeder is represented by a light blue dot. **(a-h):** Six of eight outbound portions and four of eight inbound portions of flight show the bee following the appropriate linear feature on its final approach to the goal (LF). **(i-p):** Only one outbound and two inbound portions of flight show flight along linear features (LF). The satellite image used is from Google Earth, ©2018 Google.

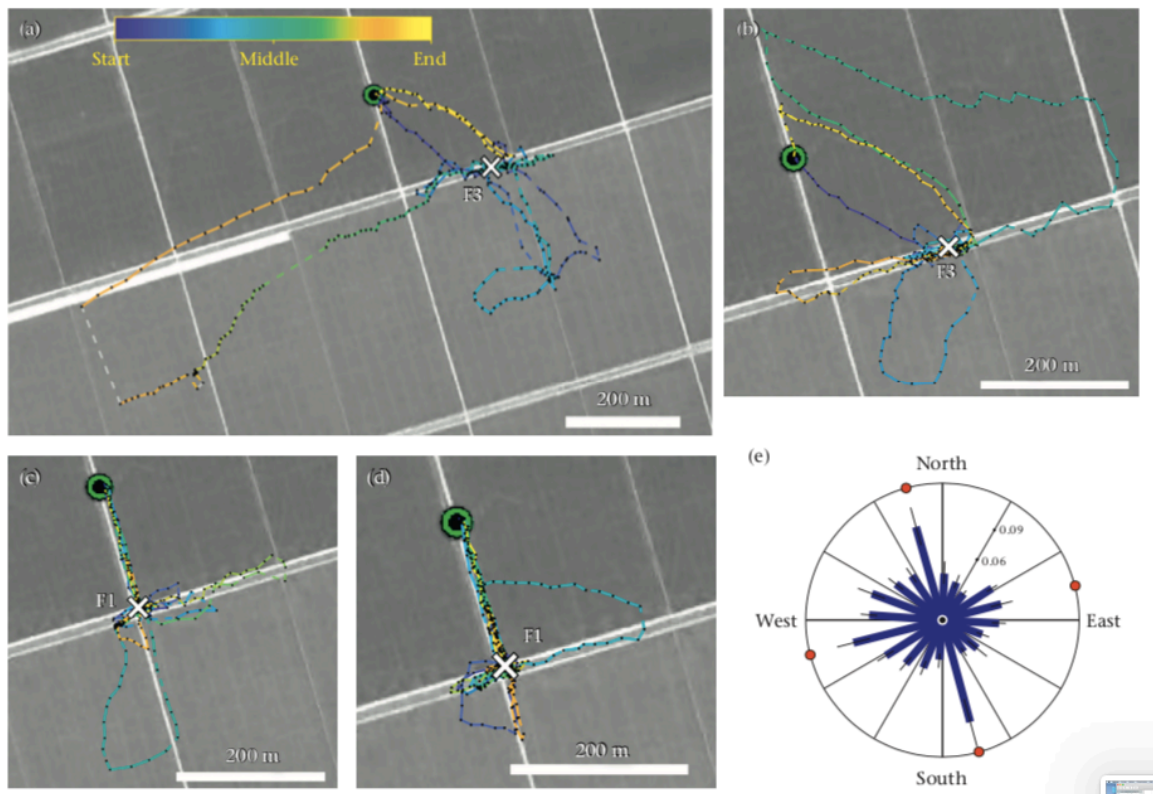


Figure 5: Bees searching for an experimentally removed feeder reduced their search space by concentrating on linear features. Every bee had prior experience foraging at the feeder (labelled F1 or F3) and was tracked searching after all feeders were removed from the field site. **(a-d):** Example flight paths of bees searching for the experimentally removed feeder. The location of this feeder before its removal is indicated by a white cross. Tracks begin dark blue, turn green then yellow by the end of the recorded track. Grey dashed lines indicate a period where the bee's position was unknown. The hive is represented by a green circle. Bees began by searching primarily along the linear feature connected to the feeder's location before expanding their search outwards. These larger loops frequently involved flight along other unrelated linear features **(a, b)**. The satellite image used is from Google Earth, ©2018 Google. **(e):** Circular bar chart representing the mean proportion of each searching flight ($N = 7$) spent flying in each direction. Black lines represent standard error of the mean for each bar. Red dots on the perimeter show the orientations of linear features in the environment.

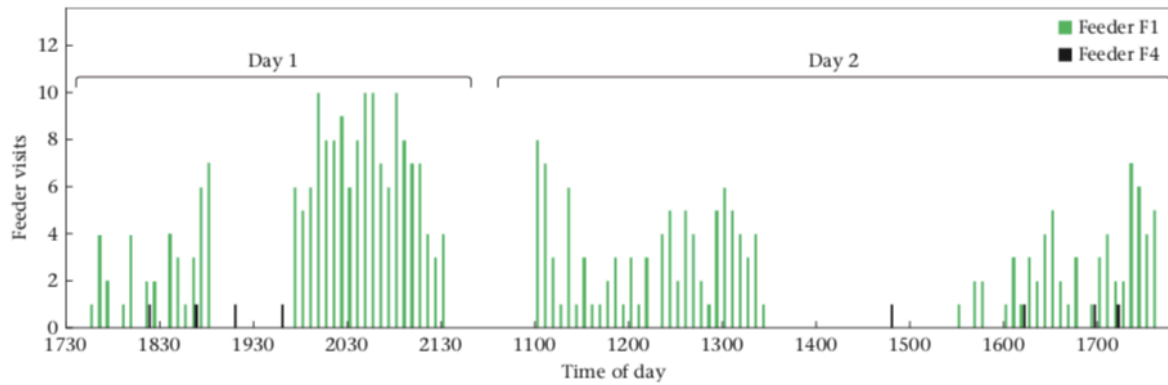
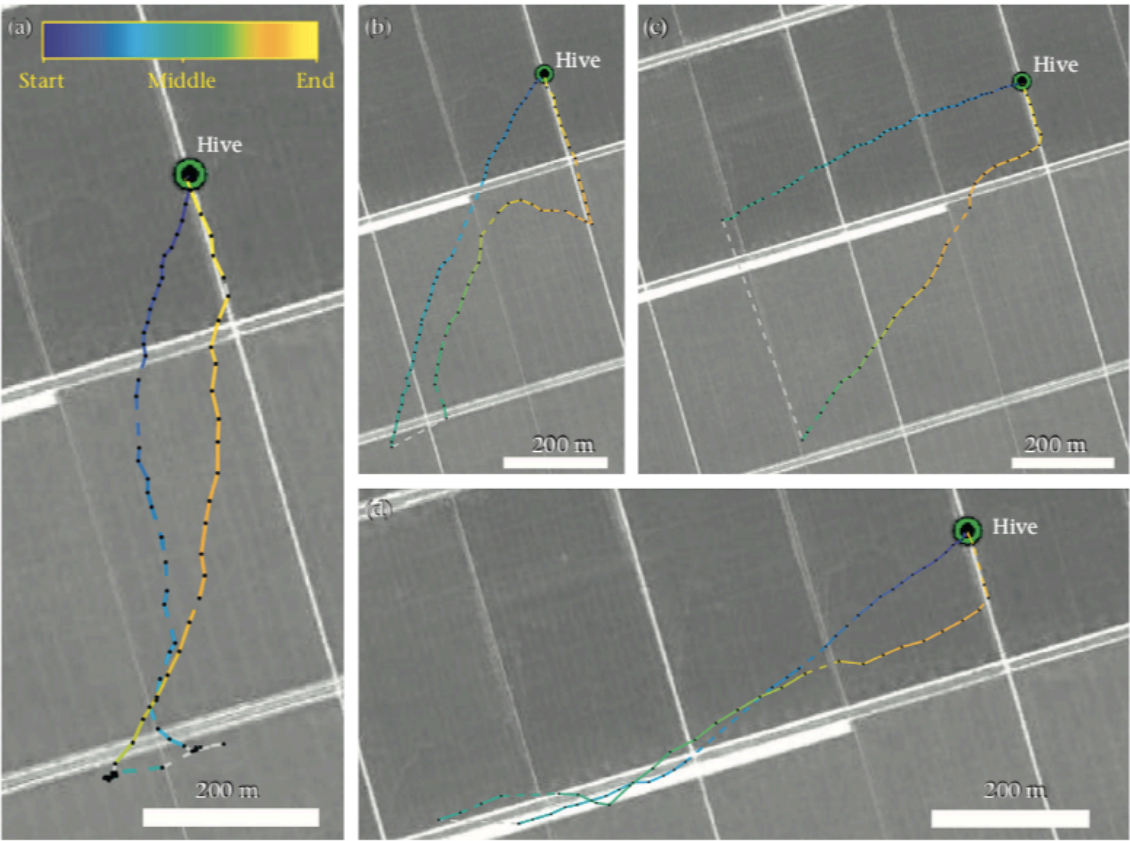


Figure A1: A feeder on a linear feature was far more visited than one not near a linear feature. Histogram showing the number of visits to two feeders in 5 m periods over two days. Feeder F1 (in green), was located along a linear feature adjacent to the hive location. Feeder F4 (in black) was placed 100 m away from the closest linear feature. Both feeders were otherwise identical and at an equal distance from the hive. Feeder visits were counted using video footage. Feeder F1 was visited a lot more frequently than F4.



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Figure A2: Bees followed linear features to reach their hive from distant foraging locations. A-D: Example flight paths of

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bees flying to and from distant foraging sources. Tracks begin dark blue, turn green then yellow by the end of the recorded

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track. Tracks cut off when bees fly beyond the range of the radar, and restart when bees re-enter the range Grey dashed

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lines indicate a period where the bee's position was unknown. The hive is represented by a green circle. Most outbound

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flights (in blue) cut across linear features and did not follow them for extended periods. Return flights differed markedly: in

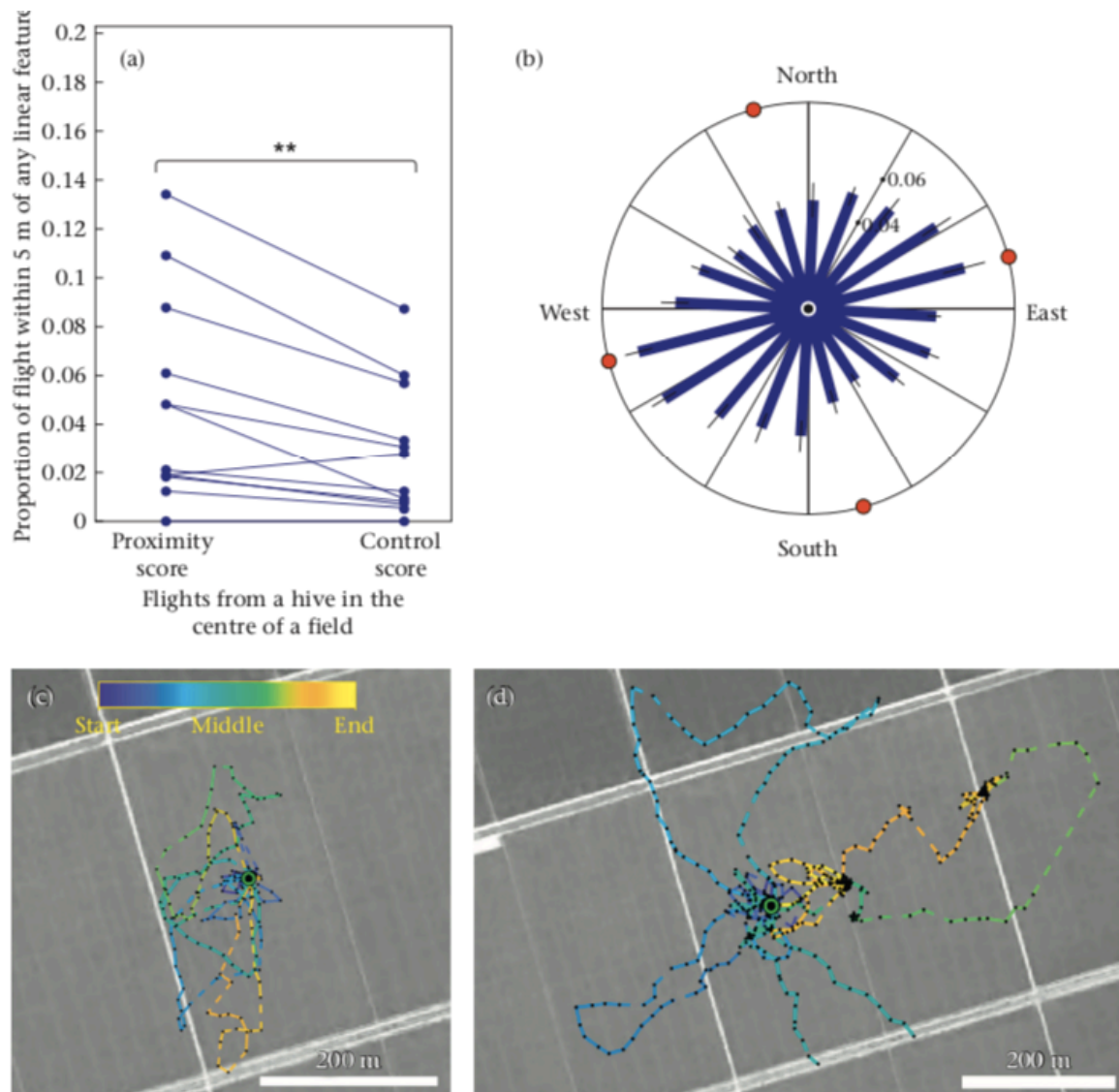
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almost all cases recorded, the bee joined the linear feature along which the hive was placed and followed it for some

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distance for the last stretch of flight. The satellite image used is from Google Earth, ©2018 Google.

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Figure A3: Bees searching for unpredictably located feeders within a field used linear features. Bees were trained to a protocol in which three feeders were moved at random within the field between foraging bouts. **(a):** Proximity of bee to linear features (initial score) compared to the track-specific control proximity (control score) of bees performing searching flights for unpredictable feeders. Each set of two linked points represents a single individual's scores. Asterisks indicate p-values from a Wilcoxon matched-pair signed-rank test: ** $P < 0.01$. **(b):** Circular bar chart representing the mean proportion of each searching flight spent flying in each direction. Black lines represent standard error of the mean for each bar. Red dots on the perimeter show the orientations of linear features in the environment. Bees showed a bias towards flying in ENE-WSW directions. **(c-d):** Example flight paths of bees searching for feeders in unpredictable locations. Tracks begin dark blue, turn green then yellow by the end of the recorded track. Grey dashed lines indicate a period where the bee's position was unknown. The hive is represented by a green circle. The satellite image used is from Google Earth,

845 ©2018 Google. **(c)**: Example flight in which the bee appeared to bound its search space using linear features, flying
846 between the hive and surrounding paths without crossing them. **(d)**: Example flight in which a bee that did cross linear
847 features to exit the field showed extensive flight along several paths.

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