

Context-dependent navigation in a collectively foraging species of ant, *Messor cephalotes*

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Abstract More than 100 years of scientific research has provided evidence for sophisticated navigational mechanisms in social insects. One key role for navigation in ants is the orientation of workers between food sources and the nest. The focus of recent work has been restricted to navigation in individually foraging ant species, yet many species do not forage entirely independently, instead relying on collectively maintained information such as persistent trail networks and/or pheromones. Harvester ants use such networks, but additionally, foragers often search individually for food either side of trails. In the absence of a trail, these ‘off-trail’ foragers must navigate independently to relocate the trail and return to the nest. To investigate the strategies used by ants on and off the main trails, we conducted field experiments with a harvester ant species, *Messor cephalotes*, by transferring on-trail and off-trail foragers to an experimental arena. We employed custom-built software to track and analyse ant trajectories in the arena and to quantitatively compare behaviour. Our results indicate that foragers navigate using different cues depending on whether they are travelling on or off the main trails. We argue that navigation in collectively foraging ants deserves more attention due to

the potential for behavioural flexibility arising from the relative complexity of journeys between food and the nest.

Keywords Harvester ants · Navigation · Collective foraging

Introduction

Navigation is an essential component of foraging in many animals, allowing directed movement through potentially complex spatial environments to find food and other vital resources. Navigational systems are specific to an animal’s sensory capacities, the availability of environmental cues and the scale of the environment being traversed (Philips et al., 2006). In social insect colonies, foragers may make multiple journeys per day between the nest and food sources. Foraging efficiency, often cited as a key factor in the ecological success of social insects (e.g. Hölldobler and Wilson, 1990), is largely dependent on the accuracy with which individuals can move between these locations. Navigation in ants has been studied extensively, and research spanning more than a century has attested to the remarkable precision with which individuals can navigate familiar and unfamiliar environments (reviewed in Collett and Collett, 2002; Wehner and Srinivasan, 2003; Cheng, 2012).

Many ant species use diverse strategies that incorporate both geocentric cues—including the Earth’s magnetic field (Camlitepe and Stradling, 1995), the position of the sun (Sommer and Wehner, 2005) and the orientation of polarized light (Wehner and Müller, 2006)—and egocentric cues, such as the panoramic view of the skyline from the position of the ant (Graham and Cheng, 2009; Philippides et al., 2011; Wystrach et al., 2011). These cues can be coupled with internal distance counters to allow effective orientation by

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path integration (Müller and Wehner, 1988; Wittlinger et al., 2006; Schultheiss and Cheng, 2011).

The use of specific navigational cues is at least to some extent dependent on environmental context, with behavioural flexibility at the individual level enabling dynamic use of cues as and when they are available (in *Cataglyphis*, Wehner, 2003; in *Melophorus*, Narendra, 2007). Furthermore, individual experience of a route from the nest may play an important role in the selection of a navigational strategy (Harrison et al., 1989; Fukushi and Wehner, 2004; Kohler and Wehner, 2005; Wystrach et al., 2012).

Yet despite the extent of the work on ant navigation, recent research has focused almost exclusively on species which make foraging excursions individually. Solitary foraging is at one end of a spectrum of foraging techniques, and most ant species show some form of collective foraging behaviour, whether by tandem running, group recruitment, or via the establishment of trails (Hölldobler and Wilson, 1990).

Many collectively foraging species of seed harvester ants live in large, territorial colonies of thousands of individuals and create persistent networks of trails to guide foragers to food sources up to 40 m from the nest (e.g. Hölldobler, 1974; Solida et al., 2010). Often, ants leave the trail to search for seeds individually (Hölldobler, 1976). On finding a seed, foragers show high accuracy in returning to the point of departure on the trail network, and then follow the main trail back to the nest. Thus, a harvester ant's outward and inward journeys are each split into two segments—an on-trail segment and an off-trail segment. This two-part journey presents an interesting navigational challenge, as foragers do not home directly from their current location after finding food, but retrace their routes back to the point at which they left the trail network, and only then reorient towards the nest (Hölldobler, 1971, 1976). As it is likely that the visual and chemical information available to a forager on the main trail will differ considerably from that available to a forager searching some distance from the trail, there is the potential for context-specific selection of navigational strategies.

In some of the earliest experiments on insect navigation, European harvester ants (*Messor barbarus*) displaced a short distance to one side of the main trail continued parallel to their previous trajectories rather than following the shortest route back to the nest, implying an ability to use information other than just the presence of pheromones or other ants on the trail for navigation (Santschi, 1911). Foragers of the North American seed harvester ants *Pogonomyrmex rugosus* and *Pogonomyrmex barbatus* can use visual cues, a sun compass and potentially also pheromones to orient along trunk trails (Hölldobler, 1971, 1976; although see Gordon et al., 2011; Prabhakar et al., 2012). However, off-trail ants of these species may depend primarily on visual landmarks to navigate back to the trail from foraging sites

(Hölldobler, 1974, 1976). Hence there is indirect evidence that during a single excursion, ants that forage using persistent trail systems may be switching between navigational strategies.

Here we take advantage of technological advances in video equipment and processing to directly and quantitatively investigate the relationship between a forager's position relative to the trail network and its navigational strategy using colonies of the Old World harvester ant *Messor cephalotes*. The genus *Messor* shows an unusually high level of variation in foraging strategy between species (Plowes et al., 2013), and to our knowledge, the foraging behaviour of *M. cephalotes* is undescribed. However, like foragers in the species *P. barbatus* and *P. rugosus* described in Hölldobler (1976), individuals in this species are observed to leave main trunk trails to search for seeds, presenting the opportunity to compare navigation behaviour between ants on the main trail and ants foraging individually.

On-trail ants (foragers travelling along the main trails) and off-trail ants (foragers on solitary excursions to the sides of the main trails) were individually removed from their routes and transferred to an experimental arena. This arena was positioned over 10 m from the experimental colony's nest and 5 m from any trail used by that colony to ensure an unfamiliar visual environment for the ants. The complete trajectories from the centre to the edge of the arena were tracked and analysed to explore the influence of context—i.e. whether ants are travelling on, or off, the main trail—on the navigational strategy used during different parts of a forager's journey. Our results indicate pronounced differences between the trajectories of off-trail and on-trail ants, providing strong evidence for context-dependent navigation in this collectively foraging species.

Methods

Study site and species

Experiments were conducted in January 2012 at Mpala Research Centre, part of a private conservancy in Laikipia County, Kenya (35°53' E, 0°17' N). Two colonies of seed harvester ants (*Messor cephalotes*), A and B, were located within 1 km² in an area of sparse vegetation (primarily grasses and small *Acacia* trees), and had one and six main trails leaving the nest, respectively. The main trail in colony A ran north to south, while the trail used for experiments in colony B ran east to west. Like other harvester ant species living in hot climates (e.g. Cole et al., 2010), these colonies tended to be active for two periods each day, during which time ants cleaned the nest and/or foraged along all or some of the trails. Consequently, experiments were carried out on

colonies in the morning from approximately 8.30 to 10.30 a.m. and in the afternoon from 3 to 6 p.m.

Experimental set-up

The experimental arena was a circular region with a radius of 50 cm on a larger rectangular board (240 × 140 cm) of 8 mm-thick plywood. The arena was placed flat in an area with relatively low vegetation deemed to be outside the main territory of the colony by an absence of clear trails or foraging ants, at a distance of 10.2 m due south of the nest for colony A and 12.4 m due east of the nest for colony B. The territorial nature of these ants and the stability of the foraging networks made it very likely that the environment of the experimental arena would be unfamiliar. During trials, the arena was positioned on the opposite side of the nest from the region in which ants were captured and oriented perpendicular to the trail being used for experiments. A tripod-mounted Panasonic HDC-HS300 video camera was positioned to the side of the board and used to film the arena during experiments with a frame rate of 30 frames per second.

Trials

In total 258 trials with ants returning with seeds were carried out: 157 off-trail (84 from colony A, 73 from colony B), and 101 on-trail (32 from colony A, 69 from colony B). Each morning or afternoon session was devoted to either off-trail or on-trail ant trials, such that both groups were tested at least once at both times of day for each colony. The process of selecting and removing an ant from its path differed slightly between off-trail ants and on-trail ants. For each off-trail trial, an ant carrying a seed back towards the trail was selected from an area of low vegetation within 7 m either side of the main trail, with a minimum distance from the trail of 0.5 m and a distance from the nest of between 3.7–8 m and 2.4–5.9 m for colonies A and B, respectively. Ants were removed from alternating sides of the main trail so that any tendency to follow the trajectory of the previously tested ant in the experimental arena could be identified. Prior to removal, each ant was observed for a period of at least 5 s, its distance from the trail recorded and its average orientation estimated using an electronic compass (GPSMAP 60Cx Handheld GPS Navigator, Garmin Ltd, error ±2 degrees). For each on-trail trial, ants returning to the nest with seeds were selected from the main trail, 4.6 and 2.5 m from the nest for colonies A and B, respectively.

For all trials, the selected ant was then captured using a small cylindrical plastic container and transferred to the experimental arena. This capture-transfer process lasted <1 min for each ant. The side of the arena from which the ant was released (either the same or the opposite side

relative to the camera) was alternated every two trials to minimize confounding effects of the position of the releaser on the ant's behaviour. The trial began when the ant was released in the centre of the experimental arena and the camera was used to film the movement of the ant until it crossed one of the arena boundaries. At the end of the trial, the ant was removed using a soft paintbrush and transferred to an inescapable plastic container for the duration of that session's experiments, to prevent individuals being repeatedly tested in the same foraging period. The wooden board was wiped with water after twenty trials to clear any debris swept onto the arena. In some trials, the ant released at the centre of the arena dropped its seed before exiting the arena (34 trials, 28 off-trails and 6 on-trails). These trajectories were not included in the analysis of differences in off-trail and on-trail navigation behaviour. In a further six trials (five off-trail, one on-trail), it was unclear from the videos whether the ant had dropped or otherwise lost its seed during the trial and these trajectories were also excluded from further analysis. The total sample size for analysis of differences between off-trail and on-trail behaviour is therefore 218 (124 off-trail, 94 on-trail).

Analysis

Video files were processed using OpenFrameworks (<http://www.openframeworks.cc>) to remove the background (i.e. arena, surrounding vegetation and shadows) leaving only the ant moving over the arena. The position of the thorax in each ant was then tracked from the processed videos at 30 frames per second using purpose-built software written in Processing (<http://www.processing.org>). Ant trajectories were cropped once they passed the boundary of the circular arena and the time taken to leave the circular arena was recorded for each ant.

In order to confirm independence of trials and eliminate the possibility of trajectory similarity arising from some form of communication between ants in consecutive trials (i.e. pheromone laying and following), the spatial overlap between consecutive trajectories was compared to the overlap between randomly selected trajectories using custom-built software (Online Resource 1). Consecutive trajectories were no more likely to be similar to each other than trajectories selected randomly from the dataset, indicating that ants navigated independently from the release point in the arena to the edge of the board.

After the total length of the path had been calculated, trajectories were discretized into segments in Matlab (The Mathworks Inc.) to facilitate analysis. The choice of segment length is subject to a trade-off between incorporating too much noise using a small segment length and sacrificing resolution by taking too large a segment length. The intermediate length of 1.5 cm chosen here is approximately

equal to the body length of the ants tested and is a compromise between reducing noise due to errors in the tracking software and maintaining a high resolution of the ant's behaviour. (Fig. S1 in Online Resource 2 shows an example trajectory discretized using this step length).

The discretized trajectories were used to obtain (1) a measure of the straightness of the path, (2) a distribution of turning angles and (3) a distribution of orientations to describe the ant's path. An index of path straightness (Batschelet, 1981; Benhamou, 2004) was calculated by computing the ratio of the minimum distance between the centre and the edge of the experimental arena to the length of the discretized path taken by the ant. This index therefore varies between values approaching 0, indicating extremely long and therefore more tortuous paths out of the arena to 1, indicating a straight line.

Mean orientations of individual trajectories were calculated for off-trail and on-trail ants from each colony and were compared within groups (i.e. on-trail, west of trail, east of trail, north of trail, south of trail) using *V* tests, which return a *p* value corresponding to the probability that a sample of angles are distributed uniformly around a circle when an expected mean direction is specified. The expected mean was the direction from the capture point to the trail for off-trail ants and from the capture point to the nest for on-trail ants.

From these data, trajectories of off-trail and on-trail ants were compared using generalized linear models and stepwise regressions (with the Matlab Statistics Toolbox), a circular statistics toolbox in MATLAB (Berens, 2009) and methods discussed in Batschelet (1981). The ant's position relative to the trail, the time of day (morning/afternoon) and the colony was included as predictors in all initial models, but was excluded during stepwise regression from the final models for the trajectory properties analysed.

Results

Trajectory properties

Off-trail ants took shorter, more direct routes and leave the arena more quickly than on-trail ants. Figure 1 shows typical trajectories (pre-discretization) for an off-trail and an on-trail ant. The position of the ant, i.e. whether it was removed from the trail or from an area to the side of the trail predicted the average time taken to leave the arena (Fig. 2, GLM $p < 0.001$). The calculated straightness index was higher for off-trail ants, indicating shorter, more direct trajectories than those of on-trail ants (Fig. 3a, GLM $p < 0.001$). In addition, the median turning angle for on-trail ants was significantly higher than the median turning angle for off-trail ants, reflecting the tendency of on-trail

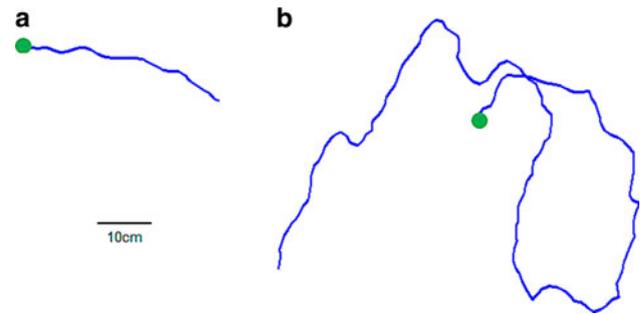


Fig. 1 Typical trajectories (pre-discretization) of an off-trail *a* and an on-trail *b* ant in the experimental arena. Circles mark the release point in the centre of the arena and the solid line shows the path of the ant from the centre to the arena boundary

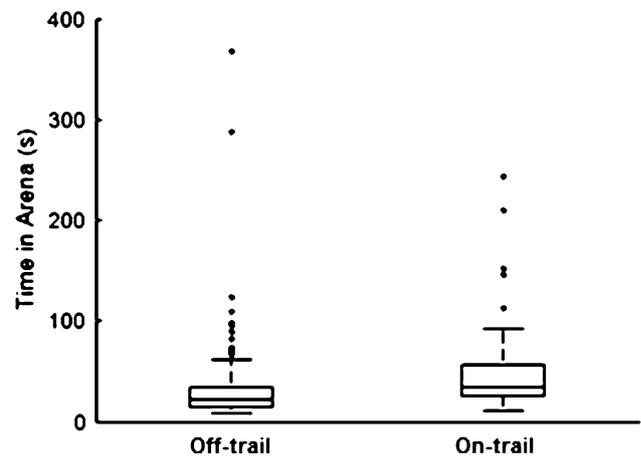


Fig. 2 Time taken to leave the arena for off-trail and on-trail ants ($p < 0.001$). $N = 124$ off-trail, $N = 94$ on-trail. Plots show median, quartile and range, dots mark outliers

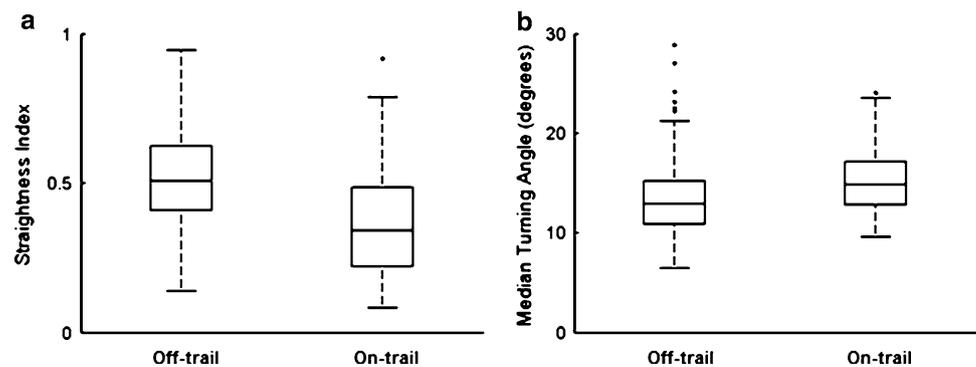
ants to make wider turns in the arena (Fig. 3b, GLM $p < 0.001$).

Orientation

Off-trail ants were able to reorient in the expected direction of the closest point in the trail relative to the capture point (*V* test for trail direction for ants from the east: $p < 0.001$; west: $p < 0.001$; north: $p < 0.001$; south: $p = 0.025$, Fig. 4a–d).

For on-trail ants, neither colony oriented in the expected direction of the nest from the capture point (*V* test for nest direction for ants in colony A: $p = 0.081$; colony B: $p = 0.900$, Fig. 4e–f). On-trail ants in colony A showed a weakly statistically significant difference from a uniform distribution, ascertained by performing a Rayleigh test ($p = 0.043$), with a south-easterly mean orientation of 236° while in colony B no such statistical difference was detected (Rayleigh test, $p = 0.368$). Note, however, that the straightness index for both colonies was significantly lower

Fig. 3 Trajectory properties for off-trail and on-trail ants: The two groups differ in **a** straightness index ($p < 0.001$) and **b** median turning angle ($p < 0.001$). $N = 124$ off-trail, $N = 94$ on-trail. Plots show median, quartile and range, dots mark outliers



in on-trail groups than in off-trail groups, reflecting far more tortuous trajectories in the arena.

Discussion

Despite such behavioural complexity, neither off-trail nor on-trail ants navigated directly towards the true position of the trail or nest from the experimental arena. Therefore, the cues used to navigate on and off the trail are specifically coupled with the ants' position relative to the trail network, and these ants cannot determine the true location of the trail or nest when displaced by a considerable distance.

On-trail ants and off-trail ants showed markedly different behaviour in the experimental arena (Fig. 1). Off-trail ants took faster, more direct paths from the centre to the edge of the arena (Figs. 2 and 3a), made smaller turns on average (Fig. 3b) and accurately oriented in the direction of the nearest point in the trail from where they were captured (e.g. due south for ants removed from the north side of a trail running west to east, Fig. 4a–d). These results indicate that off-trail ants were able to use one or a combination of the navigational cues available to them in the experimental arena to orient and walk in the expected direction of the trail, despite having been displaced.

By contrast, the trajectories of on-trail ants were characterized by wider turn angles and much longer, more tortuous paths (Figs. 2 and 3a) with larger turning angles (Fig. 3b) from the centre to the edge of the arena. Furthermore, on-trail ants did not navigate consistently in either the true direction of the nest from the arena or the direction of the nest from the capture point (Fig. 4e–f). These results suggest that on-trail ants, once displaced, were unable to retrieve their previous orientations using the information available to them in the arena.

The differences between the trajectories of the two groups strongly imply that off-trail ants and on-trail ants rely on different navigational cues. Based on the low tortuosity of off-trail ant trajectories and the high consistency of orientation towards the expected closest point in the trail,

the cues that off-trail ants used to navigate appear to have been relatively constant between the foraging area and the position of the experimental arena. The landscape of the test site was structurally complex and ants were displaced at least 10 m from the nest (and further still from the capture point). Therefore, trials took place in a markedly different visual landscape from the capture site, and we consider it unlikely that such consistency in off-trail ant orientation could be achieved using local visual cues alone. However, as this study did not exclude cues at the experimental arena, further experiments in which local visual cues are obscured (e.g. see Graham and Cheng, 2009) will be necessary to ascertain whether off-trail ants can indeed navigate in the absence of a panoramic view of the skyline.

Meanwhile, the far less direct trajectories and the low consistency of orientations of on-trail ants suggest that these individuals are unable to navigate in a homeward direction using only information available to them at the experimental arena. This result implies dependency on local trail-based cues such as the visual profile of the trail and its surroundings, or possibly chemicals deposited by other ants.

Studies in *Formica* and *Melophorus* have provided evidence for panoramic skyline matching as a mechanism of visual navigation whereby the ant compares the current view of the skyline with a stored image from part of a memorized sequence (Judd and Collett, 1998; Fukushi, 2001; Harris et al., 2005; Graham and Cheng, 2009). By moving in the direction of the least difference between these two images, an ant could move reliably back along a learned route (Baddeley et al., 2012). 'Zero-vector' foragers—ants which have already homed to the immediate vicinity of the nest—show 'indecisive' orientation behaviour when displaced from their original routes, although they eventually orient towards the nest (Narendra, 2007). Wystrach et al. (2012) interpret this result as a consequence of using variation in local perception of skyline height as a navigational cue. In this study, ants may be displaced far enough from their routes that the use of cues specific to the trail, such as local visual information or chemical cues, no longer enables

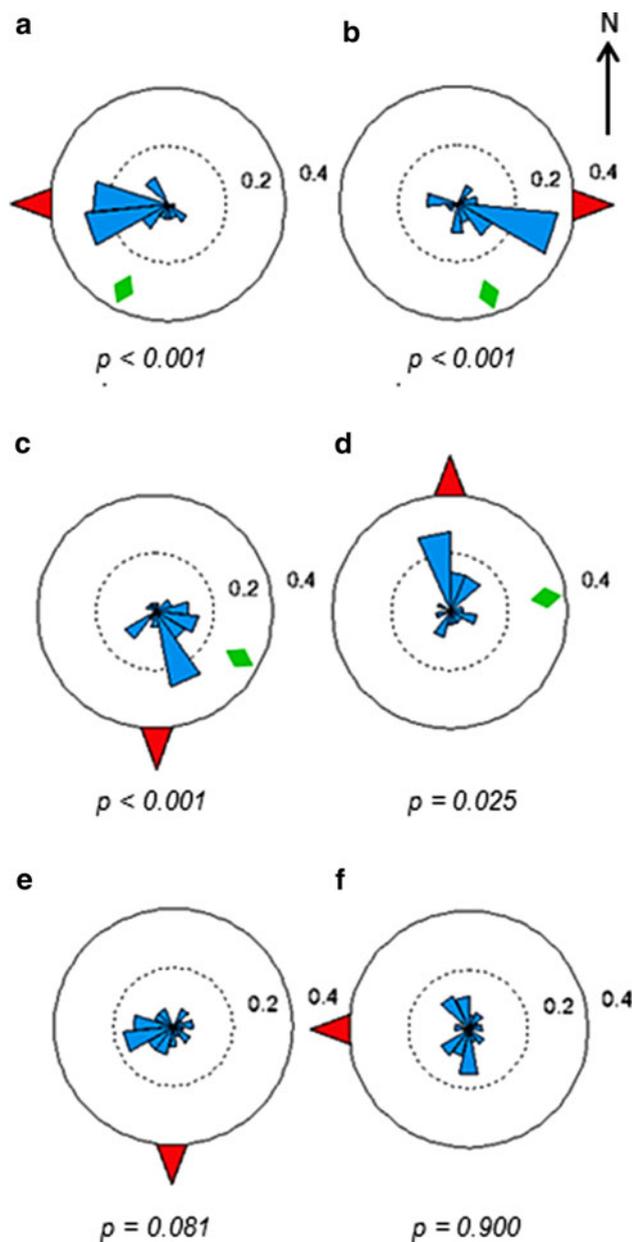


Fig. 4 Circular plots showing the mean orientations of ants from colony A removed from **a** the east side ($N = 39$), **b** the west side ($N = 29$) of the trail and ants from colony B removed from **c** the north side ($N = 34$) and **d** the south side ($N = 22$) of the trail; **e** shows on-trail ants from colony A ($N = 30$), **f** shows on-trail ants from colony B ($N = 64$). The data are presented proportionally, such that the concentric circles represent 20 and 40 % of the data for that group. Triangles point in the expected direction of the trail (**a–d**) or the nest (**e–f**) from the capture points of the ants. The displayed p values were calculated with V tests using this expected direction for each group. Diamonds mark the mean direction of the nest from the capture point for off-trail ants

accurate navigation and results in the tortuous or ‘indecisive’ trajectories of on-trail ants.

Another possibility is that on-trail ants search for the trail before attempting to use available cues to navigate

towards the nest. Off-trail ants return to the trail upon finding a seed, not the nest itself. This behaviour suggests an advantage to travelling on the trail as opposed to homing directly from foraging areas, most likely related to the high territoriality in harvester ant colonies and the cost of errors associated with solitary navigation (Hölldobler, 1974). Therefore, the more tortuous paths such as the one shown in Fig. 1b may reflect searching behaviour in ants attempting to relocate the trail. However, as noted above, further experiments excluding local cues will be crucial in evaluating the use of egocentric information during homing so that conclusions regarding specific navigational strategies may be drawn.

Our results contrast with those described by Hölldobler (1976) who found that in the North American harvester ants *Pogonomyrmex rugosus* and *Pogonomyrmex barbatus*, foragers on the main trails used the position of the sun, local visual cues and chemical cues for navigation, but off-trail ants returning to the trail engaged in searching behaviour when visual landmarks were removed. In our experiments with *M. cephalotes*, off-trail ants were consistently able to use geocentric cues to navigate in the direction of the trail, while on-trail ants apparently did not make use of globally available cues to navigate in the direction of the nest. However, ants in the genera *Cataglyphis* and *Melophorus*, along with many other insects, often couple the use of celestial navigational cues with another form of homing strategy (Fent and Wehner, 1985; Wehner, 2003; Legge et al., 2010). For example, *Cataglyphis* ants switch from using celestial cues to local visual cues when they arrive in the vicinity of the nest (Wehner and Menzel, 1969). It is likely that off-trail ants use a combination of strategies for navigation, some of which may rely on local cues that are unavailable or ambiguous at the site of the experimental arena in our study. In this case, the use of geocentric cues may provide a mechanism by which off-trail ants can relocate the trail even in the case of being displaced a small distance from their route by environmental disturbances or temporary obstacles.

It is of course possible that on-trail ants at some point are able to switch from this search-like behaviour to accurate homing, but that this switch has not been detected in the limited area of the experimental arena. However, given that the primary goal of foragers returning from foraging expeditions with seeds is to return to the nest, it would seem unlikely—despite the potential costs of leaving the territory—that ants should spend time looping around the expected position of the trail if in fact they were able to use the available navigational cues for homing. Either way, the differences in behaviour of on-trail and off-trail ants indicate a strong relationship between the primary method of navigation used and the position of the ant before displacement.

The storage of spatial information in insects is still not well understood (Collett, 2009; Baddeley et al., 2012), but context-specific navigation may allow ants to make use of the most reliable source of information available—whether that is the collectively maintained trail network or globally available cues. For example, geocentric cues, such as the position of the sun or polarized light, may represent the most reliable source of information only in the absence of local, trail-based cues. Future experiments in which visual and chemical cues are selectively examined will help to determine the reliance of individual ants on specific navigational strategies in the presence of different sources of navigational information.

The complex nature of the navigational tool kit in ants reflects the strong selection pressures acting on the efficiency of foraging in social insects. Results from this study highlight the capacity for context-dependent mechanisms of navigation in *M. cephalotes* and underscore the need for further research into the use of multiple navigational cues in collectively foraging ant species.

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