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Homing strategies of the Australian desert ant *Melophorus bagoti*

II. Interaction of the path integrator with visual cue information

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Summary

Individually foraging ants are known to return to their nest by using path-integration and recording visual information present in the environment. The interaction between the path integrator and the information provided by the visual cues in an Australian desert ant are reported here. Ants were trained to travel in a 1-m wide and 20-m long corridor of cylinders. Homeward paths of trained ants were recorded in the presence and absence of vector information and route cues in both the familiar training field and in an unfamiliar test field. Homing ants used route cue information only in a familiar context. The route cues were not essential but served to reduce the deviation of the homing trajectory from the nest–feeder line. When displaced locally, homebound ants initially oriented towards the nest using distant cues and then headed in a direction intermediate between that dictated by the path integrator and the distant cues. If in the course of travel ants encountered the familiar path they adhered to it. If not, they travelled on average half the distance of the outbound journey and initiated a search directed towards the nest. Following the search, ants headed in a direction intermediate between that dictated by the route cues and the distant cues. In an unfamiliar context neither vector nor route cue information could steer a homing ant towards the nest. The dominance of distant cues, the importance of familiar context and the interaction between different navigation strategies are discussed here.

Key words: distant cues, route cues, path integrator, context, interaction, ants, *Melophorus bagoti*.

Introduction

At the end of each foraging trip central place foraging insects such as ants, return to their nest with great precision. Ants that navigate using chemical cues, rely on visual information when a conflict arises between the visual scene and the pheromone trails (Harrison et al., 1989). Hence visual cues in the foraging territory are vital for homing ants (Collett et al., 1992; Collett et al., 2003b; Seidl and Wehner, 2006). Non-trail forming ants that inhabit landmark-rich rain forests return to the nest by either matching the contrast in the canopies (Hölldobler, 1980) or using landmark and celestial information (Beugnon et al., 2005). Individually foraging desert ants that inhabit featureless habitats are guided primarily by the path integrator to steer themselves towards the goal (Wehner et al., 1996). During path-integration, ants continuously monitor the direction and distance travelled on the foraging journey, to update a vector and compute the shortest distance to return to the nest (Wehner and Wehner, 1990; Collett and Collett, 2000; Wehner and Srinivasan, 2003).

Path-integration is a self-centred system of navigation that accumulates errors (Müller and Wehner, 1988), and because of this ants use the cues along the route, when available, to fine-tune their home vector (Collett, 1992). Path-integration is often the initial navigational strategy of non-trail-forming ants in unfamiliar terrain. With repeated foraging, an area becomes familiar and the information derived from the landmarks along the route is also used. The visual landmark information is thus utilised as a supplementary strategy (Wehner et al., 1996) for homing (Burkhalter, 1972; Wehner and Räber, 1979; Bisch-Knaden and Wehner, 2001; Collett et al., 2001). In some cases, the action associated with the visual landmarks suppresses the performance of the path integrator (Collett et al., 1998; Kohler and Wehner, 2005). However, the interaction between the path integrator and the visual cues present in the foraging territory remains obscure. This paper reports the findings of an investigation into this interaction in the Australian desert ant, *Melophorus bagoti*, which primarily navigates by establishing and adhering to individualistic routes (Kohler and Wehner, 2005).

Materials and methods

Animals

The solitary foraging Australian desert ant *Melophorus bagoti* Lubbock, constructs terrestrial nests. They are active only during the summer months from November to early April, and hibernate the rest of the year. In the summer, they forage during the hot period of the day, and begin foraging only when the soil surface temperature is over 50°C (Christian and Morton, 1992; Muser et al., 2005). *M. bagoti* ants are scavengers, and feed primarily on insects roasted in the desert heat.

Experimental set up

Ants were trained to forage within a corridor of landmarks flanking the route from the nest to a food source. Homebound trajectories of trained ants were recorded in the presence and absence of vector information and route-cues, in both the familiar training field and an unfamiliar test field.

The training field (15 m×30 m) was set up around a nest where no distinct landmarks such as trees were present. All tussocks in the foraging area were cleared using a lawn mower. Here, the ants were trained to reach a feeder by travelling north through a 20 m long route-mark corridor (20 m length and 1 m width; Fig. 1A). The route-mark corridor was constructed by erecting two rows of cylinders, each cylinder measuring 60 cm in height and 16 cm in diameter. Cylinders were placed on each side of the nest and the feeder, 0.5 m away, and along the path, where they were placed alternately 0.5 m to the left and right of the nest–feeder line, at 2 m intervals. A feeder with watermelon and cookie crumbs as food, was sunk into the ground at the end of the corridor. During training, the interior walls of the feeder was intentionally kept grainy to help ants climb out of the feeder. During testing, however, a thin coating of fluon was applied on the interior walls to prevent ants from escaping. The training field was divided into a grid of 0.5 m squares using strings and tent pegs. Paths of homing ants were recorded on squared paper.

A test field (15 m×30 m) was established in an unfamiliar area, ~250 m away from the nest site. A route-mark corridor similar to the one in the training field was set up. The test field also was cleared of tussocks and divided into a grid of 0.5 m squares wherein homebound trajectories were recorded.

Training regime

Ants that reached the feeder for the first time were marked with distinct colours for identification and allowed to return to the nest. Following marking, each ant revisited the feeder at least 20 times in a given day and were trained to reach the feeder and return to the nest for 14 consecutive days. Ants that arrived to the feeder on the 15th day and picked up a cookie crumb were captured in a plastic vial and released either in the training field or in the test field where their paths were recorded in different test conditions. Each ant was tested only once.

Testing

Based on their vector information, ants were divided to two groups: (1) full-vector ants: ants caught at the feeder before they had begun their homebound run, and (2) zero-vector ants: ants caught close (within 50 cm) to the nest entrance while returning to the nest. Zero-vector ants are so called as they have nearly run off their entire home vector.

Ant paths within the route-mark corridor

The homebound paths of ants that arrived at the feeder, after travelling through the route-mark corridor, were recorded under three conditions, full-vector ants in the presence of route-marks (FvRm+), full-vector ants in the absence of route-marks (FvRm–) and zero-vector ants in the presence of route-marks (ZvRm+), in both the unfamiliar test field and familiar training area, giving a total of six conditions. In the training field, the paths taken by the ants were recorded until they reached the nest; all the tested ants reached the nest, taking on average less than 40 s. In the test field, the paths of full-vector ants were recorded until the ants began to search, while the paths of zero-vectors ants were recorded for a 5-min period. Search was identified by a turn ⩾50° from the homing trajectory and extending for at least 0.5 m. The start of search was identified with a 100% reliability between two experimenters in an earlier sample.

Ant paths following a sideways displacement

Ants of this group were also trained within the route-mark corridor for 14 successive days. Ants that arrived at the feeder

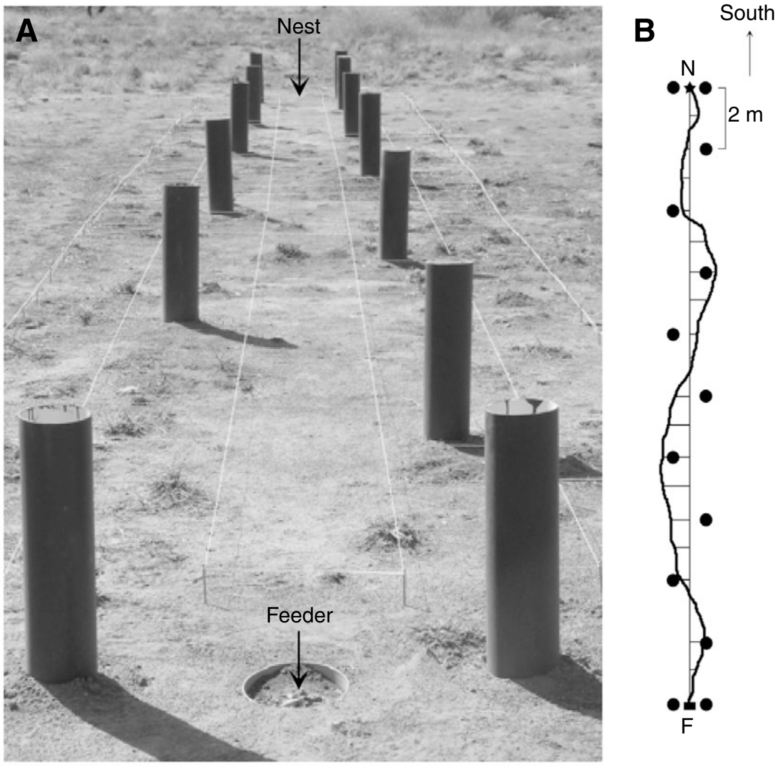


Fig. 1. (A) Experimental set-up of the route-mark corridor in the training field. (B) An example of a homing ant's trajectory (thick line), to demonstrate the method of measuring the deviation from the nest–feeder line (N–F) at every 1 m interval. Cylinders are represented as filled circles.

on the 15th day and picked up a cookie crumb, were captured and displaced sideways, 1.5 m, 3 m, 6 m and 10 m west of the nest-feeder line. Paths of homing ants were recorded on squared paper until they reached the nest. The route-marks were not moved during the tests. As a control group, zero-vector ants were captured and were displaced to a point 10 m west of the nest-feeder line.

Analysis

Trajectories of homebound paths were digitised. Data evaluation was carried out using statistical methods prescribed for circular distributed data by Batschelet (Batschelet, 1981). Circles of 0.5 and 5 m radii were drawn around the release point and angular positions were recorded when the trajectories crossed each circle for the first time. The mean direction $\boldsymbol{\theta}$ and length of the mean vector r were computed for each condition. The mean angles of circular observations was compared by Watson–Williams test using the circular statistics program Oriana (Kovach, 2004). Among ants displaced sideways, the distribution of orientations at both 0.5 m and 5 m were analysed using the V test to determine whether ants from each group were significantly oriented towards their true nest position.

Distance travelled before engaging in a search was determined for ants recorded in the test field and among ants displaced sideways. For ants whose paths were recorded in the training field, the absolute deviation of an ant's path from the nest–feeder line was measured at every 1 m interval (Fig. 1B). The overall average deviation was computed for each ant, following which the average deviation for each condition was determined. Less deviation would suggest ants adhering to a nest–feeder path, whereas greater deviation would suggest otherwise. For ants displaced sideways, the point of entry of each ant into the route-mark corridor was determined and was compared among the five laterally displaced groups. Data were checked for normality and non-parametric analyses were conducted when required. Search behaviour is described, but not analysed in detail. Another paper in preparation is devoted to the analysing the search patterns.

Trajectories of ants displaced laterally were analysed in four categories based on their search patterns: (a) zero turns: paths that did not have any turns ⩾50°; (b) one turn: paths of ants characterised by a single turn ⩾50°, these are usually 90° turns directed towards the route-mark corridor; (c) zero loops: paths of ants with more than one turn s^{-1} ⩾50°, but the paths never form loops; and (d) ⩾one loop: paths of ants that turn ⩾50° and form a loop/s.

Results

Homing in unfamiliar test field

None of the ants from the three groups FvRm+, FvRm– and ZvRm+ reached the fictive nest position located 20 m away from the release point (Fig. 2A). Ants with vector information, FvRm+ and FvRm–, path-integrated towards the fictive nest, but did not run off the entire vector, and travelled 8.84±2.35 m (44.22% of 20 m) and 8.98±2.32 m (44.94% of 20 m) respectively (means ± s.d.; t-test, P=0.84), before engaging in a search. Ants, in the absence of vector information (ZvRm+), did not travel within the familiar route-mark corridor, but engaged in a search around the release point throughout the recorded duration (Fig. 2A).

Orientation of ants in the presence of route marks (FvRm+) was directed towards the fictive nest and differed significantly from the orientation of ants in the absence of route marks (FvRm–) at both 0.5 m ($P<0.05$, Watson–Williams test) and 5 m ($P<0.05$, Watson–Williams test) after release (Fig. 3A). The initial orientation of FvRm+ ants at 0.5 m after release was significantly different from the orientation after the ants had travelled a distance of 5 m ($P<0.05$, Watson–Williams test; Fig. 3A). However, the initial orientation of FvRm– ants at 0.5 m after release did not differ from the orientation after the ants had travelled

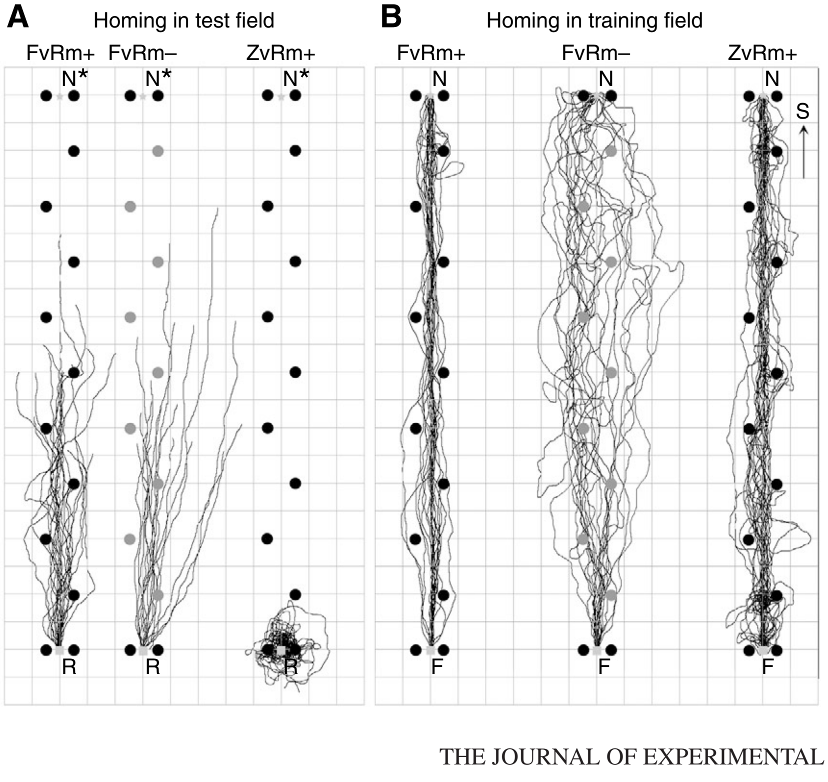


Fig. 2. Trajectories of homebound ants in (A) an unfamiliar test field and (B) the familiar training field. Each line represents the path of an ant. (A) Trajectories of FvRm+ (N=24), FvRm– (N=17) and ZvRm+ (N=15) from release point R towards the fictive nest N*. (B) Trajectories of FvRm+ (N=20), FvRm– (N=20) and ZvRm+ (N=21) from the feeder F to the nest N. Route-marks for homing ants are shown as black circles. In FvRm– condition, the grey circles indicate the location of the route-marks that were removed during test conditions. Grid size is 1 m^2.

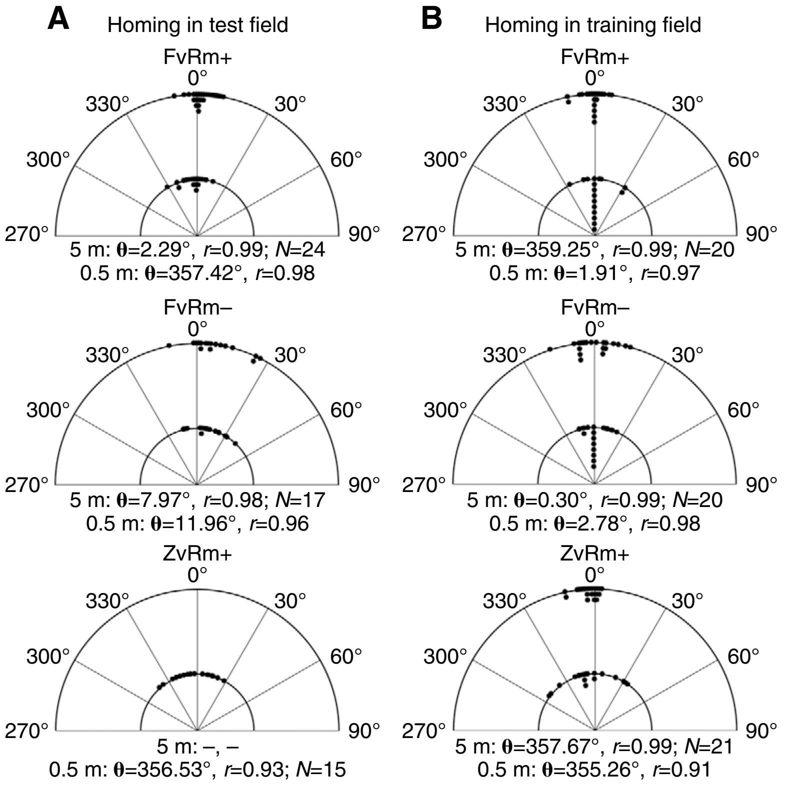


Fig. 3. Orientation of ants at 0.5 m (inner circle) and 5 m from the release point in (A) unfamiliar test field and (B) familiar training field. Mean vector θ, length of the mean vector r and sample size N are shown. Nest direction $\theta=0°$.

a distance of 5 m ($P>0.1$, Watson–Williams test; Fig. 3A). The initial orientation of ZvRm+ ants at 0.5 m was directed towards the fictive nest, but thereafter they switched to a search around the release point, and continued searching for the entire recording duration of 5 min (Fig. 2A). None of the ZvRm+ ants crossed the 5 m circle during the search and hence their orientation at 5 m is not shown.

Homing in familiar training field

(a) Ants released within the route-mark corridor

All ants from the three groups, FvRm+, FvRm– and ZvRm+, reached the nest located 20 m away from the release point (Fig. 2B). The homing paths of the three groups deviated by different extents from the nest–feeder line ($P<0.001$, ANOVA), the deviation being maximum in FvRm– (0.603±0.31 m) and minimum in FvRm+ ants (0.125±0.06 m; mean ± s.d.) The paths of FvRm+ and ZvRm– were indistinguishable except for an initial search exhibited by zero-vector ants. The deviation of the paths of ZvRm+ ants (0.178±0.07 m) from the nest-feeder line was similar to the deviation exhibited by FvRm+ ants ($P>0.05$, Bonferroni's test) and was less than the deviation of FvRm– ants ($P<0.01$, Bonferroni's test).

The mean orientations of FvRm+ ants at 0.5 m and 5 m after release did not differ ($P>0.1$, Watson–Williams test; Fig. 3B) and both were directed towards the nest ($P_s<0.001$, V test). In the FvRm– ants too, the mean orientations at 0.5 m and 5 m after release did not differ ($P>0.1$, Watson–Williams test; Fig. 3B) and both were directed towards the nest ($P_s<0.001$, V test). Zero-vector ants initially exhibited a search, but then travelled within the route-mark corridor (Fig. 2B). Their mean orientations at 0.5 m and 5 m after release did not differ ($P>0.1$, Watson–Williams test; Fig. 3B) and both were oriented towards the nest ($P_s<0.001$, V test).

(b) Ants displaced sideways

Ants displaced sideways from the nest–feeder line, 1.5 m, 3 m, 6 m, 10 m and Zv10 m, reached the nest successfully (Figs 4–6). Ants that entered the route-mark corridor travelled within the corridor until they reached the nest. The point at which they entered the route-mark corridor varied in all the five groups ($P<0.001$, ANOVA). Ants from the 1.5 m, 3 m, 6 m and 10 m group entered the corridor 12.09±4.72 m ($N=21$), 7.66±3.86 m ($N=20$), 9.87±4.65 m ($N=18$) and 1.56±0.85 m ($N=21$; means ± s.d.) respectively, away from the nest. Zero-vector ants, Zv10 m, displaced laterally entered the corridor 12.08±4.61 m ($N=15$; means ± s.d.) away from the nest.

The initial direction and halfway distance travelled by ants [as discussed in the accompanying paper (Narendra, 2007)] strongly suggest that the ants are predominantly guided by the path integrator in this section. The distance travelled by relying on the path integrator was nearly half the distance of the outbound journey of 20 m in all four groups (9.15±3.77 m, $N=10$, 1.5 m group; 11.05±2.88 m, $N=12$, 3 m group; 9.50±3.28 m, $N=18$, 6 m group; 9.23±2.35 m, $N=21$, 10 m group; means ± s.d.; $P=0.35$, ANOVA; Fig. 4). As shown in Table 1, only few ants from the 1.5 m and 3 m groups initially relied on the path integrator (i.e. ants pooled from 'one turn', 'no loop' and 'one loop' categories), and by contrast, all ants from the 6 m and 10 m group relied on the path integrator. The direction of the second segment implies strongly that ants are being guided by an aspect of the visual scene.

The majority of ants from the 1.5 m and 3 m group entered the corridor either without a turn or with a single sharp turn that identifies a switch from relying on path-integration to route following. Few ants from these two groups searched in loops before entering the route-mark corridor (Table 1). In contrast, all the ants from the 6 m and 10 m group searched in loops, following which they reached the nest, by heading towards a direction intermediate between that dictated by the nest and the route-mark corridor. Zero-vector ants too searched in loops, following which they travelled in oblique paths to reach the route-mark corridor (Table 1). In all groups, once the ant hit the route-mark corridor, it travelled within the corridor to reach the nest.

Displaced ants to which vector information was available were initially oriented towards the true nest ($P_s<0.001$, V test; Fig. 5). At a distance of 5 m from the release point, their orientation changed significantly ($P_s<0.05$, Watson–Williams test), towards a direction intermediate between that dictated by

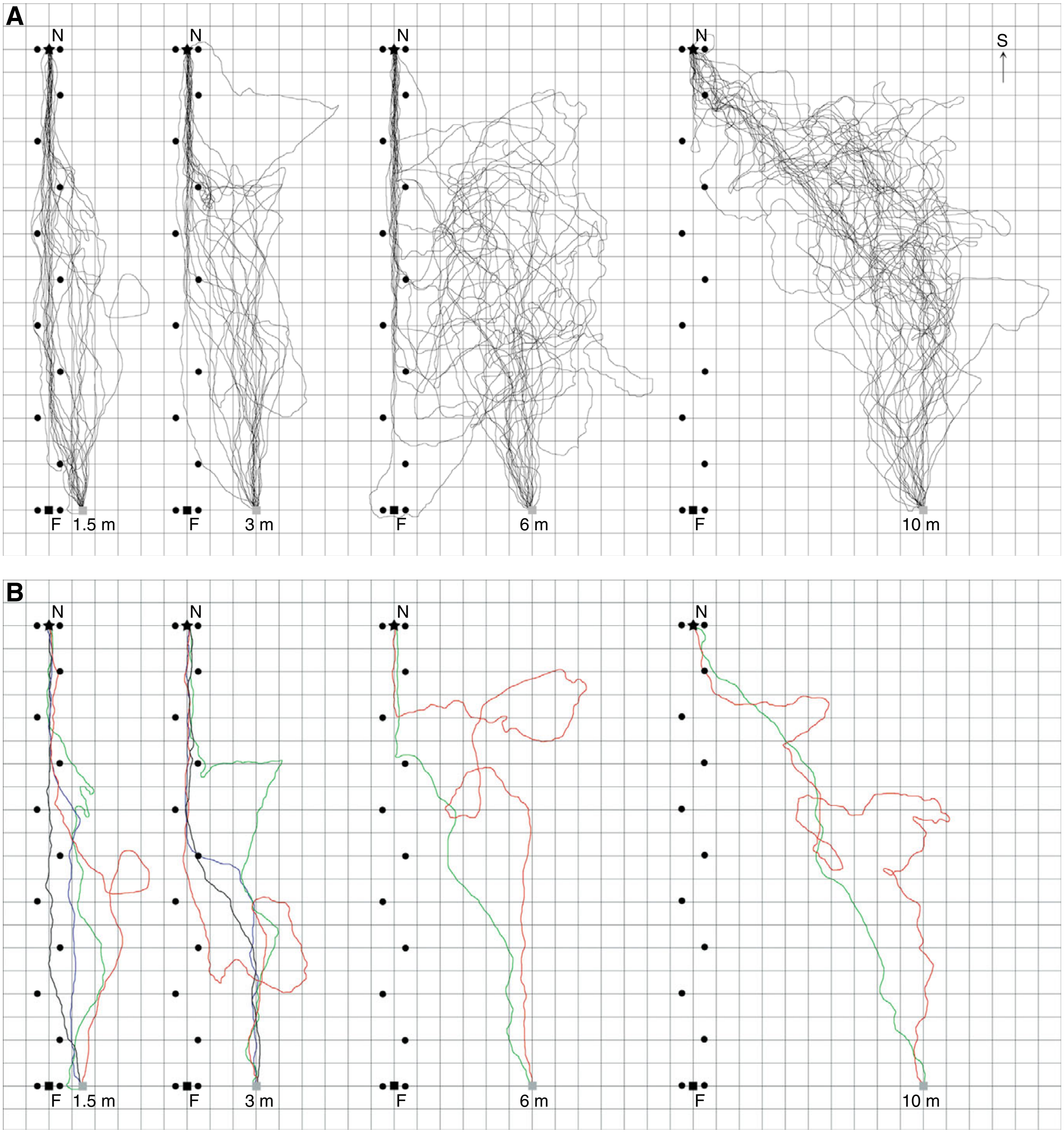


Fig. 4. Trajectories of homing ants following a sideways displacement. Ants travelled through a route-mark corridor (array of black circles) from nest N to a feeder F and were displaced from the feeder 1.5 m (*N*=21), 3 m (*N*=20), 6 m (*N*=18) and 10 m (*N*=21) from the feeder. (A) All trajectories of ants displaced sideways. (B) Example paths of ants at each displaced distance that had zero turns (black), one turn (blue), no loops (green) and ⩾one loop (red) are shown. Grid size is 1 m^2.

the path integrator and the nest (Fig. 5). Ants without vector information, Zv10 m, both initially and after 5 m were oriented towards the true nest direction (P_s<0.001, *V* test; Fig. 6). However, it is important to note that these ants initially exhibited a large directional scatter (*r*=0.38), which reduced after the ants had travelled a distance of 5 m (*r*=0.92).

Discussion

The most striking behaviour of homing *Melophorus bagoti* ants is their predominant reliance on distant nest-associated cues. Distant cues can be used for guidance and to represent a context. The lack of homing behaviour among ants in the test field does not distinguish between the two possible ways in

Table 1. *Proportion of ants that executed different searches along the travel path following a lateral displacement*

Search category	1.5 m (N=21)	3 m (N=20)	6 m (N=18)	10 m (N=21)	Zv10 m (N=15)
Zero turns	0.523	0.4	0	0	0
One turn	0.238	0.45	0	0	0
Zero loop	0.190	0.05	0.333	0.142	0.066
⩾One loop	0.047	0.1	0.666	0.857	0.933

Note: zero turns: paths that did not have any turns ⩾50°; one turn: paths characterised by a single turn ⩾50°; zero loop: paths with one or more turn s^{-1} ⩾50°, but never a loop; ⩾one loop: paths with turns ⩾50° and also a loop s^{-1}.

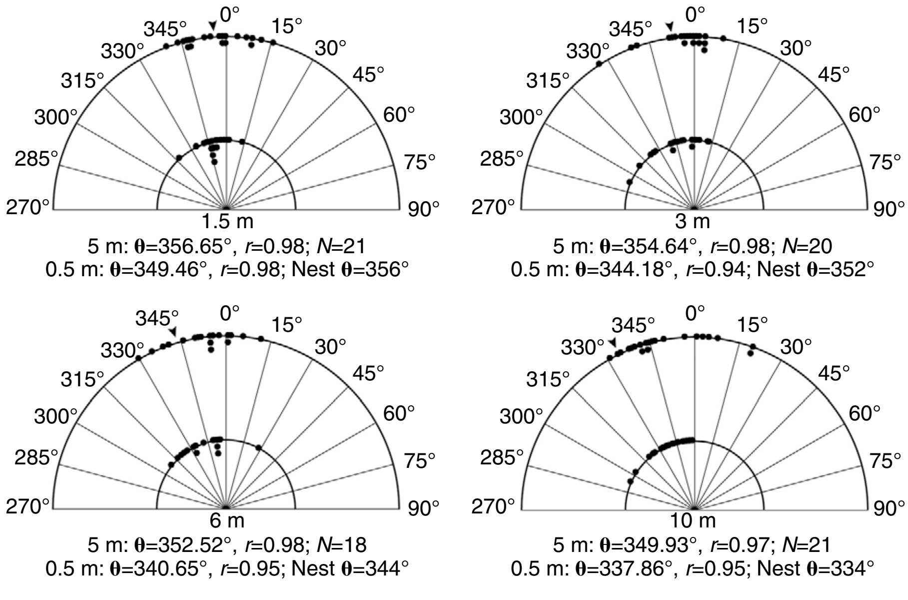
which distant cues act. In a familiar training field distant cues were utilised for guidance, but this did not exclude their role in providing contextual cues. Typically, *M. bagoti* ants forage in a particular sector (Muser et al., 2005), wherein they adhere to a particular route while returning to the nest (Kohler and Wehner, 2005). However, the ants are often exposed to severe dust storms that displace them from the familiar route. In such a scenario, relying on route cues alone would be perilous for a homing ant, and hence alternative or complementary strategies to reach the nest are required.

Homing without vector information

The initial orientation of ZvRm+ ants in the training field was towards the fictive nest position (Fig. 2B, Fig. 3B) and this was the result of a residual vector (zero-vector ants were captured close to the nest), or the direction dictated by route-marks or the familiar context consisting of micro-landmarks and distant cues. But even in an unfamiliar context, as was the case in a test field, the initial orientation of ZvRm+ ants was towards the nest (fictive) position (Fig. 2A, Fig. 3A). This was certainly because of a residual vector, or the direction dictated by the route-marks. The presence of familiar route-marks in an unfamiliar context of the test field, did not elicit homing, and the ants engaged in a search behaviour immediately after a short homeward run. Comparing the homing abilities of these ants with those that have no vector or route-mark information, ZvRm–, would be interesting. This is a condition not tested in this experiment. From the results here, I would predict that ZvRm– ants too would reach the nest, but only if in a familiar context.

Homing with vector information and the importance of contextual cues

FvRm+ ants deviated the least from the nest–feeder line in the training field, whereas in a unfamiliar test field they travelled nearly half-way towards the nest, interweaving from one route-mark to the other (compare Fig. 2A with 2B). The interweaving, which appears as if the ants are querying the presence of familiar route-marks in an unfamiliar context, was not exhibited by ants homing in a familiar context of the training field. Ants that travelled in the absence of route-marks (FvRm–) in the training field (Fig. 2B) deviated by a significantly greater distance from the nest–feeder line, whereas in the test field the lack of route-marks altered the orientation of the homing ant (Fig. 2A). In the training field the maximum deviation of the paths of FvRm– ants from the nest-feeder line was a result of the absence of familiar route-marks amidst familiar contextual cues. The deviation is quite possibly due to an interweaving search carried out by homing ants for the route-marks that were absent. The route-marks themselves could provide directional guidance when present amidst familiar contextual cues. In an unfamiliar test field, since the context was entirely different, FvRm– ants did not search for the route cues. Thus in the test field the paths of FvRm– ants were straight compared with the paths of FvRm+ ants whose paths interweaved from one route-mark to another (Fig. 2A). Thus, route cues are not essential, but when



1.5 m
5 m: θ=356.65°, r=0.98; N=21
0.5 m: θ=349.46°, r=0.98; Nest θ=356°

3 m
5 m: θ=354.64°, r=0.98; N=20
0.5 m: θ=344.18°, r=0.94; Nest θ=352°

6 m
5 m: θ=352.52°, r=0.98; N=18
0.5 m: θ=340.65°, r=0.95; Nest θ=344°

10 m
5 m: θ=349.93°, r=0.97; N=21
0.5 m: θ=337.86°, r=0.95; Nest θ=334°

Fig. 5. Orientation of ants 0.5 m (inner circle) and 5 m from the release point following a sideways displacement of 1.5 m, 3 m, 6 m and 10 m from the feeder. Nest direction, mean vector θ, length of the mean vector r and sample size N are shown. The arrowhead indicates the true nest direction, Nest θ, from the point of release.

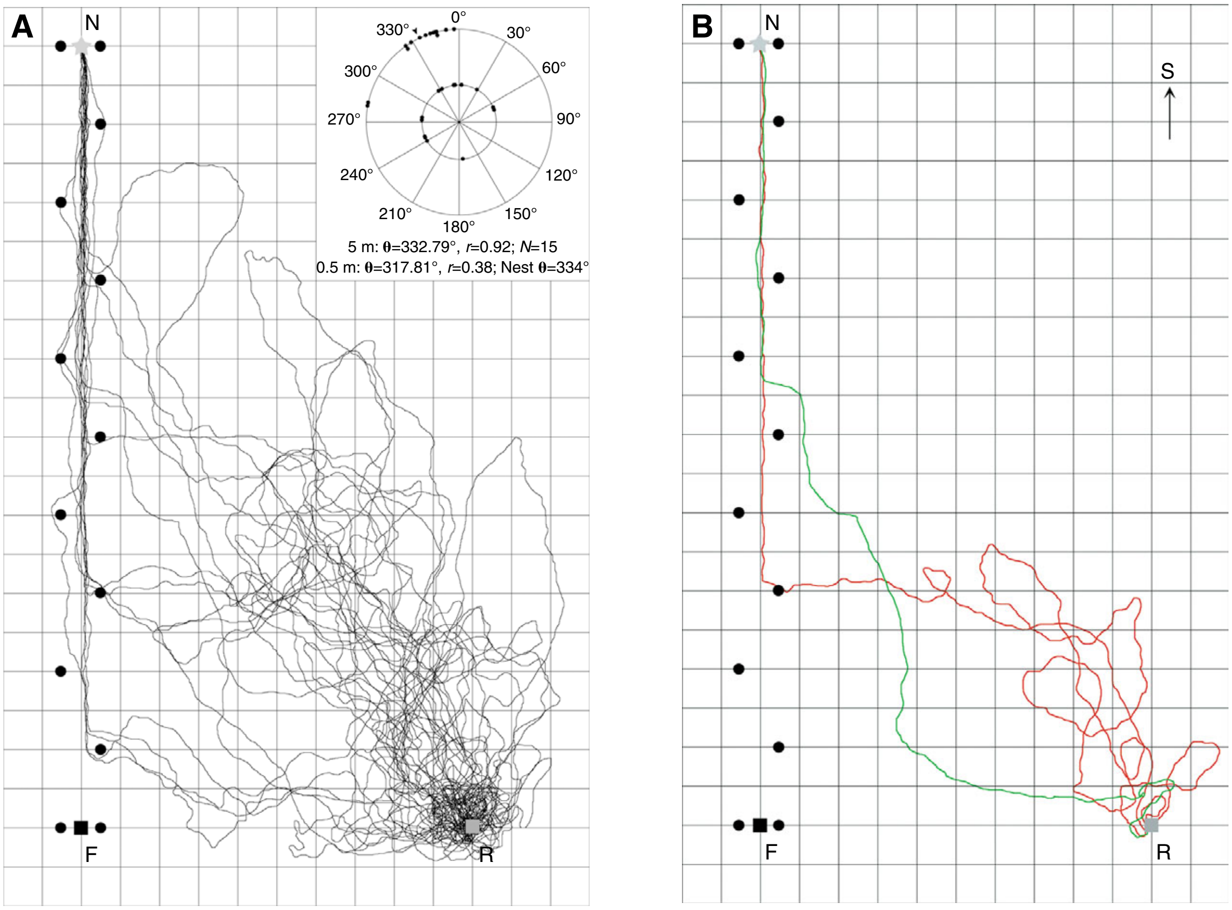


Fig. 6. Trajectories of zero-vector ants (*N*=15) displaced 10 m west of the nest–feeder line. Cylinders in the route-mark corridor are shown as black circles along with the nest N, feeder F and release position R. (A) All trajectories of ants displaced sideways. (B) Example paths of ants that had no loops (green) and one or more loops (red) are shown. Grid size is 1 m^2. Inset: Orientation of the ants at 0.5 m (inner circle) and 5 m from the release point. Mean vector **θ** and length of the mean vector *r* are shown. The arrowhead indicates the true nest direction, Nest **θ**, from the point of release.

present in a familiar context, ‘tighten’ the ant’s path. However, in the absence of familiar contextual cues, route cues alone cannot elicit homing and their role is perhaps to provide directional cues to an homing ant.

Ants with vector information, irrespective of the presence or absence of route-marks, travelled nearly half the distance of the outbound journey before engaging in a search. This partial distance travelled by relying on the path integrator was similar to the proportion travelled by ants in an unfamiliar test field after reaching a food source in an open field (Narendra, 2007). The path integrator is thus relied upon when visual cues that form a familiar context are absent. Isolated landmarks can often be misidentified hence relying on contextual cues can aid in disambiguating individual cues (Collett et al., 2003a). Hence, context plays an important role in insect navigation.

Homing by laterally displaced ants

Ants displaced laterally encounter a navigation problem similar to ants that are blown off by dust storms, i.e., a homing ant is presented with three conflicting directional choices, (1) the path integrator, (2) distant cues, and (3) the familiar route (Fig. 7). All ants with vector information displaced 6 m and 10 m away showed a distinct switch from initially relying on the path integrator to following visual cues (Fig. 4). In contrast, most ants displaced close to the route-mark corridor at 1.5 m and 3 m distance, reached the nest primarily by adhering alongside the route-mark corridor or travelling within the corridor and did not demonstrate any distinct switch from relying on path-integrating to route-following. Ants with vector information that were displaced close to the route at 1.5 m hit the route close to the release point, whereas those displaced 10 m away hit the route close to the nest. Thus the position where the ants hit the route did not bear any relevance to their route-following ability, and upon hitting the familiar route ants travelled along the route to reach the nest.

Laterally displaced ants, after initially orienting towards the nest, switched their orientation towards a direction intermediate between the dictates of the path integrator and the nest (Fig. 5). This orientation towards the nest clearly shows that ants were using distant nest-associated cues for homing. Since the

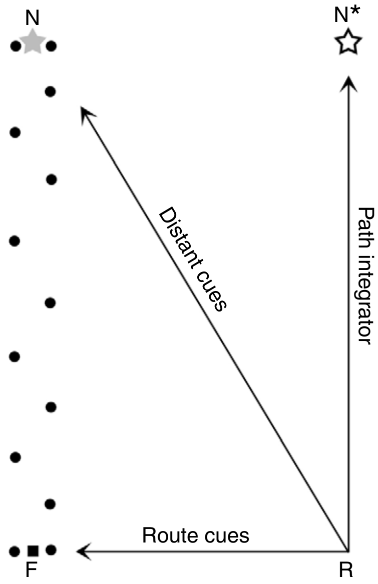


Fig. 7. Illustration of the three competing directional cues for ants displaced sideways to R. Route cues direct the ants to move laterally towards the familiar route; distant cue direct the ants towards the nest, whereas the ants' path integrator, relying on the sky compass, directs the ant to the fictive nest N*. Information from route cues, distant cues and the path integrator are in conflict in full-vector ants. Information from route cues and distant cues are in conflict in zero-vector ants.

angular differences from the release point to the true nest and to the fictive nest (as guided by the path integrator) was small, the statistical analysis indicated that all groups were significantly directed towards both these theoretical directions, at 0.5 m and 5 m from the release point. Ants that initially relied on the path integrator, i.e., all ants from the 6 m and 10 m groups and a few ants from the 1.5 and 3 m groups, travelled nearly half the distance of the outbound journey, at the end of which they turned (1.5 m and 3 m groups) or initiated a short search (6 m and 10 m groups; Table 1). The turn led the ants in the 1.5 m and 3 m groups to the familiar route, whereas those in the 6 m and 10 m groups followed the search by orienting towards a direction intermediate to the dictates of the distant cues and route cues (oblique and horizontal arrows in Fig. 7) to reach the nest. Thus, the closer the ants were to the route-mark corridor, the stronger was the pull towards the familiar path, and conversely, the farther they were, the greater was the reliance on the distant cues (initial and final orientation) and the path integrator (to travel half-way).

Information from the path integrator was, however, unavailable for zero-vector ants, Zv10 m, and hence these ants relied on distant cues for homing (Fig. 6). Upon release, the ants directed their search towards the distant cues. The search led them closer towards the familiar route-mark corridor. But rather than travelling laterally to reach the familiar path, they travelled in strikingly oblique paths, heading in a direction intermediate to that dictated by the distant cues and the route cues. Similar to the behaviour of ants in other conditions, once the zero-vector ants hit the familiar path in a familiar context, they adhered to their path until they reached the nest (Fig. 6).

The ability to adhere to a familiar route upon reaching it, corroborates with previous findings (Wehner et al., 2006), in which both full-vector and zero-vector ants were captured and displaced locally, a few meters away from the homing path. This behaviour of adhering to a familiar route is exhibited by homing pigeons as well (Biro et al., 2004; Lipp et al., 2004). Experienced birds that had been displaced nearly 3 km from the route approached the route obliquely, and once they hit the route they travelled along their familiar path to reach their goal (Biro et al., 2006). These paths were similar to their earlier flight paths before being displaced.

Nature of distant cues

In the absence of route cues and vector information, distant cues guide ants towards the nest (Fig. 7). Distant cues take precedence over vector information among ants displaced sideways, causing the ants to orient towards the nest immediately upon release. What might these distant cues be? In the ant's semi-arid desert habitat these cues could either be a distant skyline or a single conspicuous landmark such as a distant tree whose view changes little as the insect moves around the nest. The use of distant cues while homing has been demonstrated in wood ants, *Formica japonica* (Fukushi, 2001), where the ants used the distant skyline for homing. Hence the paths of laterally displaced wood ants did not remain parallel to one another but converged at the nest. Fukushi (Fukushi, 2001) suggested that the distant cues used by wood ants are panoramic cues. Further research is needed to identify the nature of these distant cues.

In summary, *M. bagoti* ants displaced from their familiar route rely on distant landmarks for homing. The ants follow routes in familiar foraging terrain, but the route marks are not essential and are utilised only when present in a familiar context. Locally displaced ants return to the nest by compromising between three navigational strategies. Ants far away from the familiar route, compromise between the directional dictates of the path integrator and the distant cues and ants nearby to the route compromise between the directional dictates of the distant cues and the familiar route cues. If the ants encounter the familiar path in a familiar context, they adhere to the familiar path until they reach the nest.

This research has demonstrated the interaction between the different navigational strategies and has highlighted the importance of distant cues and contextual information for homing desert ants.

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