

## Landmark Learning and Guidance in Insects

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# Landmark learning and guidance in insects

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## SUMMARY

Insects use terrestrial landmarks both for retrieving important places in their environment, like a nest, and for guiding their way along frequently travelled routes. Places are pinpointed by a form of image matching: the insect moves to maximize the fit between the image on its retina and its memory of surrounding landmarks as viewed from close to the goal. In this case, the insect's stored representation seems to be a filtered but relatively unprocessed replica of the image falling on the retina, which is parsed for features like the position and orientation of edges, their speed of motion and their colour. Routes need not be defined so precisely and landmarks are then employed in less demanding ways.

## 1. INTRODUCTION

A remarkable feature of insect behaviour is that individuals return repeatedly to a favoured spot. This ability is developed most highly in central place foragers, like bees and ants, which may spend much of the day shuttling hundreds of metres between their nest and foraging ground. But other examples abound: Heliconias butterflies roost nightly on the same perch in the same tree (Jones 1930); dragonflies hawk for insects and between times rest on the same twig. Such navigational feats make sophisticated demands of what is still too often billed as a simple nervous system.

Two principal mechanisms contribute to finding a place. The first is dead-reckoning: an insect is usually equipped with a vector which specifies the distance and direction of a goal. This vector is computed during the immediately preceding trip away from the goal. The insect monitors the direction of its path with reference to a celestial compass and the distance it travels and continuously updates the vector by a process akin to path integration (Müller & Wehner 1988). The vector can also be stored in memory and used to steer later journeys, as happens when an experienced honeybee leaves its hive to collect food in the morning (von Frisch, 1967).

Errors accumulate during path integration and dead reckoning is often supplemented by the second mechanism: piloting by means of familiar landmarks. In this paper I want to contrast two ways of using landmarks. The first is exemplified by Tinbergens' famous experiment on the digger wasp, *Philanthus*. While a wasp was inside her nest, a circle of pine cones was placed around the entrance. The wasp emerged, circled for a few seconds before flying off. During her absence, the array was displaced a short distance. The wasp, on her return, aimed directly at the centre of the pine cones, demonstrating that she had formed a

representation of the landmarks which enabled her to pinpoint the nest-entrance.

Landmarks distributed along a familiar route far from a goal also aid navigation. Baerends (1941), working with *Ammophila*, placed a line of small imitation trees along the wasp's habitual path to its nest. When the line was shifted and the wasp released at a point near to one end, the wasp as usual flew beside the line of plants.

If an insect uses landmarks to retrieve a place, it must store enough of the detailed geometry of the surroundings so that it can locate what may be no more than a farthing-sized hole in the sand. But route following is less demanding. So long as the insect reaches its goal economically, the exact path is unimportant. As we will see, insects exploit landmarks quite differently in solving these two navigational problems.

## 2. LANDMARK GUIDANCE CLOSE TO A GOAL

Figure 1 emphasizes how precisely landmarks can steer an insect to a goal. Single honeybees were trained to forage for sucrose at a site defined by three black, vertical cylinders on the floor of an otherwise empty room. After every visit, the landmarks and sucrose reservoir were translated en bloc to ensure that the cylinders were the only reliable cues to the position of the sucrose. In tests, the reservoir was missing and the bee flew close to the ground searching in the expected place. This section asks what an insect learns about an array of landmarks and how it uses the stored information to reach a place.

### (a) *Memories as views from a goal*

Certain properties of the bees' internal representation can be inferred from their behaviour when the

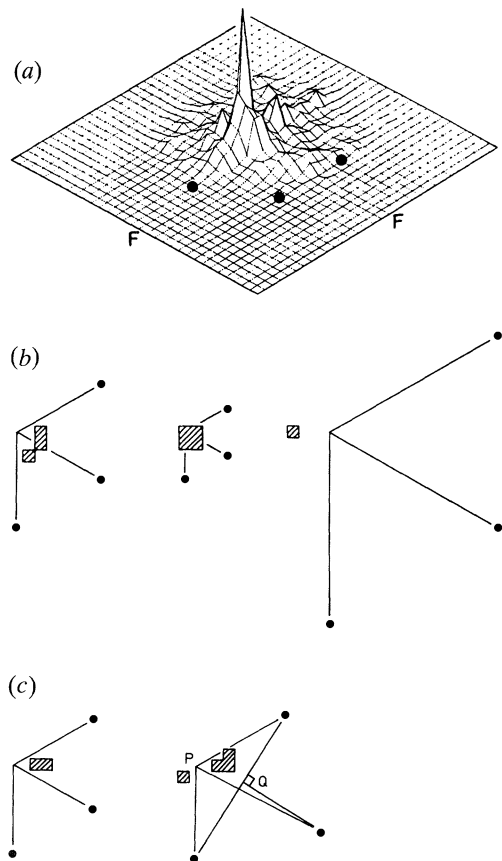


Figure 1. Honeybees searching for a missing source of sucrose at a location defined by three black, upright cylinders. (a) Relative time spent by one bee in each cell of an imaginary grid. Position of sucrose in training is marked by Fs on axes. Grid-lines are 8.7 cm apart. (b) Single bee's search when distance between landmarks is changed from the training situation. (c) Bee has choice of searching where bearings 'P' or distances 'Q' are correct. Leftmost column: search with training arrangement. Right columns: distorted arrays. Bee searches where landmarks have same bearings (shown by lines) as those experienced at the reservoir during training. Hatched areas show where search density is  $\geq 80\%$  of maximum (from Cartwright & Collett 1983).

array was distorted from the training arrangement. Bees then searched where the retinal image of the landmarks most resembled the image experienced near the sucrose during training (figure 1), as though their memory of the array was a picture of the landmarks viewed from the goal.

Bees often behaved analogously when trained to a single cylindrical landmark of one size and tested with a different sized cylinder. They searched further from a cylinder that was larger than the one to which they were accustomed and closer to one that was smaller. They positioned themselves to match the current appearance of the landmark on their retina with the one which they had stored while close to the sucrose (Cartwright & Collett 1983. See Wehner & Räber (1979); Wehner *et al.* (1983) for similar experiments on desert ants).

Various training experiments reveal that a hymenopteran's memory of landmarks is coloured (Cheng *et al.* 1986; Gould 1986) and that it includes the

position of the edges of landmarks and the speed at which those edges move over the retina as the insect flies near to the goal (see § 2e).

#### (b) *The coordinates of landmark memories*

In what coordinate system are landmarks represented? The simplest imaginable arrangement is for the memory of a landmark to be fixed with respect to the retina. Indeed, when bees are restricted to viewing a two-dimensional pattern from one spot and from one direction, the pattern is learnt in retinotopic coordinates. Bees trained to a radial grating of black and white sectors, do not recognise the same pattern when it is rotated relative to the retina so that the regions accustomed to viewing white sectors are confronted by black ones (Wehner 1981).

However, landmark guidance cannot be explained by a single stored image of landmarks painted on the retina. In some way the position of local landmarks is encoded with reference to a terrestrial coordinate system. For instance, male hoverflies, *Eristalis* sp., adopt midair hovering stations from which they make frequent excursions to pursue potential mates. The return after an abortive chase is governed by the position of nearby visual landmarks. It can be from anywhere and there is no requirement that the fly view the landmarks from a particular direction (figure 2).

An experiment by Lindauer (1960) makes the same point in a different way. He trained honeybees to feed in the afternoon at the southern corner of a large table placed to the east of their hive. After training, both hive and table were moved to a different location, the table was to the south of the hive and bees were tested in the morning. Nevertheless, bees continued to congregate at the southern corner of the table, suggesting that they had learnt the whereabouts of the food on the table with respect to its bearings given by a celestial compass.

Experiments on desert ants suggest that distant landmarks can also supply a reference frame (Wehner *et al.* (1983). Ants were habituated to seeing two small cylinders placed just north of their nest entrance. When tested with the cylinders moved a short way from the nest, so that the horizon looked the same as it usually did, the ants searched for the nest south of the cylinders. However, when the testing area was further away, so horizon cues could no longer provide directional information, ants searched equally south and north of the landmarks.

Parsimony suggests that a representation of landmarks in Earth-based coordinates should be constructed from a set of retinotopic memories. One way to do this is to learn several views from the goal while pointing in different directions. The insect would associate each view with a particular heading and on its return retrieve the memory appropriate to its current heading (Cartwright & Collett 1983).

#### (c) *Using landmark representations*

How might such a landmark representation guide an insect to a remembered spot? One model, which mimics much of the behavioural data, supposes that

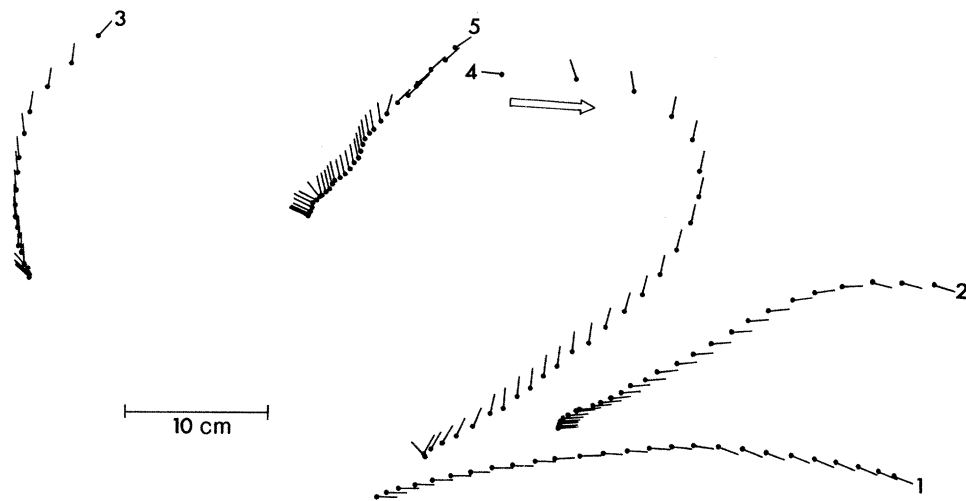


Figure 2. Five consecutive returns of a single hoverfly to its midair station showing the variability in the orientation of the body. Fly's position, viewed from below, is shown every 20 ms. Its head is indicated by the blob and its orientation by the bar (from Collett & Land 1975).

the insect continually compares its current retinal image with its memory of landmarks and moves so as to reduce the discrepancy between the two. Once the discrepancy is zero, the insect has reached its goal. The comparison is done locally. Each area on the retina of a given colour is paired with the area in memory of the same colour which has the closest bearing. Every such pairing generates unit vectors which tend to move the insect so as to reduce the difference in bearing and size between the paired areas. These local vectors are then summed to specify the direction in which the insect actually moves (Cartwright & Collett 1983).

Elegant experiments on waterstriders (Junger, 1991) show that translational movements can indeed be governed by the difference between the current and desired retinal positions of a visual landmark. Waterstriders rely on visual landmarks to keep station on fast-moving reaches of streams where they are likely to encounter prey. They face upstream and drift backwards with the current. Periodically, they jump upstream to correct for the drift.

A point-source of light in an otherwise darkened room sufficed to anchor a waterstrider in one place on an artificial stream (figure 3). The insect picked its spot on the stream and learnt the corresponding elevation of the light, which in different experiments lay between  $20^\circ$  and  $80^\circ$  above the horizon. When the position of the bulb was suddenly switched to an elevation well above the preferred one, the waterstrider reduced the frequency of its jumps and drifted downstream until the light was again at the preferred elevation (figure 3). Conversely, if the angle was lowered, the insect immediately began jumping forwards until the light was once more correctly positioned on the retina. Waterstriders thus know the sign of the difference between the desired elevation of the light and its actual position and move to eliminate the discrepancy between the two values.

#### (d) Matching memories to a scene

With a single light bulb as the only visible feature, there is no problem about pairing items in the retinal image with those in memory. But in a richer environment there are chances of mispairing which grow as the insect moves away from its goal. Not only do the bearings and sizes of landmarks become increasingly different from those at the goal, but the order of landmarks on the retina change and objects which were too small to be recorded in memory may become visible while other landmarks disappear from view. This increasing mismatch between retinal image and a memory of landmarks viewed from the goal presents several difficulties.

An initial problem is to retrieve the correct memory. A bee may forage at several places each

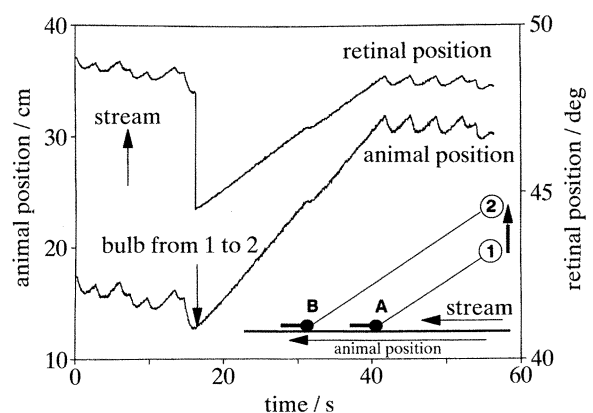


Figure 3. Waterstrider keeping station on the surface of an artificial stream flowing at  $0.75 \text{ cm s}^{-1}$ . The bulb located 115 cm from the insect was moved from position 1 to position 2. The insect compensated for the change in the bulb's height by shifting from A to B. Graph plots time-course of the insect's position on the stream and the retinal elevation of the bulb (W. Junger, unpublished data).



defined by a slightly different set of landmarks. How does the bee recall the memory appropriate to its current goal while it is still some distance away? One solution is to rely on more distant landmarks or other contextual cues to prime the retrieval of the memory of landmarks close to the goal (Collett & Kelber 1988). Bees were trained to forage from two identical white 1.8 m<sup>2</sup> platforms located 40 m apart on an area of grass. Trees and buildings from 6 to 10 s of metres away gave the bees a distinctly different view from each platform. The location of a sucrose reservoir on each platform was specified by objects on the platform. After every visit, the sucrose and these local landmarks were moved together to a new position. On platform 1 the reservoir was always 21 cm west of two yellow cylinders, and on platform 2 it was east of a blue upright triangle. When landmarks were occasionally swapped between platforms, bees searched west of the blue triangle on platform 1 and east of the cylinders on platform 2 (figure 4). In other words, they searched in the site appropriate to the platform they visited, as though the panorama associated with each platform triggered the memory of the local landmarks on that platform. And, despite their incongruous appearance, the swapped landmarks still guided the bees' search. This outcome should be contrasted with the same experiment performed inside two white huts separated by 33 m. In this case there were no visual cues by which the insect could distinguish the inside of the huts. With landmarks swapped between huts, the bees' search area was specified by landmark type and not by hut location.

A second problem caused by differences between memory and retinal image is in generating useful movement vectors. Large discrepancies between memory and retinal image mean that any matching procedure is likely to mispair items so that movement vectors no longer point at the goal. To avoid mispair-

ing, memories and retinal images should be sparse and the difference between them kept small. These conditions must be met without restricting the guidance system to a uselessly small area around the goal. A possible solution is to have several memories which are retrieved sequentially. The initial one should contain just distant landmarks, thereby reducing the likelihood of mispairings (Cartwright & Collett 1987). This memory would guide the insect to the rough area of the goal, where the current view matches that from the goal well enough to switch to a second memory emphasising close landmarks. These help the insect pinpoint the goal, while the exclusion of distant ones keeps the memory reasonably sparse (Cartwright & Collett, 1983; Zeil 1992*b*).

#### (e) Evidence for several memories

This scheme requires that bees should assess the relative distance of surrounding landmarks. In other situations, hymenoptera rely on motion parallax for range finding (Lehrer *et al.* 1990; Srinivasan *et al.* 1991), and there is evidence that bees and wasps learn the speed at which the image of a landmark moves over their retina as they fly in the vicinity of the goal. Sometimes (bees: Cartwright & Collett 1979; wasps: Zeil 1992*b*), the search position was not influenced by changes to the size of a landmark, suggesting that insects can keep a fixed distance from a landmark by matching its image speed to that stored during searching. This may only happen when there is a close resemblance between the flight path during learning and searching (see § 2*f*).

Secondly, hymenoptera locate goals using both 'near' and 'far' landmarks (e.g. Zeil & Wittmann 1987), but when they are close to the goal, they actively select near landmarks to steer their path (Cheng *et al.* 1987). Bees were trained to an array consisting of some landmarks close to the goal and some that were further away. On tests, landmarks which in training trials had been close to the food source were displaced relative to the more distant ones. Bees then searched preferentially at the location defined by the close landmarks (figure 5).

Suppose that there were one all-inclusive memory associated with a goal. Retrieval of this memory far from the goal would have disruptive effects. Stored areas corresponding to close landmarks would be readily mispaired (e.g. figure 5) and generate misleading motor commands. These considerations argue that the memory of nearby landmarks is only recalled when the insect has come close to the goal and the chances of mispairing are small.

#### (f) Orientation flights

Another perspective to the problem of retrieving memories comes from examining what insects do while they learn the disposition of landmarks around a goal. Many hymenoptera engage in stereotyped flights to acquire this information (for a review, see Wehner (1981)). These 'orientation' flights are performed by

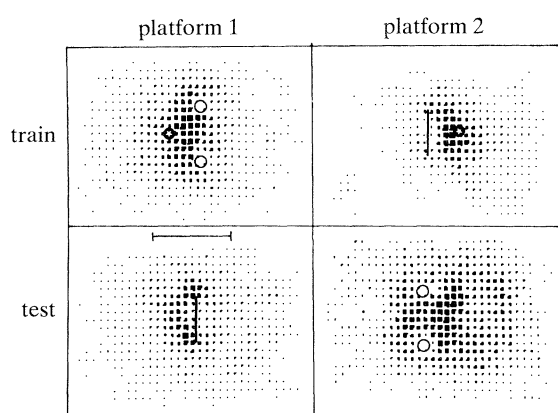


Figure 4. Search of bees trained to forage on two platforms with different landmarks on each. Top panel: search when tested with training arrangement: yellow cylinders on platform 1 are shown by circles; blue triangle on edge on platform 2 is shown by line; '\*' position of food in training. The size of black squares shows relative amount of time spent in different cells of an imaginary grid centred on landmarks. Bottom panels: search when landmarks are swapped. Calibration bar represents 50 cm (from Collett & Kelber 1988).

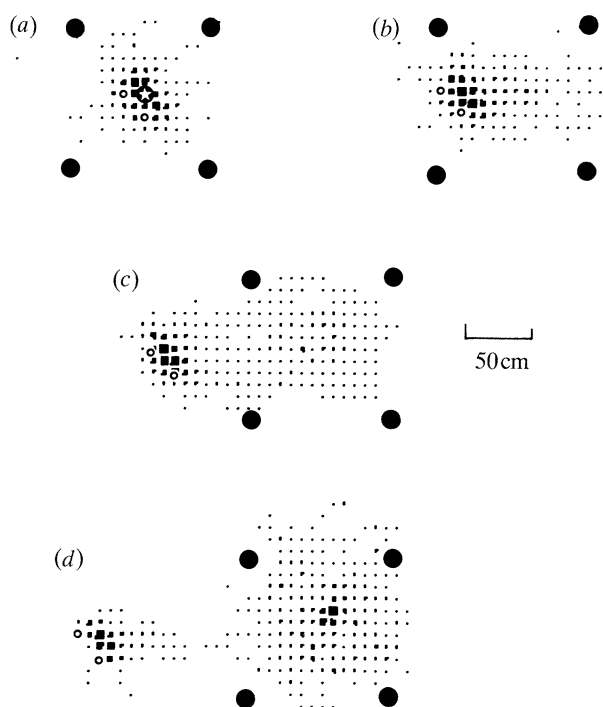


Figure 5. Search of bees trained to a site marked by two yellow (open circles) and four blue (filled circles) cylinders. (a) Tests with training array; '\*' position of food in training. (b–d) Tests with increasing displacement of yellow landmarks relative to blue. Search is preferentially determined by landmarks remembered as being close to the sucrose (from Cheng *et al.* 1987).

young honeybees when they first leave the nest to begin foraging, and by foraging bees and wasps on first departing from a new foraging area. A single flight is enough to ensure a successful return (e.g. Free 1955; Manning 1956; Tinbergen 1932; Zeil 1992*b*). In some species, the behaviour is interestingly sex-specific: males, which leave home on a one way trip with the sole purpose of impregnating a female, do not perform orientation flights.

Zeil (1992*a,b*) has analysed in detail the orientation flight that *Cerceris*, a solitary wasp, performs every morning on first leaving her nest or whenever she had difficulties in locating it on her previous return. The wasp emerges and turns to face the entrance. She then flies in a series of arcs centred on the entrance (figure 6). As the series progresses, the wasp flies higher and the arcs increase in radius. Throughout each arc, the wasp rotates her body axis to keep the nest roughly fixated by a region of retina located 60° laterally and 50° below the equator. The wasp's rotational velocity remains approximately constant during the series, and to compensate for the increasing radius, the wasp's translational velocity increases. At the end of each arc, she reverses flight direction and turns so that during the next arc the nest is fixated by the corresponding region of the other eye. The wasp, by switching eyes, ensures that both eyes view the surroundings in the vicinity of the nest entrance.

It is hard to discover what information the wasp extracts from the moving images generated during

these flights. But it is tempting to suppose that the geometry of the flight path has been shaped to aid the capture of relevant information and to filter out irrelevancies. One consequence of fixating the nest while circling around it is that landmarks close to the nest will be relatively stationary on the retina, whereas the image of distant objects will move at the wasp's rotational velocity (Cartwright & Collett 1983; Zeil 1992*a*).

Wasps could exploit this feature to furnish themselves with a set of distance-scaled, landmark memories. Suppose that wasps only learn the retinal positions and properties of those portions of the image which move below some threshold velocity. When arcs have a small radius, just landmarks close to the nest will be memorised. As the radius grows, the image velocity of landmarks progressively more distant from the nest will fall below the cut-off and so be incorporated in memory, whereas some of the small landmarks recorded earlier in the flight may drop out because their image is too small to be registered. With such memories, a wasp's return would first be guided by large landmarks that fall within a wide area around the nest. And then as she approaches closer, she would be influenced by landmarks of all sizes that are near to the nest.

If the wasp's return is to be guided by retinotopically defined memories, we might expect that to some degree the geometry of orientation flights will be reproduced during return flights. Although the exact path is not retraced, there are remarkable statistical similarities (Zeil 1992*b*). First, the wasp both faces in the same compass direction while orienting and returning and also views the landmark with the same region of retina (figure 7). She thus looks at the scene from similar vantage points on her outward and return flights. Secondly, the wasp tends to fly in the same direction relative to her long axis during orientation and return flights ( $\alpha$  in figure 7) and to adopt a similar distribution of angular velocities. By describing similar arcs in the two flights, the returning wasp can compare the motion of her retinal image with that recorded during the orientation flight and so control her distance from landmarks near to the nest (§ 2*e*). All of which suggests that wasps and bees simplify a confusingly rich scene by special purpose scanning movements and so make image matching a viable procedure.

#### (g) *The extent of image matching*

Somewhat uncertain measurements suggest that guidance by image matching may be limited to a few metres around a goal. The first estimate is given by the maximum radius of the arcs performed in orientation flights. Wagner (1907) noted that bumblebees fly in arcs facing the nest until the radius reaches about 1.75 m. They then turn and fly away. Similarly, the maximum radius of most orientation flights of *Bombix* is less than 2 m, with occasional 5 m and 10 m outliers (Chmurzynski 1964).

A second estimate comes from shifting the landmarks which are normally near to the goal until they

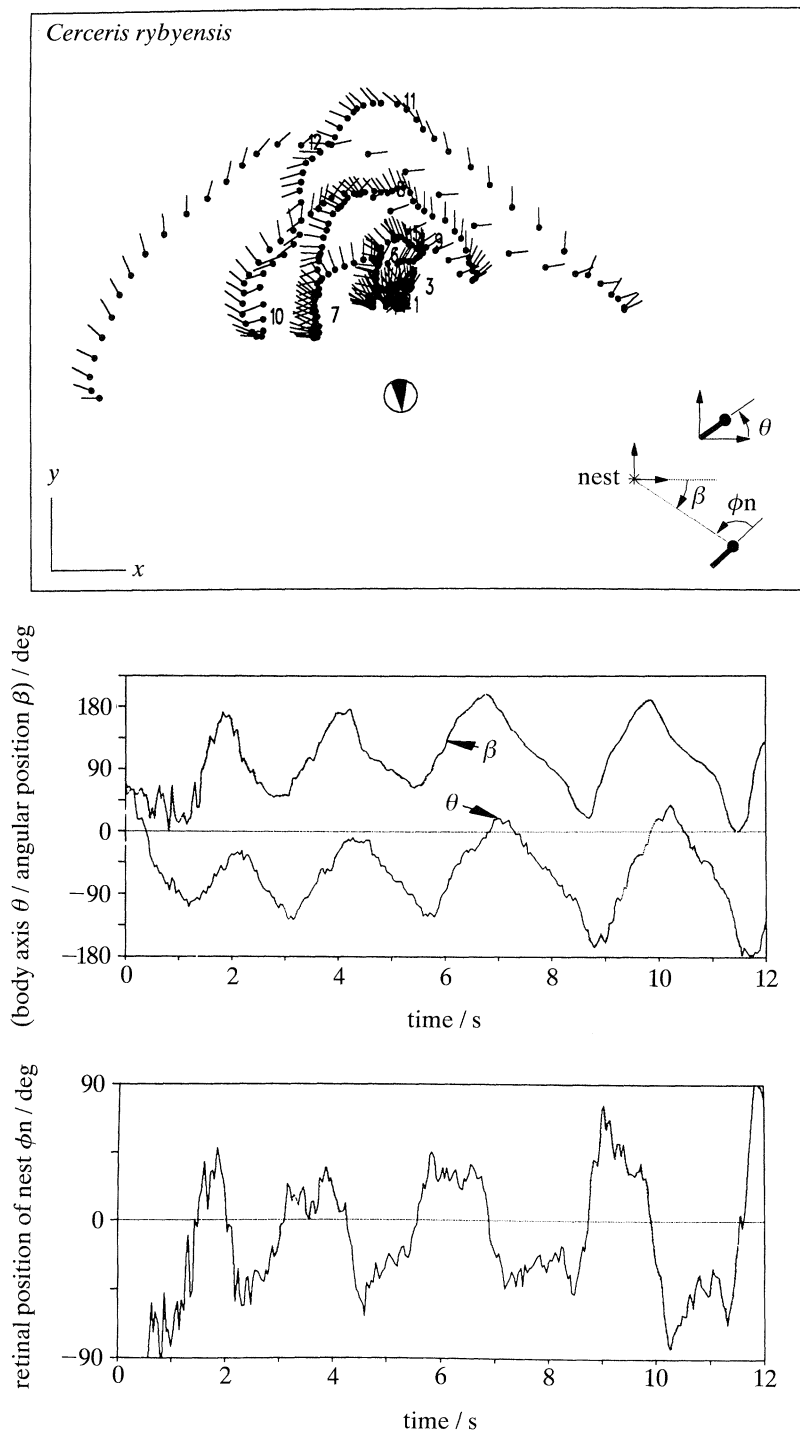


Figure 6. Orientation flight of *Cercheris* after emerging from nest (just left of 1). Top: wasp's position, viewed from above, is shown every 40 ms during the first 12.5 s of the flight. Cylinder (2.2 cm wide, 6.3 cm high) shown by arrowed circle is just below nest. Bars marked  $x$  and  $y$  are 5 cm. Wasp characteristically flies so nest lies between it and landmark. Bottom: timecourse of body orientation ( $\theta$ ), angle of line joining head to nest ( $\beta$ ), and retinal eccentricity of nest ( $\phi$ ) (from Zeil 1992a).

no longer steer an insect's search. The idea is to measure how far these landmarks can attract insects from the area to which they have been brought by other navigational aids. This distance may be an underestimate because (i) not all relevant landmarks may have been moved, and (ii) other mechanisms may actively hold an insect close to where it was brought. Fabre did the first experiment of this type. He shifted a stone with the nest of a mason-bee attached to it by 1 m and the returning bee flew

directly there. But if he moved the stone 2 m, the bee did not find the nest. More systematic manipulations showed that *Bembix* coped with at most 3 m to 4 m of displacement (Chmurzynski 1964).

### 3. LANDMARK GUIDANCE FAR FROM A GOAL

Insects often follow stereotyped routes when travelling between two familiar places. Figure 8 illustrates the

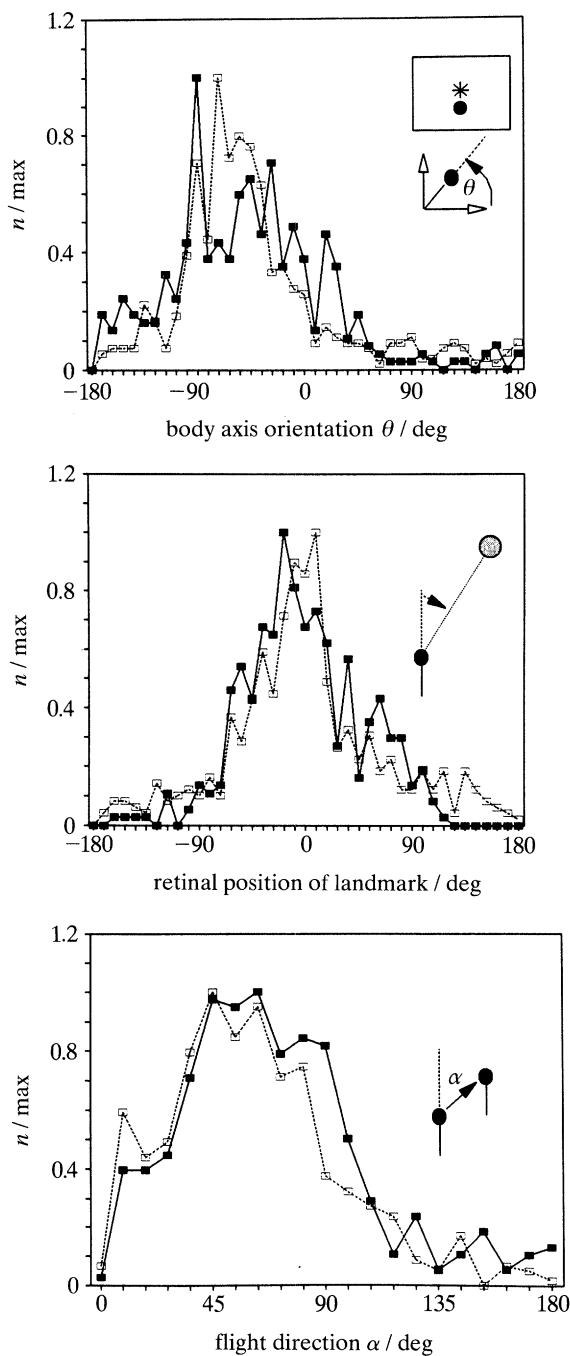


Figure 7. Comparison of flight parameters during the orientation flight of Figure 7 (closed squares) with the subsequent 39 s search flight (open squares) during which landmark was placed over nest entrance (from Zeil 1992b).

homeward trajectories of desert ants (*Cataglyphis bicolor*) foraging at a site 30 m from their nest. Four distinct landmarks were placed on the bare terrain and over several days each individual settled on one out of the possible routes around the landmarks. The similarity of the trajectories of different individuals taking the same route (figure 8c) suggests that the ants obeyed the same instructions.

*Cataglyphis* do not lay chemical trails and the details of an ant's path on its homeward route are governed by two factors: first, its 'home vector', that is its

knowledge that its nest lies a given direction and distance from its current location, and, secondly, its reaction to individual landmarks.

A simple experiment shows that ants will learn to recognize individual landmarks (figure 9). Foragers were trained to collect melon juice 30 m from their nest with two landmarks placed along the route. The first, an oil barrel, lay 2 m to the right of the direct path between melon and nest and halfway along it. The second, a pair of triangles, was stationed 2 m to the left of the direct path and 2 m from the nest. After a few days of training, ants were caught at the melon and carried to another bare area of sand. On release, they headed in the direction dictated by their home vector. One of the two landmarks was placed 10 m from the release site along the expected trajectory, so forcing the ants to detour around the obstacle. When the barrel blocked an ant's path, the insect detoured consistently to the right, but, when the triangles were in the way, detours were to the left. Ants thus distinguished between the barrel and triangles. Note that the ant detoured appropriately around the triangles although they were encountered sooner than usual. A variety of tests suggests that landmarks are recognised by their distinctive visual features and that recognition does not depend upon seeing landmarks in their accustomed sequence or at the expected distance along the home vector.

Route landmarks are used primarily to fine tune the home vector. The ant does this by adjusting its path so that a particular landmark is kept on its accustomed side. Experiments and simulations suggest that this is accomplished very simply. Contrary to behaviour close to the goal, the trajectory near a route landmark is not steered by the ant's memory of the landmark's bearing and size. The insect learns only to recognise a landmark and to associate with that landmark the decision to turn consistently to its left or right. The ant's rate of turning is dictated by the landmark's immediate appearance. In brief, as an ant approaches a landmark, it continuously measures the landmark's retinal size and turns at a speed which increases with that size (e.g. figure 9). Once the ant is abreast of a landmark, that landmark ceases to exert any effect. The ant's trajectory is then determined by the home vector and by the next landmark, if one is present. This strategy lightens memory load. But it means that the ant cannot choose the form of its trajectory around a landmark, that is imposed by the landmark's size and distance.

#### 4. MEMORY SIZE AND ROUTES WITH MULTIPLE GOALS

This account suggests that successful navigation relies more on feats of memory and recall than on elaborate information processing. The insect's stored representation of a place seems to be a filtered but relatively unprocessed image of the surroundings, which is parsed for features like the position of edges, their orientation, speed of motion and colour. An insect may store many such memories taken from different viewpoints.



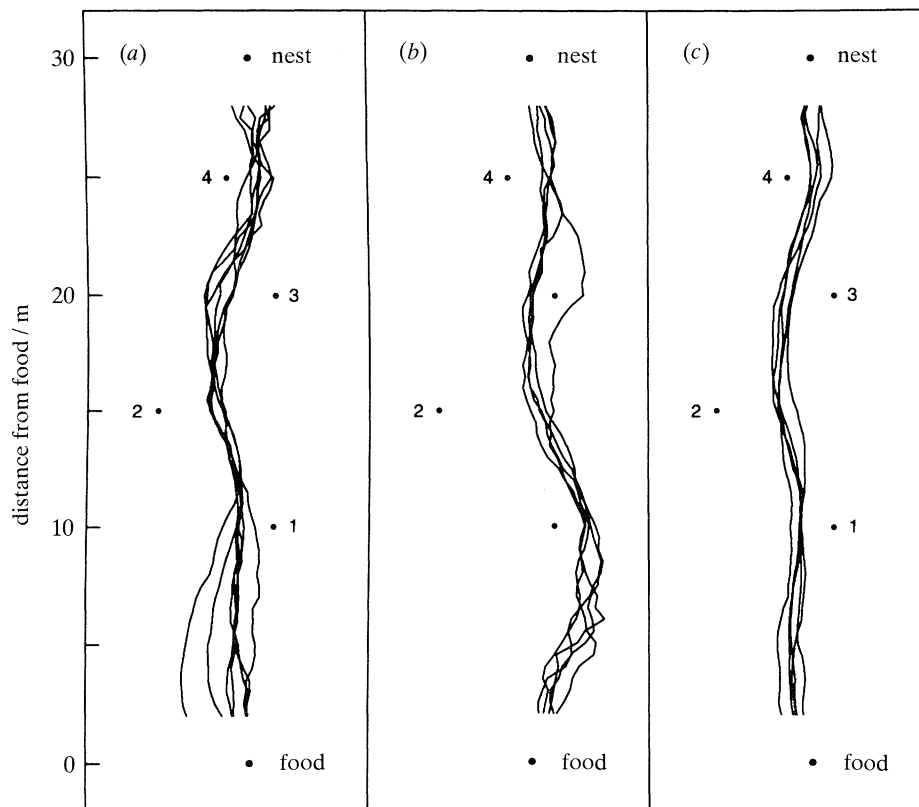


Figure 8. Homeward trajectories of desert ants. (a,b) Superimposed trajectories from two different ants one going to the left (a), the other to the right (b) of landmark 1. (c) Averaged trajectories of five ants passing left of landmark 1 (from Collett *et al.* 1992).

Moreover, insects often memorise several foraging sites at once. A bumblebee, for instance, collects nectar or pollen from a series of plants which it visits in a fixed sequence on a single foraging trip (Heinrich 1976). When it leaves a newly discovered plant, it

performs an orientation flight. Should that plant then be removed, the bumblebee continues to visit the precise site of the missing plant and to hover there for about 10 s before continuing on its route (Manning 1956). The record is set by orchid bees which regularly forage from about 40 isolated plants scattered along a 20 km path through tropical forest (Janzen 1961).

At the moment we can do little more than marvel at what can be stored in a hymenopteran brain. There are too many uncertainties to attempt a quantitative estimate of memory capacity. We do not know, for example, the spatial resolution of stored images, or how images are encoded, or how long a sequence of images represents a single place.

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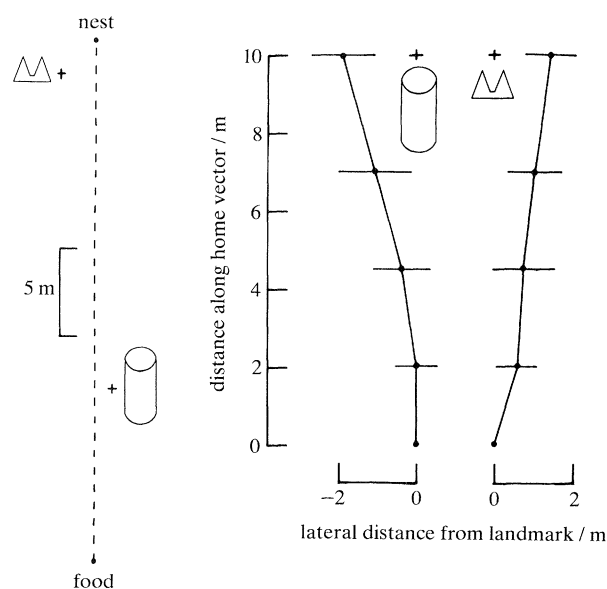


Figure 9. Homeward trajectories of ants trained to route on left and released on testing ground with either barrel or triangles in the path of the home vector, 10 m from the release site. Filled circles give mean position of ants and horizontal bars show  $\pm 1$  standard deviation of the mean (from Collett *et al.* 1992).

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