Nest-mark orientation *versus* vector navigation in desert ants

Patrick Bregy*, Stefan Sommer and Rüdiger Wehner[†]

Institute of Zoology, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland
*Present address: Institute of Cell Biology, University of Bern, Baltzerstrasse 4, CH-3012 Bern, Switzerland
[†]Author for correspondence (e-mail: rwehner@zool.uzh.ch)

SUMMARY

Foraging ants and bees use path-integration vectors and landmark cues for navigation. When in particular experimental paradigms the two types of information – vector-based and landmark-based information – are made to compete with each other, the insect may weight either source more heavily depending on the navigational context and the animal's motivational state. Here we studied the effects of a displaced nest mark on the homing performances of *Cataglyphis* ants. Foragers were trained to shuttle between the nest, which was marked by a black cylinder (the beacon), and an artificial feeder. Trained ants were captured at the feeder and transferred to a distant test field, where they experienced the nest mark at various positions relative to their home vector. When the beacon was positioned to one side of the point of release, the ants slightly drifted towards the beacon right at the start of their inbound run, but thereafter resumed their home-vector courses. When the nest mark appeared to one side further down the homing course, the ants set off in the home-vector direction, but then gradually drifted towards the beacon. The distance, at which this occurred, and the ants' drift from the home-vector course were very similar across test conditions. During the final search for the nest, landmark information dominated the ants' path integrator. The results clearly show that nest-mark memories are effective during the entire vector-based homeward course, but that they are either only partly activated or partly used unless the state of the ants' path integrator is close to zero.

Key words: beacon, *Cataglyphis*, home vector, landmark, nest search, path integration.

INTRODUCTION

Solitarily foraging desert ants and honey bees perform path integration during their extensive outdoor journeys (Wehner and Srinivasan, 2003). In doing so, they continuously derive an estimate – the 'home vector' – of the direction and the distance to their nesting site. In addition, they use landmark information to follow habitual routes as well as to pinpoint familiar goals (Wehner and Räber, 1979; Wehner, 1981; Collett, 1992; Collett, 1996; Durier et al., 2003; Graham et al., 2003; Wehner, 2003).

The vector-based and the landmark-based systems of navigation do not operate independently. Above all, the former might provide the framework within which the latter is embedded (Collett et al., 2003b; Wehner and Srinivasan, 2003). When the two usually complementary systems of navigation are experimentally set at variance – either by displacing individuals or landmarks – the animals may rely more heavily on one or the other type of spatial information depending on the navigational task, the internal motivational state, and the visual complexity of the environment (Wehner et al., 1996; Sassi and Wehner, 1997; Collett et al., 2003a; Wehner et al., 2006). For example, in visually rich habitats view-based landmark memories often dominate path-integration vectors (Wehner et al., 1996; Andel and Wehner, 2004; Kohler and Wehner, 2005; Sommer et al., 2008). However, desert ants fall back on the vector-based system of navigation when they are deprived of landmark information by removal of familiar landmarks (Knaden and Wehner, 2005) or by transfer to unknown territories (Wehner et al., 2006).

Generally, visual landmark memories are the more stable the closer the landmark(s) are to the ants' nesting site (Bisch-Knaden and Wehner, 2003). In the extreme, nest-mark memories, that is, memories of landmarks that directly define the nest position,

survive for weeks [fig. 64 in Wehner (Wehner, 1981)] (Ziegler and Wehner, 1997). They dominate the path integrator during the final stages of homing when the state of the ants' path integrator is close to zero (Knaden and Wehner, 2005). The point, at which the nest-mark memories get activated, depends to some extent on the distance the ants have ventured out from the nest; the longer the home vector at the point of return, the earlier the ants respond to a prematurely appearing nest mark (Michel and Wehner, 1995). However, previous experiments suggest that ants ignore otherwise familiar landmarks from the immediate vicinity of the nesting site if the landmarks are made to appear close to the start of the homeward run – that is, when the path-integration vector has still its full length – of a foraging journey (Michel and Wehner, 1995; Wehner et al., 1996). Here we investigate this question in more detail (1) by using a single nest-based landmark, a beacon, rather than a set of landmarks surrounding the nesting site, and (2) by performing a set of parametric tests in which the landmark is positioned at different distances from the staring point of the ant's homeward journey on either side of the ant's vector-based homeward course or directly on that course.

MATERIALS AND METHODS
Study animals and field site

The study was performed with foragers of the Saharan desert ant *Cataglyphis fortis* Forel during the ants' main activity period between July and September 2002. The four colonies used for the experiments were located within a vegetation-free area of a salt pan close to the village of Maharès, Tunisia (34°32'N, 10°32'E). The minimum distance between any two experimental nests was 80 m. The foraging activity typically started at about 08:30 h (solar time)

in the morning, reached its maximum level around solar noon, and gradually decreased towards the late afternoon.

Experimental procedures

At the start of the experiments, each focus nest was marked by a black plastic cylinder (0.45 m in diameter and 0.41 m high), which was permanently positioned at a 0.1 m distance from – and to the north of – the nest entrance. Subsequently, foragers were trained to retrieve biscuit crumbs from an artificial feeder at a distance of 15 m due south (Fig. 1A). Ants that had arrived at the feeder were marked with a day-specific colour dot on the gaster (acrylic paint; Dupli-Color, Hassmersheim, Germany). They were allowed to forage for at least 1 day before they were transferred to a distant test field, which was at least 100 m apart from the nearest experimental nest. The test field was devoid of any vegetation. It consisted of a rectangular grid of white lines with a mesh width of 1 m (Fig. 1B). The grid was painted on the sandy desert surface using commercially available emulsion paint. It measured 28 m and 30 m in the east–west and the north–south direction, respectively.

Ants were tested individually. They were caught at the feeder and, while being kept within opaque plastic vials, transferred to the test area, where they had to pick up a biscuit crumb before they were released. During test runs, a landmark identical to the one at the nest entrance (the beacon) was located at various positions along or to the side of the ants' theoretical (i.e. pre-displacement) homing direction (Fig. 1B). In one test series, the 'negative control' experiment, the landmark was removed from the field.

We recorded the path of each ant for 5 min on graph paper on a scale of 1:100. Tested ants were marked with a specific coloured dot on the alitrunk before they were released into the nest. This procedure ensured that each ant (N=327) was tested only once.

Data analyses

We manually retraced the recorded paths on a digitizer tablet (Digikon 3, Kontron, Eching, Germany) and used GEDIT software (Antonsen, 1995) to analyse the digitised runs. The ant's first turn, which marks the transition from homing to nest-search behaviour (Wehner and Srinivasan, 1981), was defined as the point at which the animal turned by about 180° and continued to run along the newly set course for at least 1 m. For any given individual, the beeline direction from the point of release to the ant's current position was taken as the average homing direction up to that point. Across ants, mean directions and 95% confidence intervals were calculated according to standard techniques used for the analyses of circularly distributed data (Batschelet, 1981). A given mean direction was considered to deviate statistically from the true homeward course (north), if the latter direction lay outside the 95% confidence interval of the sample mean.

We further investigated the ants' nest-search efforts close to the tip of the home vector and in the vicinity of the (displaced) beacon. For comparisons, we computed the search densities within two equally sized squares (edge length: 2 m) that were centred on the fictive nest entrance as indicated by the ants' home vector and the beacon, respectively (Fig. 1B; note that the beacon reduced the accessible area inside the square by about 4%). The search density per ant and square was calculated as the ratio of the ant's path length covered within a given square to the ant's total path length.

RESULTS
Homing direction and first turn

In a series of 15 critical tests a beacon (cylindrical landmark), which in the training area was positioned directly at the nest entrance, was presented to the homing ants at different distances from the ants'
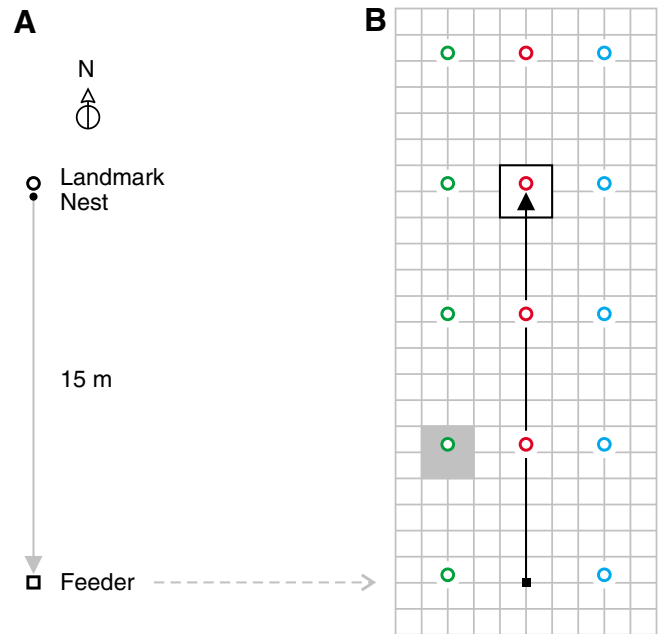

Fig. 1. Experimental paradigm. (A) Training setup. Ants were trained to a food source (open square) at 15 m due south. The nest entrance (black dot) was marked by a black cylinder, hitherto referred to as the 'landmark' (open circle). N indicates north. Ants, which had been caught at the feeder, were released on a distant field (indicated by the broken arrow between A and B). (B) Test field. Ants were released (black square) in the test field, which was marked out as a rectangular grid of white lines with a mesh width of 1 m. Coloured circles indicate alternative positions of the landmark, which was identical to the beacon presented at the nest entrance during training. In one series of experiments (the 'negative control') the landmark was removed from the test field. The open and the shaded squares indicate the areas selected to assess the ants' nest-search densities at the positions indicated by the home vector and the nest mark, respectively. In the example shown here the beacon is assumed to be set up at 5 m to the north and 3 m to the west of the point of release.

path-integration vector: either directly on the vector course (series A2–A5; Fig. 2) or to one side of it (series B1–B5 and C1–C5). Two controls were included: a 'positive control' (series A4), in which the landmark was positioned as in the training situation, and a 'negative control' (series A1), in which the landmark was removed.

The ants performed the first turn within 2 m from the fictive nest entrance when the beacon appeared at the usual position behind the goal (series A4; Fig. 2A). When the beacon had been removed (series A1) the scatter among the ants' first turns increased by a factor of about 3. Among the other test situations, in which the landmark had been displaced along the ants' home-vector course (Fig. 2A), the proportion of ants that started to search at the beacon decreased with increasing discrepancy between vector-based and landmark-based information. When the landmark had been shifted 5 m to the south (series A3) or the north (series A5), 62.5% and 88.9% of the ants initiated the nest search at the beacon, respectively. However, only 29.2% of the ants did so when the landmark had been moved 10 m to the south (series A2). This pattern remained fairly similar when the beacon had been shifted both along and to the side of the ants' home-vector course (Fig. 2B,C).

Furthermore, none of the ants started to search at the landmark 3 m to one side of the point of release (series B1 and C1; Fig. 2B,C). However, even then the animals did not ignore the beacon completely. On the first 4 m of the ants' homing paths, the running
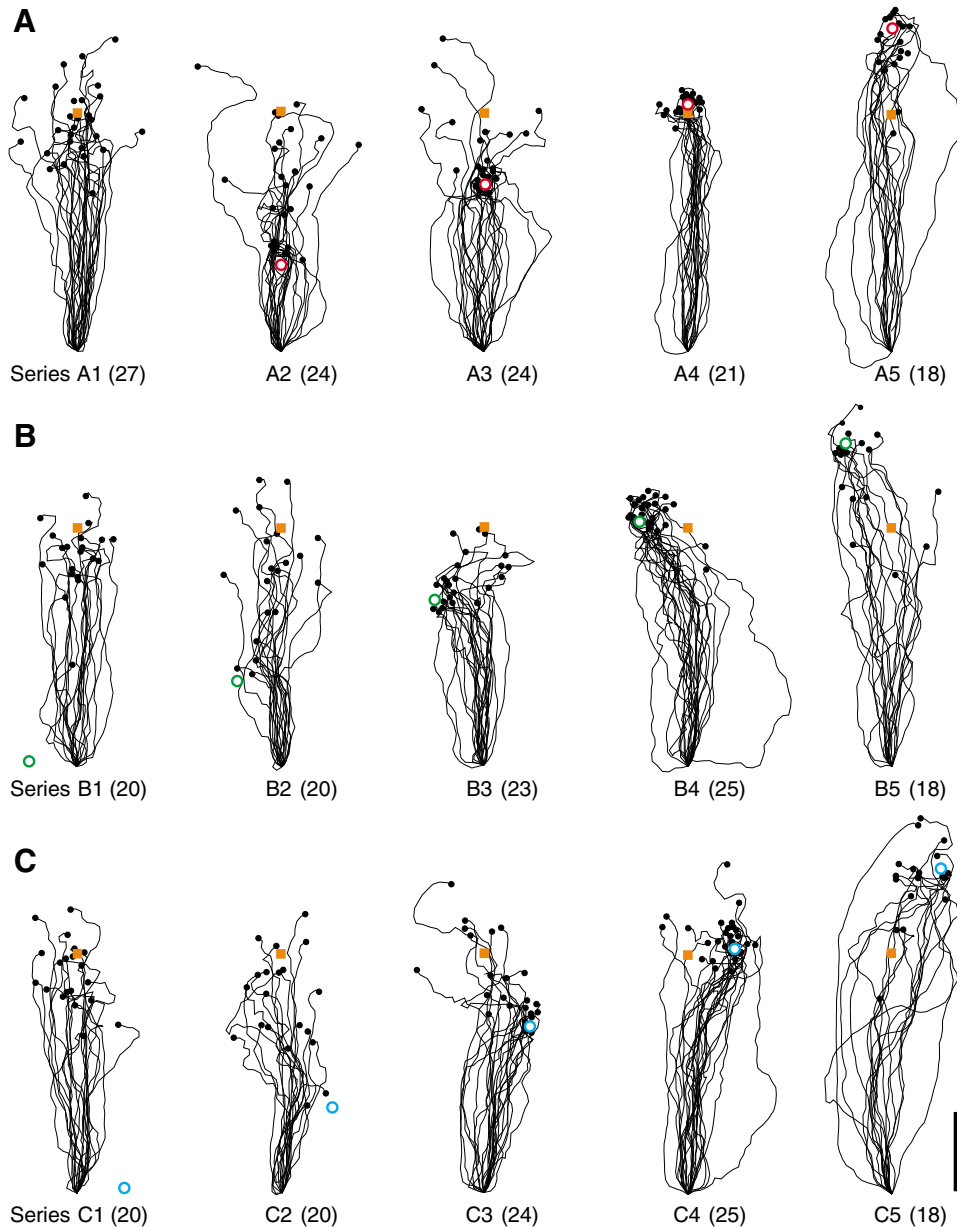
Fig. 2. Test runs. Shown are the ants' trajectories from the point of release to the first turn (black dots). The beacon (open circle) was positioned along (A), to the left (B) or to the right (C) of the ants' home-vector course. In series A1 the beacon was removed during tests. The orange square marks the position of the fictive nest entrance as indicated by the ants' home vector. Numbers in parentheses represent sample sizes. For illustrative purposes landmarks are slightly enlarged. Scale bar, 5 m.

directions deviated significantly from the home-vector course towards the side of the landmark (Fig. 3B). As expected, such an early deviation from the true homeward direction (0°) did not occur when the beacon was installed at the habitual position along the ants' home vector (Fig. 3C). Some occasional deviations might occur as shown in series A2 (Fig. 2A).

Finally, most ants were attracted by the laterally displaced beacon when it appeared further down the inward course (series B2–B5, C2–C5; Fig. 2B,C, Fig. 3A). Upon release, the ants usually set off in the home-vector direction before they started to drift towards the beacon. They did so at a fairly constant distance of about 6 m (Fig. 4). However, even if the course to be taken towards the landmark differed by almost 30° from the home-vector course (series B2 and C2; Fig. 2B,C), the ants deviated, on average, by

only <10° from the latter direction. In fact, the ants' change of direction was more or less uniform across test conditions (Fig. 4B).

By contrast, when measured in relative terms, with 100% representing a direct approach to the landmark upon release (coloured broken lines in Fig. 4B), the ants' maximal deflections from the vector course were 26.9%, 56.5% and 80.0% when the beacon was positioned to the side of the homeward course of either 5 m (orange), 10 m (green), and 15 m (blue), respectively (Fig. 4B). Hence, the ants weighted landmark-based information more heavily with decreasing length of their home vector.

Nest search
When the landmark appeared at the habitual place (position 0 in Fig. 5B) the ants spent about 30% of the nest search within the 4 m²
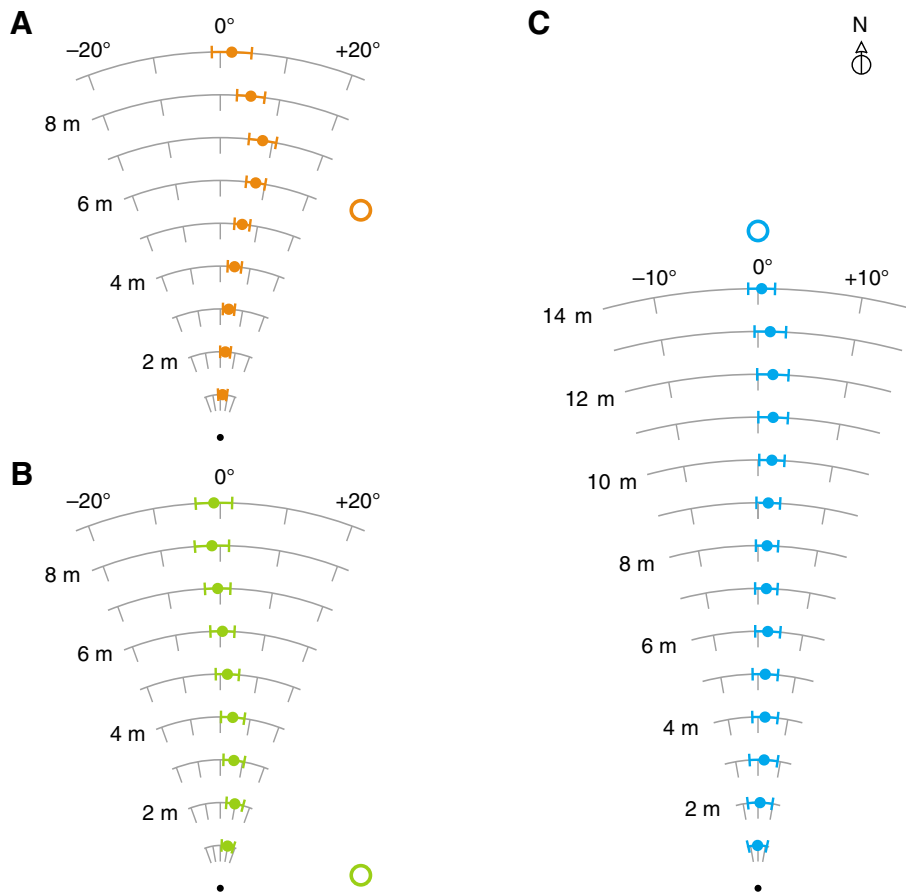
Fig. 3. Effects of the displaced nest-defining landmark on the ants' running direction. (A) Ants of series B2 (data mirrored) and C2 (see Fig. 2) experienced the beacon (open orange circle) to one side after having run off their home vector for 5 m. (B) Ants of series B1 and C1 were tested with the landmark (open green circle) at 3 m to the west (data mirrored) or to the east of the point of release (black dot), respectively. (C) The landmark (open blue circle) was positioned at the fictive position of the nest, that is, at 15 m due north (0°; series A4). Coloured dots and bars depict the ants' mean homing directions and the 95% confidence intervals, respectively. N indicates north.

area centred on the fictive nest entrance. The search density in the same area dropped to about 5% when the landmark was absent during tests (no LM in Fig. 5B). Furthermore, the ants usually searched the landmark square more intensively than the home-vector square when landmark-based and vector-based information did not coincide. However, when the beacon was set up to one side of the point of release (position –15 in Fig. 5C), the ants' search preferences changed. In this case, 37 out of 40 ants did not even enter the 4 m² area indicated by the landmark.

The farther the landmark was located from its habitual position at the (fictive) nest entrance indicated by the ants' home vector, the lower were the ants' search densities around the landmark (Fig. 5). The extent of the ants' response to the displaced beacon depended on the direction and the magnitude of the displacement. A 5 m shift towards the point of release (position –5 in Fig. 5B) reduced the average search density in the landmark area considerably less than a similar shift of the beacon in the opposite direction (position +5 in Fig. 5B). An additional 3 m sideways shift of the beacon reduced the search density further (Fig. 5C). However, the ants' search efforts at the end of the home vector were largely unaffected by the magnitude and the direction of the displacement of the beacon. They were generally low and reached their maximum values (about 5–7%) when the landmark was missing (no LM in Fig. 5B), and when it was installed 3 m to one side of the point of release (position –15 in Fig. 5C).

DISCUSSION

In the present study, we investigated the effects of a displaced visual nest mark on the homing and nest-search behaviour of desert ants, *C. fortis*. In a parametric series of competition experiments we gradually increased the discrepancy between the courses to be taken by the ants on the basis of path integration and on the basis of landmark information by installing the nest mark at various positions along and to one side of the ants' home-vector course. In order to be effective in homing at all, nest-site-associated landmark memories must be recalled while the ants are still at some distance from home. Here we show that they are active from the very beginning of the ants' homeward runs, although at later stages – during the ants' nest search – they may become ineffective, if the nest mark has been moved way out of place.

Previous experiments with *C. fortis* had shown that familiar nest-site-based landmarks elicited the nest-search behaviour only after the ants had run off the home vector almost completely (Michel and Wehner, 1995; Wehner et al., 1996). However, in these experiments the landmarks – a pair of black cylinders – had been flanking the nest at a distance of 2 m, that is, they had not been beacons indicating the nest entrance directly. Moreover, during the critical tests performed on a distant field, the landmarks had been displaced along, but not to the side of, the animals' home-vector course. Hence, vector-based and landmark-based information coincided in the directional component of the ants' inbound courses, but not in the distance to be covered in order to reach the nest. The experimental setup therefore prevented the authors from studying potential effects of displaced landmarks on the ants' homing directions. Owing to this constraint and based on the analysis of the ants' first turns, the authors had to conclude that homing ants ignored the displaced nest marks until the familiar landmarks were made to appear during the final stages of the ants' inbound runs (Michel and Wehner, 1995; Wehner et al., 1996). The results presented here point towards a more subtle influence that learnt landmarks might have on the ants' homeward courses. The current experimental setup
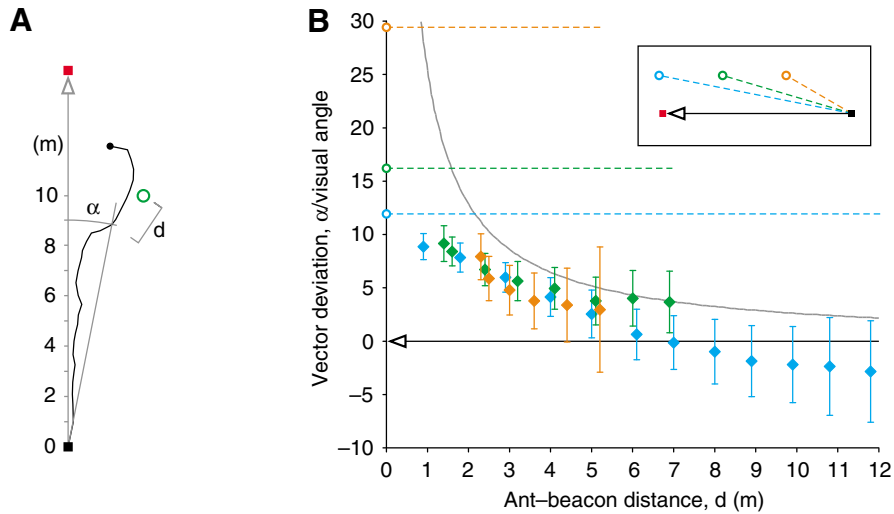
Fig. 4. Vector deviation as a function of the ant–beacon distance. (A) The ant's home-vector deviation α (in degrees) and distance d to the landmark (open green circle) were evaluated at distinct distances (in the example shown here at a 9 m distance) from the start of the ant's homeward run (see concentric circles in Fig. 3). The black and red squares depict the point of release and the fictive position of the nest, respectively. The black dot marks the ant's first turn (i.e. the onset of the ant's nest search behaviour). (B) α/d relations as computed from the ants' test runs. Visual angle is in degrees. Different colours represent different test situations. Inset: as in A the black and red squares depict the point of release and the fictive position of the nest, respectively; the open arrow indicates the ants' home vector; coloured circles show alternative positions of the landmark (data from ants with the landmark to the left of the home vector are mirrored). The open arrowhead pointing at the y-axis (0°) marks the direction of the ants' home vector. Correspondingly, the coloured broken lines indicate the direct courses towards the beacon for each test situation (see inset). Diamonds and bars depict the means and the 95% confidence intervals, respectively. The grey curve represents the horizontal visual angle of the landmark (ordinate) as seen by the observer from different distances (abscissa).

enabled us to study both the distance and the directional effects of a displaced nest mark on the ants' inbound trajectories.

When the landmark was positioned to one side of the point of release, the ants' courses were deflected to the side of the beacon during the first few metres of the inbound runs, but thereafter the

courses again aligned with the home-vector direction. When the landmark appeared to one side further down the homeward course, the ants gradually drifted towards the beacon. The fact that the ants searched more intensively in the vicinity of the landmark than at the point indicated by the home vector (see Fig. 5C) shows that the ants
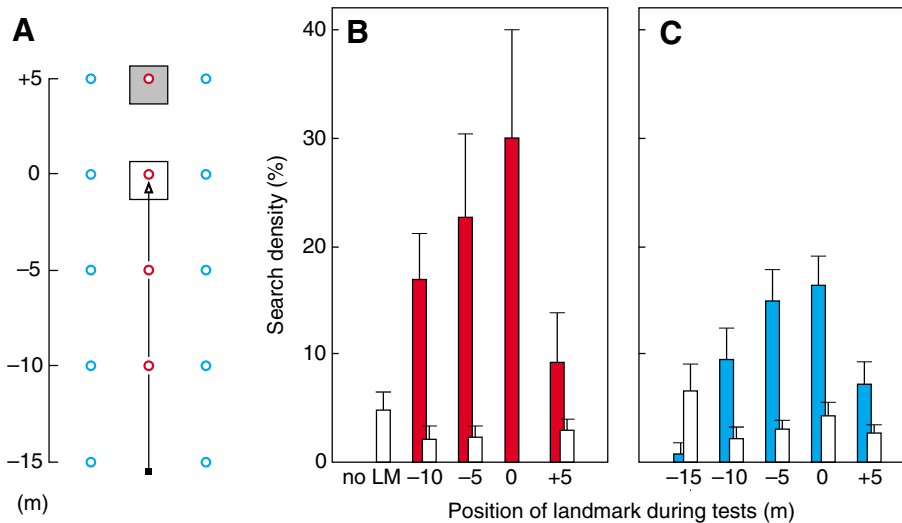

Fig. 5. Nest-search densities. (A) Conceptual scheme used for the evaluation of the ants' spatial search preferences. The open and the shaded squares indicate the areas selected to assess the search densities at the positions indicated by the ants' home vector (open arrow) and the beacon (open circle), respectively. In the example shown the landmark is assumed to be set up 5 m beyond the position of the nest entrance as indicated by the ants' home vector (at position +5). The black square marks the point of release. (B) Mean search densities with upper 95% confidence limits of the test series with the landmark positioned in the direction of the ants' home vector. Red and white bars are the search densities in the vicinity of the landmark and at the tip of the home vector, respectively. In the 'positive control' experiment (landmark position 0), the two squares coincide and the white bar is omitted. In the 'negative control' experiment (no landmark), the beacon was removed during tests. (C) Results of the experiments with the landmark positioned to one side of the ants' home vector. Data sets for the corresponding left and right series are pooled. Blue bars are the search densities in the vicinity of the landmark (white bars as above).

identified the displaced beacon as the nest mark they had experienced during training. This result makes it very unlikely indeed that spontaneous beacon aiming – as described in wood ants (Graham et al., 2003) – has been the main cause of the ants' angular drift towards the landmark. In fact, previous experiments with desert ants, *C. bicolor and C. fortis*, showed that the ants do not adjust their courses, that is, do not deviate from the direction indicated by their home vector, when a familiar route mark is displaced sideways (Collett et al., 1992). Moreover, even the wood ants mentioned above, once they have established their routes do not alter their courses when a familiar beacon along a habitual foraging path appears at an unusual position [in this case, on the other side of the direct path towards a known food source (Graham et al., 2003)]. We therefore feel confident that the deviation from the home-vector course observed in the present study reflects the ants' reaction towards a familiar visual signpost – the nest mark they had experienced during training.

The ants started to drift towards the beacon from a fairly constant distance. Motion parallax and the rate of change of the visual angle of an object are two cues that might have informed the ants about their distance to the object. During training, however, the ants approached the nest mark directly, which makes motion parallax ineffective. The visual angle of the beacon, however, increased continually and grew rapidly at distances less than 5 m (see grey curve in Fig. 4B). This value roughly coincided with the distances from which the ants started to drift towards the laterally displaced beacon. Perceived object size (Harris et al., 2007) and/or its rate of change might therefore have been the crucial cue(s) for inducing the ants to adjust their courses to the side of the beacon.

When the fictive nest entrance, defined by the ant's home vector, and the landmark-based system of navigation were less than 6 m apart, the majority of ants applied an all-or-none strategy in favour of the nest-mark cues. That is, they initiated the nest search at the beacon and concentrated their search efforts on this area. In all these cases, however, the state of the ants' path integrator was close to zero. In such situations ants usually weight landmark information more heavily than path-integration vectors (Knaden and Wehner, 2005).

During their final nest search the ants generally paid little attention to vector information as compared to landmark cues. However, the beacon gradually lost its attractiveness the further it had been moved out of place, and it was ignored completely when it was positioned to one side of the point of release. In this case, the landmark might just have been out of the ants' sight when they started the nest search.

Finally, although most ants drifted sideways when the beacon was positioned lateral to the home-vector course, none of the ants initiated the nest search at the beacon positioned to one side of the point of release, and only few ants did so when the beacon was installed to one side after the ants had run down about one third of their home vector. Moreover, the ants drifted only slightly – although significantly – from the home vector course, but they did not fully align with the direction indicated by the landmark (see difference between data points and dashed coloured lines in Fig. 4B). Such a mixed navigational strategy is puzzling, since an intermediate course is hardly ever successful. Intuitively, one would expect the ants to rely fully on one or the other type of information, that is, either to rate the beacon as familiar or unknown. In the first case, the ants should start the nest search at the landmark, that is, they should suppress path-integration information; in the second case, they should ignore the displaced beacon and continue to run along the home vector. Instead, the ants partly responded to the landmark by drifting away from the vector course, but, after having passed the beacon, proceeded to run off their home vector. Such an ambiguous behaviour raises the question of whether the landmark memories were only partly activated but fully used, or whether they were fully activated but only partly used. At the present state, this question must remain unanswered.

However, former competition experiments indicate that the weighting of landmark and sky-compass information is a dynamic process that changes with the ants' experience. If outbound foragers are consecutively presented with a situation in which landmark navigation always competes with vector navigation, in the first competition test the ants follow their reference-vector courses and move towards the landmark only after they have completed their vector course. Yet with increasing numbers of competition training sets, they more and more switch towards approaching the landmark directly and finally disregard their reference-vector course completely (Wehner, 1970).

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