

Navigation in wood ants *Formica japonica*: context dependent use of landmarks

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Summary

Wood ants *Formica japonica* can steer their outbound (foraging) and inbound (homing) courses without using celestial compass information, by relying exclusively on landmark cues. This is shown by training ants to run back and forth between the nest and an artificial feeder, and later displacing the trained ants either from the nest (when starting their foraging runs: outbound full-vector ants) or from the feeder (when starting their home runs: inbound full-vector ants) to various nearby release sites. In addition, ants that have already completed their foraging and homing runs are displaced after arrival either at the feeder (outbound zero-vector ants) or at the

nest (inbound zero-vector ants), respectively, to the very same release sites. Upon release, the full-vector ants steer their straight courses by referring to panoramic landmark cues, while the zero-vector ants presented with the very same visual scenery immediately search for local landmark cues defining their final goal. Hence, it depends on the context, in this case on the state of the forager's round-trip cycle, what visual cues are picked out from a given set of landmarks and used for navigation.

Key words: ant, *Formica japonica*, landmark guidance, navigation, path integration.

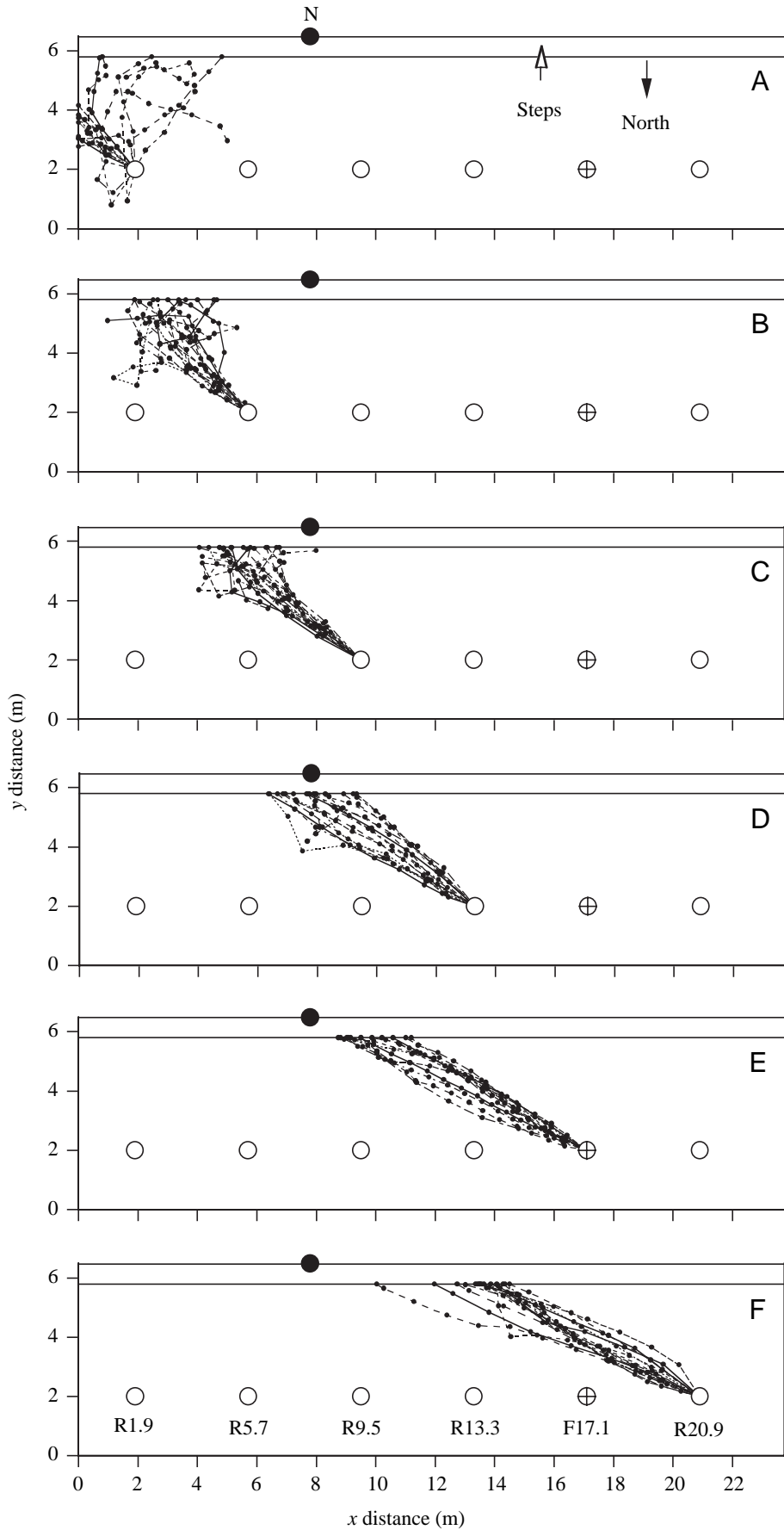
Introduction

In recent times ants have become model organisms for the study of animal navigation (Wehner, 1982, 2003; Collett and Collett, 2000). In particular, they have been shown to use path integration (vector navigation) and information about visual landmarks to steer their foraging and homing courses through familiar terrain. It has often been assumed that path integration provides the animal with a framework within which landmark information is acquired and used, but the details of how the ants structure their foraging journeys by relying on both vector navigation and view-based site recognition, and the ways of how these two modes of navigation are intertwined, have still to be worked out.

Similar to bees (Wehner, 1972; Wehner and Flatt, 1977; Cartwright and Collett, 1983), flies (Dill et al., 1993) and water striders (Junger and Varju, 1990), ants can learn visual patterns in retinotopic coordinates (Wehner and Rüber, 1979; Judd and Collett, 1998) and link these visual memories to an earth-based system of reference (Wehner et al., 1996; Åkesson and Wehner, 2002; for bees see Dickinson, 1994; Frier et al., 1996). They can store a number of views of the same object from different vantage points (Judd and Collett, 1998; Nicholson et al., 1999) and link different landmark memories by local vectors (Collett et al., 1998), which guide them from one visual signpost to the catchment area of the next (Wehner et al., 1996). In the context of following such learnt routes by playing out associations between site-based views they can use landmark information without reference to the state of their path integrator. For example, homebound desert ants such as

the North African *Cataglyphis* and the central Australian *Melophorus* follow their habitual routes through cluttered environments with the same precision independently of whether they set out directly from the feeder (full-vector ants), or whether they have already arrived at the nest and are experimentally displaced back to the feeder (zero-vector ants), or whether full-vector ants are displaced from the feeder to a place along their route halfway between nest and feeder (Wehner et al., 1996; M. Kohler and R. Wehner, manuscript in preparation). Hence, the retrieval of a sequence of landmark memories is not necessarily coupled to the state of the path integrator. What then are the cues that link the trajectories of a multi-segment path and recall the right memory at the right time?

The role of distant (skyline) landmarks as contextual cues for recalling snapshot memories of local landmarks has been studied in honey bees (Collett and Kelber, 1988). In these experiments bees have been trained to discriminate between two sets of local landmarks – between two snapshots – on the basis of panoramic cues alone. European wood ants rely on distant landmarks for selecting a particular route (Rosengren and Pamilo, 1978; Rosengren and Fortelius, 1986), and so do Japanese wood ants when steering their homeward courses (Fukushi, 2001). The present study describes how the latter rely exclusively on landmarks for locating nesting and feeding sites. Experiments were performed under various landmark situations (landmarks seen from the feeder, the nest or a set of release sites) and in different states of the ant's foraging cycle



(inbound or outbound runs, full-vector or zero-vector ants). This full set of displacement experiments was only possible because we succeeded in displacing and testing ants in the field as successfully during their foraging (outbound) runs as during their return (inbound) runs.

Materials and methods

Materials and experimental area

Japanese wood ants *Formica japonica* Motschoulsky 1866 were trained and tested on a rectangular terrace (23.8 m×5.8 m in the *x*- and *y*-directions, respectively) attached to a building in the north and surrounded by a lawn and a panoramic treetop skyline on its eastern, southern and western sides (for details, see Fukushi, 2001). The positions of the nest (N) and the feeder (F17.1) are indicated in Fig. 1 by filled and open (cross marked) circles, respectively. At the glass-tube feeder the ants were provided with diluted honey water and marked on their gaster with a colour code (Hobby Color, Gunze Ind. Co., Japan). All ants were marked at least one day prior to the experiments, so that they had performed at least 20 round-trip journeys before they were used in the displacement experiments.

Recording the ants' trajectories

As the terrace was covered with a square array of 20×20 cm² tiles, it was provided with a grid of floor lines and hence an easy method for recording the ants' trajectories. Every 10 s vial caps were placed as markers along the walking paths of individual ants, and the positions of these markers were later recorded within the *x*, *y* coordinate

Fig. 1. Inbound paths of displaced full-vector ants, i.e. ants that have been displaced from the feeder (F17.1, crossed open circle) to various release sites (R1.9, R5.7, R9.5, R13.3 and R20.9). N (filled circle), nest. (A–F) Paths of the displaced ants that upon release had started their inbound runs from the release sites mentioned above. *N*=16 ants tested in each experiment except for (E), *N*=12.

system mentioned above. Recording continued until the foraging or homing ants started their search movements, i.e. performed 180° turns or undirected zigzag walks.

Displacement experiments

Ants were subjected to sets of displacement experiments at various states of their foraging round-trip cycle. Inbound (homing) ants were captured at the feeder before starting their return runs (inbound full-vector ants) or after they had completed their return runs and were just on their way of entering the nest (inbound zero-vector ants). Similarly, outbound (foraging) ants were captured just when leaving the nest and heading for the feeder (outbound full-vector ants) or after they had completed their outward journeys and had reached the feeder for a distance of less than 30 cm (outbound zero-vector ants).

The inbound ants tested in both their full-vector and their zero-vector state were displaced in most cases to the very same set of release sites (R1.9, R5.7, R9.5, R13.3, R16.9 and R20.9; see Figs 1, 3), and so were the outbound full-vector and zero-vector ants (ER4.0, SR3.8, SR7.6, SR11.4 and SR15.2; see Figs 4, 5). In all displacement experiments the ants were captured in a glass tube and transferred in the dark to the release sites mentioned above.

Calculation of walking directions

The directions of the straight trajectories of the full-vector ants were determined by taking the mean of all 10 s segments of the ants' paths with south defined as 0°. A counter-clockwise sense of rotation was applied. In all cases where the inbound ants first ran straight in their homeward direction and then began to search (Fig. 1), only the segments pertaining to the first parts of their paths and deviating by no more than $\pm 30^\circ$ from the preceding segments were used for computing the mean directions. In the outbound paths, the segments near the feeder, where the foraging ants started searching ($x > 16$ m and $y < 2$ m) were not included in determining the mean courses. Means and angular standard deviations (S.D.) were computed by applying the methods of circular statistics (Batschelet, 1981).

In order to compare the directions of the paths between two groups of displaced ants, e.g. between full-vector ants and zero-vector ants, concentric circles (radii 2, 3 and 4 m) were laid around the point of release or – in the case of the outbound paths – around the point where the ants started their journeys on the terrace floor. Then the first crossings of the ants' paths with each circle (crossover points) were determined. However, as many zero-vector ants did not reach the 3- and 4 m circles, the statistical tests were mainly applied to the crossover points at the 2 m circle.

The Watson–Williams test was used to evaluate the difference of the directions between two experimental groups of ants. The difference of the variances of the courses between two particular groups was also tested by computing the concentration parameter described in Batschelet (1981, pp. 122–124). In order to check whether the mean direction of a

sample of displaced ants differed significantly from the nest or the feeder direction, the confidence intervals of the mean were computed (Zar, 1999, pp. 605–606).

There was no indication whatsoever that odour (e.g. trail pheromone) cues were involved in any experiment described in the present account. Even if the ants had used such cues in their way back and forth between nest and feeder (they obviously had not), they could not have relied on them in our experiments, where they had been displaced from their normal route and hence had to move over completely novel territory.

Results

Inbound paths of homing ants

The foraging activity of the colony used in the previous study (Fukushi, 2001) had declined over the years, so that in the present study another colony located at the southern edge of the terrace ($x=7.79$, $y=6.48$) had to be used (see Fig. 1). Since the landscape surroundings seen from the new nest and the new feeding site ($x=17.1$, $y=2.0$) were different from those seen from the previous locations, the displacement experiments had to be repeated. In the control experiments, in which the ants started at the feeder and moved towards the nest, the mean angle of the ants' inbound courses was $61.2 \pm 4.5^\circ$ (mean \pm S.D.; $N=53$, Fig. 1E; 95% confidence intervals $\pm 1.2^\circ$) and thus slightly different from the direction of the nest as seen from the feeder (64.3°). Eight of the 53 ants, whose inbound courses had been recorded, walked under a totally overcast sky. However, there was no statistical difference between the mean angles of the courses exhibited by these two groups of ants (total-overcast courses: $63.0 \pm 2.4^\circ$, remainder of courses: $60.9 \pm 4.8^\circ$; $P > 0.5$, Watson–Williams test).

In the displacement experiments, in which the ants were transferred from the feeder to various release sites (inbound full-vector ants; Fig. 1), the ants started to run unhesitatingly along rather straight paths in a particular direction that deviated significantly ($P < 0.001$, Watson–Williams test) from the direction taken by the controls ($61.2 \pm 4.5^\circ$). It was only in the releases from R20.9 that this difference was not significant. In each set of displacement experiments, the ants' directions were taken at 2-, 3- and 4 m distances from the start and compared with those of the controls.

In Fig. 2 the mean inbound courses of the displaced full-vector ants are included into a floor plan of the terrace and its surroundings. If these courses (solid lines) are extended beyond the position of the nest, they all intersect at a particular point ($x=-9.6$, $y=17.0$) lying between two conspicuous chestnut trees (6 and 7). It might have been towards this 'focal point' that the ants had directed their homebound runs.

If the inbound full-vector ants had relied so obviously on landmark cues rather than celestial compass information, one might ask whether the zero-vector ants that upon return had been captured directly at the nesting site and displaced to the very same points of release, behaved similarly. They did not (zero-vector ants, inbound; Fig. 3). First, the inbound runs of

the zero-vector ants are extremely convoluted as compared to the amazingly straight inbound runs of the full-vector ants. This is immediately obvious, if one compares Figs 1 and 3, and it is statistically demonstrated by the angular variances of the runs being larger in the zero-vector than in the full-vector ants (determined at the 2 m distance from the start, $P < 0.02$, concentration parameter test). Second, the directions taken by the zero-vector ants deviate highly significantly from those of the full-vector ants ($P < 0.001$ or, in one case: R13.3 at 2 m from the start $P < 0.05$; it is only at R16.9, i.e. at a release site as close as 20 cm to the feeder, that this difference does not exist). Hence, the inbound zero-vector ants took neither the true compass courses – this was to be expected – nor the courses selected by the full-vector ants. As shown by the broken lines in Fig. 2, they moved more or less in the direction of the nest. The silhouette of the three chestnut trees (11–13) might have been their guide.

Outbound paths of foraging ants

Normal outbound paths

The ants' outbound (foraging) paths from the nest towards the feeding site were fairly straight, but slightly more divergent and more curved than the inbound paths (compare Figs 1 and 4). Some ants would reach the feeder directly, but most of the ants started to search near the feeder (within 1 m) or passed the feeder and then returned to it. The mean direction of the outbound paths was $63.3 \pm 4.4^\circ$ (mean \pm s.d.; $N = 12$; the actual value was rotated by 180° to ease comparisons with the directions of the inbound courses; 95% confidence intervals $\pm 2.7^\circ$) and thus not significantly different from the direction of the feeder as seen from the nest (64.3°). There was no statistical difference between the directions of the normal outbound paths

and the inversions of the inbound paths ($P > 0.20$, Watson–Williams test).

What landmark features might have guided the outbound ants? As the feeder itself was a transparent glass tube (3.0 cm wide and 5.0 cm high), it was certainly invisible to the ants from the edge of the terrace ($x = 8.95$ and $y = 5.8$; angular height 0.32° ; width of the tube, 0.19°). The feeder was placed 2.0 m south of the building, which contained 3 m high glass windows, two boxes housing air pumps (B1 and B2; 1.0 m wide, 0.6 m deep and 1.45 m high), and five columns (C1–C5; 0.66 m wide, 0.62 m deep and 3.4 m high) framing the building (see Fig. 4). From the edge of the terrace, where the ants started their outbound runs, B1 and B2 appeared under angular dimensions of $9.3^\circ/12.7^\circ$ and $3.8^\circ/6.2^\circ$ (width/height), respectively. C4 was 5.0° wide and 18.3° high. Given these angular dimensions, all these landmarks could have been used in determining the ants' courses.

Displacement experiments

Individual ants having emerged from the nest were captured at the edge of the terrace and displaced in the dark to various release sites (outbound full-vector ants; Fig. 4). Once released, they climbed the step of the terrace either immediately or after short searches for a hiding place. They were so motivated to climb the step and to visit the feeding site that almost all of the displaced ants continued their foraging journeys. Only two ants (released at SR11.4) out of in total 63 ants returned home directly and did not start a foraging journey. In this respect, *Formica* seems to differ from *Cataglyphis*, which tends to return to the nest rather than to continue foraging when disturbed on its outbound runs (Collett et al., 1999; but see Loch and Wehner, 1997).

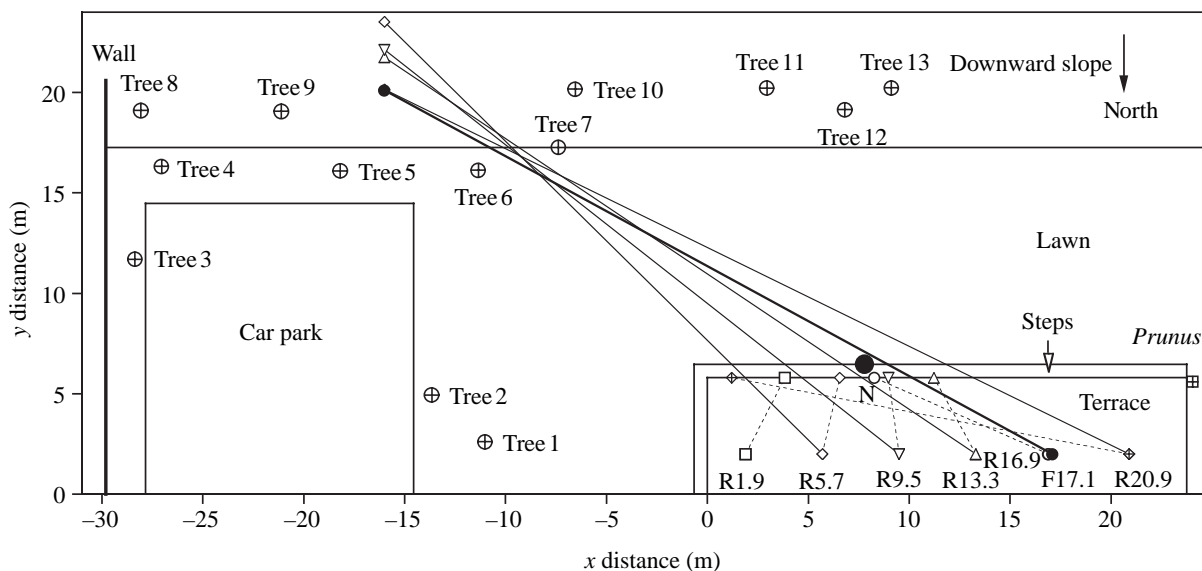


Fig. 2. Floor plan of the terrace platform and its surroundings. The mean inbound courses of the full-vector ants (Fig. 1) and the zero-vector ants (Fig. 3) are shown by solid and broken lines, respectively. The symbols marked R1.9 to R20.9 depict the sites at which the full-vector ants and the zero-vector ants were released and started their inbound (homeward) runs. In addition, the locations of 13 large horse chestnut trees (*Aesculus turbinata*) are indicated. The lower trees and bushes are omitted (see Fukushi, 2001, Fig. 3). N (filled circle), nest. Bold line, normal homeward course.

Again, as with the inbound courses of the displaced full-vector ants, the outbound courses of the displaced full-vector ants differed significantly from those of the controls and hence from a potential skylight compass course ($P < 0.001$ or < 0.01 in all cases, the only exception being the releases from SR3.8, in which the difference was not significant). When considering the kind of landmarks that the outbound ants might have used, let us have a closer look at the individual sets of displacements. Most ants released at ER4.0 started search movements after they had climbed the terrace; they stayed mainly within 6 m from the east edge of the terrace. None headed steadily towards the feeding site (Fig. 4A). When three lost ants were carried back to positions near the nest and released there, they then – even after this second displacement in a row – walked straight towards the feeding site. This shows that the ants released at ER4.0 were still highly motivated to forage, even after having searched around for several minutes. Most of the ants released at SR3.8 headed for B1, then having passed $x = 10\text{--}11\text{ m}$ changed their courses towards B2 and reached positions near the feeder (seven ants reached positions 2 m apart from the feeder; Fig. 4B). To demonstrate this directional change during the outbound courses, the regression lines of the ants' positions recorded at $x < 10\text{ m}$ (the first halves of the courses; $N = 82$) and at $10\text{ m} < x < 16\text{ m}$ (the second halves of the courses; $N = 80$) were computed for nine paths that exceeded $x = 10\text{ m}$ (see solid lines in Fig. 4B). The slopes of the regression lines of the first and second halves were significantly different ($P < 0.001$, t -test; Zar, 1999).

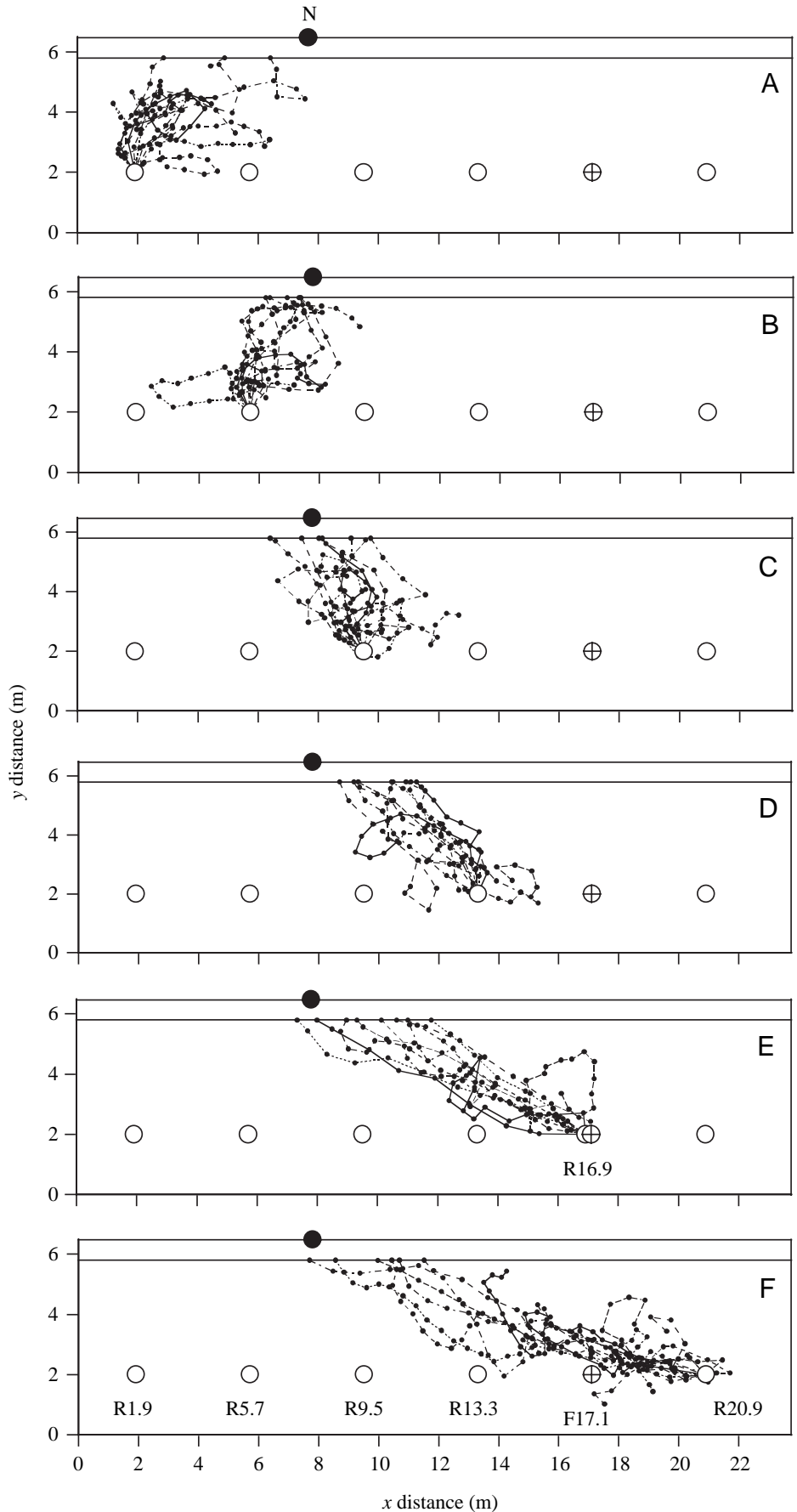


Fig. 3. Inbound paths of displaced zero-vector ants, i.e. ants that were captured shortly before they entered the nest and were displaced to the very same release sites (R1.9 to R20.9) as the full-vector ants, whose inward trajectories are shown in Fig. 1. For further conventions see Fig. 1. $N = 12$ in each experiment.

In the control experiments (releases close to the nest) the captured ants were kept in the dark for 20 s and released at the same positions as captured. The mean direction of the outbound paths was $62.8 \pm 2.2^\circ$ (mean \pm s.d.; $N=13$; Fig. 4C) and hence not significantly different from that of the normal outbound paths (see above: $63.3 \pm 4.4^\circ$; $P > 0.5$, Watson–Williams test). This shows that neither the disturbances caused by mechanical manipulations such as capturing and releasing nor keeping the ants in the dark for 20 s had any influence on the trajectories of the displaced animals. The ants released at SR11.4 headed directly towards the feeding site and moved along fairly straight trajectories (mean \pm s.d., $54.0 \pm 5.3^\circ$; $N=12$). This mean direction was significantly different from that in the control experiments ($P < 0.001$, Watson–Williams test) again showing that the ants did not rely on skylight information in determining their courses. All ants reached the feeding site, i.e. approached it for 1 m (Fig. 4D). Most of the ants released at SR15.2 were clearly attracted by B2, which was located in an almost identical position relative to the point of release as B1 was to the nest (Fig. 4E). These results suggest that the outbound ants might have used the boxes at the building as their main navigational aid.

Next we tested ants that had already arrived at the feeder and were displaced back to the nest or a number of other (nearby) release sites (outbound zero-vector ants; Fig. 5). Although the mean directions taken by these zero-vector ants do not differ significantly from those of the full-vector ants (if the intersects of the trajectories with the 2-, 3- and 4 m circles are taken as the criterion), the fine structure of the zero-vector trajectories is dramatically different from that of the full-vector trajectories.

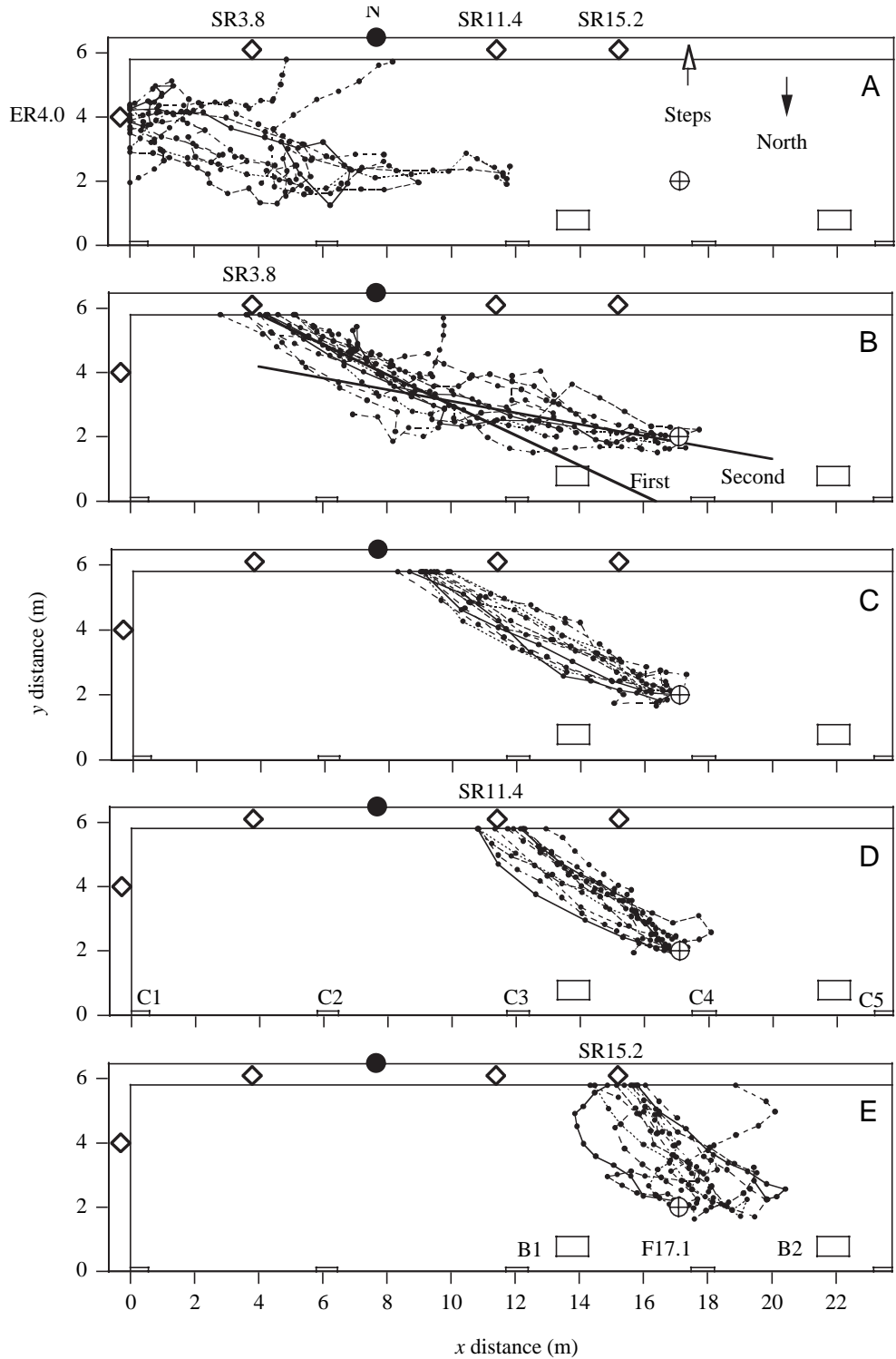


Fig. 4. Outbound paths of displaced full-vector ants, i.e. ants that had emerged from the nest and were displaced to various release sites (diamonds: ER4.0, SR3.8–SR15.2). The two solid lines in B represent the linear regressions computed for the ants' position $x < 10$ m (labelled 'First') and $10 \text{ m} < x < 16$ m (labelled 'Second'). B1, B2, C1–C5, landmarks (boxes and columns) in front of the building in the north of the terrace. $N=12$ in each experiment except for $N=13$ in C.

This is already borne out by the angular variance of the crossover points at the 2 m circle. These variances are significantly larger in the zero-vector than in the full-vector

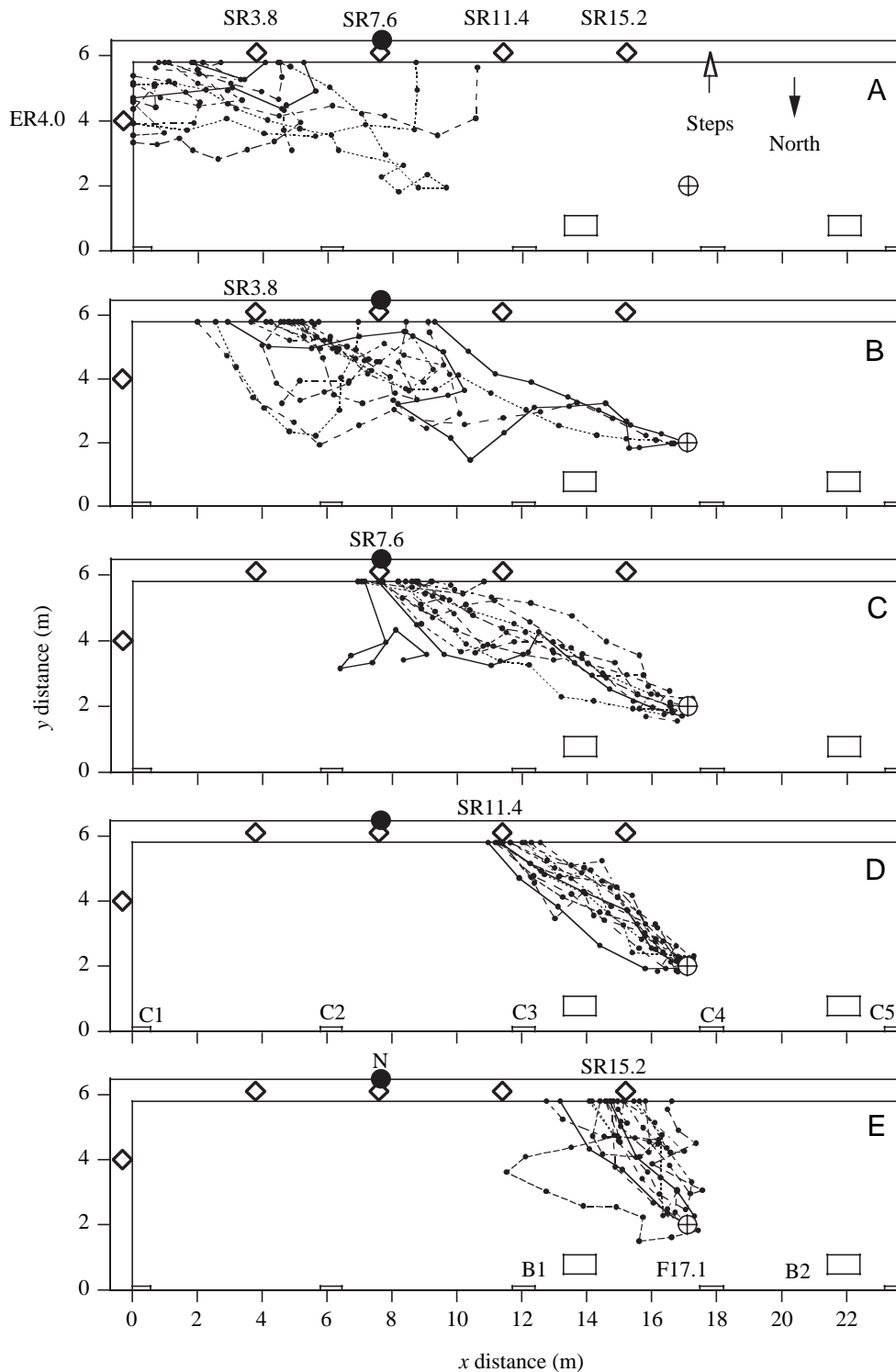


Fig. 5. Outbound paths of displaced zero-vector ants, i.e. ants that had arrived at the feeder (F17.1) and were displaced from there to the very same release sites as the full-vector ants, whose outbound trajectories are shown in Fig. 4. For further conventions see Figs 1, 4. $N=13$ in each experiment.

ants, even in those cases (SR7.6 and SR11.4), in which the paths of the zero-vector ants appear rather straight ($P<0.002$ and $P<0.05$, respectively). Furthermore, a closer look at the structural details of the ants' trajectories reveals distinct

differences between the zero-vector and the full-vector ants. For example, in contrast to what occurred in the displaced full-vector ants, the zero-vector ants once released hesitated to climb the step of the terrace immediately. Instead, they first moved about to and fro. Especially when released at the eastern step (at ER4.0) they were reluctant to proceed towards the feeder; two out of 15 ants descended from the step and headed to the east into the lawn, six ants turned on the step to the south-eastern corner of the terrace and then climbed the southern step of the terrace, and the remaining seven ants climbed the eastern step where they had been released. After having mounted the terrace, they walked tortuously, but never steered straight courses towards the feeding site (Fig. 5A). The zero-vector ants released especially at ER4.0 and SR3.8 (Fig. 5A,B), but also at SR15.2 (Fig. 5E), climbed the step in a much wider range than the full-vector ants did at the same release sites (compare Figs 4 and 5). Most of them walked in tortuous ways (see especially Fig. 5A,B). Only four out of 13 ants released at SR3.8 reached the feeder. Often, as in the releases from SR3.8 and SR15.2 (Fig. 5B,E), the ants turned backwards and returned to the step of the terrace at which they had been released. This behaviour was never observed in the full-vector ants.

Discussion

One of the most striking results of the present investigation is the finding that neither the inbound (homing) nor the outbound (foraging) ants relied on celestial compass information. Even though the full-vector ants when displaced from the feeder or the nest (in the inbound or the outbound state, respectively) to various release sites exhibited rather straight inbound and outbound trajectories, the directions

of these trajectories were not parallel to each other (what they should have been, if the ants had used a skylight compass, i.e. visual cues located at infinity). Furthermore, there was no difference in the trajectories of ants tested under full skylight or total overcast conditions. In all cases, the homebound ants seemed to have used distant landmark cues to set their courses (see also Fukushi, 2001). As shown by the solid lines in Fig. 2, the extensions of the ants' inbound trajectories intersect at a 'focal point' defined by the treetop skyline of two distant landmarks, the chestnut trees 6 and 7. These two treetops appeared at angular elevations of 27.9° and 29.1°, respectively, as seen from the nest, and under an elevation of 19.1° and 19.2°, respectively, as seen from the feeder. Hence, the angular heights of the two trees increased by 9–10° as the ants walked from the feeder to the nest. At the release site R1.9 the treetop elevations were 29.6° and 29.3° and thus already exceeded the elevations as seen from the nest, which is in accordance with the observation that most ants started to search immediately after having been released (Fig. 1A). It was also at R5.7 and R9.5 (treetop elevations 23.6° to 26.5°; see Fig. 1B,C) that the ants, while running towards the focal point for only a short distance, already reached a location at which the angular elevations of the two trees matched the stored values. In conclusion, the ants' search behaviour seemed to be elicited whenever the angular elevation of the skyline at the focal point in the frontal visual field exceeded a memorized value.

In this context it might be worth mentioning that other species of ants have been shown to exploit the elevation of panoramic cues for one navigational task or another. Desert ants *Cataglyphis fortis* pinpoint the location of their nest by responding to distant panoramic cues even smaller than 2° in elevation (Wehner et al., 1996). Furthermore, they run along the midline of a passageway formed by natural or artificial landmarks on their left and right by balancing the vertical angular subtenses of the left and right landmarks (Heusser and Wehner, 2002). Finally, when *Leptothorax albipennis* (Pratt et al., 2001) and *Formica rufa* (Graham and Collett, 2002) were trained to walk parallel to an extended landmark (a wall), they maintained a desired distance from the wall by keeping the image of the top of the wall at a particular retinal elevation.

If the same type of displacement experiments described above for the homebound ants were performed for the outbound (foraging) ants, the full-vector ants again did not use skylight information: the mean directions of the paths taken by the ants displaced to various release sites were not parallel to each other. However, the visual skyline differed between the two experimental paradigms in so far as the visual scenery experienced by the homebound ants was a structured treetop skyline, while the outbound ants walked towards a building providing a continuous horizontal roofline, which did not provide azimuthal cues. In fact, when the ants were prevented from seeing the lower background around the feeder, but were still able to see the upper rooftop skyline, they did not move towards the feeding site (our unpublished observations). Hence, the displaced outbound ants must have relied on the conspicuous landmarks – the two boxes (B1 and B2) and the

three columns (C3–C5, see Figs 4, 5) – located at the front side of the building. The white surfaces of these landmarks contrasted sharply with the dark background formed by the glass windows. Let us just give one example of how the ants behaved: when captured immediately after their emergence from the nest and released at SR3.8, they headed towards B1; having passed it they changed their courses towards B2, and finally arrived at positions close to the feeder (Fig. 4B). These results suggest that box B1 located nearer to the ants' starting position served as a first landmark cue. Upon approach of B1, the second box (B2) became more conspicuous and guided the ants on the subsequent part of their outbound journeys. This kind of target switching during foraging runs has also been observed in *Formica rufa* (Nicholson et al., 1999; Graham et al., 2003). Finally, the ants might have pinpointed the feeder by matching-to-memory processes relying on the local arrangements of these three (and possibly more but unidentified) nearby landmarks.

As the full-vector ants in both their outbound and inbound states used landmarks as their only navigational cues, the question immediately arises, whether the zero-vector ants, which can use nothing but landmarks as their guide, do so in the same way. As a comparison of Figs 1 and 4 on the one hand and Figs 3 and 5 on the other clearly shows, the ants behave differently in their full-vector and zero-vector states. In the former case, they head directly into a particular direction and perform straight outbound and inbound paths, whereas in the latter they exhibit convoluted paths, often return to the point of release, and only finally move slowly in a direction leading them to the neighbourhood of the goal (nest or feeder). It is especially in the inbound ants that the directions taken by the full-vector ants and the zero-vector ants differ significantly from each other. This means that the two groups of ants have either relied on different types of landmarks or have used the same landmarks in different ways. As discussed above, the full-vector ants had obviously used panoramic cues to set their courses. In contrast, the convoluted trajectories of the zero-vector ants do not show any relation to the panoramic cues used by the full-vector ants. Apparently, upon release the zero-vector ants look immediately for the local arrangements of objects defining the goal. In any case, if the path integrator (Collett et al., 1999; Wehner et al., 2002) is at zero state, information about distant landmarks does not suffice for letting the ants choose straight inbound and outbound courses. In conclusion, if ants are presented with the same set of landmarks, they use these landmarks in different ways depending on the state of their foraging and homing round-trip cycle.

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