

## HOMING IN WOOD ANTS, *FORMICA JAPONICA*: USE OF THE SKYLINE PANORAMA

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### Summary

Homeward orientation was studied in wood ants *Formica japonica* that, while foraging, shuttled back and forth along a 7.9 m route between the nest and a feeding site located on a wide terrace platform surrounded by a conspicuous landmark panorama. The return runs of the ants were amazingly straight, not only in the controls (starting at the feeding site) but also in ants displaced for various distances to the left and right of the feeding site. These courses, however, were oriented neither parallel to the predisplacement courses nor directly towards the nest. This result excludes the use of chemical cues and celestial compass cues. Furthermore, the nest itself, or some object close to it, could not have served as a beacon.

The extensions of the homeward paths taken by ants that had been displaced to various release sites up to 11 m sideways from the training route intersected at a point far (approximately 13 m) behind the nest. This result suggests that the ants used distant landmarks seen by them in their frontal fields of view.

To test this hypothesis, the distant landmark panorama

was concealed by an opaque sheet mounted at right angles to the normal return route of the ants and extending up to different elevations. Shielding the lower part of the landmark panorama had no effect on the homeward paths. However, when the screen was mounted in such a way that the ants could only see the top skyline, represented by the upper edges of a line of trees, for part of their return run, it was only during these parts that their path was oriented in the homeward direction.

When, during the course of displacement experiments, the ants were deprived of their familiar skyline panorama, they moved in their home direction only for an extremely short distance (0.1–0.4 m rather than the usual 7.9 m) and then started a systematic search programme. Hence, in the present context, skylight information is not used, at least not extensively. Instead, ants use the distant skyline as a navigational guidemark.

Key words: homing, navigation, landmark guidance, skyline panorama, ant, *Formica japonica*.

### Introduction

Several species of wood ant (genus *Formica*) have been shown to exhibit high degrees of site or route fidelity based mainly on visual memories of environmental landmarks (Rosengren, 1971; Rosengren and Pamilo, 1978; Rosengren and Fortelius, 1986). Similar behaviour patterns, especially the dominance of visual-landmark over chemical-trail information, are displayed by representatives of many other ant genera under a variety of field and laboratory conditions (for a review, see Wehner, 1992).

In nearly all these studies, landmark guidance has been investigated by using conspicuous nearby landmarks specifying either the nest or the feeding site, or in some exceptional cases (e.g. Wehner et al., 1996) the route between the two sites. For example, if desert ants *Cataglyphis fortis* are trained to search midway between two identical black cylinders (Wehner and R ber, 1979) or in the centre of a triangular array of three such cylinders (Wehner et al., 1996), they persistently search at the fictive position of the goal, in this case the nest entrance. They move so as to decrease the discrepancy between

a memorised ('snapshot') image of the landmark panorama around the goal and the current image of the landmarks (for landmark learning in honeybees, see Cartwright and Collett, 1983, who designed a computer model simulating this matching-to-memory behaviour).

A detailed analysis of the walking trajectories of the ants reveals that, when wood ants *Formica rufa* leave a newly discovered feeding site, they repeatedly turn back and face the landmarks positioned close to the feeder (Judd and Collett, 1998; Nicholson et al., 1999). This turn-back-and-look behaviour was first described for honeybees (Lehrer, 1993), but in wood ants it has also been shown that if food is placed between two different landmarks the ant revisits the feeder by first fixating the more conspicuous landmark and then being directed towards the less conspicuous one positioned closer to the feeder. In general, the ant appears to take several snapshots of the landmarks from different vantage points, i.e. it holds the landmark images steady on its retina at several discrete positions.

In the present account, the behaviour of wood ants *Formica japonica* was studied with respect to distant rather than nearby landmarks. It was found that these distant landmarks formed such a conspicuous skyline that they were used by the ants as a guidemark overriding even celestial compass information.

## Materials and methods

### *Materials and experimental area*

Experiments were carried out on a terrace attached to the south of a 30.4 m wide and 8.1 m high building. The dimensions of the terrace were 23.8 m (east–west direction,  $x$ -axis) by 5.8 m (north–south direction,  $y$ -axis). The terrace floor was raised 0.32 m above ground level. In all graphs, the northeast corner of the terrace defines the origin of the  $x,y$  coordinate system used for recording the positions of the ants and the positions of the surrounding landmarks (see Fig. 1, Fig. 3). The terrace was surrounded by a short-mown lawn at its eastern, southern and western sides and by the 3 m high glass windows of the building at the northern side. Its surface was paved with tiles measuring 20 cm $\times$ 20 cm, each tile consisting of a square array of 36 parts (see Fig. 4). This rectangular grid of floor lines was used for recording the positions of the ants.

The terrace was used by the experimental animals, diurnally foraging wood ants of the species *Formica japonica*, as their food-searching ground and was used by the experimenter as the main test arena.

### *Nest and feeding site*

The nest used in all experiments was located near the southeastern corner of the terrace (filled circle in Fig. 1,  $x=0.53$  m,  $y=6.80$  m). It opened to a grass-covered surface through a few inconspicuous entrance holes (approximately 3 mm in diameter). The feeding site was established at position  $x=9.5$  m,  $y=2.0$  m (referred to as F9.5 and indicated by the open circle with a cross in Fig. 1). The feeder consisted of a glass tube (3.0 cm wide and 5.0 cm high) filled with honey water (1/3 dilution), which was placed upside down on a dish (5.3 cm wide and 0.8 cm high) covered with filter paper (see Fig. 4). The ants visited the feeding site freely, consumed honey water and returned to their nest. They returned to the feeder approximately every 10 min. During feeding, the ants were marked on their gaster with dots of a water-soluble colour paint. Only marked ants that had performed several round trips were used in the experiments. Ants from other nests were removed from the feeder.

## Experiments

### *Recording the trajectories of the ants*

To record the trajectories of the ants on the terrace, vial caps (1.3 cm in diameter) were placed every 10 s on the walking paths of individual ants. After the ants had completed their return runs, the positions of the vials were recorded using the  $x,y$  coordinate system described above.

### *Displacement experiments*

*Displacements within the training area (terrace).* When the ants started to move from F9.5 towards N, they were captured in a glass tube and carried in the dark to a position located 7.6 or 3.8 m east of F9.5, or 3.8, 7.6 or 11.4 m west of F9.5, where they were released. Hence, the coordinates of the release sites are (1.9, 2.0), (5.7, 2.0), (13.3, 2.0), (17.1, 2.0) and (20.9, 2.0). The sites themselves are referred to as R1.9, R5.7, R13.3, R17.1 and R20.9, respectively (see Fig. 2). After the ants had been released, their walking trajectories were recorded.

*Displacements beyond the training area.* Ants caught at F9.5 were carried in the dark either to a football field located approximately 500 m northeast of the terrace (an approximately 7 min walk) or to the roof of the building to which the terrace belonged. In both places, a 6 m $\times$ 6 m test area was prepared which contained a square array of coloured dots (grid width 0.5 m) and was used to record the trajectories of the ants. The former area was mostly bare ground with a sparse cover of short grass. The latter area was located at a vertical distance of 7.7 m above the terrace, and the centre of the test area was positioned at  $x=17.58$  and  $y=-4.50$  (corresponding to the Cartesian system of coordinates described for the terrace floor). The ants were released at the centres of the test areas, and their trajectories were recorded on graph paper using a reduced scale (2.8/100). Recording was completed when the ants had reached the borders of the test areas. Data were not included in the analysis if the ants stayed within the test area for more than 20 min. The trajectories of all ants were later read by a scanner and digitized as series of 12 cm line segments using the public-domain NIH image programme.

### *Visual deprivation experiments*

To screen off the frontal views of the returning ants, a wide opaque sheet of silver polyethylene film, normally used for agricultural purposes (Tokan Kyosan Co., Ltd, Japan), was placed perpendicular to the mean courses of the ants (from F9.5 to the nest). The distance of the sheet from F9.5 and its height were varied systematically.

### *Calculation of walking directions*

#### *Walking directions on the terrace*

The directions of all segments of the paths taken by the ants were recorded every 10 s in a counterclockwise (positive) sense of rotation. South is defined as 0°. As the walking trajectories were fairly straight, the directions of particular paths were computed as the mean of all segments pertaining to a particular path. The ants displaced to R17.1 and R20.9 first ran straight in the homeward (southeast) direction and then occasionally turned sideways towards the left (northeast direction) (see Results). In such cases, only the segments pertaining to the first part of a particular path, which were directed towards southeast, were used to calculate the mean direction. In each experiment, the mean and the angular standard deviations of the directions of all runs recorded were calculated according to circular statistical methods (Batschelet, 1981).

*Walking directions on the two additional test areas*

The trajectories of ants displaced to the nearby football field and to the roof of the building were not straight but tortuous, so the walking direction of a particular path was represented by the frequencies of heading directions. The trajectory was divided into a series of 12 cm line segments, and the percentages of the segments falling into four angular quadrants (A–D) were calculated. Quadrant A was centred about the fictive home direction. Within each quadrant, the percentages were averaged for all runs tested.

**Results**

*Return paths between F9.5 and the nest*

As shown in Fig. 1A, the homeward paths from F9.5 to the nest were fairly straight. The mean direction chosen by the ants was  $61.3 \pm 6.0^\circ$  (see Table 1). This direction coincided extremely well with the direction of the nest as measured from F9.5 ( $61.9^\circ$ ). The outward paths from the nest to F9.5 are depicted in Fig. 1B. Their mean direction was  $60.6 \pm 5.7^\circ$  (Table 1). Note that the directions of the outward paths were rotated by  $180^\circ$  to make them directly comparable with the directions of the inbound courses (see above). Apart from this  $180^\circ$  discrepancy, there was no statistical difference between the mean angles of the inbound and outbound paths ( $P > 0.25$ ). What cues do the ants rely on to enable them to head straight towards the nest over a distance of 7.9 m? This question will be tackled by the displacement experiments described in the next section.

*Displacement experiments from F9.5 to various release sites within the training area (terrace)*

Homebound ants were displaced from F9.5 to various release sites on the terrace. The resulting paths are shown in Fig. 2. Ants displaced to R1.9, R5.7 and R13.3 took fairly straight courses (Fig. 2A), but those released at R17.1 (Fig. 2B) and R20.9 (Fig. 2C) exhibited a range of courses from straight to smoothly curved. In these ants, the initial path was straight and directed towards home, but then turned sideways towards the left, i.e. towards the side of the building, and finally was again directed towards home (Fig. 2B,C). The mean directions of the displaced ants are shown in Table 1. The mean angles of ants displaced eastwards (R1.9 and R5.7) decreased, whereas those of ants displaced westwards (R13.3, R17.1 and R20.9) increased, in comparison with the directions of the controls, i.e. the ants returning from F9.5. The angular changes are proportional to the displacement distances (Table 1). However, the directions taken by the displaced ants did not coincide with the directions towards the nest as viewed from the sites of release (Table 1).

These results show, first and foremost, that the return courses of the displaced ants are not guided by chemical trails. Furthermore, if the displaced ants had relied mainly on skylight cues, their courses starting from various release sites should have been parallel to the

Table 1. Mean walking directions of ants starting at feeding site F9.5, at the nest and at various release sites

Starting site	Number of runs recorded	Mean path angle (degrees)	Nest direction (degrees)	Statistical differences <sup>1</sup>
Nest	11	$60.6 \pm 5.7^2$		$P > 0.25^3$
R1.9	10	$49.8 \pm 4.6$	15.9	$P < 0.001$
R5.7	10	$57.1 \pm 2.9$	47.1	$P < 0.05$
F9.5	43	$61.3 \pm 6.0$	61.9	$0.05 < P < 0.10$
R13.3	10	$65.0 \pm 4.3$	69.4	$0.05 < P < 0.10$
R17.1	10	$68.8 \pm 4.0$	73.8	$P < 0.025$
R20.9	10	$73.5 \pm 4.0$	76.9	

Values are means  $\pm$  angular s.d.

<sup>1</sup>Differences between the directions taken by the ants at two neighbouring sites (Watson–Williams test).

<sup>2</sup>Actually  $60.6 + 180 = 240.6^\circ$  (see Results).

<sup>3</sup>Difference between the directions taken by the ants at the nest and F9.5.

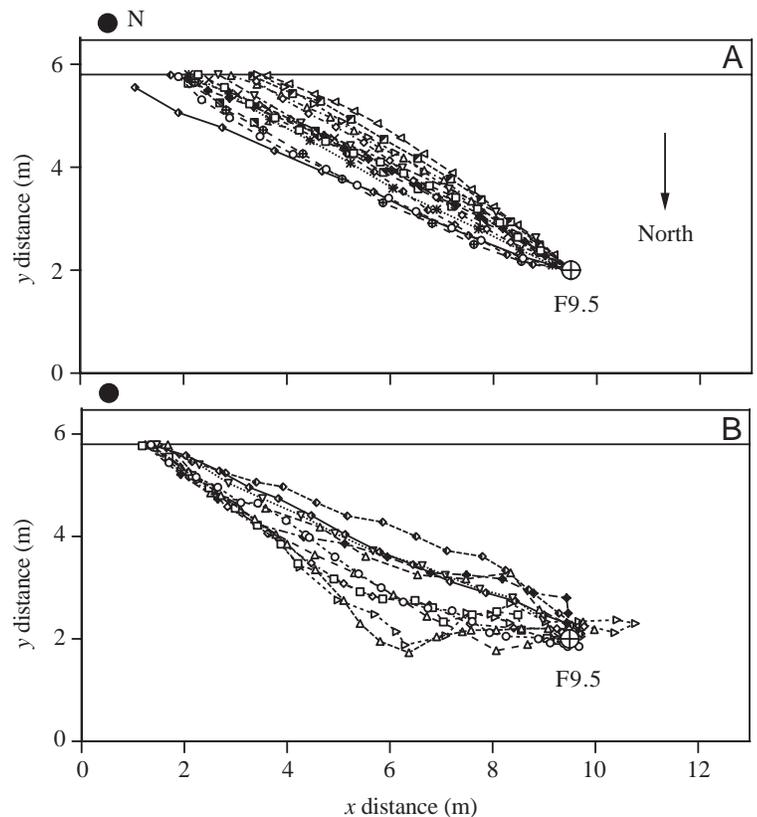


Fig. 1. (A) Inbound (return) and (B) outbound (foraging) paths of individual ants shuttling back and forth on the terrace platform between the feeding site (F9.5; open circle with cross) and the nest (N; filled circle). Only the eastern half of the terrace is shown. The northeast corner of the terrace is taken as the origin of the x,y coordinate system. The positions of the ants were recorded every 10 s.  $N=15$  (A) and  $N=11$  (B).

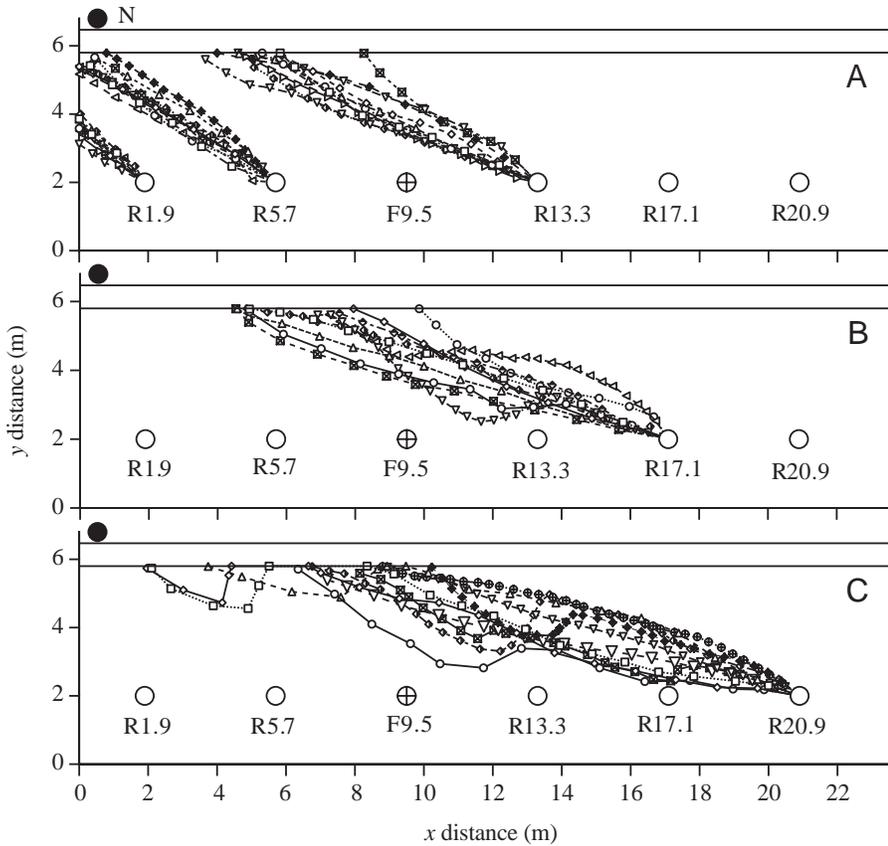


Fig. 2. Homeward (return) paths of ants displaced from F9.5 to various release sites (open circles). (A) Paths from R1.9, R5.7 and R13.3. (B) Paths from R17.1. (C) Paths from R20.9.  $N=10$  in each experiment. N, nest.

nest itself could not be seen by the returning ants because the terrace floor was elevated 0.32 m above the ground and the subterranean nest was located 1 m south of the southern edge of the terrace. Hence, ants walking on the terrace were unable to see the nest directly until they reached the southern edge of the terrace. Furthermore, within an area of 6 m around the nest, there were no tall objects recognisable as landmarks by the ants on the terrace.

Thus, if the ants were using visual guidemarks, these must have been provided by the trees and bushes in the distance. Fig. 3 illustrates the two-dimensional topography of the terrace and its surroundings. The mean homeward courses of the ants (data from Fig. 1 and Fig. 2) have been added to this topographical sketch, in which the positions of trees and bushes are indicated.

homeward direction as seen from the feeding site at F9.5. The results show that this is not the case.

The remaining possibility is that the ants relied on the visual landmarks in the surroundings of the training platform. The

indicated. If the lines of the courses followed by the ants are extended, they all (with the exception of the R20.9 line) intersect at a particular position ( $x=-11.3, y=13.3$ , i.e. around the southwest corner of the car park). This point will

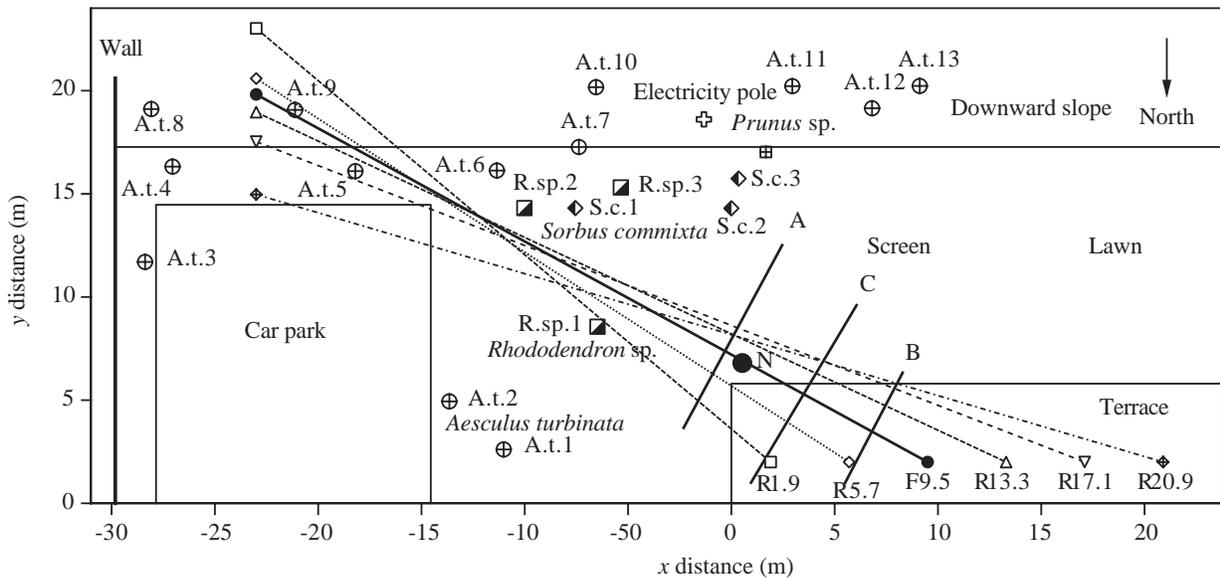


Fig. 3. Topographical layout of the terrace platform and its surroundings. The mean homeward courses of the ants starting at F9.5 and at the various release (R) sites (see Fig. 1, Fig. 2) and their extensions beyond the nest (N) area are included. The positions of trees, bushes and other conspicuous objects are marked. The lines labelled A, B and C indicate the positions of the screen used in the deprivation experiments. For further details, see text.

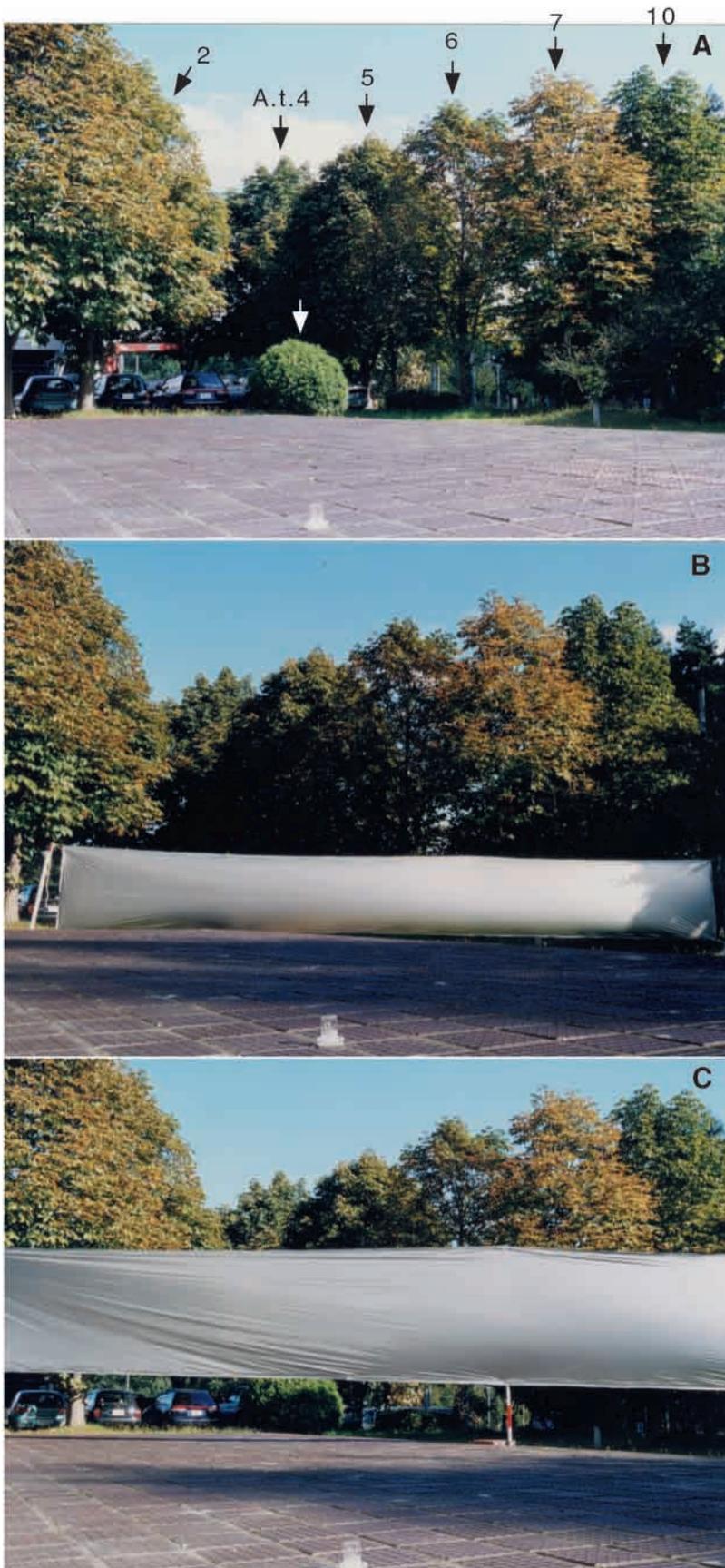


Fig. 4. (A) Photograph depicting the experimental area taken from behind F9.5, where the feeder can be seen in the foreground. The hemispherical bush in the centre is a rhododendron plant (white arrow; R.sp.1 in Fig. 3), and the surrounding trees are horse chestnuts (black arrows labelled with individual numbers corresponding to those in Fig. 3). The ants returning from F9.5 walk in a direction coinciding approximately with the right edge of R.sp.1. The yellow dots on the ground running back from the feeder are vial caps placed on the path taken by the ant. (B) The same landscape but with screen A mounted in the experimental area. (C) The same landscape but with screen C mounted in the experimental area.

subsequently be termed the focal point. The fact that the straight homeward courses of ants released at various sites aimed at a point located more than 13 m behind the nest raises the question of whether the ants were guided by distant landmarks positioned in their frontal visual fields.

Before proceeding with this argument, the results of preliminary experiments, in which the ants after having returned home from the feeding site were captured near the nest entrance and displaced to various release sites, will be briefly described. After release, ants displaced to R17.1 and R20.9 started their searching behaviour (see below), while those displaced to R1.9, R5.7 and R13.3 took straight homeward paths as seen in the displaced ants from F9.5 ( $N=5-7$  in each experiment; data not shown).

#### *Behaviour of ants deprived of their frontal field of view*

A conspicuous high silhouette of trees and bushes surrounds the focal point defined above (see Fig. 4A). Skyline panoramas seen from the nest, from the feeding site and from various release sites are shown in Fig. 5 as horizontograms measured every  $10^\circ$  of azimuth. What features of this skyline panorama might have been exploited by the ants? We tried to answer this question by screening off different parts of the visual panorama and recording the behaviour of the ants.

#### *Deprivation of the lower field of view*

In a first series of experiments, the lower fields of view of the homing ants were screened off by a vertical sheet placed 1 m behind the nest and arranged perpendicular to the main courses of the ants from F9.5 to the nest (screen A in Fig. 3 and Fig. 4B). The sheet was extended vertically from 0.3 m to 1.6 m (the gap between the bottom edge of the sheet and the ground cannot be seen by the ants

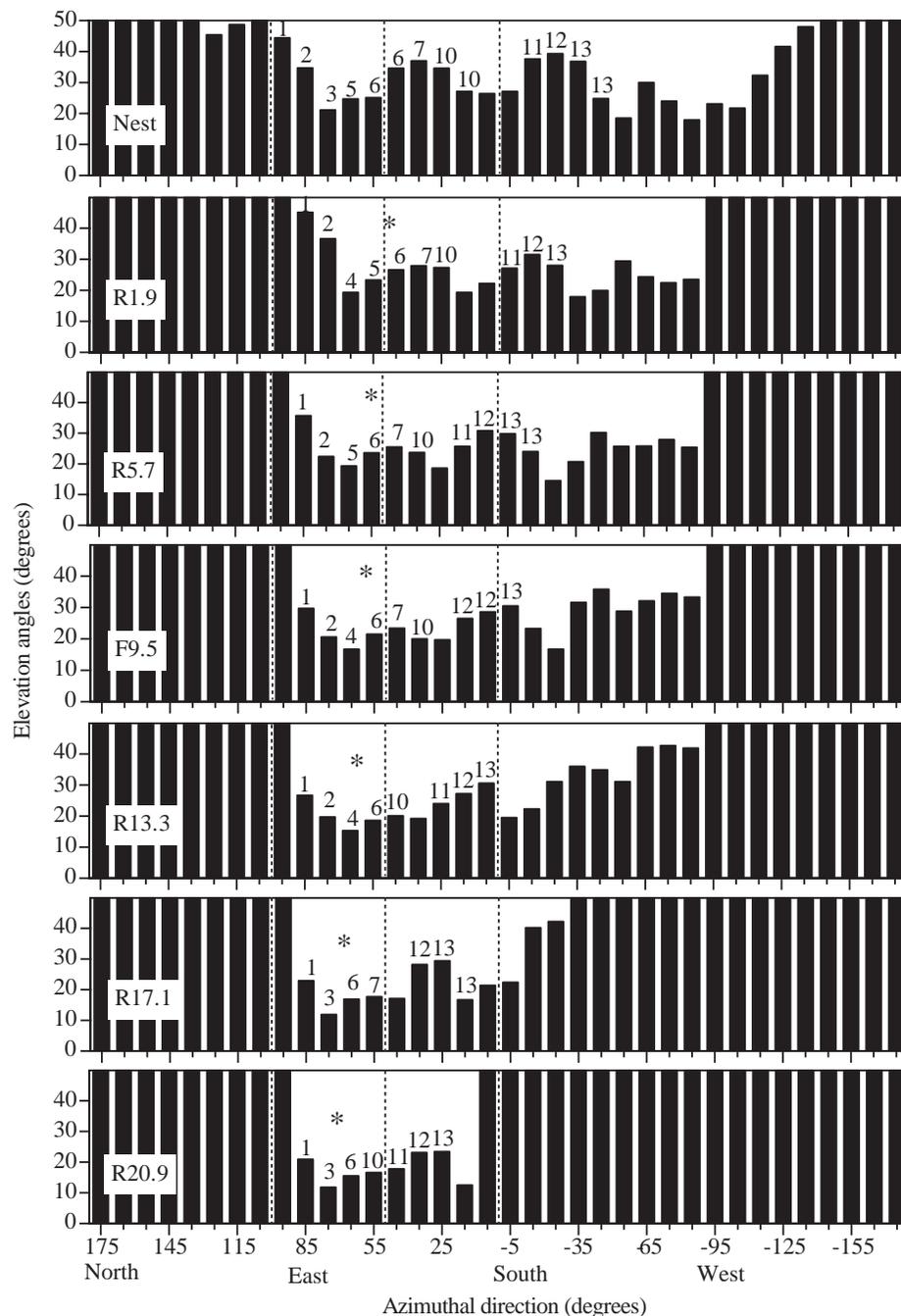


Fig. 5. Horizontograms as seen from the nesting site (Nest), the feeding site (F9.5) and the various release sites (R1.9–R20.9). The abscissa shows the azimuthal direction; south defines 0° in a counterclockwise (positive) sense of rotation. Elevation angles of the skyline (ordinate) were measured every 10° of azimuth using a transit (Tracon S-25, Ushikata Co., Ltd, Japan). As the measurable angle of elevation using the transit was up to 50°, all elevation angles higher than 50° are represented as 50°. The numbers at the top of each column corresponds to the numbers of chestnut trees in Fig. 3 (A.t.1–A.t.13). The asterisk shows the mean homeward direction of ants starting from their respective feeding or release site (see Table 1). The high elevation angles for the north side were due to the building positioned next to the terrace, and those for the south to west side in the plots for R17.1 and R20.9 were due to a cherry tree (10.0 m in height) located near the southwest corner of the terrace ( $x=24.5$  and  $y=5.6$ ; not shown in Fig. 3), the branches of which overhung the west side of the terrace. For reference, vertical dotted lines are drawn at 0°, 50° and 100°.

#### Deprivation of the entire frontal field of view

In this experiment, the vertical sheet (1.8 m high and 6.0 m wide) was placed 3.1 m from F9.5 (screen B in Fig. 3). Its dimensions (30.2°×88.5° as seen by the ants from their starting point) ensured that none of the chestnut trees (see Fig. 3; A.t.1–A.t.10, which were 10.3–12.5 m tall and located more than 20 m away from F9.5) located within the 60° frontal fields of view of the ants could be seen by the ants as they left F9.5, with the exception that the tip of

on the terrace because the terrace floor is raised 0.32 m above the ground) and 10 m in the horizontal direction and, hence, exhibited angular dimensions of 6.5°×48.2° as seen by the ants from F9.5. This arrangement completely deprived the ants of the lower part of their frontal fields of view; e.g. on leaving F9.5, they could not see the rhododendron bushes (R.sp.1 and R.sp.2 in Fig. 3, which were 1.8 and 0.5 m high, respectively) or the lower parts of the chestnut trees (in the case of A.t.5, up to a height of 3.6 m).

As shown in Fig. 6A, the screen had almost no effect on the homeward courses taken by the ants. The mean course angle (60.3±11.0°,  $N=20$ ) was not statistically different ( $P>0.25$ ) from the homeward courses of the controls (61.3±6.0°, Fig. 1A).

A.t.1 was visible, but soon dropped out of sight behind the screen after the ants had proceeded 23 cm from F9.5 along their homeward course.

In spite of this severe obstruction of their frontal skyline, the ants still ran straight towards the sheet, but their courses deviated from the true home direction (Fig. 6B). The mean course angle (49.7±8.8°,  $N=13$ ) differs significantly ( $P<0.001$ ) from that of the controls. Have the animals, in this situation, relied on their skylight compass? Or did they use visual landmarks positioned in their lateral fields of view? These questions will be discussed below.

In the next experiment, the size and position of the vertical shield were the same as those in the previous experiment

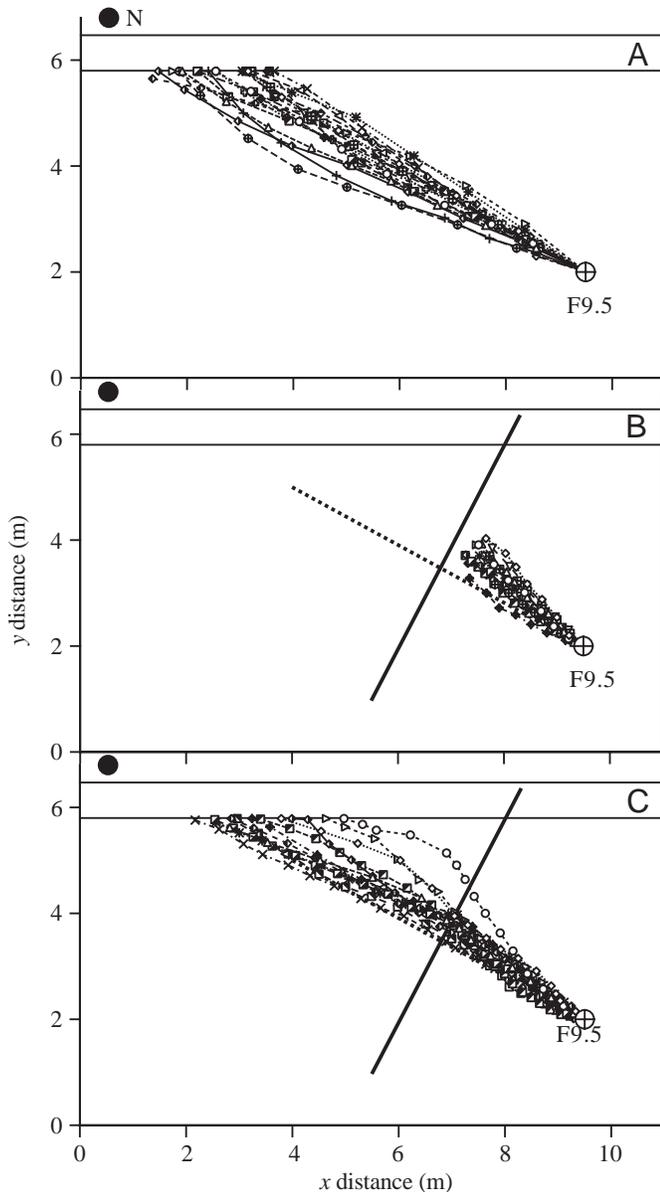


Fig. 6. Deprivation experiments. The frontal fields of view of the ants were obscured by screens (for exact positions, see Fig. 3). The heavy dotted line (in B and C) indicates the normal homing direction. (A) Homeward paths of ants deprived of the lower parts of their frontal fields of view (screen A positioned 1 m behind the nest; see Fig. 4B).  $N=20$ . (B) Homeward paths of ants deprived of their entire frontal fields of view (screen B, positioned 3.1 m from F9.5, as indicated by the heavy black line; height 1.8 m).  $N=13$ . (C) The same screen as in B, but raised by 10 cm, so that the ants were able to pass underneath it.  $N=13$ . N, nest.

(screen B in Fig. 3), but the screen was raised by 10 cm, so that the ants could pass through the resulting opening between the bottom edge of the screen and the surface of the platform. Again, the starting courses of the ants were fairly straight, but a marked directional change occurred after they passed the screen (Fig. 6C). The mean angle of approach before passing the screen was  $53.1 \pm 9.9^\circ$  and that after passing the screen

was  $63.9 \pm 8.1^\circ$  ( $N=13$ ). Although the two means differed significantly from each other ( $P < 0.01$ ), the first ( $53.1^\circ$ ) was not significantly different from angle of approach in the previous experiment ( $49.7^\circ$ ;  $P > 0.25$ ) and the second ( $63.9^\circ$ ) not significantly different from the normal homing direction ( $61.3^\circ$ ;  $P > 0.10$ ).

#### *Deprivation of the upper parts of the frontal fields of view*

The screen used in the first shielding experiment was now positioned 6.8 m away from F9.5 and extended vertically from 0.6 m to 1.9 m, and 10 m in the horizontal direction (screen C in Fig. 3; see Fig. 4C). With this arrangement, ants at F9.5 could see the lower parts of their frontal skyline (up to an elevation of  $5.0^\circ$ ) and the uppermost parts (from an elevation of  $15.5^\circ$  upwards). When proceeding along their homeward courses, these ants experienced a continuous decrease in the upper part of their landmark panorama, while the angular extent of the lowermost part gradually increased. When the ants had reached the sheet, the entire landmark scenery was again available to them.

Under these experimental conditions, 36 homing paths were recorded (Fig. 7A). Although not generally straight, they were roughly directed towards the nest. In the initial phase of their homeward journey, the ants followed their normal homebound course (up to the position  $x=6.8$ , the mean course angle of  $61.7 \pm 5.6^\circ$  was not statistically different from the normal homeward course,  $P > 0.25$ ). Of the 36 paths, 22 exhibited a characteristic sigmoidal shape (Fig. 7B; for the remaining paths, see Fig. 7C). The middle phases of the sigmoidally shaped paths start and end at positions of approximately  $x=7.0$  and  $x=4.5$ , respectively. The ants then reoriented themselves towards the nest. During the middle phase, the paths deviated to the left.

#### *Displacements to test areas located outside the training platform*

All experiments described above were carried out on the terrace platform where the ants could experience familiar surroundings. The next question, of course, is how the ants would behave if they were deprived of these landmarks, i.e. displaced to novel terrain. For example, would they then rely on celestial compass cues?

In trying to answer these questions, the ants were displaced from F9.5 either to a distant football field or to the roof of the building positioned next to the training platform. There, their 'homeward' paths differed substantially from those on the terrace platform. As shown in Fig. 8, on being released, the ants did not walk in their homeward direction for any length of time, but chose straight courses only for extremely short distances (in most cases, for approximately 10–40 cm); they then turned sharply and began to search in wide loops. The size of the loops increased gradually until the ants reached the edge of the test area. Occasionally, while exhibiting this looping search pattern, the ants returned to their point of departure (release). There was no difference between the trajectories recorded on the football field and on the roof of the building.

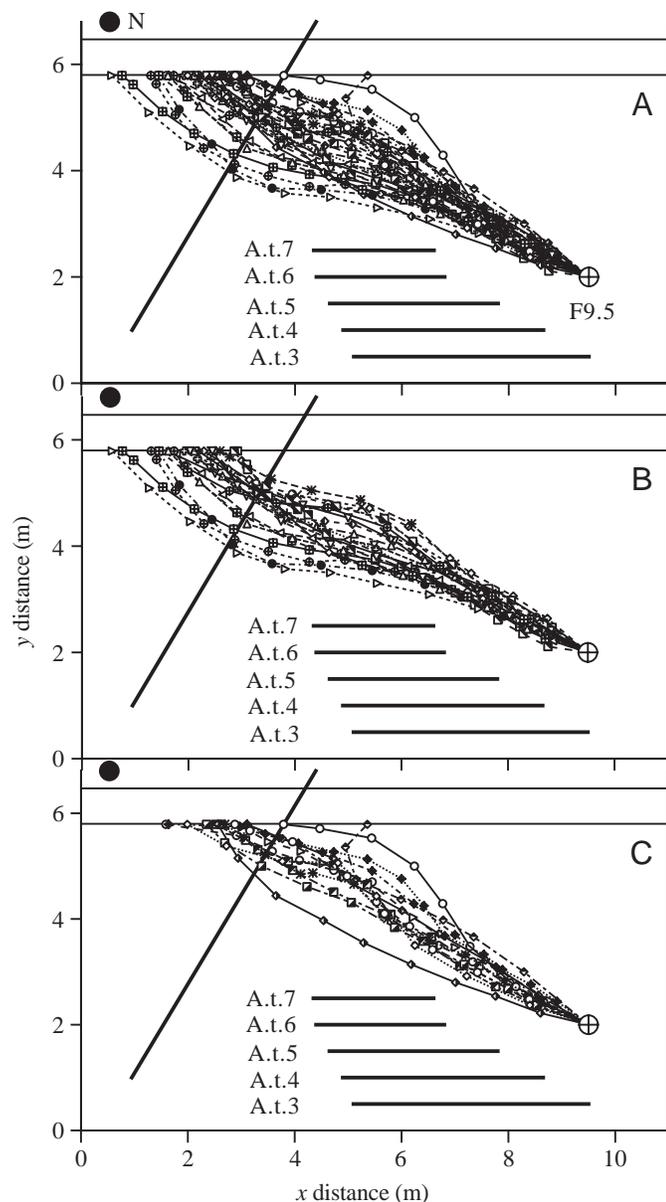


Fig. 7. Deprivation experiments. The upper parts of the frontal fields of view of the ants were obscured by a screen. Screen C (oblique heavy black line) was positioned 6.8 m from F9.5 in the direction of the nest (N) (see Fig. 4C). Assuming that the ant walks along its normal homeward course ( $y = -0.548x + 7.206$ ) from F9.5, the positions where the top of a chestnut tree drops out of sight behind the screen and reappears under the screen were calculated by advancing the position of the ant by a 5.0 cm step along the  $x$ -axis. Horizontal bars indicate the top parts of individual chestnut trees (A.t.3–A.t.7; see Fig. 3) that could not be seen by the ants on their homeward courses. (A) Paths of all runs tested.  $N=36$ . (B) Paths exhibiting a characteristic sigmoid bend, selected from A.  $N=22$ . (C) The remaining paths shown in A but not in B.  $N=14$ .

The trajectories were analysed by calculating the frequencies of heading directions (directions of path segments) in each run (Fig. 9). The most preferred heading direction was that of quadrant A, i.e. the quadrant that included the direction

of the fictive nest. The circular distributions of all segments distributed across the four quadrants were significantly different from a random distribution ( $P < 0.001$ ,  $\chi^2$ -test). The differences between the segment numbers in quadrants A and C (the largest and the second largest values) were also significant ( $P < 0.02$ ,  $\chi^2$ -test). When only the first segment of each run was used in the evaluation, approximately 60% of all ants tested preferred quadrant A. In Fig. 9, these values are given in parentheses. After testing, the ants were returned to their familiar route on the terrace. Almost every ant ran immediately homewards along a straight course.

## Discussion

### *Use of distant landmarks in homeward orientation*

The experiments described here show (see Fig. 1A) that wood ants *Formica japonica*, foraging within an environment that is characterised by a skyline with conspicuous landmarks, exhibit straight homebound paths over a distance of 7.9 m. What are the cues used by the ants while accomplishing this task?

When the ants are displaced from the feeding site to various release sites on the terrace platform, they take fairly straight courses (Fig. 2), but the directions of these courses are not oriented towards the nest and are not parallel to the usual homeward course taken by the ants when homing from the feeding site at F9.5 (Table 1). The courses of the displaced ants depend on the direction of displacement (east or west from F9.5) and on the distance of displacement (Table 1). These results clearly show that, while homing on the terrace platform, the ants are neither using chemical trails nor relying on a skylight compass as their principal directional aid.

The most striking observation of the current study was that, when the homebound courses of the ants were extended, they intersected at a point located more than 13 m behind the nest (Fig. 3). When returning home, the ants were guided by the distant landmark-rich skyline available in their frontal fields of view, especially by the horse chestnut trees indicated in Fig. 3 as A.t.5 and A.t.6 and by the rhododendron bushes R.sp.1 and R.sp.2. As the ants proceeded along their homeward path, the upper edge of the skyline silhouette represented by these trees and bushes increased in mean elevation by  $10.2^\circ$  (from  $20.1^\circ$  at F9.5 to  $30.3^\circ$  at the nest; compare the horizontogram taken from F9.5 with that from the nest in Fig. 5). The ants might have learned that it is this change in the retinal image that is associated with a successful homeward journey. This would be in accord with observations in wood ants *Formica rufa* that retinal images memorized in the frontal field of view are used in goal navigation (Nicholson et al., 1999).

The sigmoidal path trajectories exhibited by ants displaced to more distant release sites (R17.1 and R20.9, Fig. 2B,C) might be indicative of some kind of correction behaviour. The more distantly the ants were displaced, the more frequently was this course correction behaviour observed. The most likely hypothesis to explain this behaviour is that, whenever the ants experienced too large a mismatch between the stored image of

the skyline and the current one, they started some kind of course correction behaviour. In the present case, this 'correction' always resulted in a turn to the left. This might mean that the ants can use the lateral fields of view to supplement the frontal ones in matching stored and current retinal images; e.g. the ants starting from R20.9 towards the focal point see the chestnut trees A.t.11–A.t.13 (see Fig. 3; 18.3 m distant and  $29.7^\circ$  elevated as seen from F9.5 on average) in the direction  $34.5^\circ$  (on average) on the right, while those from F9.5 see them in the direction  $51.3^\circ$  (see the horizontograms taken from R20.9 and F9.5 in Fig. 5). To compensate for this discrepancy, the ants have to turn to the left. As a result of this compensation, the match in the frontal retinal image will be gradually improved and the ants might again be able to use the skyline panorama in their frontal fields of view.

*What are the particular landmark cues used in homeward orientation?*

An answer to this question emerges if we take a closer look at the visual deprivation experiments. When the opaque sheet shown in Fig. 4B was used to screen off the lower parts of the field of view of the ants (up to an elevation of  $6.5^\circ$  at F9.5 to  $90^\circ$  at the screen itself), their homeward courses were not affected (Fig. 6A). The ants may not make use of this part of the landscape because the contrast differences within the lower parts of the landmark panorama surrounding the nest might be small and unreliable; for example, they might change in different illumination conditions such as occur during the course of a day.

An interesting situation arises when the sheet was placed such that there was a pronounced gap between its lower edge and the terrace platform (see Fig. 4C). In this situation, when the ants were proceeding along their homeward courses, they could first see the crowns of the trees, which then disappeared from their field of view but later reappeared when the ants approached the gap. Once they had passed through the gap, the whole landmark panorama was again at their disposal. Straight (and mainly homeward oriented) courses occurred in the first and final parts of the courses, while the intermediate part, when the top skyline was hidden behind the screen (see heavy black inset lines in Fig. 7), was characterized by the sigmoidal deviation shown in Fig. 7B. Hence, during their homeward runs, the ants seem to be guided by the crowns of the distant horse chestnut trees (particularly by A.t.5 and A.t.6) and the troughs between them. These tree tops constitute a steadily reliable, dark contour that clearly contrasts against the bright sky.

What is unresolved at the moment is the observation that the ants maintained a straight (but not correctly homeward-bound) course even when their entire frontal field of view was obscured by the screen (Fig. 6B). Did they refer to 'skymarks' or to terrestrial cues in other parts of their visual field?

We might get some hints of how to answer this question by displacing the ants to novel territory. This was performed under two conditions: by displacing the ants from the feeder either to a distant football field or to the roof of a building. In both situations, the ants started to search along tortuous paths (Fig. 8). But there was one important difference between the two test areas. From the roof of the building, the crowns of the chestnut trees could be seen above the 0.35 m high fence surrounding the roof, but they were not used by the ants as guidemarks. Apparently, the difference in elevation ( $4.9^\circ$  for the top of A.t.5 and  $5.3^\circ$  for the top of A.t.6, as seen on the roof, in contrast to  $19.9^\circ$  and  $23.6^\circ$ , respectively, as seen during training on the ground) was too large to allow for a match to be made between the stored and

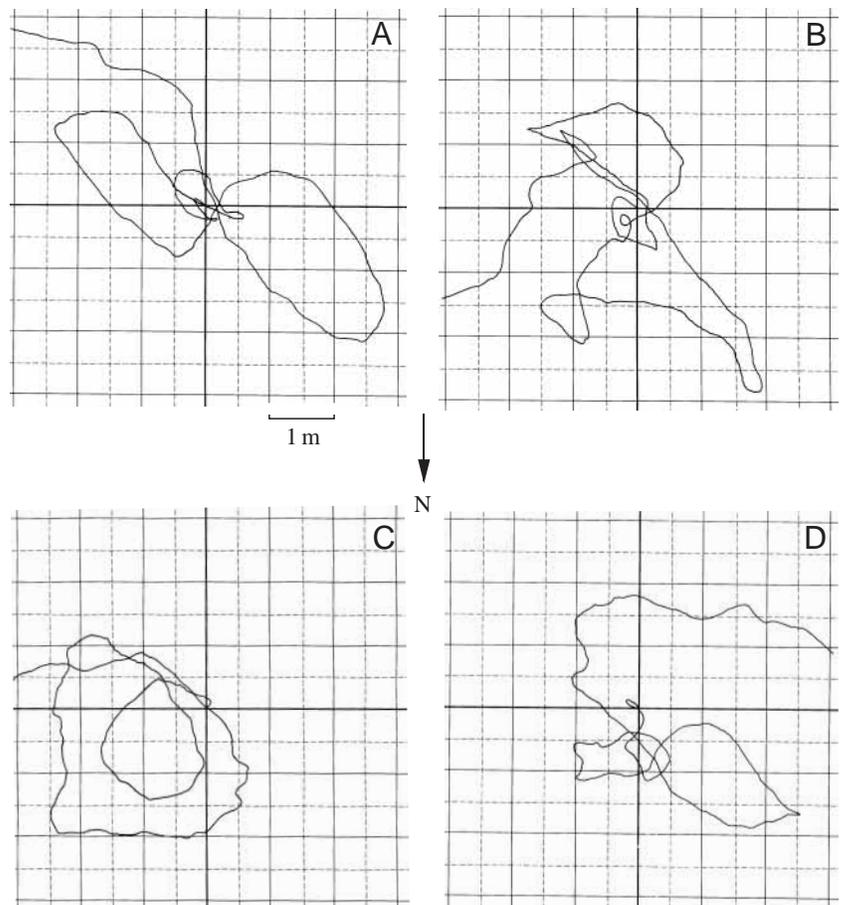


Fig. 8. Two examples each of search trajectories of ants displaced from F9.5 to either a distant football field (A,B) or the roof of the building attached to the terrace (C,D). The ants were always released at the centre of the test area (the crossing point of the two heavy black lines). Walking time recorded: (A) 8 min 22 s, (B) 8 min, (C) 7 min 40 s and (D) 6 min 47 s.

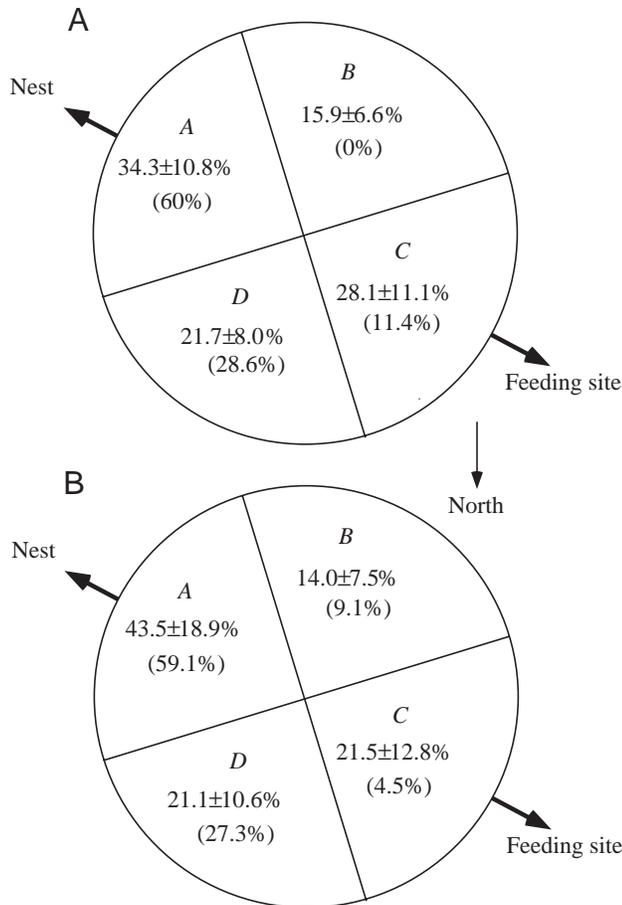


Fig. 9. Mean heading directions (computed from individual path segments) of ants displaced from F9.5 to either the football field (A) or the roof (B). Quadrant A is centred about the fictive home direction. Numbers in parentheses refer to the direction of the initial path segment of each run.  $N=35$  (A) and 22 (B) runs. For details see Materials and methods.

the current retinal image, as described by Wehner et al. (Wehner et al., 1996) and Judd and Collett (Judd and Collett, 1998).

#### Skylight cues and the path integration system

At first glance, it might be surprising that, when displaced from the feeding site to territories in which they could not experience their familiar skyline panorama, the ants did not select their homeward courses, or did so only in the initial phase after release (Fig. 9). Instead, they quickly switched on their systematic search programme (see Wehner and Srinivasan, 1981; Müller and Wehner, 1994). As the initial segments of the walking trajectories show, the ants are informed about their skylight-compass direction (for a review, see Wehner, 1994; Wehner, 1997), but apparently do not rely further on it if the proper skyline is absent.

Usually, when ants that have already arrived at the nest are displaced back to the feeder, they immediately start their

search behaviour if, and only if, no reliable landmark information is available (Wehner and Srinivasan, 1981; Wehner, 1982). As shown here, the ants usually do this for the more distant release sites (R17.1 and R20.9), but choose straight paths more-or-less parallel to the predisplacement paths when displaced from the nest to release sites close to the feeder or to their familiar route (R1.9, R5.7 and R13.3). When we compare the horizontograms taken from various release sites with those from F9.5 and the nest (Fig. 5), it appears that the ants have used the skyline panorama as some kind of guidemark at release sites close to the feeder, but that they have not proved sufficient as guidemarks when seen from more distant release sites, thus causing the ants to start their searching behaviour. These results would be in accord with observations that ants of the species *Cataglyphis* followed a familiar route even when their homebound vector store has already been emptied (Wehner et al., 1996).

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