The Journal of Experimental Biology 210, 1798-1803
Published by The Company of Biologists 2007
doi:10.1242/jeb.02768

Homing strategies of the Australian desert ant *Melophorus bagoti*

I. Proportional path-integration takes the ant half-way home

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Accepted 5 March 2007

Summary

Highly evolved eusocial insects such as ants return from a food source to their nest by the shortest possible distance. This form of navigation, called path-integration, involves keeping track of the distance travelled and the angles steered on the outbound journey, which then aids in the computation of the shortest return distance. In featureless terrain, ants rely on the path integrator to travel the entire distance to return to the nest, whereas in landmark-rich habitats ants are guided by visual cues and in the absence of the visual cues homing ants rely on the path integrator to travel only an initial 10–60 cm of the homebound distance. The functioning of the path integrator in a habitat of intermediate landmark density is unknown. The findings reported here show that when the outward journey is on a familiar foraging area, and the inward journey is on an unfamiliar area, the Australian route-following desert ant *Melophorus bagoti* relies on the path integrator and consistently travels half the distance of the outward trip. However, when both the outward and inward trips are performed in plain and featureless channels, which blocks the distinct terrestrial visual cues, ants travel the entire distance accurately. A similar half-way abbreviation of the home vector occurs when the ant's outward trip is in an L-shaped channel and the homeward trip is over an open and unfamiliar region. The ecological significance of these new findings is discussed.

Key words: orientation, path-integration, abbreviation, desert ant, *Melophorus bagoti*.

Introduction

Precise homing strategies are essential for central place foragers such as ants, as they need to return to the nesting site at the end of each foraging journey. Although most ants form trails, and orient using pheromones, some are solitary foragers and exhibit a remarkable diversity in homing behaviour. In landmark-rich habitats ants utilise the available visual cues for homing, wherein they match the contrast in canopies [*Paltothyreus tarsatus* (Hölldobler, 1980)], follow routes [*Gigantiops destructor* (Beugnon et al., 2001; Beugnon et al., 2005)] and rely on distant cues [*Formica japonica* (Fukushi, 2001)] to reach the nest. In featureless deserts where landmarks are absent or less distinct, ants such as *Cataglyphis fortis* compute the shortest return distance to the nest, by integrating the angles steered and the distance travelled on their outward journey (Wehner and Wehner, 1990; Collett and Collett, 2000). This homing strategy, called path-integration (Mittelstaedt and Mittelstaedt, 1980), is accomplished by relying on the celestial compass for directional cues (Wehner, 1994) and some form of step-counting to estimate distances (Wittlinger et al., 2006).

While computing the shortest distance, the path integrator accumulates errors with increasing nest-feeder distance (Müller and Wehner, 1988). Perhaps owing to this, desert ants that normally rely on path-integration for homing, use visual cues when available (Wehner et al., 1996). On the other hand, when familiar cues are unavailable along the homebound journey, visually oriented ants such as *Gigantiops destructor* (Beugnon et al., 2005) and *Formica japonica* (Fukushi, 2001) rely on the path integrator to travel an initial distance of 10–60 cm and then engage in a systematic search. The functioning of the path integrator in ants is known only from contrasting landscapes of featureless saltpans and landmark-rich rain forests. I report here that in a sparse but not featureless environment, a primarily route-following Australian desert ant relies on the path integrator and consistently travels half the distance of the outward trip in the absence of familiar cues along the homebound journey. This novel strategy allows the ants to travel half-way towards the nest in the absence of familiar cues.

Materials and methods

Study area and study species

The study was carried out in a semi-arid desert habitat with sandy clayey soil, and tussocks of Buffel grass (*Cenchrus* *ciliaris* L.) and sparse woody vegetation of *Acacia* and *Hakea* species at Alice Springs, Northern Territory, Australia. The thermophilic ant *Melophorus bagoti* Lubbock is widespread in the semi arid desert habitat of central Australia (Christian and Morton, 1992). In their familiar foraging area, *M. bagoti* ants establish and adhere to individualistic routes along their homeward journey (Kohler and Wehner, 2005). The ants are diurnally active, forage individually and begin activity when ground temperature approaches 50°C (Muser et al., 2005). These ants are primarily scavengers and feed on insects roasted in the desert heat.

Experiment 1: open field path-integration

Ants reached a feeder placed 6 m, 12 m, 20 m or 35 m south of the nest (Fig. 1A), by travelling in a familiar foraging area. Only for the 6 m group were feeders set up at four different directions: north, south, east and west of the nest. The feeder was a rectangular box sunk into the ground with its interior walls coated with fluon to prevent ants from escaping. Cookie crumbs were provided as food. Ants that arrived at the feeder and picked up a cookie crumb were captured and displaced to an unfamiliar test field, where both familiar distant cues and route cues were absent. Here, their homing paths were recorded on squared paper. No differences in homing from different directions were found at 6 m, and the data from different directions was pooled. Data were collected from four nests and were pooled as no differences between the nests were found.

Experiment 2: distance estimation in linear channels

This experiment determined if in the absence of visual route cues, ants can measure the distance travelled on the outbound journey and use this estimate to return to the nest. Both outbound and inbound journeys were in white non-textured plastic channels. Ants had to reach a feeder by travelling in outbound channels of 6 m or 12 m in length (10 cm wide, 10 cm high). The nest was enclosed from all sides, with manned exits leading into white plastic channels (Fig. 1D). Ants that reached the feeder and picked up a cookie crumb were transferred to the far end of a 30 m test channel. All the three channels were placed in parallel with a distance of 10 cm between adjacent channels. A measuring tape beside the test channel enabled the observer to note the turns taken by the ants. The distance from the release point to the first turn (U-turn measuring at least 0.2 m) gave an ant's estimate of the homebound distance (Ronacher et al., 2000; Cheng et al., 2006; Narendra et al., 2007). The distance estimates of ants with 6 m and 12 m outbound distance were compared with the estimates of ants from the path-integration experiments. Data were collected from three nests and were pooled as no differences were found between the nests.

Experiment 3: path-integration in L-shaped channels

In this experiment, the outbound journey of ants was in channels whereas their homebound journey was in an unfamiliar open field. The experimental group of ants reached a feeder by travelling in a white L-shaped channel (10 cm wide, 10 cm high). The length of the first leg was always 6 m, but the length of the second leg was either 6 m (Fig. 1B) or reduced to 3 m (Fig. 1C). A control group of ants for each two-leg condition were tested. The control ants travelled only the first leg of 6 m to reach a feeder. The feeder itself was sunk into the ground, and its interior walls were coated with fluon to prevent ants from escaping. Ants that reached the feeder and picked up a cookie crumb were collected in a plastic tube and transferred to a test field, where the homing paths were recorded.

Recording of trajectories

The test field (20 m×40 m) was located in a distant unfamiliar area and divided into 1-m grids using strings and tent pegs. Ants that had reached the feeder and picked up a crumb were captured, transferred in the dark and released in the middle of the test field. Trajectories of ants were recorded individually within 5 min after their reaching the feeder. Paths of homing ants, including the first two search loops were recorded on squared paper by an observer. The search loops were recorded, as the exact point of the start of search was difficult to identify in the field. During recording, the observer continuously shifted positions, to make certain of not being used as a landmark. Recording of all homing paths was carried out within a 1-hour period (15:30–16:30 h local time) under clear skies. Thus, all ants were tested under similar polarisation patterns in the sky. After testing, the ants were marked and released to the nest, thus ensuring that no ants were tested twice.

Trajectory analysis

The paths were digitised and the start of the search of a homing ant was identified as deviations of $\geq 50°$ and more than 0.5 m, on either side of the homebound trajectory. Determination of the start of search proved 100% reliable between two experimenters for a subset of the data. The vector from the release point to the start of search gave the compass direction and the distance of the ant's path-integration guided homeward journey. For directions, the mean vector θ and length of the mean vector r, for each group were computed according to Batschelet (Batschelet, 1981). The mean angles of circular observations was compared by pair-wise and multi-sample Watson–Williams tests using the circular statistics program Oriana (Kovach, 2004). A V test was carried out to test whether ants' orientations were significantly different from the predicted direction. For distance, data were analysed for normality, and where required, non-parametric tests were carried out.

Results

Experiment 1: open field path-integration

Ants with outbound distances of 6 m, 12 m, 20 m and 35 m were oriented towards the fictive nest $\theta=0°$ ($P_s<0.001$, V test; Fig. 2A). The mean orientation of ants from the different outbound distances did not differ significantly ($P>0.10$,

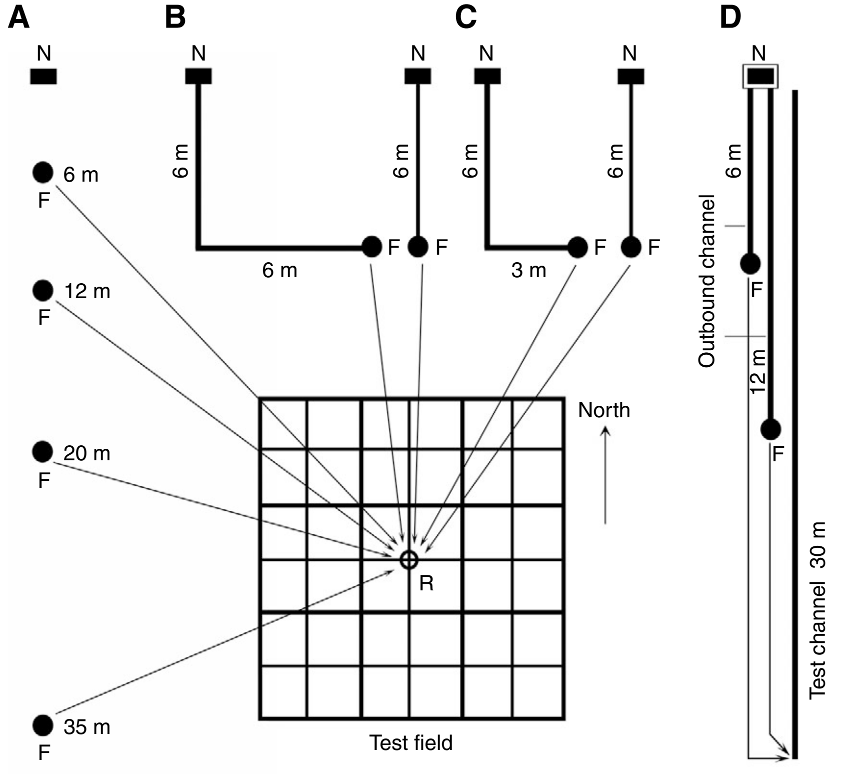

Fig. 1. Experimental set-up. Ants reached a feeder (F) in three different conditions: by travelling 6 m, 12 m, 20 m and 35 m from the nest (N) in an open field (A); by walking in an L-shaped channel (thick lines), where experimental ants travelled either 6 m (B) or 3 m (C) on the second leg and the control ants travelled only the first leg of the journey; and by travelling in linear outbound channels of 6 m and 12 m (D). In A–C, ants that picked up a cookie crumb were displaced to the test field where their paths were recorded. In D, ants that picked up a cookie crumb were captured and displaced to the end of the 30 m test channel, where their distance estimate was measured. Thin lines with arrows show the displacement of ants from the feeder either to a release point (R) in the test field or to the test channel. Note: figures not to scale.

Watson–Williams test). None of the ants travelled the entire distance towards the fictive nest and the distance travelled varied in absolute terms ($P<0.001$, ANOVA; Fig. 2B). However, as a proportion of the nest–feeder distance, the distance travelled by ants with a nest–feeder distance of 6 m (42.99%±20.39), 12 m (47.83%±15.44), 20 m (43.71%±15.45) and 35 m (40.30%±10.95; means ± s.d.) remained similar ($P>0.05$, ANOVA).

Experiment 2: distance estimation in linear channels

Homing ants that travelled in a test channel with an outbound distance of 6 m and 12 m, travelled nearly the entire distance to the nest. Thus the distance travelled varied in absolute terms ($P<0.001$, ANOVA; Fig. 2C). However, as a proportion of the nest–feeder distance, the distance travelled by ants with a nest–feeder distance of 6 m (94.23%±40.44) and 12 m (98.95%±47.81; means ± s.d.) remained similar ($P>0.05$, ANOVA). Interestingly, the distances estimated by ants in the channels (Fig. 2C) and in the open field (Fig. 2B) were significantly different at nest–feeder distances of both 6 m ($P<0.001$, *t*-test) and 12 m ($P<0.001$, *t*-test).

Experiment 3: path-integration in L-shaped channels

Ants from the 6 m×6 m group

The direction of the (fictive) nest from the release point for a homing ant of the experimental and control groups was 315° and 0° respectively. Ants from both the experimental and control groups were orientated towards the fictive nest ($P_s<0.001$, *V* test; Fig. 3A,B). The mean orientation of ants from the experimental and control group differed significantly ($P<0.001$, Watson–Williams test). The distance to the (fictive) nest from the release point for a homing ant of the experimental and control group was 8.48 m and 6 m, respectively. Ants from both the groups did not path integrate the entire homebound distance. The distance travelled by ants from the experimental and control group varied in absolute terms (Fig. 3C; $P<0.001$, *t*-test), but not as a proportion of the nest to feeder distance (experimental: 43.43%±7.91; control: 43.75%±14.24; means ± s.d.; $P=0.92$, *t*-test).

Ants from the 6 m×3 m group

The direction of the (fictive) nest from the release point for a homing ant of the experimental and control groups was 333° and 0°, respectively. Ants from both the experimental and control groups were orientated towards the fictive nest ($P_s<0.001$, *V* test; Fig. 3D,E). The mean orientation of ants from the experimental and control group differed significantly ($P<0.001$, Watson–Williams test). The distance to the (fictive) nest from the release point for a homing ant of the experimental and control group was 6.70 m and 6 m, respectively. Ants from both the groups did not path integrate the entire homebound distance. The distance travelled by ants from the experimental and control group did not vary either in absolute terms (Fig. 3F; $P=0.36$, *t*-test) or as a proportion of the nest to feeder distance (experimental: 43.97%±15.84; control: 44.9%±11.68; means ± s.d.; $P=0.83$, *t*-test). Since the homebound distances for the control ants (6 m) and the experimental ants (6.70 m) were similar, the difference in the distance travelled was not significant.

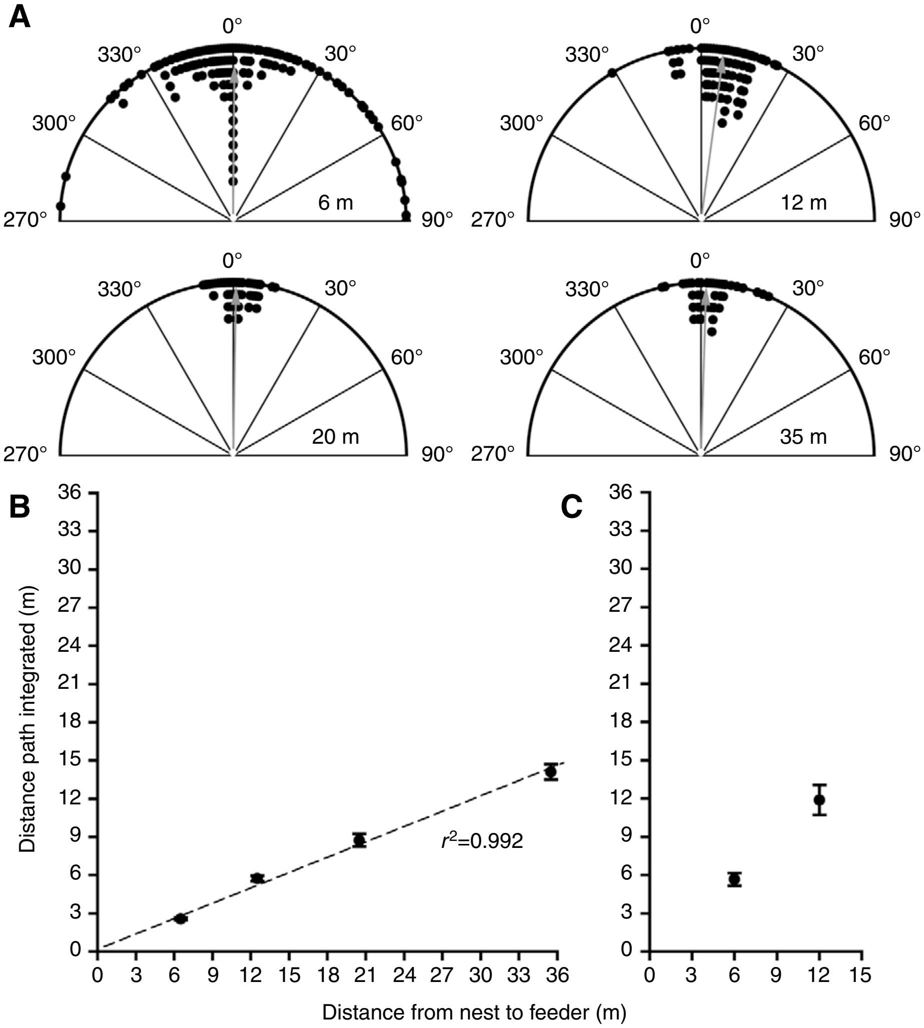

Fig. 2. Path-integration in *Melophorus bagoti* ants. (A) Homebound orientation of ants with outbound distance of 6 m (**θ**=1.22°, *r*=0.89, *N*=128), 12 m (**θ**=7.62°, *r*=0.98, *N*=80), 20 m (**θ**=1.34°, *r*=0.99, *N*=40) and 35 m (**θ**=3.21°, *r*=0.99, *N*=40), when released in the test field. Home direction=0°. The mean vector direction **θ** is indicated by the grey arrow. The length of the arrow represents *r*. (B) Distance path-integrated (means ± s.e.m.) by ants at nest-feeder distances of 6 m (*N*=128), 12 m (*N*=80), 20 m (*N*=40) and 35 m (*N*=40) in the open field. (C) Homebound distance travelled by ants in linear channels (means ± s.e.m.) with an outbound distance of 6 m (*N*=24) and 12 m (*N*=24).

Discussion

The most interesting result of this study is that the homing Australian desert ant, *Melophorus bagoti* relies on the path integrator to travel the entire homebound distance if outward and inward trips are in uniform channels, but when the outward trip is on familiar terrain and inward trip is on unfamiliar terrain, ants rely on the path integrator to travel consistently half the distance of the outward trip. A similar abbreviation is found when the outward trip is in an L-shaped channel and the homeward trip is over an open and unfamiliar terrain.

When the outward and inward journeys of the ant were in uniform featureless channels, ants were accurate in estimating the entire homebound distance (Fig. 2B). However, ants that reached the feeder by travelling in an open and familiar field, upon displacement to an unfamiliar test field, travelled neither the entire distance nor a constant initial distance towards the nest. They travelled nearly half the distance of their outward journey (44.09%±17.48; means ± s.d., for data pooled from 6 m, 12 m, 20 m and 35 m; Fig. 2B). Ants whose inward and outward journeys were restricted to linear channels relied on estimating distance instead of using distant landmarks for homing. If the ants homing in the channels had relied on frontally visible distant landmarks, ants from both the 6 m and 12 m group should have travelled the entire length of the 30 m test channel before beginning to search, which was not the case. Thus, consistently travelling a specific proportional distance in the open field, along with the ants' ability to estimate the entire homebound distance accurately, suggests that *M. bagoti* ants can estimate distances accurately. Distant landmarks could, however, be used to set a heading (Fukushi, 2001) or to provide contextual information to inform the ant about familiar surrounds (Collett and Collett, 2002).

The orientation of the homing ants in the open field after an outbound journey in an L-shaped channel indicate that the ants had path-integrated the two legs of the 'L'. But according to the computational theory of Müller and Wehner (Müller and Wehner, 1988), the 90° turn the ants were forced to take in the L-shaped channels, should have caused a systematic error during path-integration, in which they turn too sharply. The systematic error in *Cataglyphis* ants causes the ants to orient towards the first leg of their outbound journey. It has been proposed that such errors might in fact be an ecological adaptation for a homing ant (Hartmann and Wehner, 1995), with the errors steering the ants towards the familiar route

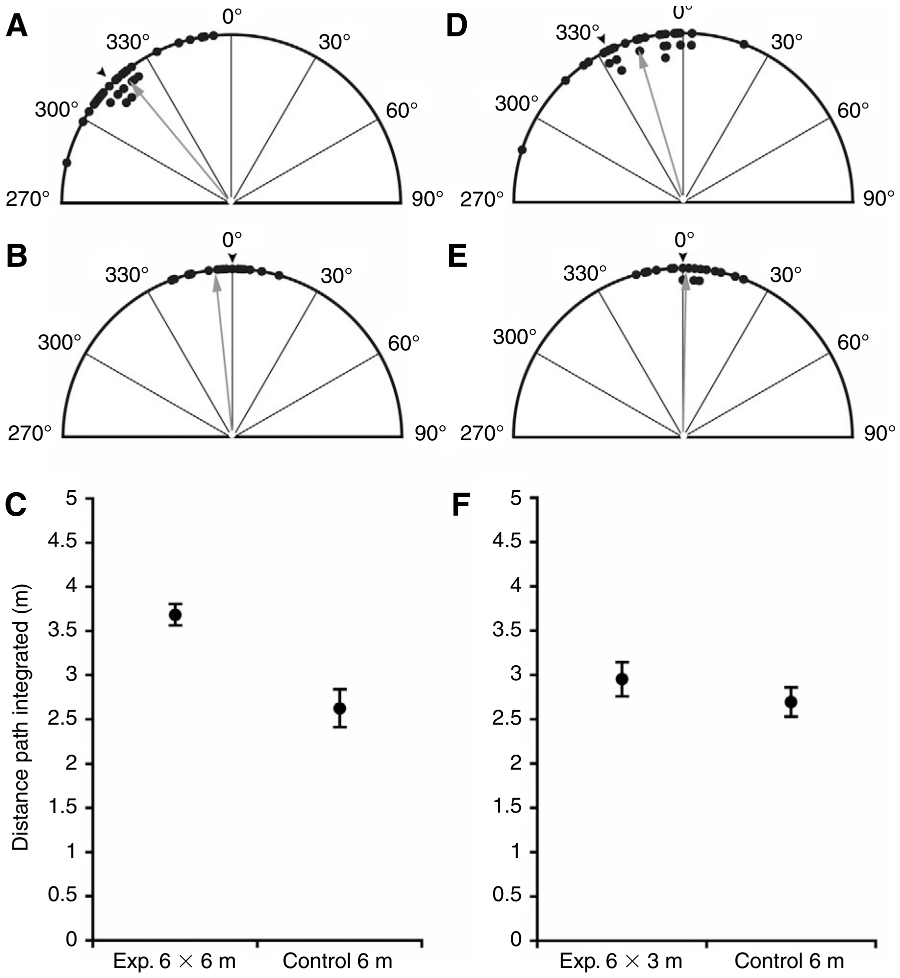

Fig. 3. Path-integration of ants in L-shaped channels. Orientation and distance travelled by ants from the 6 m×6 m condition (A–C), and 6 m×3 m condition (D–F). Orientation of (A) experimental ants (6 m×6 m: θ=319.52°, r=0.96, N=30) and (B) control ants (6 m: θ=356.82°, r=0.98, N=16) that travelled only the first leg. Orientation of (D) experimental ants (6 m×3 m: θ=343.71°, r=0.95, N=30) that travelled a two leg trajectory and (E) control ants (6 m: θ=2.0°, r=0.98, N=18) that travelled only the first leg. Home direction is shown by the arrowhead outside the semi-circle. The mean vector direction θ is indicated by the grey arrow. r is represented by the length of the arrow. Distance path-integrated (means ± s.e.m.) by ants from experimental and control groups of the 6 m×6 m (C) and 6 m×3 m (F) conditions are shown.

rather than to the nest itself. Interestingly, *M. bagoti* ants that were forced to take a 90° turn (Fig. 3A,D) were oriented towards the (fictive) nest. Furthermore, the orientation of homing *M. bagoti* ants whose outward and inward journey was in the open field increased in accuracy with increase in nest–feeder distance (Fig. 2A). There was a large degree of scatter in the orientation of ants at 6 m outbound distance. The scatter is perhaps the result of the short homing distance of 6 m, for which the ants might rely on visual cues rather than the path integrator, which results in erroneous orientation of some individuals. This interpretation has to be treated with some caution as the 6 m data comes from four different direction and this may have increased the scatter. Nevertheless, the mean orientation of ants from the 6 m group was directed towards the nest (Fig. 2A).

Abbreviated path-integration in ants is known to occur in two scenarios: (1) when ants [*Formica japonica* (Fukushi, 2001) and *Gigantiops destructor* (Beugnon et al., 2005)] are displaced to an unfamiliar terrain, and (2) when ants (*Cataglyphis fortis*) are trained in channels and tested on open ground (Collett et al., 1999). Such an abbreviation is likely due to the sensitivity of the path integrator to the context of the ant's foraging route; hence, if the context is unfamiliar the ants follow their home vector, but travel only a constant distance instead of the entire distance. Unlike in some ants where the home vector is abbreviated at a constant distance, the home vector of *M. bagoti* ants is abbreviated at an exact proportion of the distance travelled along the outbound journey. The most likely reason for the path-integration to be abbreviated at an exact proportion rather than at a constant distance, is that travelling half the outbound distance may get the ants into a familiar catchment area from where other visual cues (distant landmarks) guide the homing ant. But whether travelling nearly half-way towards the nest is an optimum strategy for these ants has yet to be determined.

This ability to travel only about half of the outbound journey, could be a functional adaptation of the path integrator. In featureless plains, because of the unavailability of landmarks, ants rely on the path integrator to travel the entire distance from the food source to the nest (Wehner and Wehner, 1990). In cluttered landmark-rich habitats ants follow routes, and only when the familiar visual cues are absent, do they rely on the path integrator but travel only an initial distance of 50 cm towards the nest (Beugnon et al., 2005). However, in a habitat of intermediate landmark density, as in the Australian semi-arid desert, homing *M. bagoti* ants travel half the distance travelled on the outbound journey, following the path-integrated home vector. It thus seems possible that the landscape of the habitat could dictate the distance travelled by an ant following the path-integrated home vector in the absence of familiar visual cues.

But why is path-integration required for route-following ants? Homing *M. bagoti* ants establish idiosyncratic routes to reach the nest (Kohler and Wehner, 2005). These ants often get blown off course by strong dust storms that displace them from their familiar route. The maximum distance these ants have been observed to be displaced from their familiar route is 6 m (A. Narendra, personal observation); thus most displacements are local, from wherein familiar distant landmarks are visible, but familiar visual route cues are not. Since the ants would not 'know' how far away have they been displaced, they do not travel laterally to reach the familiar route, but instead rely on the path integrator to travel only about half the distance to get close to the nest and home-in using distant nest-associated cues (Narendra, 2007). The path integrator may also serve as a scaffold to guide naïve foragers while they learn the visual information along the route.

In conclusion, the Australian desert ant *Melophorus bagoti* monitors the distance travelled and directions steered along the food-ward route both in the channels (wherein visual route cues are absent) and in the familiar terrain, but on open and unfamiliar terrain the performance of their home vector is half the expected distance. The cues that determine this specific proportion of distance path-integrated will be examined in a subsequent study.

I thank the entire research team at the Alice Springs field station for their support during this work. Discussions with Andrew Beattie, Jan Hemmi, Thomas Collett, Dinesh Rao and Marie Herberstein improved the earlier versions of the paper. Comments from two anonymous reviewers improved the manuscript substantially. I thank Ken Cheng and Rüdiger Wehner for their logistical and financial support (Australian Research Council grant #DP0451173) during this work. I am grateful for the scholarship offered by Macquarie University, NSW, Australia.

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