RESEARCH ARTICLE

Vector-based and landmark-guided navigation in desert ants of the same species inhabiting landmark-free and landmark-rich environments

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SUMMARY

The central Australian desert ant *Melophorus bagoti* lives in a visually cluttered semi-arid habitat dotted with grass tussocks, bushes and trees. Previously, it was shown that this species has a higher propensity to switch from vector-based navigation to landmark-guided navigation compared with the North African desert ant *Cataglyphis fortis*, which usually inhabits a visually bare habitat. Here, we asked whether different colonies of *M. bagoti*, inhabiting more and less cluttered habitats, show a similar difference. We compared ants from typically cluttered habitats with ants from an exceptional nest located in an open field largely devoid of vegetation. Ants from both kinds of nests were trained to forage from a feeder and were then displaced to a distant test site on the open field. Under these conditions, ants from cluttered habitats switched more readily from vector-based navigation to landmark-guided navigation than ants from the open field. Thus, intraspecific differences caused by the experience of particular landmarks encountered *en route*, or of particular habitats, influence navigational strategies in addition to previously found interspecific, inherited differences due to the evolutionary history of living in particular habitats.

Key words: ant, vector-based navigation, path integration, landmark guidance, intraspecific comparison.

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INTRODUCTION

One of the big open questions in research on ant navigation in particular, and insect navigation in general, is the relative role that path integration, also known as vector-based navigation, and landmark guidance routines play in the animal's overall behaviour. As previous studies have shown, landmark-defined route guidance (LG) usually out-competes guidance based on the path integration home vector (HV) (Andel and Wehner, 2004; Kohler and Wehner, 2005; Wystrach et al., 2011), but even if the ant's behaviour is governed by LG, the path integrator continues to run in the background until the ant has finally returned to and re-entered the nest (Sassi and Wehner, 1997; Andel and Wehner, 2004; Knaden and Wehner, 2005; Knaden and Wehner, 2006).

Results such as those obtained in the LG–HV competition experiments cited above as well as other indications (Wehner et al., 1996; Narendra, 2007a; Narendra, 2007b) raise the question of whether (i) ants of colonies inhabiting cluttered or landmark-free environments differ in the relative weights they attribute to HV and LG routines (intraspecific, environment-dependent differences), and whether (ii) ants of different species or even genera differ in this respect as well (interspecific, inherited differences). The latter has already been shown to be the case. The North African desert ant *Cataglyphis fortis*, which inhabits largely landmark-free salt-pan areas, and the central Australian desert ant *Melophorus bagoti*, which inhabits richly cluttered, steppe-like environments, were subjected to the same experimental protocol. When trained to run along an artificial landmark corridor and later transferred to a landmark-free test field, *C. fortis* relied much more strongly on its HV routine than *M. bagoti* did (Bühlmann et al., 2011). In the present study, we

tested whether similar differences also occur intraspecifically, as a function of natural variations in the landmarks encountered by the ants. We did so by comparing ants of the species *M. bagoti* taken from colonies located either in an open-field area ('open-nest ants') or in very cluttered environments ('cluttered-nest ants'), and testing them all at the same location on the open field, some distance from the open nest.

Disparate results from past studies suggest that full-vector ants from cluttered nests do not run as far as ants from open nests before engaging in a search for landmarks they usually encountered *en route*. Thus, Bühlmann and colleagues displaced the open-nest ants (the same nest as used in this study), and found that they ran most of the accumulated vector (Bühlmann et al., 2011). In another condition from the same study, artificial landmarks placed along the training corridor were presented to ants of the same nest. When these artificial landmarks were absent in a test on the open field (but distant from the nest), the ants did not run as far before engaging in searching behaviour. This result suggests that experience with artificial landmarks matters.

But artificial landmarks are not natural, and affect the foraging behaviour of the ants in other ways. For example, the paths of travel are straighter when the ants travel down a corridor of landmarks as opposed to travelling on an open field (Bühlmann et al., 2011). Would experience with natural landmarks produce a similar effect, leading ants tested on the open field to run a shorter distance, and perhaps a more tortuous path, before engaging in a search, in comparison with ants from the nest on the open field, which experience nothing by way of landmarks along the route? Based on comparisons between studies, we predicted so. Narendra displaced

ants from nests in typical cluttered habitats to a different but similarly cluttered habitat, and found that the ants ran only about 44% of the accumulated vector before engaging in search (Narendra, 2007a), a much shorter proportion than the *M. bagoti* ants in Bühlmann and colleagues' (Bühlmann et al., 2011) study. Therefore, we set out to test this hypothesis of intra-specific variation in navigation within a single study.

For the intraspecific comparison, we selected *M. bagoti* as the test species because even though this species usually inhabits cluttered environments, one nest was found that was located on an open plain largely free of vegetation (see Bühlmann et al., 2011). However, *C. fortis*, the typical open-habitat salt-pan ant, could not be found in the type of cluttered environment characteristic of *M. bagoti*. Furthermore, it should be noted that the interspecific comparison performed by Bühlmann and co-workers was actually an intergeneric one (a *Cataglyphis versus Melophorus* species). It was originally conceived as an interspecific comparison performed within the genus *Cataglyphis*, i.e. between *C. fortis* and the cluttered-habitat species *C. bicolor*, but as recently colonies of the latter species could not be located at proper sites in the vicinity of our field station at Maharès, Tunisia, *M. bagoti* was used rather than *C. bicolor* for the interspecific study to which we repeatedly refer in the present account.

MATERIALS AND METHODS
Species
The red honey ant *M. bagoti* Lubbock 1883 is found over a large expanse of semi-arid Central Australia. Like all members of the genera *Cataglyphis* and *Ocymyrmex* in the Afro-Asian and southern African deserts, respectively (Wehner, 1987; Wehner and Wehner, 2011), ants of this *Melophorus* species fill a thermophilic niche (Christian and Morton, 1992), and come out to forage in the heat of the day during the summer months. Foragers carry home various plant materials and nectar, and also scavenge for dead arthropods (Muser et al., 2005). The study was conducted in January and February of 2008.

Experimental location and set up
Thanks to permission from the Alice Springs Airport Authority, experimentation took place at and around a field cleared of most vegetation, normally used for launching hot-air balloons. The balloon-launching field was surrounded by fairly uniformly tall trees, but the field itself was devoid of the usual vegetation of the area (Fig. 1A). On the balloon-launching field we found one active nest, which served as the 'open' nest. All around the balloon-launching field, the vegetation was typical for the area, cluttered by tussocks mostly of the invasive buffel grass (*Cenchrus cilialis*), along with bushes and trees of *Hakea* and *Acacia* genera (Fig. 1B,C). The area around the balloon-launching field was wild and not maintained at all, and as a result contained even more plants and leaf litter than the sites on well-maintained properties used for past research on *M. bagoti* route learning (Wystrach et al., 2011; Wystrach et al., 2012). Around the balloon-launching field we located three nests ('cluttered' nests) active enough and suitable for experimentation. Suitable meant having no trees or large bushes within 12 m south of the nest, because we set up a feeder 12 m south of each nest. The feeder consisted of a small plastic container (~20 cm square) sunk into the ground in which crumbs of cookie were placed.

On the balloon-launching field, a test grid of 1 m squares was constructed ~70 m from the open nest. The grid consisted of strings wound around tent pegs stuck in the ground, 20 m long north to south, 10 m wide east to west. The path of ants on tests was traced on grid paper.

Fig. 1. Photographs of the habitats near Alice Springs Airport where the experimental nests were found. (A) The open balloon-launching field where the open nest was found. (B,C) The sites where two of the cluttered nests were found. Photographs by R.W. (A) and E.J.T.M. (B,C).

Procedure
For logistical reasons, one nest was experimented on at a time. When an ant arrived for the first time at the feeder, it was painted with a

dot of paint and then followed back to the nest. For cluttered nests, which were found in sufficient density, this was crucial for ensuring that the ant came from the experimental nest. A painted ant that returned was painted again with more dots for individual identification, and allowed to run home with a piece of food. On its fifth trip to the feeder, the ant was captured in a tube and carried to the test field in the dark. After the ant had grabbed a piece of cookie, it was released at the southern end of the test grid, in the middle. Its path was traced on grid paper for 5 min, after which the ant was captured and returned to her nest. Each ant was tested only once (N=20 for the open nest, N=10 for each cluttered nest).

For the three cluttered nests, we also obtained the ants' headings from the feeder in the training area, using different ants from those tested (N=10 for Nest1 and Nest3, N=9 for Nest2, which was becoming inactive). This was done by timing the ant as she ran home from the feeder, and marking her location 15 s into her journey. The direction from the start of the run to this point was taken as an estimate of heading direction.

Data analysis

Each path from the test field recorded on paper was scanned as an electronic file and then digitised using the software GraphClick (www.arizona-software.ch/graphclick), which delivered the x and y coordinates of successive points of the path in metres. We digitised the path into as many straight segments as could be readily resolved on the screen at 100% viewing scale. We stopped digitising when the path went off the grid.

The point at which the ant first ended her straight run and started searching was then determined according to criteria closely matching those used previously (Bühlmann et al., 2011). Some ants performed turns and loops right at the beginning of the test, and we ignored these, not counting any turns and loops within the first metre of travel. Otherwise, the start of search was defined as the point at which the ant turned by at least 60 deg and did not revert back to the original direction of travel for at least 3 m, or if the ant turned and made a loop (crossed her original path).

The beeline distance d_0 was used as a measure of the distance travelled to the fictive nest before searching began. This was the y coordinate of the start of search, i.e. the projection of the start of search onto the line connecting the start of the run and the fictive nest. The path length l to the start of search was calculated by adding up the lengths of all the segments delivered by GraphClick. A straightness measure was defined as the straight-line distance d from the start of the run to the start of search divided by the path length, i.e. d/l. A perfectly straight run has a straightness measure of 1.0.

For a directional measure, we could not use the previous definition (Bühlmann et al., 2011) of where the path intersected a circle of 5 m radius because not every path was 5 m long. Instead, we took the direction to be defined by the point closest to 80% of the path length from the start of the run to the start of search. We did not want to use the start of search to define direction as the ant might have started veering off course on a search already when she met the criterion for the start of search. In point of fact, the two definitions of direction produced similar results (Pearson correlations >0.9). The target direction was defined as 90 deg, with positive errors counter-clockwise, following traditional trigonometric conventions.

Directional measurements were compared using circular statistics (Batschelet, 1981). For cluttered nests, the distributions of directions at the training site and on the test field were compared for each nest singly. The cluttered nests as a group were then compared with the open nest in terms of their performance on the test field. The Watson–Williams test was used to compare differences in mean
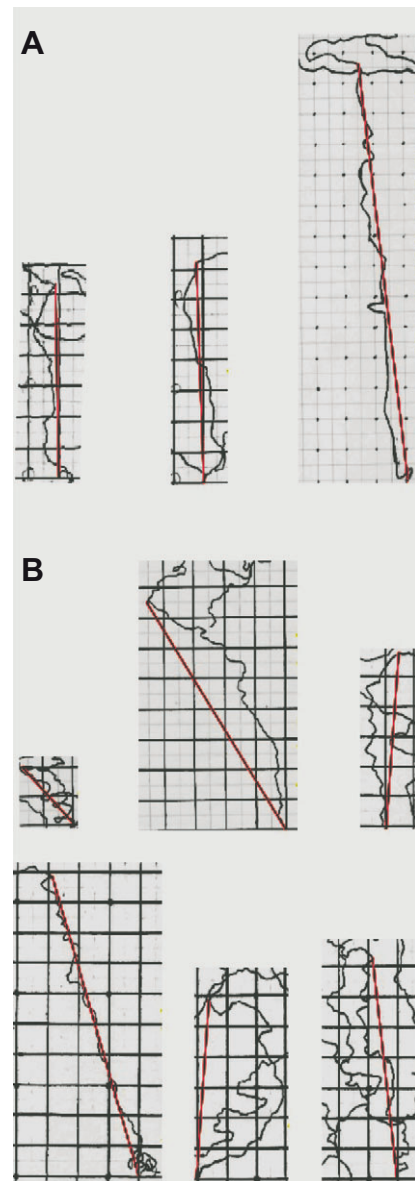

Fig. 2. A few examples of the paths taken by tested ants from the open nest (A) and from the cluttered nests (B), obtained from the data sheets on which the paths were drawn. The red line indicates the start of the run to the point at which search began. Each square represents 1 m².

heading direction, while the K-test was used to compare differences in directional scatter.

Linear measurements were compared using the standard parametric technique of analyses of variance (ANOVA). Ants that did not run onto the test grid, but headed in the direction opposite to the fictive nest at the start of their runs, were not counted. As only ants from cluttered nests did this, this exclusion biases against finding differences in lengths between open and cluttered nests. We used O'Brien's test (O'Brien, 1979), available in the statistical package JMP (SAS, 2002), to compare variances between groups. We prefer this test because it is not overly influenced by occasional outliers, compared with other tests such as Levene's or the F_{max} test. Should a significant difference (P<0.05) in variance be found, Welch's ANOVA, also available in JMP, was used to test for differences in means. Otherwise, a standard ANOVA was used.
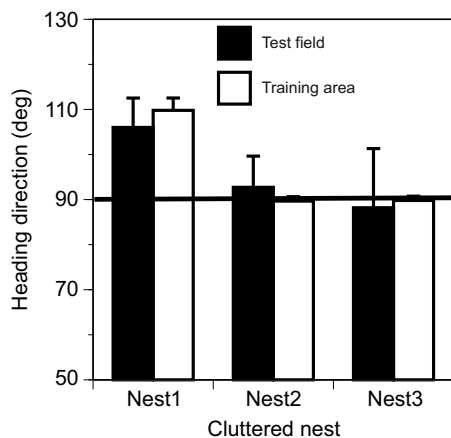
Fig. 3. Heading directions (means ± 95% confidence interval, CI) of ants from the cluttered nests at their training site ($N=10$, 9, 10 for Nest1, Nest2 and Nest3, respectively) and on the test field ($N=10$ for each nest). At the training site, headings were taken after 15 s of travel from the feeder. On the test field, headings were taken at 80% of the path length to the point where searching behaviour began. The thick horizontal line at 90 deg indicates the feeder–nest direction. The graphs are actually circular plots, with values calculated according to circular statistics, but are presented linearly because the overall scatter in heading was small.

RESULTS

In general, the ants ran off in the direction towards the fictive nest on a test, sometimes after a few twists and turns at the start (see Fig. 2 for some examples). All 20 ants from the open nest did this. A few ants from the cluttered nests, however, did not run onto the test grid, but in the opposite direction; that is, somewhere in the half-circle opposite to the direction of the fictive nest ($N=2$, 1 and 2 out of $N=10$ ants in Nest1, Nest2 and Nest3, respectively). Thus, few ants from any nest failed to run onto the test grid (Fisher's exact test between open and cluttered nests, $P=0.075$). On the whole, the ants were oriented in the general direction of the fictive nest (Fig. 3). Cluttered Nest1 showed a small bias to the left of the nest/fictive nest, on both the training and test fields. At their training site, the ants had an obstacle (tussock) in the direct path between feeder and nest, which they detoured around to the left.

Directions

We first compared mean directions of the cluttered nests on the training field *versus* the test field. These were not significantly different for any nest (Watson–Williams test, $P>0.24$). In directional scatter, all three nests showed significantly more scatter on the test field than on the training field (K-test, Nest1: $P=0.034$; Nest2 and Nest3: $P<0.001$). Thus, on the unfamiliar test field, headings were more variable across ants.

We then compared the directions of travel on the test field of the open nest *versus* the three cluttered nests combined. Because Nest1 showed a bias from the fictive nest direction on both the training field and test field (Fig. 3), we adjusted the target direction on the test field for each cluttered nest. The direction of the mean vector at the training site was coded as 90 deg. For the open nest, the fictive nest direction remained 90 deg. Bühlmann and colleagues' results showed that this nest was oriented approximately in the fictive nest direction on average at both the training and test fields [see fig. 2 of Bühlmann et al. (Bühlmann et al., 2011)]. Fig. 4A shows that the two groups performed similarly. The statistical comparisons between the cluttered nests and the open nest revealed neither a significant
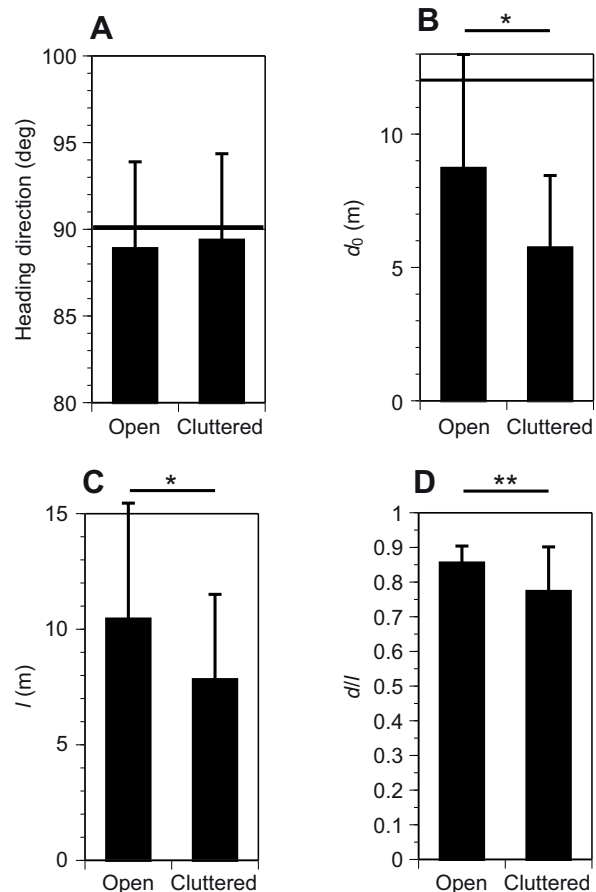

Fig. 4. Comparing the performance of the ants from the open nest ($N=20$) and from the cluttered nests (combined, $N=25$) in (A) heading direction (means ± 95% CI), (B) beeline distance to the nest at the point of first searching (d_0, the y-axis value at the point where searching first started; means ± s.d.), (C) total path length (l) to the point where searching first started (means ± s.d.) and (D) straightness (d/l), defined as the straight-line distance to the point where searching first started (d) divided by the total path length to that point (l) (means ± s.d.). Heading directions in A for the cluttered nests were calculated relative to the mean heading in the training area of each nest (which equals 90 deg, indicated by the thick horizontal line), while the headings of open-nest ants were not adjusted. The graph is a circular plot, with values calculated according to circular statistics, but presented linearly because the overall scatter in direction was small. The thick horizontal line in B indicates the target distance. *$P<0.05$; **$P<0.01$.

difference in mean direction (Watson–Williams test, $P=0.891$) nor a significant difference in directional scatter (K-test, $P=0.625$).

Distances travelled

In terms of the distance travelled in the fictive nest direction at the start of search (d_0; Fig. 4B), ants of the cluttered nests displayed a significantly smaller variance than ants of the open nest (O'Brien's test, $F_{1,43}=5.02$, $P=0.030$). Welch's ANOVA then showed that the ants from the open nest travelled farther before searching ($F_{1,30.7}=7.37$, $P=0.011$). The coefficient of variation (ratio of s.d. to mean), however, was similar between the two groups (open nest: 0.49; cluttered nests: 0.47), replicating the linear scaling of standard deviations to means in odometry found in this species (Narendra et al., 2007) and also in *C. fortis* (Cheng et al., 2006).

In terms of total path length (l, determined up to the point where searching began; Fig. 4C), the open- and cluttered-nest ants showed

no significant difference in variance (O'Brien's test, $F_{1,43}$=2.20, P=0.145). The open-nest ants ran longer mean paths ($F_{1,43}$=4.08, P=0.050). Moreover, the variance in straightness (d/l) was much greater in the ants from the cluttered nests (Fig. 4D; O'Brien's test, $F_{1,43}$=9.60, P=0.003). Furthermore, in terms of mean values, the open-nest ants had straighter paths (Welch's ANOVA, $F_{1,32.2}$=8.62, P=0.006).

DISCUSSION

In a previous paper (Bühlmann et al., 2011) we showed that the open-habitat species *C. fortis* relied more strongly on its path integration home vector when tested in the absence of familiar landmark cues than the cluttered-habitat species *M. bagoti* did. The switch between vector-based and landmark-mediated behaviour occurred more readily in the latter than in the former species. Across a range of conditions, *M. bagoti* switched from running off a vector to searching, presumably for familiar landmarks, after a shorter distance than did *C. fortis*. It was concluded that the open-habitat and cluttered-habitat species had higher and lower propensities, respectively, to adhere to their vector-based strategy when presented with unfamiliar landmark situations. Comparisons across past studies suggested that intraspecific, environment-dependent differences would be found in addition to these interspecific propensities. The present results provide further evidence by confirming this hypothesis within a single test situation in a single season.

Ants of the species *M. bagoti* inhabiting either (exceptionally) an open-field habitat or (more usually) cluttered-field habitats were tested and compared. Having been trained in their natural habitats to forage at a feeder placed at a 12 m distance from the nest, they had to perform their home runs in an open test field free of nest- or route-defining landmarks. Ants of both groups selected their home direction by relying on information provided by their path integrator. The angular spreads of their home runs did not differ between the two groups (Fig. 4A), similar to the findings for the two species *M. bagoti* and *C. fortis* [see fig. 5 of Bühlmann et al. (Bühlmann et al., 2011)]. This behaviour indicates that the same path integration mechanism was used by ants of both species and both environments. What did differ significantly, however, between the ants from the open nest and those from the cluttered nests were (i) the beeline distances (d_0) they covered in the test field and (ii) the indices of straightness (d/l) of their trajectories. First, the beeline distance was significantly larger for the open-nest ants than for the cluttered-nest ants, meaning that the latter broke off their vector-based home runs much earlier than the former did (Fig. 4B). Note that Fig. 4B corresponds to fig. 3 in Bühlmann et al. (Bühlmann et al., 2011), blue boxplots [−/−] and [+/−], respectively. The [−/−] condition in Bühlmann et al. resembled our open-nest group, in that ants from the same open nest were displaced to a test site on the balloon-launching field. The [+/−] condition in Bühlmann et al. paralleled that encountered by our cluttered-nest ants, in that artificial route marks were set up in training but were missing in tests. It seems that the artificial landmark array with which *M. bagoti* had been presented in the former study had about the same effect on the ants' behaviour as the naturally cluttered environment had in the present study. In each case, the missing landmarks resulted in about 25% shorter runs before the start of search. Second, the home runs in the cluttered-nest ants were distributed over a much larger area and thus exhibited smaller indices of straightness (d/l) than the home runs of the open-nest ants did (Fig. 4D). Parametric manipulations on this species have shown that the larger the mismatch in views between training and test situations, the more the ants tend to meander, zigzagging around the direction of travel [see fig. 5 of

Wystrach et al., 2011 (Wystrach et al., 2011)]. We interpret this wiggling during travel as indicating a propensity to search for familiar scenery even as the ants integrate a path.

We attribute the differences between the open and cluttered nests to the foraging experience that the ants had had; in particular, to the different visual input that they encountered in foraging on their respective terrains. We think it highly unlikely that the open nest would have evolved different innate tendencies from those found in the other nests in the vicinity. The balloon-launching field was only cleared very recently in evolutionary time, within the last two centuries, and we doubt that adaptive specialisations to such an environment would have evolved in that time.

The question arises as to how much experience of the visual surround is necessary for the observed effect to appear; that is, for ants deprived of familiar landmarks to run a shorter straight leg before engaging in searching. Indeed, even a couple of foraging trips to food provided near the nest suffice to enable the ant learn something of the visual panorama (Wystrach et al., 2012). In the context of the present study, the question is hard to test practically because ants make a number of trips before arriving at a feeder 5 or 10 m away (E.J.T.M. and K.C., personal observations), so that first-time arrivals at the feeder are not truly naive. In Wystrach et al.'s (Wystrach et al., 2012) study, some ants that arrived for the first time at a feeder at the end of their experimental route were tested, although the results of these ants were not reported in the publication. The behaviour of these ants was more similar to than different from that of ants that were highly experienced with the route.

In summary, the results of the present study clearly show that differences in the readiness with which individual ants switch from vector-based to landmark-mediated behaviour depends on the landmark information that the ants have gained in their foraging area. The more cluttered the environment, the less strictly do conspecific ants rely on their path integration routine when deprived of familiar landmark cues. A species-specific, inherited propensity unravelled in the previous study (Bühlmann et al., 2011) is further and finally shaped by environment-dependent, individually gained information.

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