Landmark guidance and vector navigation in outbound desert ants

Tobias Merkle[1],* and Rüdiger Wehner[2]

[1]Centre for Visual Sciences, Research School of Biological Sciences, Australian National University, Canberra ACT 2601, Australia and [2]Institute of Zoology and Brain Research Institute, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland
*Author for correspondence (e-mail: tobias.merkle@anu.edu.au)

SUMMARY

This study deals with the influence landmark information has on the foraging behaviour of the desert ant, *Cataglyphis fortis*, especially with the interaction of such landmark information with the ants' path integration system. We show in the first experiment that desert ants that are captured immediately after leaving their nest and then transferred to a remote test area search for the nest rather than activate their previous path integration vector. In a second experiment, the ants had been trained to a landmark corridor on their way to the feeder. In the critical test situation, they were again captured immediately after they had left the nest and transferred to a test field where they faced one of the following three situations: (1) the same landmark corridor as used during the training phase, (2) no landmarks at all and (3) a landmark corridor rotated by 90 deg. as compared with the training situation. Nearly all ants in test situation (1) eventually followed the landmark corridor but most of them never reached the fictive feeder. In situation (2), the ants searched around the nest entrance. In situation (3), approximately one half of the ants searched for the nest, whereas most of the other ants followed the landmark corridor, i.e. headed in a completely wrong direction. Hence, familiar landmarks do not only influence the foraging behaviour of desert ants, e.g. in making the ants start their foraging runs but can even out-compete the ants' path integration system.

Key words: desert ants, *Cataglyphis*, foraging, landmark guidance, path integration.

INTRODUCTION

Desert ants, *Cataglyphis fortis*, live and forage in the salt-pans of the northern Sahara, a mostly featureless habitat devoid of vegetation and other visual markers that could be used for orientation. Therefore, the most important and most frequently used navigational tool in desert ants is their path integration system (Wehner, 1968; Wehner, 2003; Wehner and Srinivasan, 2003). This system enables them to approach the nest on a direct route from any position by providing them with a continually updated home vector (for reviews, see Collett et al., 1999; Wehner and Srinivasan, 2003; Merkle et al., 2006b). When an ant has found and loaded up a food item, it simply plays out its home vector and returns to the nest *via* the shortest possible way. Playing out the reverse of the home vector enables it to return to a feeding site (Wehner et al., 2002).

However, the path integration process is error prone (Wehner and Wehner, 1986; Müller and Wehner, 1988; Merkle et al., 2006a; Merkle and Wehner, 2008b). Therefore, the ants require a backup system that allows them to compensate for those errors that have been accumulated during foraging and homing. When the home vector has not led them exactly to the nest entrance, they switch on a systematic search programme, thereby performing loops of increasing size that are interrupted by regular returns to the starting point of the systematic search (Wehner and Srinivasan, 1981; Müller and Wehner, 1994). The ants even take into account the length of the preceding foraging excursion by altering their search patterns accordingly (Merkle et al., 2006a).

In addition, desert ants also make use of external cues, mainly landmark information, in order to keep the path integration errors to a minimum. When foraging in cluttered environments or when confronted with artificial landmarks, they are able to use this landmark-based information to find the nest or a familiar feeder, or to establish routes between nest and feeder (Collett et al., 1998;

Heusser and Wehner, 2002; Wehner, 2003; Wehner and Srinivasan, 2003). Several studies have shown that the information obtained by use of landmarks can even override the information provided by the path integrator (Wehner et al., 1996; Collett and al., 1998; Andel and Wehner, 2004). What information is actually used when the information provided by nest-site landmarks conflicts with the information obtained by the path integrator of homing ants, depends on the context and the relationship between the position of the landmarks and the state of the path integrator (Bregy et al., 2008).

Ants that live in cluttered environments, for example the Australian desert ant, *Melophorus bagoti*, rely mainly on landmark information. These ants establish landmark-based routes during inbound and outbound runs (Kohler and Wehner, 2005; Wehner et al., 2006), and in acquiring such routes use nearby as well as distant (panoramic) landmarks [for the latter, see Narendra (Narendra, 2007)].

When desert ants have a different route to the feeder as compared with the nest, their motivational state (homing or foraging) decides which landmark route (inbound or outbound) is followed (Harris et al., 2005; Wehner et al., 2006) [see also Dyer et al. for honey bees (Dyer et al., 2002)]. In a previous study, we showed that the reverse also occurs, i.e. that landmarks can change the foragers' motivational state (Merkle and Wehner, 2008a). Animals that were halfway between their nest and a familiar feeding site were captured and transferred to a remote test field. When no landmarks were present during training and test, nearly all ants immediately changed from an outbound to an inbound state of their vector, i.e. they aborted their foraging trip and headed back towards the nest. However, when landmarks were present within the second half of the outbound run during both training and test, a remarkable number of ants continued their foraging runs to the feeder.

In the present study, we further investigate the influence of landmarks on the ants' foraging rather than homing behaviour. The

ants were captured immediately after they had left the nest and were transferred to an unknown test area. These ants were just about to commence foraging and, hence, had not put any effort into foraging at this stage. Thus, they differed from the ants tested in the experiment mentioned above that had already been on their foraging trips. We show that it depends on the presence of landmark cues whether the ants really start foraging or rather try to return to the nest. In addition, we investigate the interaction between landmark information and information provided by the path integrator on outbound rather than the more commonly studied inbound journeys.

MATERIALS AND METHODS
Field site and study species

The experiments were carried out with desert ants, *Cataglyphis fortis* Forel 1902 (Wehner, 1983), in a salt-pan at our traditional field site near Maharès in southern Tunisia (34 deg. 32′N, 10 deg. 32′E) from June until August 2005. All ants that were trained and tested belonged to the same colony. The area around the entrance of the colony was devoid of any conspicuous landmarks; this also held true for the area in which the feeder was established (see below) and for the area between nest and feeder.

Experiments
Experiment one (no landmarks)

The ants were trained to an artificial feeder (containing small biscuit crumbs) 10 m south of their nest entrance (Fig. 1A, left). Ants that had encountered the feeder were marked with a non-specific colour-code and allowed to forage to and fro between the nest and the feeder for at least another 24 h. This way, we ensured that all ants had performed similar numbers of foraging trips between the nest and the feeder when they were due to be tested.

During the test, the ants were captured by means of a small plastic ring (diameter 20 cm) immediately after they had left the nest (0%-out ants) (see also Merkle and Wehner, 2008a). They were then put into small plastic flasks and transferred in complete darkness to a test field that was approximately 60 m away from the nest. In addition, a sand mound was situated between the nest and the test field, making it very unlikely that ants of this colony had ever been in the test field before. The test field consisted of a white grid that had been painted on the desert floor (size 20×20 m, mesh width 1 m) (Fig. 1A, right). No landmarks were in or around the test field. The plastic flasks were opened and carefully put on the desert ground in the middle of the test field. After the ants had left the plastic flasks, their trajectories were recorded, with reference to the painted grid, on graph paper (scale 1:100) for five minutes each. Altogether, 25 ants were tested; each ant was tested only once.

Experiment two (landmarks)

Again, foraging ants were trained to the feeder 10 m south of their nest. In contrast to experiment one, a landmark corridor consisting of six black cylinders (height 30 cm, diameter 20 cm) was set up between the nest and the feeder. Pairs of cylinders were placed at distances of 2 m, 4 m and 6 m south of the nest; each of them had a lateral distance of 1 m to the beeline between the nest and the feeder (Fig. 1B, left). As in experiment one, ants were marked at the feeder (this time individually with a specific two-colour code) and allowed to forage for another 24 h. They were then captured after leaving the nest (0%-out-LM ants) and transferred to the test field (for more details on the capturing and release procedures, see Experiment one).

Each ant was released in the middle of the test field and confronted with one of the following three conditions: (1) no
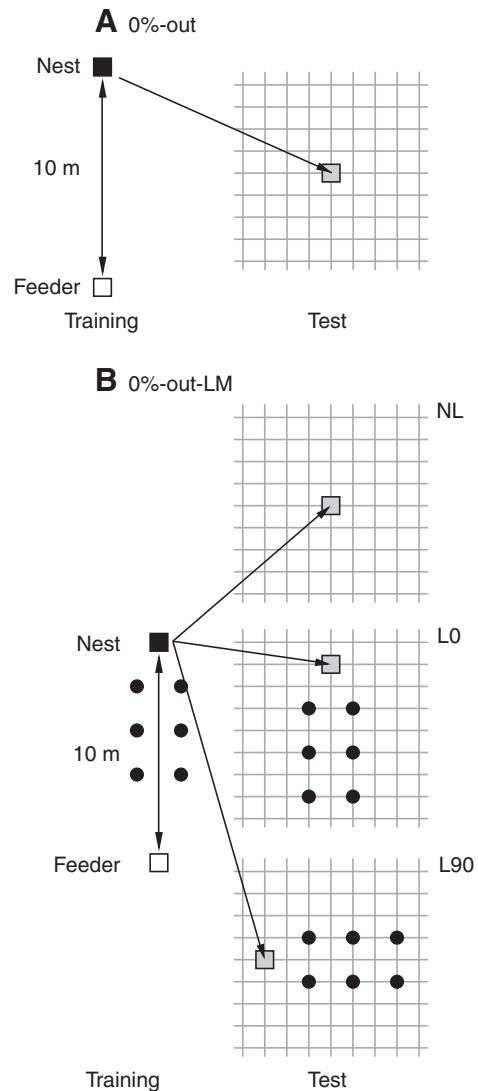

Fig. 1. Experimental setups. (A) Experiment 1 (no landmarks). Ants trained to a feeder located 10 m south of the nest entrance were captured immediately after leaving the nest (0%-out ants) and transferred to the test field, where they were released. (B) Experiment 2 (landmarks). As in experiment 1, ants were trained to a feeder located 10 m south of the nest. A landmark corridor consisting of six black cylinders was set up between the nest and the feeder. The ants were captured immediately after leaving the nest (0%-out-LM ants) and transferred to the test field, where they were confronted with no landmarks (NL), a landmark corridor as during training (L0) or a landmark corridor rotated by 90 deg. (L90). Grey squares indicate points of release.

landmarks (NL), (2) a landmark corridor arranged in exactly the same way (heading south) as in the training situation (L0) and (3) a landmark corridor as experienced during training but rotated by 90 deg. to the east (L90) (Fig. 1B, right).

Again, the trajectory of each ant was recorded for 5 min (for details of the recording procedure, see experiment one). The ant was then captured and brought back to the nest entrance where it was released. It entered the nest without hesitation. After having performed at least two runs to the feeder and back to the nest, the same ants were captured again and tested in a different condition. Afterwards, they had to perform at least two successful foraging trips to the feeder and back to the nest before they were captured and tested for the third and last time. After an ant's trajectories were recorded for 5 min

in all three test conditions (NL, L0, L90), this ant was excluded from further investigations.

Altogether, 25 ants were tested in all three conditions. The order in which the ants were presented with the three different test conditions was changed systematically.

Data analysis
Digitizing procedure

The recorded trajectories were digitized using a graphics tablet (Digikon 3, Kontron, Eching, Germany) and GEDIT Graphics Editor and Run Analyser and GEDIT Tracking Software (Antonsen, 1995). After the digitization procedure, we transformed the paths into cartesian coordinates (approximate step length of 5 cm), which were used for further analyses.

Analyses and comparisons

The first question we asked was whether the ants headed towards one particular direction or tried to find their nest, i.e. commenced their systematic search programme. As the search for the nest entrance consists of more or less symmetric loops around the starting point of the search (Wehner and Srinivasan, 1981; Müller and Wehner, 1994), we determined whether an ant headed towards one particular direction by determining the largest extension of its path in each of the four cardinal directions (Fig. 2, north, east, south, west). However, the radii of search loops increase over time and are never even close to each other in size (Wehner and Srinivasan, 1981; Merkle et al., 2006a). Therefore, we defined a 2 m limit; if the extension of the ant's path in one direction exceeded the extensions in all other directions by at least 2 m, this ant was considered as having a preferred direction. These preferred directions were assigned to north, east, south and west quadrants. This procedure was applied for all ants tested in experiment 1 (0%-out ants, N=25) and for each ant and each condition of experiment 2 (0%-out-LM ants, N=25 for each of the three conditions NL, L0, L90). It resulted in ratios for all groups that showed how many ants of a group had a directional preference and how many only searched for the nest. These ratios were compared between the 0%-out ants and the 0%-out-LM ants tested in condition L0 (same landmark arrangement in training and test). By doing so, we could define whether or not and to what extent landmarks had changed the ants' behaviour. In addition, the ratios were compared between the 0%-out-LM ants in conditions NL, L0 and L90.

As we found directional preferences for most of the 0%-out-LM ants tested in conditions L0 and L90 but no such preferences in condition NL (see Results), we compared groups L0 and L90 but included only those ants that exhibited directional preferences in both conditions. Altogether, we computed three values that were compared between conditions L0 and L90. First, we determined the directions the animals were heading towards. Because even the paths of ants that displayed a directional preference were quite tortuous as compared with the training situation and because most ants did first search for the nest before they headed in one direction (see below), we did not determine the directions of the paths by laying a circle with a fixed radius around the release point or by using the minimization method applied previously (Merkle and Wehner, 2008b). Instead, we determined the direction of the path of an ant by connecting the point of release with the point of the path at which the ant reached the maximal distance from the release point (Fig. 3). We checked these directions for deviations from the preferred directions (i.e. 90 or 180 deg., depending on whether the ants headed east or south). The absolute values of these deviations were then
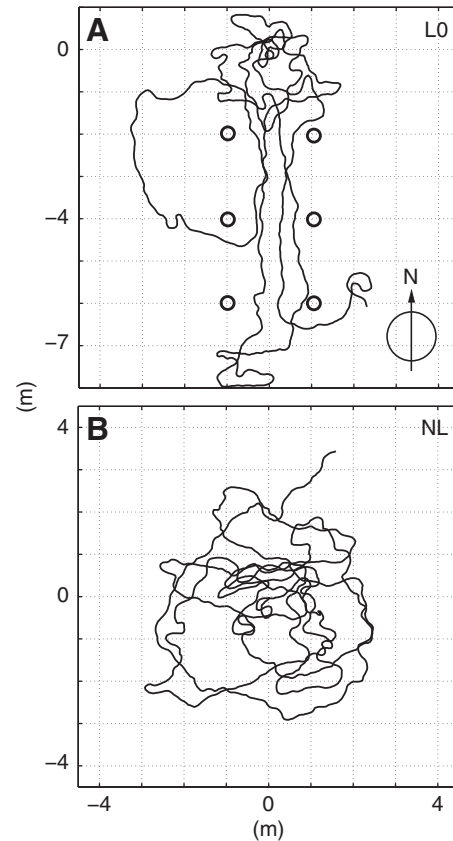

Fig. 2. Example of a 0%-out-LM ant in test condition L0 (A) and NL (B). Point of release was at 0/0. Landmarks are shown as black circles.

compared between the groups. In addition, we determined the maximum distance an ant reached in their preferred direction.

In order to determine how long it took an ant until it showed its directional preference, we computed the path length covered until the point at which it started heading out in that direction. The switch from searching for the nest to foraging was defined as the first point from which an ant headed in one direction without deviating from the former course by more than 45 deg. for at least 2 m (see Fig. 3, in which all three values described above are illustrated by a sample path). Ants that did not search for the nest at the beginning but immediately headed off in one direction exhibited a search-path length of zero.

Most of the 0%-out-LM ants in condition NL showed no directional preferences, i.e. they behaved in a similar way to those that were trained and tested without landmarks (0%-out ants, see Results). We, therefore, compared these two groups. The few ants that exhibited a directional preference were, again, excluded from the analysis, that is only the paths of ants that behaved as the majority behaved were analysed and compared. We determined the centre of the systematic search as the square with side length of 0.5 m that displayed the highest path density, i.e. the square where the path length divided by the overall path length of that particular ant showed the highest relative value [for more details regarding this procedure, see Merkle et al. and Merkle and Wehner (Merkle et al., 2006a; Merkle and Wehner, 2008a)]. The distances between search centres and release points were then calculated and compared between the two groups. As the search centres of both groups turned out to be very close to the release point (see Results), we did not determine
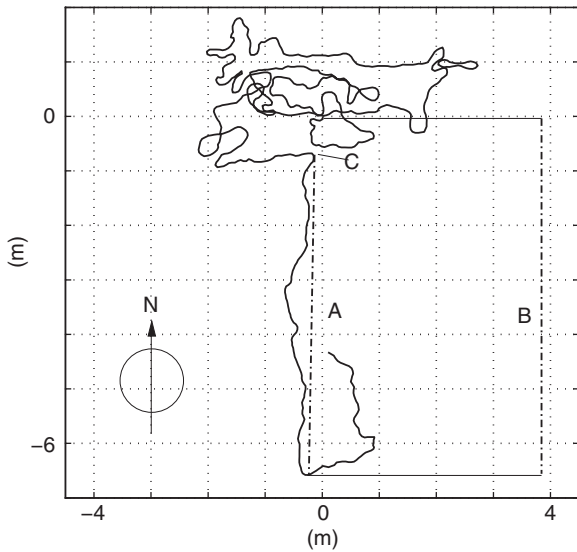
Fig. 3. Sample path showing the values that were determined for ants with directional preferences: (A) direction the ant headed towards, (B) distance reached by the ant in its preferred direction and (C) distance covered until the ant exhibited its directional preference (for more explanations, see text). Point of release was at 0/0.

the search centres and release points in the three different conditions in which the 0%-out-LM ants were tested (L0, NL, L90). For this comparison, all 25 0%-out-LM ants were compared for all three conditions, irrespective of whether an ant had a directional preference or not.

Statistics

The ratios of ants heading out towards one particular direction and those searching for the nest were compared using either Fisher's Exact test (comparisons between different ants, i.e. 0%-out and 0%-out-LM ants) or McNemar's test (tests between different conditions with which 0%-out-LM ants were confronted).

Directional deviations, distances and path lengths covered before the ants headed off in one direction were compared using the Wilcoxon-test for paired samples between 0%-out-LM ants in conditions L0 and L90.

The positions of the systematic search centres and the systematic searches spatial extensions were compared using Mann–Whitney's U-test (different test groups, 0%-out and 0%-out-LM ants).

By means of Friedman's rank analysis of variance for related samples, we could decide whether there were differences with regards to the systematic search centres between the three test conditions (L0, NL, L90), which the 0%-out-LM ants had to face.

Results were assessed as significant when $P<0.05$. All P-values given are two-tailed.

directions for the search centres. In addition, the spatial extension of the systematic search was determined by multiplying the distances between the two most extreme values on the x-axis (east–west direction) and y-axis (north–south direction). This multiplication yielded an area characterising the spatial layout of the systematic search pattern (Merkle et al., 2006a). To compare this value between the two groups, it was crucial that the ants had covered the same path lengths. Thus, the paths of the ants were cut to a length of 54.42 m (the shortest path length measured throughout all of the experiments) before the spatial extension was computed.

Finally, we determined the path centre, as described above, for the 0%-out-LM ants that were tested in conditions L0 and L90, i.e. in the conditions in which most ants displayed directional preferences. We then compared the distances and angles between

RESULTS

Five out of the 25 tested 0%-out ants showed a directional preference; four of them tended to head towards a southern direction, i.e. they headed towards the position where the feeder had been situated during the training. One ant set out in a westerly direction.

With regards to the 25 0%-out-LM ants that were tested in the three different conditions described in the Materials and methods section, the result was clear – when the test situation resembled the training situation (with the landmark corridor pointing towards the position of the feeder, L0), 23 of the 25 ants showed a directional preference for the southern direction (where the feeder had been during training). Thus, the behaviour of 0%-out ants (that had never experienced a landmark corridor) and 0%-out-LM ants in condition L0 differed significantly (Fisher's Exact test: $P<0.001$, $N=25$) (Figs 4, 5 and 6).

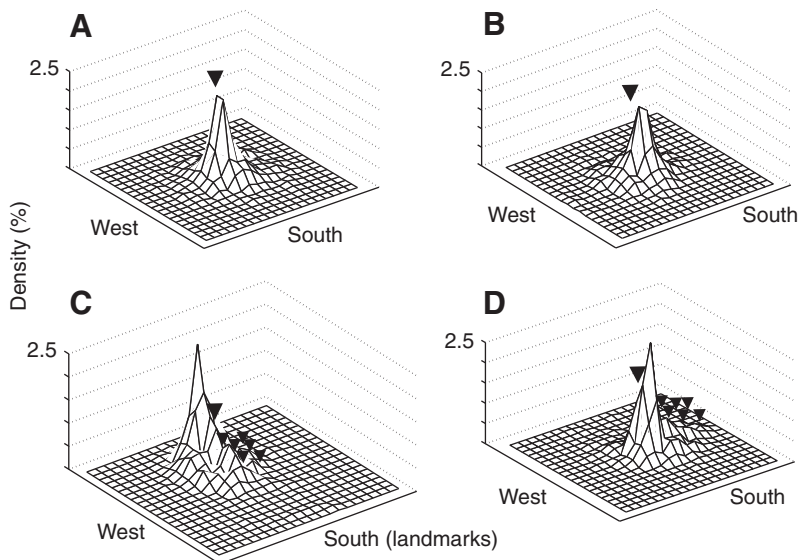
Fig. 4. Path layouts in different conditions. Density profiles of paths of (A) 0%-out ants ($N=25$) and 0%-out-LM ants in the three conditions (B) NL, (C) L0 and (D) L90 ($N=25$ in each condition). Density was calculated as the percentage of path length within each square divided by the total path length of all ants in the respective condition. Release points and landmark positions are indicated by large or small arrowheads, respectively. Side length of squares, 1 m.
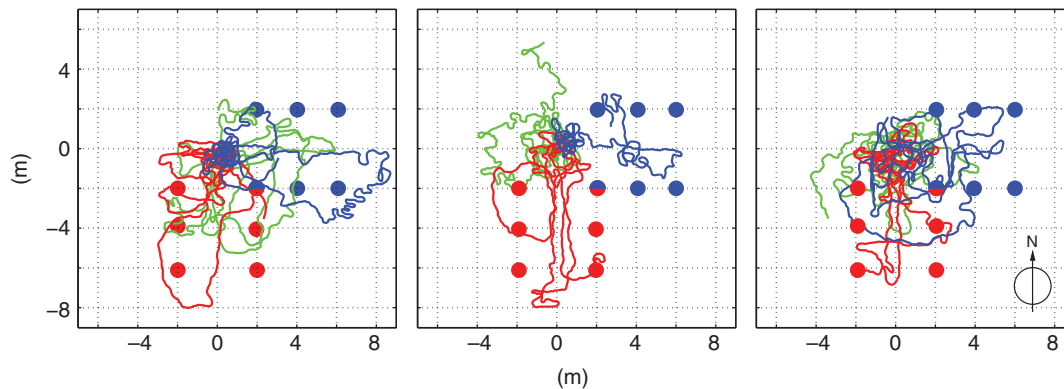
Fig. 5. Sample paths. Paths of three 0%-out-LM ants in the three conditions NL (green), L0 (red) and L90 (blue). Point of release was at 0/0. Landmarks in conditions L0 and L90 are shown as red or blue circles, respectively.

When the 0%-out-LM ants were tested without a landmark corridor (NL), only five individuals displayed a directional preference – four headed southwards and one westward. Finally, the ants were confronted with a landmark corridor that pointed towards the east (L90). In this situation, 11 ants were influenced by the corridor and tended to forage to the east, two ants headed south and 12 ants searched for the nest. Thus, the percentage of 0%-out-LM ants with a directional preference differed significantly between the different test conditions (McNemar's test: $P<0.05$ for all comparisons) (Figs 4, 5 and 6). Although the 0%-out-LM ants tested in condition L90 showed a tendency to follow the landmark corridor towards east, the relative number of ants that did so differed significantly from that of the ants tested under condition L0 (a path indicated by landmarks in the 'proper' position and direction), where nearly all ants headed south.

In the next step, we compared the 0%-out-LM ants facing the two different landmark corridor arrangements L0 and L90. Twelve of the 25 ants displayed a directional preference in both situations (L0, all headed southwards; L90, ten headed eastwards and two headed southwards). These 12 ants were included in the following comparison (see Materials and methods). With regards to the directional deviations, the ants tested in condition L0 were more accurate than those tested in condition L90 (the medians of directional deviation were 9.1 deg. and 15.6 deg. in L0 and L90, respectively). However, pairwise comparisons between the different experimental situations revealed that this difference was not significant (Wilcoxon test for pairwise comparison, $P=0.136$, $N=12$) (Fig. 7A). Even though the ants did not walk the entire distance of 10 m in either of the two landmark conditions, there were differences between the two conditions; when the ants were confronted with condition L0 during the critical test, they headed out further than when tested in condition L90 (L0, median of distance=7.98 m; L90, median of distance=7.23 m; Wilcoxon test for pairwise comparison, $P=0.015$, $N=12$) (Fig. 7B). Finally, we examined whether the ants' behaviour differed in the two landmark conditions in terms of when they started heading towards their preferred directions. In this regard, there were no remarkable differences in the ants' behaviour (L0, median of distance covered before heading out towards the preferred direction=21.92 m; L90, median=19.92 m; Wilcoxon test for pairwise comparison, $P>0.5$, $N=12$) (Fig. 7C). It should be noted that only one ant in condition L90 immediately headed for the feeder, whereas all of the other ants in either condition (and this ant in condition L0) searched for the nest first before they started setting out into one direction.

The 0%-out ants and the 0%-out-LM ants tested in condition NL (i.e. without a landmark array in any direction) searched very close to the point of release. The median distance of the systematic search centres of both groups amounted to 0.5 m and the groups did not differ markedly (Mann–Whitney U-test for independent samples, $P>0.5$, $N=20$). With regards to the spatial extensions measured for the searches of both groups, the result was similar (0%-out ants, median=35.74 m^2; 0%-out-LM ants tested in condition NL, median=29.95 m^2; Mann–Whitney U-test for independent samples, $P>0.3$, $N=20$).

Finally the positions of the search centres of 0%-out-LM ants during all three critical test conditions (NL, L0, L90) were compared. In all three conditions, the ants searched most intensely very close to the fictive nest position: the median distance between search centres and the fictive nest position amounted to 0.71 m in condition NL and L0. When tested in condition L90, the ants searched even closer to the nest position (median distance=0.5 m). However, the differences in the three test conditions proved not to be significant (Friedman's rank analysis of variance for related samples, $P>0.2$, $N=25$). The latter also held true for the directions between release points and search centres; the majority of the search centres were
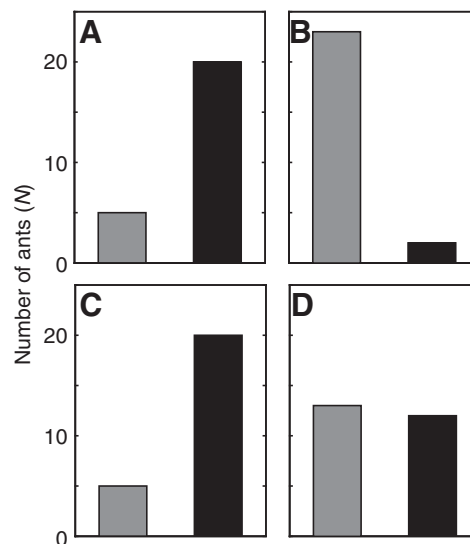

Fig. 6. Number (N) of ants that showed a directional preference (grey) and ants that searched for the nest instead (black) for 0%-out ants (A) and 0%-out-LM ants in conditions L0 (B), NL (C) and L90 (D).
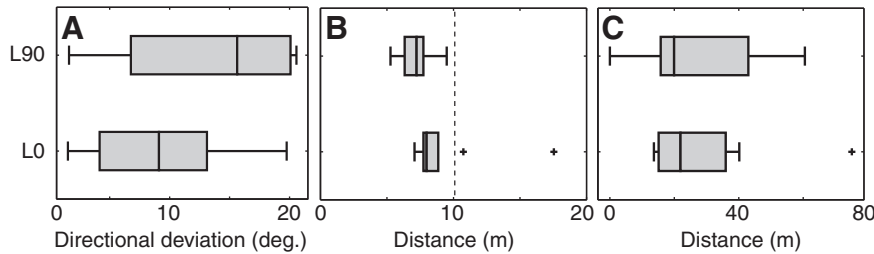
Fig. 7. Comparison of ants that showed directional preferences in conditions L0 and L90: (A) Directional deviations (deg.), (B) maximum distances covered (broken line represents the distance between the release point and that of the fictive feeder, m) and (C) distances covered until the ants showed their directional preferences (m). Boxplots indicate medians (middle vertical lines), quartile ranges (boxes), whiskers (error bars) and outliers (crosses).

north of the release point, and the ants did not behave differently in the various test situations (Friedman's rank analysis of variance for related samples, $P > 0.2$, $N = 25$).

DISCUSSION

Most of the experimentally displaced 0%-out ants (trained and tested without landmarks) did not start their foraging routines but rather searched for their nest entrance. As shown in an earlier study (Merkle and Wehner, 2008a), desert ants switch from an outbound to an inbound state of the path integration vector much more readily than they do in the reverse direction. In other words, ants that are disturbed during their foraging runs tend to return to the nest rather than to continue foraging. As disturbances under natural conditions are mainly caused by predators (Harkness and Wehner, 1977; Schmid-Hempel and Schmid-Hempel, 1984), a useful strategy in such cases is to try to reach the nest as quickly as possible. In the current study, we present evidence that this also holds true for ants that are about to begin their foraging or homing runs. If the experimental displacement takes place at the feeder, they start homing without hesitation (e.g. Burkhalter, 1972; Wehner and Flatt, 1972; Müller and Wehner, 1988; Wehner et al., 2002; Merkle and Wehner, 2008b; Merkle et al., 2006a). However, if captured shortly after leaving the nest, when they have their full outbound vector available, they do not play out the latter but instead start searching for the nest.

The ants behaved differently when a landmark corridor was presented in both the training and the test situation (0%-out-LM ants tested in condition L0). In this case, even after the experimental displacement, nearly all animals started at least one foraging excursion towards the fictive feeder. Hence, landmark information can influence the foraging behaviour of desert ants in a way that induces the ants to start foraging if they are in their full-outbound-vector-state, that is, the information provided by the landmarks helps them to handle the disturbance they experienced during the capturing and relocation procedure. In this respect, the foraging behaviour of *Cataglyphis* resembles the behaviour of other ants that mainly or even exclusively rely upon landmarks for orientation. Wood ants, *Formica japonica*, for example, use panoramic landmarks as their main means of navigation (Fukushi, 2001). If they are experimentally displaced from their nest entrance in the same way as *Cataglyphis* foragers have been displaced in the experiments of the current study, they start foraging without hesitation; this even happens after the displaced ants, having failed to locate the feeder, are brought back to the nest (Fukushi and Wehner, 2004).

However, the trajectories of 0%-out-LM ants in condition L0 differed from those performed in the training area. In the training area, the ants foraged to and fro between the nest and the feeder. When doing so, they displayed a high level of precision from the start, and only rarely had to switch to their systematic search behaviour to locate the feeder or the nest. This was the case even after the ants had been tested in one of the three conditions (L0, L90 or NL) in the test field and were brought back to perform another

two training runs before being tested again (Merkle and Wehner, personal observation). However, during the critical test in condition L0, only two ants reached a distance from the point of release that was larger than the distance between the nest and the feeder in the training situation (10 m). Moreover, all ants first searched for the nest and only after having covered a remarkable path length (around 20 m) did they venture out towards the fictive feeder. Finally, the paths were much more tortuous than those observed in the training area. In this regard, foragers of the genus *Cataglyphis* and *Formica* behave differently, as the latter start foraging after being displaced without a lengthy search and also faithfully recapitulate their outbound paths, i.e. head straight towards the position of the (fictive) feeder.

As a control, we tested the 0%-out-LM ants without providing the landmark corridor (condition NL). The results were very similar when compared with those of the 0%-out ants that had never experienced landmarks before. The percentages of ants with directional preferences were the same in both conditions and the two groups did not differ markedly with regards to their systematic searches (centres and spatial extensions). Thus, if the ants were deprived of the landmark information that they had experienced during the training procedure, they did not start foraging. This result strengthens our conclusion that the landmark information does indeed change the foraging behaviour of ants in such a way that they now start foraging in spite of the preceding disturbance.

There still remains the question why the 0%-out-LM ants in condition L0 did not immediately head off towards the feeder. In addition, why did most ants only make one attempt to reach the feeder and why did none conduct a search for the feeder? The latter becomes obvious when the positions of the search centres of the 0%-out-LM ants in the three different test conditions are compared. The distances and directions of the systematic search centres relative to the release points did not differ significantly between the conditions NL, L0 and L90. Thus, the presence of landmarks induced only one or two excursions towards the feeder position but did not simultaneously alter the spatial distribution of the paths. Obviously, the landmark corridor on its own did not induce the ants to react in exactly the same way as they had done during training.

Thus, apart from the landmark information, there seem to be additional cues that influence the foraging behaviour of desert ants. This conclusion becomes even more obvious when we investigate the paths in more detail (see Figs 4 and 5). Most ants aborted their foraging trips shortly after the landmarks had vanished out of their field of view. It might well be that during the first part of the of the journey, that is, when the landmarks were within their field of view, the ants made use of them during their foraging trips but as soon as they could no longer rely upon these landmarks, other cues became more important. Also, as these cues were very likely to be different in the test and in the training area, the ants did not continue to forage but returned to the nest instead. However, the nature of these other contextual or external cues [surface structure (see Seidl

and Wehner, 2006; Merkle and Wehner, 2008b); the presence of nest mates or distant panoramic landmarks (see Collett et al., 2003)] and how they might interfere with the path integrator remains elusive.

The fact that the ants first searched around the point of release before they started venturing out towards the feeder position may also explain the somewhat surprising result that nearly all of the ants performed at least one trip towards the feeder when landmarks were present. We found in a previous study that when foragers were captured in the middle of their outbound runs, only approximately half of them could be induced by landmarks to continue foraging (Merkle and Wehner, 2008a). This is surprising because these ants had already covered 50% of the outbound route and, therefore, had put more effort into their foraging excursion than ants that were just about to start foraging. This might suggest that it should be easier to make the former group continuing foraging. However, in this previous study, the ants only had the choice of continue foraging or returning to the nest and had to make an immediate decision, so to speak, whereas in the present study, the ants could search for the nest after having been released and, after spending some time with nest searching, could then start their foraging trips.

By confronting the 0%-out-LM ants with a corridor that was rotated by 90 deg., i.e. pointed towards east (L90), we created an experimental paradigm in which the two crucial orientation cues, path integrator and landmark information, were made to compete with each other. In the critical test, the behaviour of the ants changed dramatically, as 11 out of the 13 ants that started foraging followed the landmark corridor eastwards. This indicates that the landmark information is considered to be more important than the information provided by the path integrator. Several experiments in homing desert ants have shown that under specific conditions landmark information can override the information gained by the path integrator (Michel and Wehner, 1995; Wehner et al., 1996; Bregy et al., 2008). However, landmark information seems to be more robust when the landmarks are close to the nest (Bisch-Knaden and Wehner, 2003). Moreover, homing desert ants rely more on landmark information the closer they are to the nest entrance (Knaden and Wehner, 2005) and ignore nest-site marking landmarks when they are about to begin their home runs (Michel and Wehner, 1995). The results we present here indicate that the situation is different when the ants are in their full outbound vector state. In this state, they rely more on landmark information than on their path integrator. However, the percentage of ants that started a foraging excursion was significantly lower than in condition L0. Obviously, although the presence of landmarks induced some of the ants to commence foraging, the conflict between the two sources of information prevented a number of ants from doing so. Thus, the somehow reassuring effect of the landmark information decreases when landmark information and information provided by the path integrator are set into conflict.

As in condition L0, nearly all ants that headed for the feeder first switched on their systematic search programme and searched for the nest before they made an attempt to reach the feeder. Moreover, the path lengths they covered during the nest searches were similar in both conditions. Also, the ants that displayed a directional preference in both conditions (L0 and L90) did not differ remarkably with regards to their deviations from the correct direction. These findings again raise the question as to which other cues influence the foraging behaviour of desert ants.

The excursions to the feeder in condition L90 were shorter than in condition L0. This implies that the ants tested in condition L0 might have fallen back on their path integrator information when they could no longer rely on landmark information and, therefore, ventured out slightly further than the ants did in condition L90.

Approximately 50 years ago, von Frisch and Lindauer set the polarization compass and the landmark information in conflict in foraging honeybees (von Frisch and Lindauer, 1954; von Frisch, 1967). The results of these experiments were quite similar to the results we present here – if a great number of landmarks flanked the outbound paths of the bees, most of them followed the route indicated by the landmarks. More recent studies on honeybees have shown that familiar landmark cues can also override the odometric input when both sources of information are set into conflict (Chittka et al., 1995; Vladusich et al., 2005). However, in contrast to our findings, bees made extensive use of their skylight-based compass system when they were about to start their foraging excursions, whereas desert ants seem to put more emphasis on landmark information when they start foraging.

Finally, the conclusions that can be drawn from the results reported in the present study are: (1) the presence of landmarks can make disturbed ants start their foraging runs, (2) when information provided by landmarks and the path integrator are set into conflict the effect of the landmarks on the foraging behaviour of ants decreases and (3) landmark guidance can out-compete vector-based navigation not only in homebound runs as shown in a number of previous experiments (Wehner et al., 1996; Collett and al., 1998; Andel and Wehner, 2004; Bregy et al., 2008) but also in outbound runs when the ants start their foraging journeys.

REFERENCES

Andel, D. and Wehner, R. (2004). Path integration in desert ants, *Cataglyphis*: how to make a homing ant run away from home. *Proc. R. Soc. Lond., B, Biol. Sci.* **271**, 1485-1489.

Antonsen, N. (1985). *MbasaSoft GEDIT for Windows, v. 2. 5.* Zürich, Switzerland.

Bisch-Knaden, S. and Wehner, R. (2003). Landmark memories are more robust when acquired at the nest site than *en route*: experiments in desert ants. *Naturwissenschaften* **90**, 127-130.

Bregy, P., Sommer, S. and Wehner, R. (2008). Nest-mark orientation *versus* vector navigation in desert ants. *J. Exp. Biol.* **211**, 1868-1873.

Burkhalter, A. (1972). Distance measuring as influenced by terrestrial cues in *Cataglyphis bicolor*. In *Information Processing in the Visual System of Arthropods* (ed. R. Wehner), pp. 303-308. Berlin: Springer.

Chittka, L., Kunze, J. and Geiger, K. (1995). The influences of landmarks on distance estimation of honeybees. *Anim. Behav.* **50**, 23-31.

Collett, M., Collett, T. S., Bisch, S. and Wehner, R. (1998). Local and global vectors in desert ant navigation. *Nature* **394**, 269-272.

Collett, M., Collett, T. S. and Wehner, R. (1999). Calibration of vector navigation in desert ants. *Curr. Biol.* **9**, 1031-1034.

Collett, T. S., Fauria, K. and Dale, K. (2003). Contextual cues and insect navigation. In *The Neurobiology of Spatial Behaviour* (ed. K. J. Jeffery), pp. 67-82. Oxford: Oxford University Press.

Dyer, F. C., Gill, M. and Sharbowski, J. (2002). Motivation and vector navigation in honey bees. *Naturwissenschaften* **89**, 262-264.

Fukushi, T. (2001). Homing in wood ants *Formica japonica*: use of the skyline panorama. *J. Exp. Biol.* **204**, 2063-2072.

Fukushi, T. and Wehner, R. (2004). Navigation in wood ants *Formica japonica*: context dependent use of landmarks. *J. Exp. Biol.* **207**, 3431-3439.

Harkness, R. D. and Wehner, R. (1977). Cataglyphis. *Endeavour* **11**, 115-121.

Harris, R. A., de Ibarra Hempel, N., Graham, P. and Collett, T. S. (2005). Priming of visual route memories. *Nature* **438**, 302.

Heusser, D. and Wehner, R. (2002). The visual centring response in desert ants, *Cataglyphis fortis*. *J. Exp. Biol.* **205**, 585-590.

Knaden, M. and Wehner, R. (2005). Nest mark orientation in desert ants *Cataglyphis*: what does it do to the path integrator? *Anim. Behav.* **70**, 1349-1350.

Kohler, M. and Wehner, R. (2005). Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: how do they interact with path-integration vectors? *Neurobiol. Learn. Mem.* **83**, 1-12.

Merkle, T. and Wehner, R. (2008a). Landmark cues can change the motivational state of desert ant foragers. *J. Comp. Physiol.* **194**, 395-403.

Merkle, T. and Wehner, R. (2008b). Repeated training does not improve the path integrator in desert ants. *Behav. Ecol. Sociobiol.* DOI:10.1007/s00265-008-0673-6.

Merkle, T., Knaden, M. and Wehner, R. (2006a). Uncertainty about nest position influences systematic search strategies in desert ants. *J. Exp. Biol.* **209**, 3545-3549.

Merkle, T., Rost, M. and Alt, W. (2006b). Egocentric path integration models and their application to desert arthropods. *J. Theor. Biol.* **240**, 385-399.

Michel, B. and Wehner, R. (1995). Phase-specific activation of landmark memories during homeward-bound vector navigation in desert ants, *Cataglyphis fortis*. *Proc. Neurobiol. Conf. Goettingen* **23**, 41.

Müller, M. and Wehner, R. (1988). Path integration in desert ants *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**, 5287-5290.

Müller, M. and Wehner, R. (1994). The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. *J. Comp. Physiol.* **175**, 525-530.

Narendra, A. (2007). Homing strategies of the Australian desert ant *Melophorus bagoti*. II. Interaction of the path integrator with visual cue information. *J. Exp. Biol.* **210**, 1804-1812.

Schmid-Hempel, P. and Schmid-Hempel, R. (1984). Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Ins. Soc.* **31**, 345-360.

Seidl, T. and Wehner, R. (2006). Visual and tactile learning of ground structures in desert ants. *J. Exp. Biol.* **209**, 3336-3344.

Vladusich, T., Hemmi, J. M., Srinivasan, M. V. and Zeil, J. (2005). Interactions of visual odometry and landmark guidance during food search in honeybees. *J. Exp. Biol.* **208**, 4123-4135.

von Frisch, K. (1967). *The Dance Language and Orientation of Bees*. Cambridge, MA: The Belknap Press, Harvard University Press.

von Frisch, K. and Lindauer, M. (1954). Himmel und Erde in Konkurrenz bei der Orientierung der Bienen. *Naturwissenschaften* **41**, 245-253.

Wehner, R. (1968). Optische Orientierungsmechanismen im Heimkehrverhalten von *Cataglyphis bicolor* (Formicidae, Hymenoptera). *Rev. Suisse Zool.* **75**, 1076-1085.

Wehner, R. (1983). Taxonomie, Funktionsmorphologie und Zoogeographie der saharischen Wüstenameise *Cataglyphis fortis* (Forel 1902) stat. nov. (Insecta: Hymenoptera: Formicidae). *Senckenb. Biol.* **164**, 89-132.

Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *J. Comp. Physiol.* **189**, 579-588.

Wehner, R. and Flatt, I. (1972). The visual orientation of desert ants, *Catagyphis bicolour*, by means of terrestrial cues. In *Information Processing in the Visual System of Arthropods* (ed. R. Wehner), pp. 295-302. Berlin: Springer.

Wehner, R. and Srinivasan, M. V. (1981). Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J. Comp. Physiol.* **142**, 315-338.

Wehner, R. and Srinivasan, M. V. (2003). Path integration in insects. In *The Neurobiology of Spatial Behaviour* (ed. K. J. Jeffery), pp. 9-30. Oxford: Oxford University Press.

Wehner, R. and Wehner, S. (1986). Path integration in desert ants: approaching a long-standing puzzle in insect navigation. *Monit. Zool. Ital.* **20**, 309-331.

Wehner, R., Michel, B. and Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129-140.

Wehner, R., Gallizzi, K., Frei, C. and Vesely, M. (2002). Calibration processes in desert ant navigation: vector courses and systematic search. *J. Comp. Physiol.* **188**, 683-693.

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