Radar Tracking and Motion-Sensitive Cameras on Flowers Reveal the Development of Pollinator Multi-Destination Routes over Large Spatial Scales

Mathieu Lihoreau¹ab*, Nigel E. Raine¹b*, Andrew M. Reynolds², Ralph J. Stelzer¹, Ka S. Lim², Alan D. Smith², Juliet L. Osborne²ac, Lars Chittka¹*

¹ Biological and Experimental Psychology Group, School of Biological and Chemical Sciences, Queen Mary University of London, London, United Kingdom, ²Rothamsted Research, Harpenden, Hertfordshire, United Kingdom

Abstract

Central place foragers, such as pollinating bees, typically develop circuits (traplines) to visit multiple foraging sites in a manner that minimizes overall travel distance. Despite being taxonomically widespread, these routing behaviours remain poorly understood due to the difficulty of tracking the foraging history of animals in the wild. Here we examine how bumblebees (Bombus terrestris) develop and optimise traplines over large spatial scales by setting up an array of five artificial flowers arranged in a regular pentagon (50 m side length) and fitted with motion-sensitive video cameras to determine the sequence of visitation. Stable traplines that linked together all the flowers in an optimal sequence were typically established after a bee made 26 foraging bouts, during which time only about 20 of the 120 possible routes were tried. Radar tracking of selected flights revealed a dramatic decrease by 80% (ca. 1500 m) of the total travel distance between the first and the last foraging bout. When a flower was removed and replaced by a more distant one, bees engaged in localised search flights, a strategy that can facilitate the discovery of a new flower and its integration into a novel optimal trapline. Based on these observations, we developed and tested an iterative improvement heuristic to capture how bees could learn and refine their routes each time a shorter route is found. Our findings suggest that complex dynamic routing problems can be solved by small-brained animals using simple learning heuristics, without the need for a cognitive map.

Citation: Lihoreau M, Raine NE, Reynolds AM, Stelzer RJ, Lim KS, et al. (2012) Radar Tracking and Motion-Sensitive Cameras on Flowers Reveal the Development of Pollinator Multi-Destination Routes over Large Spatial Scales. PLoS Biol 10(9): e1001392. doi:10.1371/journal.pbio.1001392

Introduction

Animals moving in familiar environments often follow habitual routes to navigate between important locations, such as the nest and feeding sites. Most knowledge on route following behaviours has been deduced from the stereotyped paths insects [1–4] and birds [5] develop when travelling between home and a single other site. In contrast, very little is known about the routing decisions made by animals that must visit multiple sites before returning home. These routing challenges are common in central place foraging nectarivores and frugivores, which typically exploit familiar food resources that replenish over time. Many of these animals develop stable foraging circuits (traplines) between distant food patches [6–10] and must sometimes cover several kilometres to fill their crop [11].

Developing an efficient route to reduce the travelling costs between multiple foraging locations is an optimisation task analogous to the well-known travelling salesman problem (finding the shortest route to visit a set of locations once and return to the origin) [12]. The most direct approach to solve this mathematical problem is to compare all the possible routes, which often requires extensive computational power as the number of routes increases factorially with the number of locations to be visited (e.g., 5! = 120 possible routes in a problem with only 5 locations). For animals, this problem is of a different nature as they cannot plan a route in advance, using a geographic map, but must gradually acquire information about the locations and the paths linking them. Therefore many animals [13–16], including humans [17,18], navigating between multiple locations are thought to find efficient routes using heuristic strategies, such as linking nearest unvisited sites or planning a few steps ahead.

Recent laboratory studies have shown that bumblebees foraging in simple arrangements of artificial flowers in indoor flight cages develop near optimal traplines after extensive exploration, based on learning and spatial memories [15,19–21]. However, whether similar strategies are observed at larger spatial scales, when
Author Summary

Many food resources, such as flowers refilling with nectar or fruits ripening on a tree, replenish over time, so animals that depend on them need to develop strategies to reduce the energy they use during foraging. Here we placed five artificial flowers in a field and set out to examine how bumblebees optimize their foraging routes between distant locations. We tracked the flight paths of individual bees with harmonic radar and recorded all their visits to flowers with motion-sensitive video cameras. This dataset allowed us to study how bees gradually discover flowers, learn their exact position in the landscape, and then find the shortest route to collect nectar from each flower in turn. Using computer simulations, we show that the level of optimisation performance shown by bees can be replicated by a simple learning algorithm that could be implemented in a bee brain. We postulate that this mechanism allows bumblebees to optimise their foraging routes in more complex natural conditions, where the number and productivity of flowers vary.

Bees discovered flowers sequentially and had visited all five flowers at least once after an average of eight foraging bouts (here, and throughout the text, means are reported ± s.e.m.; 0.14 ± 2.43 bouts, n = 7 bees; Figure 2A). The two flowers closest to the nest (F1 and F3) were located first, by all individuals. The flower furthest from the nest (F3) was found last by four bees, whereas it was the penultimate flower discovered by the other three. Individual bees consistently approached flowers from the same quadrant of the landing platform (Video S1), irrespective of the flower visited and of their experience (Generalized Linear Mixed Model (GLMM), effect of quadrant on the frequency of visits, \( F_{4,1328} = 90.23, p < 0.001 \); effect of flower identity, \( F_{5,1328} = 1.82, p = 0.08 \); effect of the number of bouts completed, \( F_{3,1328} = 0.07, p = 0.791 \); all interactions, \( p > 0.05 \)). Frequency distributions of approaches in each quadrant were significantly different among bees (\( \chi^2_{15} = 996, p < 0.05 \); Figure 2B), indicating that each bee approached and landed on flowers from a different preferred angle. Furthermore, bees departed from the same quadrant as they arrived (and thus in opposite directions) in 71.41% ± 1.72% (n = 7 bees) of visits. The frequency of visits when arrivals and departures occurred in the same quadrant did not vary significantly in relation to flower location or to the foraging experience of bees (GLMM, effect of flower identity on the frequency of visits where arrival and departure occurred in the same quadrant, \( F_{4,1328} = 2.27, p = 0.065 \); effect of the number of bouts completed, \( F_{2,1328} = 0.46, p = 0.649 \); interaction, \( F_{4,1328} = 4.87, p = 0.022 \)). We also found no significant difference in the frequency of these visits among bees (\( \chi^2_{9} = 10.29, p = 0.113 \)). Therefore, our data suggest that each bee acquired a directional preference in arrivals to and departure from flowers before the observations began, possibly during the pre-training phase when the bees became familiar with the flower design, and used their directional preference consistently for visiting flowers in all novel locations discovered.

As they gained experience, bees increased the number of different flowers visited per foraging bout (first five bouts, 2.29 ± 0.35 flowers; last five bouts, 4.97 ± 0.06 flowers; n = 7 bees; GLMM, effect of the number of bouts completed on the number of flowers visited, \( F_{4,1328} = 149.62, p < 0.001 \) and reduced the frequency of revisits to empty flowers (first five bouts, 2.83 ± 0.58 revisits; last five bouts, 1.31 ± 0.55 revisits; n = 7 bees; GLMM, effect of the number of bouts completed on the frequency of revisits, \( F_{4,1328} = 6.50, p = 0.012 \)). In every bout, a bee’s probability to link the nest and a flower or to link two flowers together was determined by its experience. Thus, transition vectors between any two locations used in previous bouts were used more often in subsequent bouts than transition vectors never previously experienced (GLMM, effect of the cumulative frequency of all possible transition vectors in previous bouts on their frequency of usage at each bout, \( F_{5,1328} = 1.209.5, p < 0.001 \)). Among the paths already used, the probability of repeating a transition vector in two successive foraging bouts increased significantly with the optimality ratio (straight line length of the observed visitation sequence divided by straight line length of the shortest possible sequence to visit the same number of flowers) of the first bout (GLMM, effect of optimality ratio of the first bout on the frequency of transition vectors repeated in the second bout, \( F_{1,106} = 82.64, p < 0.001 \); Figure 2C). In other words, transition vectors that generated short routes were likely to be used again in subsequent bouts, while transition vectors producing long routes were gradually abandoned, thus limiting the number of novel transitions over time (Figure 2D).

With increasing experience, the sequence in which flowers were visited became more similar over successive foraging bouts (similarity index—see Materials and Methods—between the first

Results

Trapline Development between Five Flowers Arranged in a Regular Pentagon

Our first aim was to establish whether bees develop repeatable foraging circuits between stable feeding locations. We pre-trained naive bees to collect sucrose solution rewards from a patch of five artificial flowers (Figure S1) in the middle of the experimental field (Figure 1). After a day of pre-training, bees of known foraging experience were tested individually with the five flowers arranged in regular pentagon (50 m side length). Each flower provided a sucrose reward equivalent to one-fifth of the bee’s crop capacity and was refilled after each foraging bout. We tested seven bees for seven consecutive hours each on a different day. All visits to the flowers were video recorded with motion-activated webcams at each feeding station (Video S1). The first flight of an inexperienced forager and the final flight paths of five experienced foragers were recorded with harmonic radar (Videos S2, S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13).
two bouts, 0.2±0.05; similarity index between the last two bouts, 0.89±0.07, n = 7 bees; GLMM, effect of the number of bouts completed on similarity index, F_{1,187} = 78.14, p < 0.001), leading to a regular repeatable sequence, or “trapline”: the most common five-flower visitation sequence excluding revisits used by each individual bee (Figure 2E; Table S1). On average, the trapline was used in 27.13±3.46% (n = 7 bees) of each bee’s foraging bouts. It first appeared after 17.57±1.79 bouts (n = 7 bees) and was stabilized (repeated in at least three consecutive bouts at the end of training) in six bees after 30±0.8 bouts. Among the 120 possible sequences to visit all five flowers once and return to the nest, each bee selected one of the two shortest possible sequences as its trapline, either by visiting the flowers in a clockwise (sequence, 12345; n = 4 bees) or an anti-clockwise order (sequence, 54321; n = 3 bees).

Radar tracks obtained from five experienced bees, near the end of the training phase, confirmed that the routes followed were highly repeatable and close to minimizing the overall travel distance (Figure 3B–F; Videos S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13). Flight paths were composed of relatively straight segments linking either the nest and a flower or two flowers together. During each bee’s final foraging bout, these flight segments were on average 26.09%±0.10% (n = 30 segments) longer than a straight line. Overall, the bees travelled 458.10±29.14 m (n = 5 bees), which is 146.92±29.14 m longer than the shortest possible path to visit the five flowers (311.8 m). This value contrasts sharply with the 1,953.01 m travelled by a naïve bee during its first foraging bout in the pentagonal array (Figure 3A; Video S2; for further tracks see Figure S2). Thus, over multiple bouts, bees effectively minimized their travel distances using a relatively direct path to visit all flowers once in an optimal order.

**Trapline Adjustment after Removal of a Flower and Introduction of a More Distant One**

Our second aim was to investigate how experienced bees modify their trapline in response to changes in the spatial configuration of flowers. Immediately after radar-tracking the bees in the regular pentagonal array, we removed the flower located in the top corner (location 3) and established a new flower east of the initial pentagon (location 6). This new location was chosen to maximise the probability that search flights would be performed in the catchment area of the radar (Figure 1). We recorded the flight paths of three of the seven trained bees for eight consecutive foraging bouts (Videos S14, S15, S16, S17, S18, S19, S20, S21, S22, S23, S24, S25, S26, S27, S28, S29, S30, S31, S32, S33, S34, S35, S36, S37).

After the removal of the familiar flower, the bees increased their flight duration by around five times (last bout in initial array, 245.00±32.87 s; first bout in modified array, 1,221.67±894.81 s; n = 3 bees), their travel distance more than doubled (last bout in initial array, 455.75±33.91 m; first bout in modified array, 970.93±264.24 m; n = 3 bees), and they once again started to

---

**Figure 1. Aerial view of the experimental field.** The area was structured both by landmarks providing global references (edges between different types of cut grass, lines of trees) and by local features (isolated trees). Naïve bees were pre-trained to forage on the five artificial flowers positioned in a linear array midway between location 1 and 5 (red line). In the first phase of the experiment, bees were observed foraging on the five flowers positioned in locations 1–5. The shortest possible route to visit all five flowers once and return to the nest box was 311.8 m long (blue line). In the second phase of the experiment, the flower at location 3 was removed and a new flower was established at location 6 (50 m from both location 4 and location 5). The shortest possible route in the modified array was 342.6 m (yellow line). In both spatial arrangements, the minimum distance between nearest neighbour flowers was 50 m. Open white arrow (bottom left) indicates north. White square indicates the location of the anemometer station. Black triangles represent the locations of the small generators used to power the motion detection equipment at each feeding station. GPS data (WGS 84) were recorded on an iPad (Apple, Cupertino, CA). Satellite image from Rothamsted estate, Hertfordshire, UK (http://maps.google.com). Scale is in metres. doi:10.1371/journal.pbio.1001392.g001
Figure 2. Trapline development in the initial pentagonal array of flowers. (A) The average number of foraging bouts (mean ± s.e.m., n = 7 bees) before a bee made its first visit to each flower (F1–F5). Letters above columns indicate significant differences (GLMM, effect of flower on the...
number of bouts, t test: \( p < 0.05 \). (B) Proportion of arrivals (a) and departures (d) made by each bee in the four quadrants (90° sectors) of the landing platform on all flower visits. (C) Proportion of transition vectors (either nest-flower, flower-flower, or flower-nest) repeated in two successive bouts in relation to the optimality ratio (straight line length of the observed visitation sequence divided by the straight line length of the shortest possible sequence to visit the same number of flowers) of the first bout. (D) Cumulative frequency of different transition vectors experienced in relation to the cumulative number of foraging bouts completed. Each bee used on average 25 ± 1.13 different vectors (mean ± s.e.m., \( n = 7 \) bees) out of a total of 30 possible. (E) Cumulative frequency of trapline usage (the most common five-flower visitation sequence, excluding revisits, used by each bee) in relation to the cumulative number of foraging bouts completed. Traplines were first observed between bout 11 and 23, and became stabilized (used in at least three consecutive bouts at the end of training) in six bees between bouts 24 and 35. Labels 1–7 refer to the same individuals in all figures and tables.

doi:10.1371/journal.pbio.1001392.g002

revisit empty flowers (last bout in initial array, 0 revisits; first bout in modified array, 4.33 ± 2.33 revisits; \( n = 3 \) bees). Bees continued to follow their trapline, visiting all four familiar flowers and the empty feeding location (location 3) in the same sequence as before the spatial arrangement was modified (Figure 4, Table S1). However, as bees could not fill their crop to capacity by visiting

Figure 3. Flight paths in the initial pentagonal array of flowers. Black dots show the position of bees at 3 s intervals as recorded by the radar. Red dots indicate the locations of the artificial flowers (F1–F5) and the nest-box (N). (A) First flight of a naïve bee (for further tracks, see Figure S2). (B–F) Flight paths of experienced bees towards the end of training (flight paths for each bout are plotted in different colours, with the final flight in black). White arrows indicate the general directionality of the flower visitation sequence (clockwise or anticlockwise). Grey arrows indicate mean wind direction (degrees) and speed (m.s\(^{-1}\)). The open black arrow (bottom left of each panel) indicates north. Stars indicate search loops between immediate revisits to flowers. Distances are in metres. Labels 1–5 refer to the same individuals in all figures and tables. Videos of all radar tracks are available (Videos S2, S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13).

doi:10.1371/journal.pbio.1001392.g003
only four flowers, they repeated the entire circuit once, sometimes twice before returning to the nest, a stereotyped pattern observed in 33.33%±15.02% of all of their foraging bouts (n=8 bouts per bee).

At the same time, bees engaged in local searching manoeuvres, exploring new areas of the experimental field (Figure 4). Azimuthal directions of the mean flight vectors (sum of all vectors of the radar track, see Materials and Methods) indicate that bees did not investigate the entire field (Watson’s test for circular uniformity, p<0.01 for every bee), but each one restricted their searching activity to a different sector (average angle for individual 1, 75.09±2.91°; individual 2, −32.17±11.40°; individual 3, 32.38±13.14°; n=8 tracks per bee; ANOVA for circular data, F2,23 = 30.31, p<0.001). Sixteen out of 24 flight paths included loops of varying length (range, 5.10–509.26 m) between immediate revisits to flowers. White arrows indicate the general directionality of the flower visitation sequence (clockwise or anticlockwise). Grey arrows indicate mean wind direction (degrees) and speed (m.s⁻¹).

Figure 4. Flight paths in the modified pentagonal array of flowers. Red dots indicate the location of artificial flowers (F1, F2, F4, F5, F6) and the nest-box (N). One familiar flower (location 3) was removed and a new one was introduced (location 6). The red cross indicates the empty feeding location (artificial flower removed, formerly F3). Black dots show the position of the bees at 3 s intervals as recorded by radar. Movement patterns of the three bees were recorded during eight successive foraging bouts (one column per bee, flight paths shown in chronological order from top to bottom). Red arrows represent the mean flight vector of the flight path (see Materials and Methods). Stars indicate search loops between immediate revisits to flowers. White arrows indicate the general directionality of the flower visitation sequence (clockwise or anticlockwise). Grey arrows indicate mean wind direction (degrees) and speed (m.s⁻¹).

The open black arrow (bottom left of each panel) indicates north. Distances are in metres. Labels 1–3 refer to the same individuals in all figures and tables. Videos of all radar tracks are available (Videos S1, S2, S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13, S14, S15, S16, S17, S18, S19, S20, S21, S22, S23, S24, S25, S26, S27, S28, S29, S30, S31, S32, S33, S34, S35, S36, S37).

doi:10.1371/journal.pbio.1001392.g004

Trapline Optimisation by Iterative Improvement

Having established that bees develop optimal traplines without trying all possible solutions and start exploring again if some flowers are removed from and/or introduced to the array, we further examined bees’ optimisation strategy by comparing the observed visitation sequences to sequences generated by simple optimisation heuristics.

First, we tested the “nearest neighbour” heuristic, in which a model bee chooses the nearest unvisited flower as its next move until all flowers have been visited. This heuristic has been suggested to explain the routing behaviour of some animals [13,14,17,19], including bees [19], at small spatial scales. When applied to our experimental situation (five flowers arranged in a regular pentagon) the nearest neighbour heuristic predicts that bees should always move between neighbouring flowers along the edges of the pentagon. Although a large proportion of the bees’ movements involved linking nearest neighbour flowers, especially in the early bouts when all flowers were not yet discovered (77% of all transitions between flowers, n=50 bouts) and after the stabilization of an optimal trapline (100% of all transitions between flowers, n=19), this unique rule of thumb is not sufficient to fully explain our data since bees were observed moving between non-nearest neighbour flowers in 52% of the bouts in which all five flowers were visited (n=42 bouts; Table S1).

Second, we tested the “discovery order” heuristic in which a model bee visits flowers in the order it discovered them. This heuristic has been previously proposed for the establishment of long-distance traplines by bees [16]. However, we found it incompatible with our observations as none of the bees used the discovery order of the flowers as their trapline sequence (Table S1). There was no significant relationship between the discovery order of the flowers and the directionality (clockwise or anticlockwise) of final traplines (GLMM, effect of discovery order of flowers on their order in the trapline, F1,25 = 41.16, p<0.001). For each bee, the similarity index between the discovery order sequence and the trapline sequence was not different than expected by chance (similarity index range, 0.29–0.67, n=7 indices; p>0.05 for all bees, see Materials and Methods).

Third, we tested random optimization and implemented a simple random “k-opt” iterative improvement heuristic [12] assuming that (1) a model bee tries to improve the route between known flowers by randomly shuffling the order in which a number (k) of randomly selected flowers are visited and (2) the route change is kept if the new route is shorter than the previous one (otherwise it is rejected). This heuristic predicts the appearance of an optimal visitation sequence only after completion of around 100 foraging bouts, which is far higher than the 17.57±2.179 bouts (n=7 bees) observed in our experiments. In general, random optimization processes do not produce stable repeatable sequences and are therefore not compatible with our data.

We therefore developed an iterative improvement heuristic based on our analysis of bees’ movement patterns. In this heuristic, the probability of model bees visiting a particular flower or flying back to the nest is determined by its experience, allowing them to explore, learn, and sequentially optimise their routes (Figure 5). We assume that (1) bees can uniquely identify the flower locations using information from path integration and/or the visual context.
Figure 5. Principle of the iterative improvement heuristic for flight path optimization. At each stage, a model bee chooses to move between flowers according to six assumptions: (1) the bee can uniquely identify each flower; (2) the bee has a finite probability of using transition vectors joining each pair of flowers; (3) the initial probability of using a vector depends on the distance between the two flowers (in our simulations nearest neighbour flowers are visited with a probability = 0.6 and more distant locations are visited with a probability = 0.1); (4) the bee computes the net length of the route travelled by summing the distances of all vectors comprising the flower visit sequence; (5) having completed a route passing through all the flowers at least once, the bee compares the net length of the current route to the net length of the shortest route experienced so far; (6) if the new route is shorter, the probabilities of using the vectors forming this new route in the next foraging bout are increased by a common factor (in our simulation, a factor of 2). The figure illustrates a late stage of trapline development between five flowers arranged in a regular pentagon (where three different paths starting and finishing at the nest-box have been selected over time (N12354N, N13245N, N12345N)). Strengthening the vectors forming the shortest route (N12345N) makes this route more “attractive” (the thickness of the arrow is proportional to the probability of the vector being used). As the bee is more likely to take the shortest route, longer routes will be gradually abandoned (see simulations in Figure S3). doi:10.1371/journal.pbio.1001392.g005

Discussion

We have recorded complete flower visitation sequences and successive flight paths of bumblebees foraging in field-scale conditions, allowing us to examine the learning processes underpinning multi-destination routing strategies of animals with known foraging history. Over multiple bouts, bees minimized their overall travel distance by flying relatively straight vectors between learnt feeding locations and visiting all flowers once in a stable optimal sequence. When the spatial configuration of flowers was gradually abandoned (see simulations in Figure S3), bumblebees' flight paths were optimized as a trapline (e.g., sequence, 12453) is shorter than the shortest route experienced so far by that bee, then the probabilities linking movements between pairs of flowers within this circuit (1-2, 2-4, 4-5, and 5-3) are enhanced by a common factor. Gradual strengthening of the transition vectors forming the shortest route experienced so far allows the bee to sequentially optimise its visitation sequence and select an optimal route as a trapline (for more details about the model, see Text S1).

Simulation data from this novel heuristic predict that model bees (1) occasionally visit fewer than all flowers especially during early bouts, (2) regularly revisit empty flowers during the same bout, (3) decrease their frequency of revisits with experience, (4) establish stable optimal routes after about 20–25 bouts, and (5) can sequentially adjust their routes to incorporate newly discovered flowers in an optimal way (Figure S3). Quantitative evaluation of the simulated data with the optimisation performance of real bees in the experimental field showed full agreement for the number of bouts to the first appearance of an optimal sequence, the number of bouts to the stabilization of an optimal sequence into a trapline, the number of different routes experienced, the net route length travelled per bout, the number of revisits per bout, and the similarity indices between successive bouts (Table 1). Therefore, bees’ optimization strategy can be captured in a simple iterative improvement routine in which an individual compares the net length of their current route to the net length of the shortest route experienced so far, and increases its probability of reusing the flight vectors comprising this new route if it is shorter.
modified, the bees engaged in localised search flights to find new flowers.

The observed dynamic of trapline acquisition in our large-scale setup is incompatible with random movements or with an extensive exploration of all possible routes. We also ruled out the hypothesis that bees rely on a single rule of thumb such as visiting all locations in the initial discovery order or moving between nearest neighbour locations. Although a large proportion of the bees’ movements involved linking nearest neighbour flowers, especially in the first few foraging bouts, this strategy alone cannot explain our data. Rather, bees developed their traplines through trial and error by combining exploration, learning, and sequential optimisation, thus confirming hypotheses derived from previous observations in smaller enclosed environments [15–19]. Interestingly, however, the optimisation performance of bees under field-scale conditions was much higher as all the bees tested selected an optimal route as their trapline, compared to a maximum of 75% in laboratory studies using comparable numbers of feeding locations (range, 4–10 flowers) and training durations (range, 20–80 foraging bouts per bee) [15,19–21]. Presumably, bees’ motivation to optimise their routes increases with spatial scale because the costs of travelling long (suboptimal) distances are greatly magnified. It is also possible that celestial cues, such as the position of the sun or polarized light patterns that are not typically available in laboratory settings but are known to be involved in navigation [28,29], allow bees to orientate more accurately and develop routes faster in natural environments.

How, then, did the bees optimise their routes? Based on our detailed analysis of bee movement patterns, we implemented a simple iterative improvement heuristic, which, when applied to our experimental situation, matched the behaviour of real bees exceptionally well. The proposed heuristic demonstrates that bees can develop optimal routes by following multi-segment journeys as evidence for “map-like” memory [25,35], suggesting that bees process in an insect brain is a matter of long-standing debate [25,34–37]. Recent observations of honeybees using shortcuts between separately learnt foraging locations have been interpreted as evidence for “map-like” memory [23,33], suggesting that bees acquire a coherent representation of the spatial connectivity between important locations in their environment (such as the nest, flowers, and prominent landmarks), allowing them to compute new vectors. Although our study was not conceived to test this hypothesis, our results indicate that the routing behaviour of bumblebees can be replicated without assuming such a map-like representation of space. The proposed heuristic suggests that bees can develop optimal routes by following multi-segment journeys composed of learnt flight routines (local vectors), each pointing towards target locations (flowers) and coupled to a visual context (landmarks and/or panoramas). Such a decentralized representation of space is akin to the “route-based” navigation of desert ants, where spatial information is thought to be processed by separate, potentially modular, guidance systems [4,34,37,38]. The fact that trained bees continued to visit the familiar location from which a flower had been removed (location 3) further supports the hypothesis that foragers in our experimental situation relied on a simple iterative improvement heuristic, which, when applied to our experimental situation, matched the behaviour of real bees exceptionally well.

The optimisation process we describe is analogous to the iterative improvement approach developed in “ant colony optimisation” heuristics, which has been increasingly used to explore solutions to combinatorial problems in computer sciences [32]. The rationale of these swarm intelligence heuristics is based on a model describing how ants collectively find short paths between a feeding location and their nest using chemical signals [33]. “Memory” in ant colony optimisation algorithms has no neurobiological basis but instead takes the form of pheromone trails marking established routes. The shortest route becomes more attractive due to increases in pheromone concentration as multiple ants forage simultaneously along it and continue to lay pheromone, while longer routes are abandoned because of pheromone evaporation. Of course, identification of a similar iterative optimisation principle in bees, although based on very different mechanisms (bumblebees forage individually and do not recruit using pheromone trails), does not imply that bees would equal the performance of swarm algorithms in finding solutions to complex combinatorial problems. However, iterative improvement heuristics are flexible, suggesting that bees can develop functional traplines in their natural environments, where the numbers of flowers, their spatial configuration, and reward values vary over time.

The question of how spatial information is encoded and processed in an insect brain is a matter of long-standing debate [25,34–37]. Recent observations of honeybees using shortcuts between separately learnt foraging locations have been interpreted as evidence for “map-like” memory [23,33], suggesting that bees acquire a coherent representation of the spatial connectivity between important locations in their environment (such as the nest, flowers, and prominent landmarks), allowing them to compute new vectors. Although our study was not conceived to test this hypothesis, our results indicate that the routing behaviour of bumblebees can be replicated without assuming such a map-like representation of space. The proposed heuristic suggests that bees can develop optimal routes by following multi-segment journeys composed of learnt flight routines (local vectors), each pointing towards target locations (flowers) and coupled to a visual context (landmarks and/or panoramas). Such a decentralized representation of space is akin to the “route-based” navigation of desert ants, where spatial information is thought to be processed by separate, potentially modular, guidance systems [4,34,37,38]. The fact that trained bees continued to visit the familiar location from which a flower had been removed (location 3) further supports the hypothesis that foragers in our experimental situation relied on a simple iterative improvement heuristic, which, when applied to our experimental situation, matched the behaviour of real bees exceptionally well.

### Table 1. Quantitative evaluation of the iterative improvement heuristic for flight path optimization.

| Optimization Index | \(p_1\) | \(p_2\) | \(p_3\) | \(p_4\) | \(p_5\) | \(p_6\) | \(p_7\) |
|-------------------|---------|---------|---------|---------|---------|---------|---------|
| Number of bouts to first appearance of an optimal sequence | 0.87    | 0.91    | 0.95    | 0.84    | 0.97    | 0.73    | 0.91    | 0.81 |
| Number of bouts necessary for the stabilization of a sequence | 0.72    | 0.65    | 0.88    | 0.81    | 0.71    | 0.71    | 0.65    | 0.65 |
| Total travel distance per bout | 0.4     | 0.61    | 0.51    | 0.35    | 0.38    | 0.24    | 0.46    |
| Number of revisits per bout | 0.62    | 0.76    | 0.73    | 0.48    | 0.57    | 0.42    | 0.63    |
| Similarity index between successive foraging bouts | 0.34    | 0.39    | 0.36    | 0.35    | 0.29    | 0.29    | 0.44    |

Comparisons between empirical (\(n = 7\) bees) and simulation (\(n = 1,000\) runs; for details, see Text S1) data were made for six optimization performance indices. \(p_1\)–\(p_7\), average value for all bees (see Materials and Methods). \(p_n\), average value for bee \(n\). Labels 1–7 refer to the same individuals in all figures and tables.

doi:10.1371/journal.pbio.1001392.t001
heavily on learnt sensory motor routines as route-based navigation constrains the ability of individuals to rapidly adjust their routes, in contrast to map-like navigation that should allow for fast computation of entirely novel solutions [36]. Future studies should clarify whether similar learning heuristics apply to insect pollinators foraging at different spatial scales and configurations, and to other animals faced with similar routing problems (e.g., hummingbirds [9], bats [7], and primates [6, 10, 13, 14]). Ultimately, characterizing the neural-computational implementation of functional multi-destination routing solutions in small-brained animals holds considerable promise for identifying simple solutions to dynamic combinatorial problems in situations lacking central control.

Materials and Methods

Subjects and Study Site

Experiments were carried out in a flat, open area of mown pasture (approximately 700 x 300 m) on the Rothamsted estate (Hertfordshire, UK; Figure 1). Global landmarks (edges between different types of cut grass, tree lines) and local features (isolated trees) were available. The observation period (October 2010) was chosen because there were very few natural sources of pollen and nectar present during this time. The radar equipment was located on the south-east corner of the experimental field to allow maximum catchment area. The Bombus terrestris colony was housed in a wooden nest-box located south of the experimental field. A transparent tube with shutters was fitted at the entrance to control bee traffic. Bees were individually marked with numbered plastic tags within a day of emergence from pupae in order to monitor their complete foraging history.

Artificial Flowers and Video Tracking

Artificial flowers (Figure S1) were made of a plastic cylinder (height 8 cm) covered with a blue horizontal landing platform (diameter 6 cm). Bees could access the flowers equally well from all angles and collect a drop of 40% (w/w) sucrose solution from a yellow plastic square (2.4 cm side) in the middle of the landing platform. Each flower was positioned on top of a truncated cone-shaped support (base diameter 30 cm, top diameter 20 cm, height 18 cm) placed on the ground. A webcam (Logitech c250, Fremont, CA) was mounted directly above the centre of each flower on an independent vertical support (height 50 cm) to capture footage of bees when they visited. Webcams were fitted with light filters (neutral density 0.6) to attenuate sunlight illumination and connected to a laptop running video motion detection software (Zone Trigger 2, Omega Unfold, Quebec, Canada). A video clip (minimum duration 5 s) was recorded each time a bee moved into the camera field of view (Video S1). Recording continued until movement stopped, thus capturing complete flower visits from when the bee landed to its departure. Feeding stations were arranged sufficiently far apart (minimum distance 50 m) such that each station would be undetectable by the bee visual system from any other. The maximum dimension of a feeding station (including the flower, webcam, and laptop) was 70 cm. Given bumblebee’s failure to detect targets that subtend less than ca. 3° [39], a bee should visually detect a feeding station this size from no more than 13.4 m away. Each laptop was powered by a small petrol generator (850 W, length 38 cm, width 33 cm, height 32 cm) placed 10 m from the feeding station, located outside the pentagonal flower array (Figure 1). Generators provided potential local landmarks, although due to their small size they should only have been visually detectable for bumblebees at a range of 7.3 m and were therefore less prominent to bees than feeding stations. In addition, there is solid experimental evidence that bees could not visually detect feeding stations over the distances tested, since two out of three bees failed to find the new location after a displacement (see Results).

Harmonic Radar Tracking

The harmonic radar and transponders have been previously described [23]. The radar equipment provided coverage over a range of 700 m and an altitude of about 3 m above the ground. Transponders consisted of a 16 mm vertical dipole (mass 0.8 mg) that does not affect bees’ flight behaviour [24]. Individual bees were caught on departure from the colony, the transponder was attached using double-sided foam tape over the plastic number tag and released at the nest-box entrance tube. Coordinates of the transponder-tagged bee in the experimental field were recorded every 3 s by the radar with a spatial resolution of approximately ±2–3 m [40]. When the bee returned to the nest entrance, the transponder was removed before it re-entered the nest. Wind speed and direction were measured every 10 s by a recording anemometer fixed 2 m above the ground, located 10 m west of the nest-box (Figure 1).

Experimental Procedure

Experiments were performed between 09:00 and 18:00 on days when the sun or blue sky was visible. Bees were individually pre-trained to collect sucrose solution from the five artificial flowers arranged in a linear array (150 cm length), located 50 m north-west of the nest entrance (Figure 1). Flower rewards were refilled ad libitum with 10 µL. The mean volume of sucrose solution ingested by a given bee during three successive foraging bouts was used to estimate its crop capacity (range = 75–100 µL) [20]. We tested seven bees, each on a different day.

In the first phase of the experiment, bees were observed foraging on the five flowers arranged in a regular pentagon (50 m side, Figure 1), until they visited all flowers in at least five consecutive foraging bouts. This required about 7 h of observation and 28.86 ± 2.22 foraging bouts per bee (n = 7 bees). Each flower contained a sucrose reward equivalent to one-fifth of the test bee’s crop capacity (volume range = 15–20 µL) and was refilled after each foraging bout. All departure and arrival times at the nest-box were recorded by an experimenter. Flower visits were automatically recorded using motion-activated webcams (Video S1). Flight paths of five bees were tracked with harmonic radar towards the end of training (up to four foraging bouts per bee, including the final bout).

In the second phase of the experiment, one flower was removed from location 3 and a new one was established at location 6 (Figure 1). Three bees were observed for eight additional foraging bouts in this new spatial arrangement (all these bouts were monitored by both webcam recordings and radar tracking). The five remaining bees were not tested because of insufficient daylight to pursue the observations on the day they were trained. In total, 230 foraging bouts, 1,334 video clips, and 36 radar tracks of flight paths were analysed.

Data Analysis

Video data. Evaluation of the webcam video clips provided detailed information about the behaviour of bees during their visits to flowers. For each clip, we divided the landing platform of the flower into four quadrants (90° sectors) and established in which quadrant the bee landed and left the flower (Video S1). Time-coded video clips from all flowers allowed us to reconstruct the visitation sequence for every foraging bout of each bee. We examined how a bee’s tendency to repeat visitation sequences increased with experience using a similarity index.

Large-Scale Traplining in Bumblebees

September 2012 | Volume 10 | Issue 9 | e1001392
described in [20], which quantifies the similarity between pairs of flower visitation sequences. This index takes into account the length of sequences and the order of visits to flowers. The similarity index ranges between 0 (completely different sequences, e.g., 123 versus 456) and 1 (identical sequences, e.g., 12345 versus 12345). To establish whether two sequences of five flower visits were significantly more similar than expected by chance, we computed 1,000 similarity indices from 2,000 visitation sequences in which a bee visited the five locations once in a random order. Because 95% of the randomly generated similarity indices fall below a threshold of 0.67, two sequences were significantly more similar than expected by chance (at the 5% level) if the similarity index is greater than this threshold.

**Radar data.** Radar tracks gave us the flight trajectory, travel distance, and ground speed for each foraging bout. For each radar track, we calculated a mean flight vector, defined as the average of all vectors formed between each point of the flight path and the barycentre (geometric centre) of the hexagon formed by the nest-box and flower locations 1–5. A bee using the shortest possible path to visit all five flowers once would have a null mean vector. Any deviation from this optimal path is revealed by a non-null vector. Videos of all radar tracks are available (Videos S2, S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13, S14, S15, S16, S17, S18, S19, S20, S21, S22, S23, S24, S25, S26, S27, S28, S29, S30, S31, S32, S33, S34, S35, S36, S37).

**Quantitative analysis of simulation data.** Using our heuristic for bee optimization, we predicted the distribution of values for six optimization performance indices by model bees ([1] the number of bouts to the first appearance of an optimal flower visitation sequence, [2] the number of bouts to the stabilisation of a visitation sequence (when repeated in at least three consecutive bouts and all subsequent bouts are similar), [3] the number of different routes used in total, [4] the route lengths per bout, [5] the number of revisits per bout, and [6] the similarity index) foraging on five locations arranged in a regular pentagon (Table 1). The distribution was based on 1,000 simulation runs. From these data, we calculated the probability of a real bee doing at least as well as observed given that the model is correct (null hypothesis). This probability is a p value, so the model can therefore be rejected if this probability is less than 0.05. For the number of bouts to the first appearance of an optimal sequence, the number of bouts to the first appearance of a stable sequence, and the number of different routes used, we calculated the average p value for all bees. For route lengths per bout, number of revisits per bout, and similarity indices between pairs of visitation sequences, we calculated the average p value for each bee using \( \frac{p_1 + p_2 + \ldots + p_n}{n} \) where \( p_1 \) is the p value for bout 1, \( p_2 \) is the p value for bout 2, and so forth.

**Supporting Information**

**Figure S1** Artificial flowers and video tracking system. (A) Complete feeding station including an artificial flower, a webcam, and a laptop computer. (B) Details of an artificial flower. A bee equipped with a radar transponder is collecting a drop of sucrose solution from the yellow square in the middle of the blue landing platform. The webcam above the landing platform is controlled by a motion detection software (running on the laptop) that triggers the recording of a video clip when a bee lands and feeds on the flower, thus enabling us to identify the bee, the timing of its visit, and its arrival and departure directions (Video S1).

**Figure S2** Flight paths followed by a naïve bee in the initial pentagonal array of flowers. Black dots show the position of the bee at 3 s intervals as recorded by the radar. Red dots indicate the locations of flowers (F1–F5) and the nest-box (N). Movements of the bee (black lines) were recorded during its first four foraging bouts. Stars indicate search loops between immediate revisits to flowers. Grey arrows indicate mean wind direction (degrees) and speed (m.s\(^{-1}\)). The open black arrow (bottom left of each panel) indicates north. Distances are in metres. Unlike experienced bees (Figure 3), the naïve bee did not visit the five flowers in a stable, repeatable sequence and travelled more than 1,000 m per bout. (TIF)

**Figure S3** Simulated example of trapline development using our heuristic for flight path optimization. Arrows represent the movements of a model bee between the five flowers (F1–F5) arranged in a regular pentagonal array and the nest-box (N). Numbers above each diagram indicate the foraging bouts in chronological order. An optimal (shortest) route first appears at bout 18 and is stabilized (repeated in at least three consecutive bouts and all subsequent bouts are similar) at bout 25. (TIF)

**Table S1** Complete list of visitation sequences to artificial flowers. Sequences were reconstructed from a compilation of video data recorded at each flower. For each individual bee, the visitation sequences are presented in chronological order (down a column). Numbers in the table (1–6) refer to the spatial location of each flower in the experimental field (Figure 1). For each bee, the trapline (the most common five-flower visitation sequence excluding revisits) is highlighted in bold. Optimal bouts (shortest possible sequence visiting all flowers once) are highlighted in yellow. *, sequences recorded during the second phase of the experiment when the flower was removed from location 3 and a new flower was established at location 6. **, radar-track sequence. Labels 1–7 refer to the same individuals in all figures and tables. (DOC)

**Text S1** Numerical simulations of our iterative improvement heuristic for flight path optimization. In this text, we describe how we selected the probability values used in the simulations. (DOC)

**Video S1** Video clip of a bee visiting flower. Top view of a bee (unically identified by a plastic number tag) collecting sucrose solution from the middle of the circular landing platform. Recording by the webcam above the flower was triggered by motion detection software run on a laptop (Figure S1). The bee landed and left the flower from the south-west quadrant of the landing platform (181–270°). Recording date and time are displayed in the bottom left corner of the screen. (MP4)

Videos of radar tracks (Video S2, S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13, S14, S15, S16, S17, S18, S19, S20, S21, S22, S23, S24, S25, S26, S27, S28, S29, S30, S31, S32, S33, S34, S35, S36, S37). Here we present links to videos of all the radar tracks (\( n = 36 \)) overlaid on a drawing of the experimental field. Numbered circles in videos indicate the location of flowers. The blue line indicates the bee’s flight paths as recorded by the harmonic radar. Pink arrows indicate wind direction and speed. Time is accelerated ten times.

Links to Videos S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13 of the radar tracks of five experienced bees (individuals 1–5) towards the end of training in the array of five artificial flowers arranged in a regular pentagon. We also provide the radar track of a naïve bee (different from the test bees) during its first foraging bout (Video S2):

**Video S2** Naïve bee on foraging bout 1. (MP4)
Video S3  Individual 1 on foraging bout 36. (MP4)
Video S4  Individual 1 on foraging bout 37. (MP4)
Video S5  Individual 2 on foraging bout 24. (MP4)
Video S6  Individual 2 on foraging bout 25. (MP4)
Video S7  Individual 2 on foraging bout 26. (MP4)
Video S8  Individual 3 on foraging bout 22. (MP4)
Video S9  Individual 3 on foraging bout 23. (MP4)
Video S10 Individual 3 on foraging bout 24. (MP4)
Video S11 Individual 3 on foraging bout 25. (MP4)
Video S12 Individual 4 on foraging bout 37. (MP4)
Video S13 Individual 5 on foraging bout 28. (MP4)

Links to Videos S14, S15, S16, S17, S18, S21, S22, S23, S24, S25, S26, S27, S28, S29, S30, S31, S32, S33, S34, S35, S36, S37 of the radar tracks for three experienced bees (Individuals 1–3) after removal of a flower (from location 3) and the establishment of a more distant one (at location 6):

Video S14  Individual 1 on foraging bout 38. (MP4)
Video S15  Individual 1 on foraging bout 39. (MP4)
Video S16  Individual 1 on foraging bout 40. (MP4)
Video S17  Individual 1 on foraging bout 41. (MP4)
Video S18  Individual 1 on foraging bout 42. (MP4)
Video S19  Individual 1 on foraging bout 43. (MP4)
Video S20  Individual 1 on foraging bout 44. (MP4)
Video S21  Individual 1 on foraging bout 45. (MP4)
Video S22  Individual 2 on foraging bout 27. (MP4)
Video S23  Individual 2 on foraging bout 28. (MP4)
Video S24  Individual 2 on foraging bout 29. (MP4)
Video S25  Individual 2 on foraging bout 30. (MP4)
Video S26  Individual 2 on foraging bout 31. (MP4)
Video S27  Individual 2 on foraging bout 32. (MP4)
Video S28  Individual 2 on foraging bout 33. (MP4)
Video S29  Individual 2 on foraging bout 34. (MP4)
Video S30  Individual 3 on foraging bout 26. (MP4)
Video S31  Individual 3 on foraging bout 27. (MP4)
Video S32  Individual 3 on foraging bout 28. (MP4)
Video S33  Individual 3 on foraging bout 29. (MP4)
Video S34  Individual 3 on foraging bout 30. (MP4)
Video S35  Individual 3 on foraging bout 31. (MP4)
Video S36  Individual 3 on foraging bout 32. (MP4)
Video S37  Individual 3 on foraging bout 33. (MP4)

Acknowledgments

We thank M. Becher, A. Haughton, P. Kennedy, A. P. Martin, O. Ramos-Rodriguez, D. R. Reynolds, and J. Swain for their help during data collection. We thank C. Denholm for his assistance with the video files of radar tracks. We are also grateful to Syngenta Bioline Bees (Weert, The Netherlands) for supplying bumblebees.

Author Contributions

The author(s) have made the following declarations about their contributions: Conceived and designed the experiments: ML NER LC. Performed the experiments: ML NER RJS ADS. Analyzed the data: ML AMR. Contributed reagents/materials/analysis tools: AMR KSL ADS JLO. Wrote the paper: ML NER AMR ADS JLO LC.

References

1. Riley JR, Greggers U, Smith AD, Reynolds DR, Menzel R (2005) The flight paths of honeybees recruited by the waggle dance. Nature 435: 205–207.
2. Graham P, Cheng K (2009) Ants use the panoramic skyline as a visual cue during navigation. Curr Biol 19: R35–R37.
3. Sommer S, von Beeren C, Wohrler R (2008) Multiroute memories in desert ants. Proc Natl Acad Sci U S A 105: 317–322.
4. Collett M (2012) How navigational guidance systems are combined in a desert ant. Curr Biol 22: 927–932.
5. Biro D, Freeman R, Meade J, Roberts S, Guilford T (2007) Pigeons combine compass and landmark guidance in familiar route navigation. Proc Natl Acad Sci U S A 104: 7471–7476.
6. Di Fiore A, Suarez SA (2007) Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. Anim Cognit 10: 317–329.
7. Lenke TO (1984) Foraging ecology of the long-nosed bat, Glossophaga soricina, with respect to resource availability. Ecology 65: 538–548.
8. Ohashi K, Thomson JD (2009) Trapline foraging by pollinators: its ontogeny, economics and possible consequences for plants. Annals of Botany 103: 1365–1378.
9. Healy SD, Hurly TA (2003) Cognitive ecology: foraging in hummingbirds as a model system. Adv Stud Behav 32: 325–359.

10. Noser R, Byrne RW (2010) How do wild baboons (Papio ursinus) plan their routes? Travel among multiple high-quality food sources with inter-group competition. Anim Cognit 13: 145–153.

11. Wilczek M, Moles J, Eaton-Mordas MM, Holland R, et al. (2010) Large-range movements of neotropical orchid bees observed via radiotelemetry. PLoS ONE 5: e10730. doi:10.1371/journal.pone.0010730.

12. Appleget DE, Bixby RE, Chvatal V, Cook WJ (2006) The traveling salesman problem: a computational study. Princeton, NJ: Princeton University Press. 593 p.

13. Menzel EW (1973) Chimpanzee spatial memory organization. Science 182: 943–945.

14. Cramer AE, Gallistel CR (1997) Vervet monkeys as travelling salesmen. Nature 387: 464–464.

15. Liaboeau M, Chittka L, Le Comber SC, Raine NE (2012) Bees do not use nearest-neighbour rules for optimization of multi-location routes. Biol Lett 8: 16.

16. Janzen DH (1971) Euglossine bees as long-distance pollinators of tropical plants. Science 171: 203–205.

17. Blaser RE, Ginchansky RE (2012) Route selection by rats and humans in a navigational traveling salesman problem. Anim Cognit 15: 239–250.

18. Wiener JM, Ebbarner NN, Mallot HA (2009) Planning paths to multiple targets: memory involvement and planning heuristics in spatial problem solving. Psychol Res 73: 644–658.

19. Ohashi K, Thomson JD, D’Souza D (2007) Trapping foraging by bumble bees: IV. Optimization of route geometry in the absence of competition. Behav Ecol 18: 1–11.

20. Liaboeau M, Chittka L, Raine NE (2010) Travel optimization by foraging bumblebees through readjustments of traplines after discovery of new feeding locations. Am Nat 176: 744–757.

21. Saleh N, Chittka L, Rainen J, Deneubourg JL, Pasteels JM (1989) Self-organized shortcuts in the argentine ant. Naturwissenschaften 76: 579–581.

22. Dornhaus A, Chittka L (1999) Evolutionary origins of bee dances. Nature 401: 31–31.

23. Riley JR, Smith AD, Reynolds DR, Edwards AS, Osborne JL, et al. (1996) Tracking bees with harmonic radar. Nature 379: 29–30.

24. Osborne JL, Clark SJ, Morris RJ, Williams IH, Riley JR, et al. (1999) A landscape-scale study of bumble bee foraging and constancy, using harmonic radar. J Appl Ecol 36: 519–533.

25. Menzel M, Greggers U, Smith A, Berger S, Branda R, et al. (2005) Honey bees navigate according to a map-like spatial memory. Proc Natl Acad Sci U S A 102: 3040–3045.

26. Collett T, Landau D, Collett TS (2002) The use of landmarks and panoramic context in the performance of local vectors by navigating honeybees. J Exp Biol 205: 807–814.

27. von Frisch K (1967) The dance language and orientation of bees. Cambridge, MA: Harvard University Press. 592 p.

28. Wellington WG (1974) Bumblebee ocelli and navigation at dusk. Science 183: 550–551.

29. Kraft P, Evangelista C, Deck M, Labhart T, Srinivasan MV (2011) Honeybee navigation: following routes using polarized-light cues. Phil Trans R Soc B 366: 793–798.

30. Wehner R, Srinivasan MV (2003) Path integration in insects. In: the neurobiology of spatial behaviour, K.J . Jeffery, ed. Oxford, UK: Oxford University Press. pp. 9–30.

31. Chittka L, Kunze J, Shipman C, Buchmann SL (1995) The significance of landmarks for path integration in homing honeybee foragers. Naturwissenschaften 82: 341–343.

32. Dorigo M, Stützle T (2004) Ant colony optimization. Cambridge, MA: The MIT Press. 319 p.

33. Goss S, Aron S, Deneubourg JL, Pasteels JM (1989) Self-organized shortcuts in the argentine ant. Naturwissenschaften 76: 579–581.

34. Cruse H, Wehner R (2011) No need for a cognitive map: decentralized memory for insect navigation. PLoS Comp Biol 7: e1002009. doi:10.1371/journal.pcbi.1002009.

35. Menzel R, Kirbach A, Haas W-D, Fischer B, Fuchs J, et al. (2011) A common frame of reference for learned and communicated vectors in honeybee navigation. Curr Biol 21: 545–550.

36. Cheng K (2012) How to navigate without maps: the power of taxon-like navigation in ants. Curr Biol 19: R1103–R1107.

37. Wehner R, Boyer M, Loetscher F, Sommer S, Menzi U (2006) Ant navigation: one-way routes rather than maps. Curr Biol 16: 75–79.

38. Collett T (2009) Spatial memories in insects. Curr Biol 19: R1103–R1107.

39. Kapustjansky A, Chittka L, Spaethe J (2010) Bees use three-dimensional information to improve target detection. Naturwissenschaften 97: 229–233.

40. Ovaskainen O, Smith AD, Osborne JL, Reynolds DR, Carreck NL, et al. (2008) Tracking butterfly movements with harmonic radar reveals an effect of population age movement distance. Proc Natl Acad Sci U S A 105: 19090–19095.