

RESEARCH ARTICLE

Polarised skylight and the landmark panorama provide night-active bull ants with compass information during route following

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SUMMARY

Navigating animals are known to use a number of celestial and terrestrial compass cues that allow them to determine and control their direction of travel. Which of the cues dominate appears to depend on their salience. Here we show that night-active bull ants attend to both the pattern of polarised skylight and the landmark panorama in their familiar habitat. When the two directional cues are in conflict, ants choose a compromise direction. However, landmark guidance appears to be the primary mechanism of navigation used by forager ants, with those cues in the direction of heading having the greatest influence on navigation. Different colonies respond to the removal of these cues to different degrees, depending on the directional information provided by the local landmark panorama. Interestingly, other parts of the surrounding panorama also influence foraging speed and accuracy, suggesting that they too play a role in navigation.

Key words: nocturnal foraging, navigation, *Myrmecia pyriformis*, ant, orientation, polarised skylight, landmark panorama.

INTRODUCTION

Central place foragers, such as ants, require robust navigational systems to explore their environment and return to the nest successfully. Although the majority of studies have focused on the navigational mechanisms foragers use to return to the nest, relatively little is known on how foraging ants navigate back to a familiar food source without the aid of pheromone trails. To do so, individuals must remember and control heading direction with the aid of external compass cues and, once they have come close, possess a memory of the location of the goal (Collett and Collett, 2009). Individually foraging ants cannot follow pheromone trails or vector instructions as honeybees do (e.g. Riley et al., 2005) and thus must remember a 'food vector' (Collett and Collett, 2009; Collett et al., 1999) or route landmarks from their previous journeys (reviewed by Collett et al., 2006).

We were interested in identifying the compass cues used by individually foraging, night-active Australian bull ants, which would appear to have a harder task in controlling heading direction than their day-active relatives. Day-active ants are known to be guided by a number of compass cues, including the pattern of polarized skylight (Carthy, 1951; Jander, 1957; Vowles, 1950). In featureless habitats such as deserts, ants determine direction with reference to the sun or to the pattern of polarised skylight (Wehner, 1997; Wehner, 2001; Wehner and Müller, 2006). In landmark-rich environments the landmark panorama provides beacons (e.g. Graham et al., 2003; Nicholson et al., 1999) or more general compass information (Jander, 1957; Fukushi, 2001; Graham and Cheng, 2009b) that in many cases has been shown to override directional information provided by celestial cues when the two are in conflict (Andel and Wehner, 2004; Collett et al., 2007; Fukushi, 2001; Fukushi and Wehner, 2004; Graham and Cheng, 2009a; Narendra, 2007b). Ant foragers leaving the nest on a foraging excursion

remember the direction of a goal using beacons when landmarks are present (Graham et al., 2003), or celestial cues when deprived of visual landmarks (Collett et al., 1999). Landmark guidance again dominates when there is a discrepancy between celestial and terrestrial cues (Merkle and Wehner, 2008), suggesting that the degree to which one or the other drives behaviour depends on their salience, i.e. the relative strength and reliability that the respective signals provide.

We know most about the use of celestial and terrestrial cues from ants operating in a range of environments, from featureless to landmark-rich environments. However, a similar change in the availability of cues might also exist between diurnal and nocturnal lifestyles: as light levels drop, visual compass cues in general become less reliable because of the decreasing number of photons. The relative signal strength that celestial and terrestrial compass cues provide may change accordingly as the signal-to-noise ratio in photoreceptors decreases. How reliably and strongly these cues are represented on a neural level, depends, in the first case, when comparing featureless and landmark-rich environments, on the topography of the environment and on the spatial resolution and polarization sensitivity of the eyes. In the second case, when comparing the situation during day and night, their relative salience depends, in addition, on the relative light sensitivity of those parts of the compound eyes that are sensing polarised skylight or the landmark panorama. We know that during twilight the pattern of polarised skylight is in a particularly simplified form and has a high degree of polarisation (Cronin et al., 2006), potentially providing a stronger directional cue to animals than during the day. Indeed, twilight-active arthropods have been shown to re-orientate strongly in response to experimental changes to the pattern of polarised skylight (Dacke et al., 2001; Dacke et al., 1999; Dacke et al., 2003; Labhart et al., 1992). However, we lack measurements of the degree

to which the absolute and relative salience of compass cues changes from day to night. What we do know is that, qualitatively, landmarks seen against the bright western sky will have a higher contrast at twilight, compared with landmarks seen against the dark eastern sky, so that their use as beacons may depend on the direction of view.

We report here on an investigation into how foragers of the night-active bull ant *Myrmecia pyriformis* Smith determine their direction of heading during their nightly foraging journeys. *M. pyriformis* are solitary foragers, with no evidence of recruitment, who leave the nest shortly after sunset to forage on nearby trees (Narendra et al., 2010a). The majority of individuals make only one foraging trip per night and visit the same tree each time. They move along idiosyncratic routes, following the same path on successive evenings (S.F.R., unpublished data). The bulk of activity to and from the nest is restricted to the dusk and dawn twilight (Greiner et al., 2007; Narendra et al., 2010b) and has been shown to be triggered by ambient light intensities (Narendra et al., 2010a).

Foragers of *M. pyriformis* have eyes with enlarged lenses and rhabdoms, boosting light sensitivity by a factor of approximately 27, compared with their diurnal relatives (Greiner et al., 2007). These adaptations to vision in dim light cannot by themselves compensate for the huge drop in ambient light levels of eight log units between day and night (e.g. Warrant, 2004; Greiner et al., 2005), but still suggest that vision plays an important role in the ants' nightly foraging trips. In fact, one reason why these ants might determine the onset of foraging by monitoring ambient light levels is so that they are able to use visual compass cues in the remaining light before it gets too dark (Narendra et al., 2010a). *M. pyriformis* is thus a particularly appealing species in which to study the relative importance of these cues as a source of directional information for a night-active animal. Do bull ants, like dung beetles, rely solely on celestial cues? Or does the increased sensitivity of their compound eyes allow them to rely predominantly on landmarks, like some day-active ants (e.g. Graham and Cheng, 2009a)? We found, instead, that they do attend to both, and that celestial and terrestrial compass information combine to provide a directional estimate.

MATERIALS AND METHODS

Study site and study species

Experiments were carried out on three nests of *M. pyriformis* located in the Campus Field Station of The Australian National University, Canberra (35°16'50"S, 149°7'50"E; Fig. 1A). The vegetation in the area consisted of Eucalyptus trees, regularly cut grass and weeds, and no distinct undergrowth. All nests were within 35 m of one another and located near Eucalyptus trees, which individuals climb to forage on sap, homopteran honeydew and insect prey. All experiments were carried out during the onset of activity in the evening twilight and were concluded before the end of astronomical twilight. A head torch fitted with a red filter was used for observations, which did not appear to disturb the ants.

The primary foraging direction from each nest was determined by recording the tree towards which the majority of foragers headed. Only foragers leaving the nest 90 deg either side of this dominant foraging direction were used for experiments. At Nest 1 the majority of foragers headed 192 deg to a tree 9.3 m away (Fig. 1A). At Nest 2 the primary foraging direction was 119 deg to a tree 8.1 m away, and at Nest 3 the majority headed 81 deg to a tree 3.7 m away.

Orientation to polarised skylight

To determine whether *M. pyriformis* uses a polarisation compass for orientation, we manipulated the direction of skylight polarisation

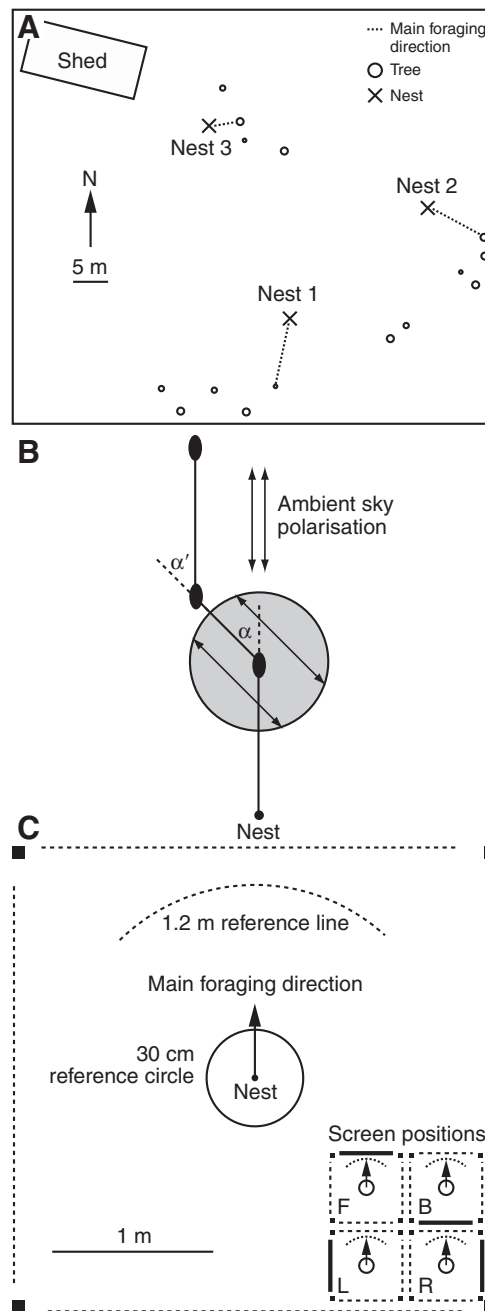


Fig. 1. Experimental setup. (A) The study site. All nests were within 35 m of one another and located near Eucalyptus trees. (B) Polarisation experiment. A polarisation filter was placed over an ant with its e-vector transmission axis 45 deg to the left (as in this example) or right of the dominant direction of skylight polarisation. We recorded exit orientation (α) and reorientation (α') of individuals. (C) Landmark-blocking experiment. A square was marked out around the nest and a screen was erected on one side at a time (insert shows screen position with respect to the main foraging direction; F, front; B, behind; L, left; R, right). We recorded the time individual foragers took to exit a 30 cm reference circle around the nest, the exit orientation upon leaving the reference circle and the proportion that crossed a 1.2 m reference line in the main foraging direction.

perceived by individual ants. A polarising filter (Polaroid HN22) 42 cm in diameter, supported by four 8 cm high thin metal legs, was placed over an individual ant after it had travelled 50 cm from the nest, such that it was centred over the ant (Fig. 1B). The line from

the nest to this point underneath the filter was taken as the initial heading direction of the ant. The e-vector transmission axis of the filter was oriented either 45 deg to the left (−45 deg) or 45 deg to the right (+45 deg) of the dominant direction of skylight polarisation at this time of day. To an ant underneath the filter the direction of polarised skylight would thus appear to have suddenly rotated 45 deg to the left or right, respectively. Once the ant exited from underneath the filter its position was marked, giving the ‘exit orientation’ (α ; Fig. 1B). Following this, we marked the position of the ant after it travelled another 50 cm, giving an individual’s ‘reorientation’ (α' ; Fig. 1B). This experiment was conducted on ants from Nest 1 and Nest 3. These two nests were chosen because ants from Nest 1 travelled the furthest (9.3 m) to reach their trees, whereas those from Nest 3 travelled the shortest distance (3.7 m; Fig. 1A).

To test for differences between the orientation changes of the ants in the −45 deg and +45 deg conditions of the rotated filter at a single nest, results were analysed using the Mardia–Watson–Wheeler test, available in the circular statistics program Oriana3 (Kovach Computing Service, Anglesey, UK), which tests whether two distributions are identical. If polarised skylight is used for orientation, individual ants should turn in the direction the filter was rotated. If not, there should be no difference between the two conditions. By rotating the polarising filter by either plus or minus 45 deg, we controlled for potential changes in the ants’ behaviour resulting from changes in light levels that are an unavoidable consequence of placing the filter over an ant. To determine whether the presence or phase of the moon had any influence on exit orientation we performed a Spearman’s correlation (SPSS, SPSS Inc., Chicago, IL, USA).

The use of the landmark panorama for orientation

To determine if foragers rely on the landmark panorama for orientation, a screen was erected in one of four directions around each of the three nests, obscuring different portions of the visual panorama as the ants left for foraging. Four posts were hammered into the ground, creating a square of 3×3 m, aligned with the dominant foraging direction and centred on the nest entrance (Fig. 1C). A taut dark blue fabric screen 1.5 m high and 3 m long was attached to the posts roughly 3 cm off the ground to allow ants to walk underneath the screen. This effectively blocked 90 deg in the horizontal and 45 deg in the vertical of the visual scene, as seen from the nest. A reference circle with a radius of 30 cm was marked around the nest entrance. A video camera positioned above the nest entrance allowed us to record the initial heading direction of individual ants as they crossed the 30 cm circle, as well as the time taken to exit the circle. In order to determine whether the ants were able to navigate over a long distance towards their foraging sites when the screen was erected, a reference arc centred on the main foraging direction 1.2 m from the nest (with an angular extent of just under 90 deg at the nest) served to record the proportion of ants, relative to the number exiting the 30 cm circle, that crossed this 1.2 m reference line.

During an experiment, only one of the four screens was erected at a time, either in the main foraging direction (front), behind the main foraging direction (behind), to the left (left) or to the right (right) of the nest (Fig. 1C). This allowed us to test what effect removing different portions of the panorama has on the ants’ ability to head towards their goal. For each direction the experiment lasted for 40 min and was performed twice on different days. On one occasion, the screen was up for the first 20 min of the daily foraging bout then down for the second 20 min. On another occasion, the screen was down for the first 20 min and up for the second 20 min.

The positioning of the screen relative to the nest and whether it was up or down for the first 20 min was carried out in a pseudo-random order. The results from both days were combined, allowing for a comparison of the effect when the screen was up and down for each direction around the nest.

Results from initial orientation measurements were analysed for differences between the screen-up and screen-down condition for each direction using the Mardia–Watson–Wheeler test. Data obtained for the time to exit the 30 cm reference circle were not normally distributed. We therefore used the Kolmogorov–Smirnov non-parametric test (SPSS) to test for differences between the distributions of the screen up and screen down condition for each direction. Finally, the proportions of ants crossing the 1.2 m reference line (relative to the number exiting the 30 cm circle) were analysed using a Fisher’s exact test. For all statistical procedures a Bonferroni correction was applied to account for multiple comparisons (four), lowering the level for a significant effect to 0.0125.

Displacement experiment

At Nest 3 it was necessary to carry out an additional experiment to establish whether foragers use landmark information for orientation. Similar to the other two nests, foragers at Nest 3 form habitual routes between the nest and tree (S.F.R., unpublished data). A grid with 1 m squares was marked out around Nest 3. After travelling half of the foraging distance from the nest to the northern tree, an individual ant was captured in a light-tight container. Only ants that crossed the halfway point and were within 50 cm of the nest-to-tree line were used for displacements. Individuals were then displaced either 2 m to the left or 2 m to the right of the nest-to-tree line (see Fig. 4). After release, the individual’s path was marked with a small pin every 20 s until it reached the foraging site. The pin-marked path was transcribed onto paper and later digitised. Only six ants were used (three at each displacement site) as it was merely necessary to determine whether foragers at Nest 3 use landmark information or not.

Panoramic images

We analysed differences in the visual structure of the local environment at each nest site by recording panoramic snapshots at the entrances of the three nests during the evening twilight, the time the ants usually begin activity. We used an obstruction-free panoramic imager (see Stürzl et al., 2008) with a visual field of 360 deg in azimuth and 150 deg in elevation. The imager was mounted on a video camcorder (Sony Handycam DCR-HC21E PAL). Individual frames of the recordings were digitised using VirtualDub (<http://www.virtualdub.org/>), unwarped using a program written in Matlab (MathWorks, Natick, MA, USA), following established procedures (Chahl and Srinivasan, 1997), to a rectangular image of 787 horizontal and 328 vertical pixels, corresponding to 0.46 deg pixel^{−1}. Images were low-pass filtered with a Gaussian filter with half-width of 2 deg to account for the estimated visual acuity of bull ants (Via, 1977).

RESULTS

Do bull ants use the pattern of polarised skylight for orientation?

By rotating a polarising filter either 45 deg to the left or right of the dominant direction of skylight polarisation, we manipulated the perceived direction of polarisation to an ant underneath the filter. If ants monitor their direction of travel using polarised skylight, individual ants should turn in the direction the filter is rotated. Indeed, when the filter was rotated left (−45 deg), the average exit

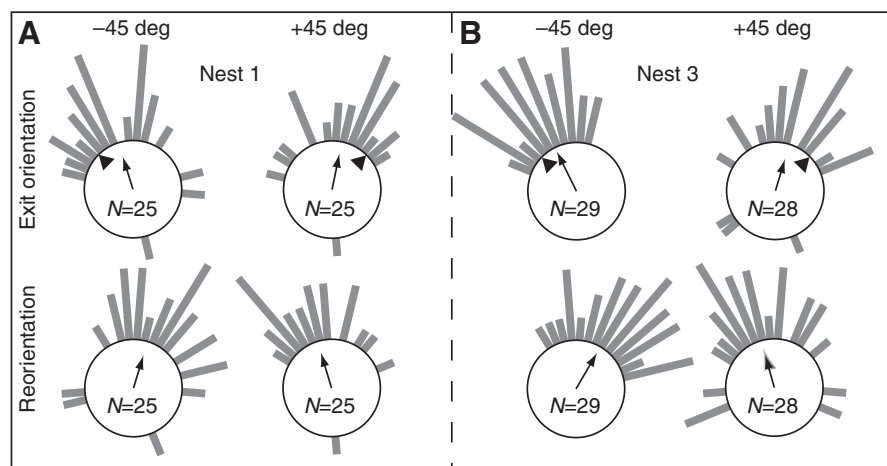


Fig. 2. Polarisation experiment. Circular histograms showing the exit orientation of ants when the polarising filter was rotated left (-45 deg) or right (+45 deg), and their reorientation after exiting, for (A) Nest 1 and (B) Nest 3. Arrows show the average orientation and length of mean vector. Triangles indicate the -45 deg or +45 deg rotation of the filter; N is the sample size.

orientation was to the left (mean \pm s.e.m., Nest 1: $\theta = -17.31 \pm 9.35$ deg; Nest 3: $\theta = -26.28 \pm 4.09$ deg, $N = 25-29$; Fig. 2A,B). When the filter was rotated right (+45 deg), the average exit orientation was to the right (Nest 1: $\theta = 11.49 \pm 8.27$ deg; Nest 3: $\theta = 16.75 \pm 9.41$ deg). The difference was significant between the two conditions (Nest 1: $W = 9.58$, $P = 0.008$; Nest 3: $W = 21.94$, $P < 0.001$), but not between the same conditions at different nests ($P > 0.05$ for both conditions). After exiting the area covered by the filter, individuals re-orientated, matching their exit orientation but in the opposite direction [Nest 1: (-45 deg) $\theta = 16.91 \pm 9.46$ deg, (+45 deg) $\theta = -16.80 \pm 7.78$ deg; Nest 3: (-45 deg) $\theta = 30.40 \pm 5.53$ deg, (+45 deg) $\theta = 15.86 \pm 9.40$ deg; Fig. 2A,B].

Experiments were performed when the moon was both present and absent from the night sky, as well as when it was in 17 different phases. However, no effect on exit orientation was seen when we analysed the results controlling for the presence and phase of the

moon (Spearman's correlation: no moon, $r = -0.05$, $P = 0.70$, $N = 49$; moon, $r = -0.11$, $P = 0.34$, $N = 53$). This suggests that neither the moon itself nor the polarisation pattern induced by its light affects forager orientation.

These results indicate that it is the pattern of polarised skylight formed around the sun that *M. pyriformis* uses for orientation. However, the ants clearly undercompensated for the 45 deg rotation of the filter, indicating that they must have attended to other compass cues as well. One possibility is the landmark panorama, which has been shown to provide strong directional information to diurnal ants (Jander, 1957; Fukushi, 2001; Fukushi and Wehner, 2004; Graham and Cheng, 2009a).

The landmark panorama as a directional cue

To determine whether *M. pyriformis* uses landmark information for controlling their heading direction, we erected a screen in different

Table 1. The results of the visual blocking experiment

Nest	Direction	Screen	N	Initial orientation \pm s.e.m. (deg)	Length of vector (r)	Average time to exit \pm s.e.m. (s)	Median time to exit (s)	% Crossing 1.2m reference line
1	Front	Down	38	190 \pm 2.2	0.97	20.4 \pm 2.8	15.0	100.0
		Up	36	189 \pm 6.8	0.77	57.6 \pm 8.2	41.2	36.2
	Behind	Down	40	191 \pm 1.6	0.99	18.3 \pm 2.1	13.0	97.6
		Up	40	184 \pm 3.8	0.92	43.0 \pm 7.1	29.0	86.6
	Left	Down	36	186 \pm 3.7	0.93	28.2 \pm 6.1	15.6	62.5
		Up	56	192 \pm 1.8	0.97	30.4 \pm 4.4	17.2	83.1
	Right	Down	32	190 \pm 3.0	0.96	22.6 \pm 5.1	13.2	93.9
		Up	40	187 \pm 2.2	0.97	21.0 \pm 1.4	20.2	95.2
2	Front	Down	99	124 \pm 1.9	0.95	12.5 \pm 1.0	10.0	100.0
		Up	119	122 \pm 1.8	0.94	17.6 \pm 1.4	13.2	61.1
	Behind	Down	89	126 \pm 2.1	0.94	11.8 \pm 0.8	9.6	92.2
		Up	81	124 \pm 2.0	0.95	14.4 \pm 1.3	11.3	90.7
	Left	Down	74	123 \pm 2.2	0.95	13.4 \pm 1.1	10.4	94.3
		Up	98	110 \pm 2.4	0.92	17.5 \pm 1.2	13.2	86.3
	Right	Down	85	119 \pm 2.6	0.92	11.6 \pm 0.9	9.6	94.3
		Up	80	128 \pm 2.1	0.95	17.5 \pm 1.8	12.0	79.1
3	Front	Down	30	80 \pm 4.4	0.92	18.6 \pm 1.3	19	100.0
		Up	50	82 \pm 4.4	0.86	20.7 \pm 2.1	15.4	83.3
	Behind	Down	54	76 \pm 3.1	0.93	18.7 \pm 1.1	15.6	91.8
		Up	55	86 \pm 3.7	0.89	20.1 \pm 1.2	17.6	86.3
	Left	Down	36	89 \pm 4.6	0.89	17.7 \pm 0.9	15.8	88.6
		Up	30	77 \pm 3.5	0.95	20.4 \pm 1.4	19.2	85.7
	Right	Down	37	83 \pm 3.3	0.94	19.2 \pm 1.2	18.0	100.0
		Up	45	81 \pm 3.5	0.92	21.2 \pm 1.3	19.2	94.1

N, number of ants.

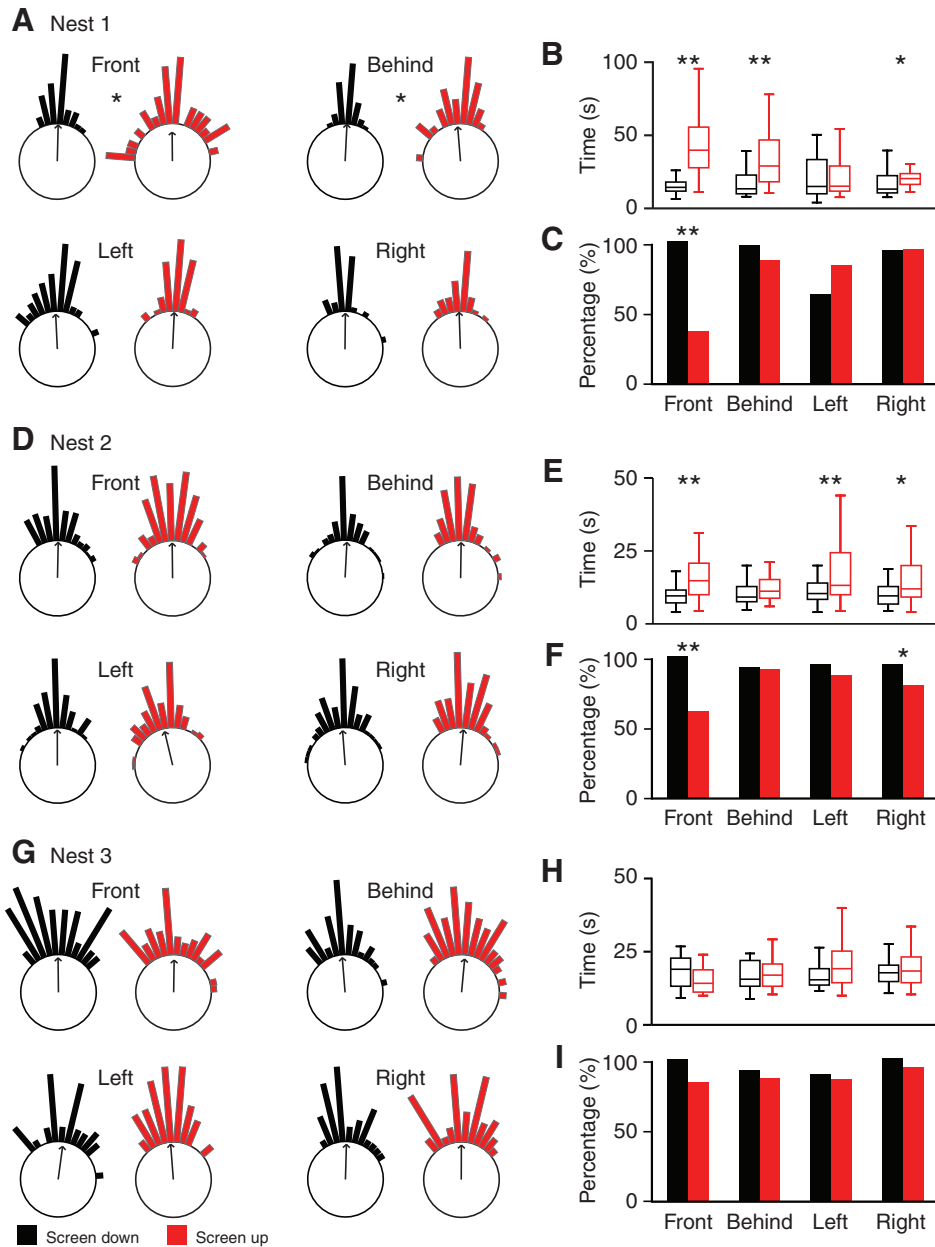


Fig. 3. Visual blocking experiment. We recorded the initial orientation of individual ants at the three nests (A,D,G), the time taken to exit the 30 cm circle (B,E,H) and the proportion that crossed the 1.2 m reference line (C,F,I) when the screen was down (black) and up (red) for the four directions (front, behind, left, right) around each nest. *Significance at $P < 0.0125$; **significance at $P < 0.0025$. Box plot conventions: the lower whisker is the minimum value, the bottom of the box is the first quartile, the middle line is the median, the top of the box is the third quartile and the top whisker is the maximum value. The box contains the middle 50% of values.

positions around each of the nest sites as individuals left for foraging. The effect of the screen at each nest site differed and is reported separately.

Nest 1

Initial orientation upon leaving the nest was significantly affected when the screen was in front of the nest ($W=10.43$, $P=0.005$; for sample size, see Table 1; Fig. 3A, Table 1). Individuals appeared to be disoriented immediately upon leaving the nest and were not directed in their usual manner towards the trees. Instead, they wandered in circles between the nest and the screen. This behaviour was only seen when the screen was in front of the nest, blocking the view in the direction of heading. However, the screen also had a significant effect on initial orientation when behind the nest ($W=9.90$, $P=0.007$; for sample sizes, see Table 1), but not when to the left or right ($P=0.07$; $P=0.55$, respectively). The time taken to exit a 30 cm reference circle was significantly affected when the screen was in front, behind and to the right of the nest ($Z=2.66$,

$P < 0.001$; $Z=2.46$, $P < 0.001$; $Z=1.71$, $P=0.006$, respectively; Fig. 3B). Once again, the effect was most pronounced when the screen was placed in front of the nest (Fig. 3B, Table 1). The only condition in which the proportion of individuals crossing the 1.2 m reference line fell significantly was when the screen was in front of the nest ($P < 0.0001$; Fig. 3C, Table 1), indicating that navigation broke down completely for some individuals. Of those ants that did cross the line, none were observed to walk underneath the screen, unlike at nest 2 and 3 (S.F.R., personal observation). It is also worth noting that when the screen was removed at the end of experiments, individuals quickly reoriented themselves towards the trees and immediately set off in their usual foraging direction.

Nest 2

The pattern of results at Nest 2 was similar to that observed at Nest 1, but less extreme and with a different spatial pattern. The screen again had the strongest effect when in front of the nest, but this effect was not as pronounced as at Nest 1. Initial orientation at Nest 2

was not significantly affected in any condition, but there was a trend towards significance when the screen was to the left (front, $W=1.33$, $P=0.51$; behind, $W=0.88$, $P=0.65$; left, $W=7.65$, $P=0.022$; right, $W=2.67$, $P=0.26$; for sample sizes, see Table 1; Fig. 3D, Table 1). However, the time taken to exit a 30 cm reference circle was significantly affected when the screen was in front, to the left and to the right of the nest ($Z=2.32$, $P<0.001$; $Z=1.94$, $P=0.001$; $Z=1.61$, $P=0.012$, respectively; Fig. 3E). The average increase in the time taken to exit the 30 cm circle was similar across all three conditions, but far less than the time taken by ants at Nest 1 (note different y-axis scales in Fig. 3B,E; Table 1). The proportion of ants crossing the 1.2 m reference line fell significantly in two conditions (front, $P<0.0001$; right, $P=0.004$; Fig. 3F) but again less than at Nest 1. In contrast to Nest 1, those ants that did cross the reference line at Nest 2 travelled underneath the screen and continued towards the trees (S.F.R., personal observation). However, a few ants continued to wander between the screen and the nest, and these individuals did not head in the right direction until the screen was removed. As seen at Nest 1, when the screen was removed, the ants immediately reoriented and moved quickly towards the trees.

Nest 3

At Nest 3, the screen had no measurable effect regardless of its position relative to the nest (front, $W=0.23$, $P=0.89$; behind, $W=3.84$, $P=0.15$; left, $W=3.26$, $P=0.20$; right, $W=2.85$, $P=0.24$; for sample sizes, see Table 1). There was no significant differences in the initial orientation, the time taken to exit the 30 cm circle or the proportion of ants that crossed the 1.2 m reference line when the screen was up or down (Fig. 3G,H,I, Table 1). There was, however, a trend towards a significant drop in the proportion crossing the 1.2 m reference line when screen was placed in front of the nest ($P=0.04$; Fig. 3I, Table 1).

Lateral displacement of foragers at Nest 3

We know from other experiments that foragers at Nest 3 (as well as those from Nest 1 and Nest 2) form habitual routes from nest to tree, indicating that landmarks are used for navigation (S.F.R., unpublished data). However, because the screen had almost no effect on foragers at Nest 3 it was necessary to perform a displacement experiment to determine whether individuals do use landmark information. During the experiment, three foragers were displaced 2 m to the left or 2 m to the right of the nest-to-tree line. When displaced at both release sites individuals re-oriented and headed towards the tree (Fig. 4), indicating that foragers at Nest 3 do indeed use landmark information for orientation.

DISCUSSION

After leaving the nest during the evening twilight, the Australian bull ant, *M. pyriformis*, climbs nearby trees to forage. Our results show that within their familiar habitat, foragers are guided by both the pattern of polarised skylight and the landmark panorama to determine their heading. A rotated polarising filter does influence the direction of travel of individual ants, but does so only partially. As well as using polarised skylight, *M. pyriformis* also attends to directional information provided by the landmark panorama. In particular, those landmark cues in front of foragers appeared to be important for the control of heading direction in this experiment. Foragers were less directed, took longer to travel and were unable to orient towards the trees when the landmark panorama in the direction of heading was obscured. However, views of the scene in directions other than in front of the foragers also influenced accuracy and speed, suggesting that the full panorama is used to

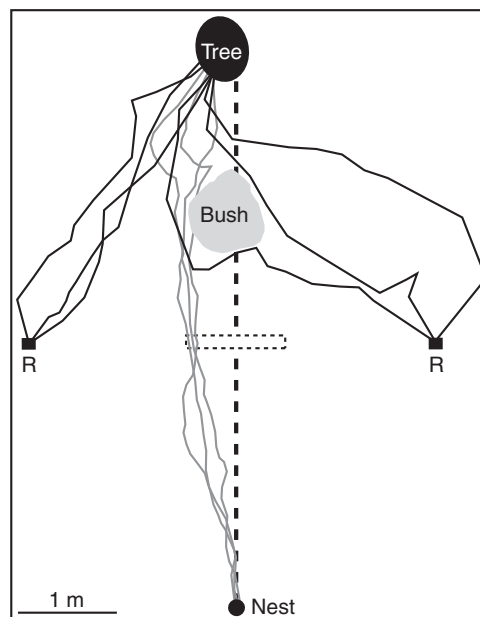


Fig. 4. Displacement experiment. Six ants were captured halfway between the nest and tree and within 50 cm of the nest-to-tree line (dashed rectangle). They were then displaced either 2 m to the left or 2 m to the right of the nest-to-tree line (R). Normal foraging paths are shown in grey, displaced paths are in black.

determine the direction of heading. Interestingly, the effect of screening parts of the landmark panorama differed at each nest site, particularly when placed in front of the nest, with a strong effect at Nest 1, an intermediate effect at Nest 2 and almost no effect at Nest 3. However, as shown by displacement experiments, foragers at Nest 3 do use landmark information for orientation. Why then does the effect of the screen differ so dramatically between nest sites?

The relationship between polarised skylight and the landmark panorama

Previous studies investigating the interaction between path integration (which relies on celestial compass information) and landmark guidance have shown that when travelling along a familiar route, landmark guidance dominates and often suppresses the output of the path integrator when there is a discrepancy between the two cues, during both inbound (Graham and Cheng, 2009a; Kohler and Wehner, 2005; Narendra, 2007a; Narendra, 2007b) and outbound (Merkle and Wehner, 2008) foraging excursions. However, all these studies have involved large-scale discrepancies between the two cues in question (but see Jander, 1957). Here we show, by manipulating the direction of polarised skylight perceived by an individual ant travelling along its habitual route, that both polarised skylight and the landmark panorama are used concurrently for orientation within the familiar foraging habitat. The resultant exit orientations from the polarising filter were a compromise between the information provided by polarised skylight and that provided by the landmark panorama, suggesting that both cues simultaneously affect the directional estimate of individual ants (Jander, 1957). In our particular experimental situation, the two compass cues were weighted equally.

At two of the nests, foragers were severely affected when the view in the foraging direction was blocked. It was not until the screen

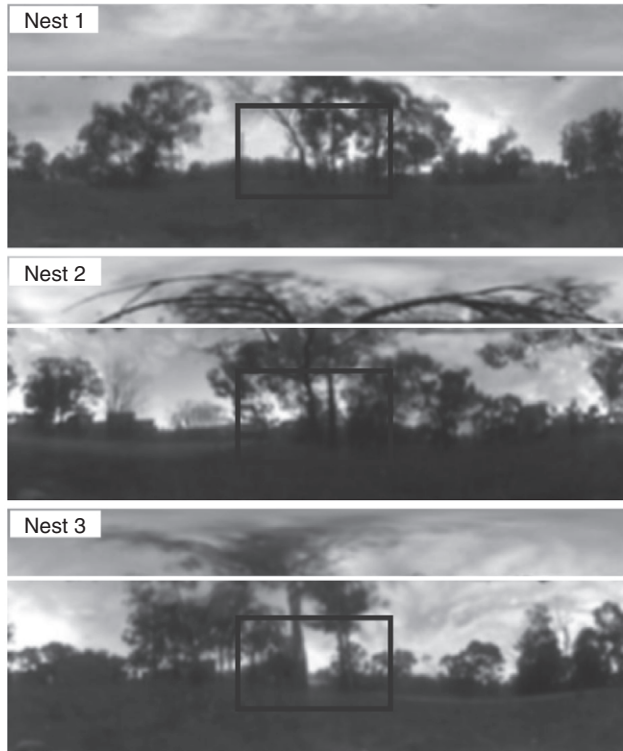


Fig. 5. View of the local environment. 360 deg panoramic images from the entrances of the three nests, together with the position of the screen (black rectangle) when blocking the view towards the main foraging direction.

was removed, and the visual scene returned to normal, that individuals were once more correctly oriented. This observation shows just how important visual landmark information is for *M. pyriformis*. It also highlights that the pattern of polarised skylight alone is unable to guide foragers past the obstruction. What use, then, is orientation to polarised skylight if it alone is unable to guide a forager towards its goal? An answer to this question may come from work on honey bees, which associate the landmark panorama with a given compass direction (Towne and Moscrip, 2008). This association would have a number of benefits for a forager. Both Fukushi and Wehner (Fukushi and Wehner, 2004) and Narendra (Narendra, 2007b) observed that foragers which were attempting to return to the nest after a displacement did so with less convoluted paths when they had full vector information (and thus an internal compass target). Collett et al. also argue that in ant species that path integrate in landmark-rich habitats, the path integrator may act as a contextual cue providing directional information to ensure foragers focus their attention on the relevant landmarks (Collett et al., 2007). This may also be the case in *M. pyriformis*. Because polarised skylight alone could not guide foragers to their goal, but did influence the direction of travel considerably, its use may be to ensure that individuals move in the right direction so that familiar landmarks can be recognised, thereby complementing the landmark guidance system. Individual foragers move along idiosyncratic routes that often do not lead directly to their foraging trees (S.F.R., unpublished data; see also Fig. 4). These routes are stable over days and indicate that landmarks do not simply serve as beacons to orient the animal in the correct direction, but also provide information on location along the paths.

What parts of the landmark panorama are used during navigation?

From our results it is clear that landmark guidance is the primary mechanism of navigation in *M. pyriformis* and that the landmark panorama in the direction of heading plays an important role. At the low light levels they operate in, *M. pyriformis* may be using the high contrast silhouette of objects cast against the relative brightness of the evening sky. The landmark panorama is known to be used by a number of diurnal ants (Jander, 1957; Fukushi, 2001; Fukushi and Wehner, 2004; Graham and Cheng, 2009a; Narendra, 2007b), and has been shown to provide directional information (Möller, 2002; Stürzl and Zeil, 2007; Zeil et al., 2003). This extends to the canopy pattern seen against the sky, which also provides high contrast compass information (Hölldobler and Taylor, 1983; Klotz and Reid, 1993; Taylor, 2007).

M. pyriformis foragers tend to head towards Eucalyptus trees that are closest to the nest and thus offering the largest and most salient landmark feature, perhaps explaining why the screen had such a strong effect when placed in front of foragers. In fact, a single feature rising above the horizon in the direction of travel can be sufficient to guide a foraging ant (Fourcassié, 1991; Fukushi, 2001), because it would be seen along the route with the frontal part of the retina (Judd and Collett, 1998; Nicholson et al., 1999). One way of using landmarks would thus be to fixate on those cues that are aligned with the direction of travel. However, our results do show that cues in other directions around the nest also play a part in navigation. When obscured, they reduced the accuracy and speed of travel, and even disrupted navigation completely for some foragers (see Fig. 2F). This indicates that the whole panorama contributes to the control of heading, and the fact that the screen in our experiment had an effect in only some directions must be a reflection of local differences in the amount of directional information the panorama provides.

The effect of the screen differed at each nest site, especially when in front of the nest. We attribute this to visual differences in the local environments. Fig. 5 shows 360 deg views from the nest entrances of the three nests, together with the position of the screen when in front of the main foraging direction (black rectangle). Although the three nests were within 35 m of one another (Fig. 1A), the visual appearance of the local environment, and the extent of visual information hidden by the screen, was quite different at each site (Fig. 5). In all cases, the screen obscured high contrast features in the direction of heading. However, the amount of ‘canopy’ features above the screen differed markedly between the three nests. At Nest 2 and 3, a large portion of canopy cues were still available, which could have provided directional guidance to the ants. In the case of Nest 3, in particular, a second close tree provided a prominent, large and salient directional cue.

Conclusion

To conclude, the night-active bull ant *M. pyriformis* uses both the pattern of polarised skylight and the landmark panorama, in concert, to control their heading direction. Landmark guidance appears to be the primary mechanism of navigation used by foragers, with those cues in the direction of heading having the greatest influence on navigation. However, other parts of the panorama also influenced foraging speed and accuracy, suggesting that they too play a role in navigation. Finally, there is also a possibility that subtle changes in the information content of a scene can have large effects on the use of navigational cues.

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