

Research article

Navigation using visual landmarks by the ant *Leptothorax albipennis*

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Summary. We examined visual navigation by *Leptothorax albipennis*, a small-eyed ant generally thought to orient principally with non-visual cues. We found that workers can use a prominent visual landmark for navigation between nest sites during colony emigration. When a landmark standing to one side of the ants' route was moved to the opposite side midway through an emigration, the ants' paths shifted toward the landmark's new position. The shift was apparent both at the point of departure from the old nest, and at the midpoint between nest sites. This result is consistent with the ants using the landmark as a beacon toward which they aim during the early stages of their journey. In contrast, no evidence was found for a simpler means of visual navigation in which the ants plot a course by consistently detouring to one side of a given landmark. When a landmark was shifted from one side to the centre of the ants' route, the ants did not adjust their paths to keep the landmark on the accustomed side.

Key words: Navigation, vision, ants, landmarks, beacons.

Introduction

The impressive navigational feats of social insects are often guided by visual cues (Wehner, 1992; Wehner et al., 1996; Collett and Zeil, 1998). Two general navigational strategies can incorporate visual information. The first is path integration, in which an exploring insect continuously tracks the distance and direction of its home, by integrating the distance it has travelled at each heading (Collett and Collett, 2000). The second is piloting with the aid of landmarks, in which the insect learns prominent visual features pinpointing the location of a familiar goal or delineating a frequently-travelled route (Collett, 1996; Collett and Zeil, 1997; Fukushi, 2001).

Extensive research has shown how highly visual species, such as the honey bee *Apis mellifera* and desert ants of the genus *Cataglyphis*, can use visual cues to return to their nests from forays of hundreds or even thousands of meters (Wehner et al., 1996). For ants of the genus *Leptothorax*, as indeed for most other ants, the role of vision in navigation is much less well understood. These small-eyed insects are generally thought to navigate chiefly via mechanosensory or chemical cues, including orientation pheromones produced by the ants themselves to mark a route or destination (Maschwitz et al., 1986; Hölldobler and Wilson, 1990). Although they clearly attend to visual cues (Aron et al., 1988; Pratt et al., 2001), the extent and manner of their use of vision for navigation is largely unknown.

In this paper, we examine how the ant *Leptothorax albipennis* uses visual landmarks for navigation during colony emigration. When a colony's nest is destroyed, forcing it to move to a new home, a subset of active ants making up approximately one-third of the colony's workers repeatedly travel between the old and new nests, retrieving nestmates and brood (Mallon et al., 2001; Pratt et al., 2002). To find their way between the nests, the active ants rely in part on odour cues (Pratt et al., 2001), perhaps from individual-specific trails known in this and other *Leptothorax* species (Maschwitz et al., 1986; Mallon and Franks, 2000). Previous work has shown, however, that visual cues can also play a role: when a prominent wall runs beside the emigration route, workers steer a parallel path by moving to keep the wall's retinal image at a constant position (Pratt et al., 2001).

How else might emigrating workers use landmarks for navigation? We consider two strategies previously demonstrated in other insects. The first consists of making biased detours around prominent landmarks. Foragers of the desert ant *Cataglyphis* use this simple strategy to fine-tune a route largely guided by path integration (Collett et al., 1992). The

forager learns the location of specific landmarks along the route, and chooses its path so that each landmark lies on the accustomed side. Thus, if a landmark is experimentally moved to the centre of the ant's path, she consistently detours to the landmark's left if she is used to seeing it on the right, and to the landmark's right if she is used to seeing it on the left.

The second strategy consists of plotting a course toward a prominent beacon. The beacon may mark the ant's ultimate destination, or it may lie along the route and thus guide only a portion of the path. For example, honey bee foragers sometimes approach a food source by first heading toward an intervening landmark, and then shifting course to head toward the food source itself (von Frisch, 1967; Chittka et al., 1995).

To determine whether *L. albipennis* uses either of these strategies, we induced ants to emigrate along routes passing to one side of a prominent landmark. Midway through the emigration, we shifted the position of the landmark, and then noted differences in the paths taken by the ants before and after the shift. We used this method to ask two questions: 1) Do ants detour in a preferred direction around the landmark when it is moved to the centre of their path? 2) Do ants shift their paths to follow the landmark if it is moved to the opposite side of their route?

Methods

Five colonies of *Leptothorax albipennis* were collected in February 2000 at Portland Bill in the United Kingdom (50°32'N, 2°27'W). Each colony had a single queen, 150 to 300 workers, and 100 to 200 brood items. Colonies were housed in artificial nests consisting of thin cardboard perimeters sandwiched between microscope slides (75 × 50 mm).

Emigrations were observed in a circular arena 1 m in diameter and 40 cm high, designed to present a minimum of visual cues. The arena walls were constructed of translucent white Plexiglas, and the base of transparent Plexiglas underlain with white poster board. The arena was centred immediately below a fluorescent ceiling lamp to eliminate light gradients to the left or right.

In each experiment, a colony in its old nest was placed on the arena floor and induced to emigrate by removing the nest's roof. An intact new nest was provided nearby, and made more attractive by moistening the cardboard and darkening the interior with a cover of red acetate film. Halfway between the nests, and displaced to the left or right of the shortest route connecting them, stood a cylindrical black plastic film canister 33 mm in diameter and 50 mm in height. Emigrations began once scouts discovered the new nest and recruited nestmates to it. In pilot runs, the initiation of recruitment was greatly retarded in comparison to previously observed emigrations in visually richer surroundings. To hasten the process, the new nest was at first placed only 4 cm from the old nest, where it was rapidly discovered. After two successful recruitments, the new nest was moved back a further 4 cm. After two more recruitments, it was shifted another 4 cm, and so on, until the distance between the nests had reached 30 cm. At each relocation of the new nest, we also moved the landmark, so that it constantly lay to the side of the ants' route, and equidistant from both nests. Accurate placement of landmark and nests was achieved with the help of a faint grid of 2-cm squares drawn on the poster board underlying the arena floor.

Immediately after the nests and landmark reached their final positions, we began to map the routes taken by emigrating ants. One ant at a time was observed and her path traced on a sheet of paper marked with a smaller-scale version of the grid squares on the arena floor. Paths were

traced only for ants carrying brood or nestmates from the old nest to the new. Unladen ants leaving either nest were not necessarily participating in the emigration; hence it could not be assumed that they were navigating from one nest to the other. Ants sometimes reversed direction and walked back toward the old nest. We ceased to track any ant that backtracked for more than three grid squares, to minimize time wasted following lost ants. During each emigration, we traced 25 complete journeys to the new nest, shifted the landmark, and then traced another 25 complete journeys.

Path locations were measured in two ways. First, we recorded the location at which each ant crossed the row of grid squares at the halfway point between the nests. Second, we recorded the region of the old nest at which each ant began her trip. Because the old nest's roof had been removed, ants were not restricted to leaving via the exit hole. Hence, for each ant we recorded whether she left through the centrally positioned hole, climbed over the left side of the perimeter, or climbed over the right side of the perimeter.

Because the ants may navigate in part through pheromone trails, we took steps to eliminate trails laid before the landmark was moved. At the start of the experiment, sheets of clear acetate film were placed on the floor of the arena, between the old nest and the final location of the new nest. When the landmark was shifted, the sheets were removed, so that trails laid in the first part of the emigration could not guide the ants along their old path, potentially overriding any effects of the changed visual scene. After removing the sheets, we waited until a transporting ant successfully travelled all the way from the old to the new nest before tracing any new paths. This typically occurred about 15 minutes after removal of the sheets.

Ants were not individually marked, because the large arena size left observers at too great a distance to detect marks on these small ants. Previous studies have shown that transporters make repeated journeys between the old and new nests, and usually continue working until the emigration is complete (Mallon et al., 2001; Pratt et al., 2002). Thus we can reasonably assume that the same population of ants was sampled before and after the landmark shift, although we cannot expect complete identity between the two samples.

Results

Experiment 1: Biased detours

To determine whether ants learn to make biased detours around a prominent landmark, each colony was induced to emigrate along a route running to the right of a single landmark (Fig. 1A). Midway through the emigration, we shifted the landmark to the centre of the route between the nests, forcing the ants to detour to its left or right. We then noted the side chosen by a sample of ants, to determine whether they showed a preference for the right side.

The results did not support the use of biased detours (Fig. 2). Before the landmark shift, ants in four of the five colonies passed significantly more often on the right side of the landmark than on the left. Once the landmark was moved to the centre, however, none of these four continued to show a significant rightward bias. Indeed, two colonies showed a significant leftward bias, and two others showed no preference for either side. Ants in the fifth colony (Colony 7) passed equally often to either side, even before the landmark was moved. After the shift, they showed a bias to the left.

A closer look at path location suggests that landmarks may nonetheless influence the ants' choice of route, by acting as beacons toward which workers bias their route. Figure 3

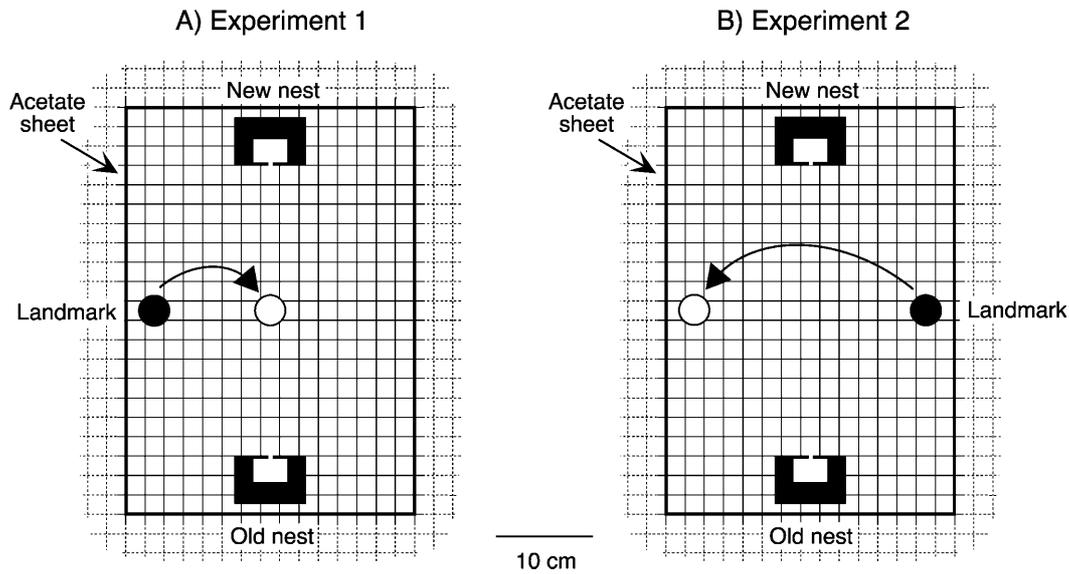


Figure 1. Arrangement of nests and landmarks for Experiments 1 and 2. Closed circles show the position of the landmark in the first part of each emigration. Open circles show the position to which the landmark was shifted midway through the emigration. The grid on the arena floor was used to track the position of the ants. Nests and landmarks rested on a sheet of clear acetate film

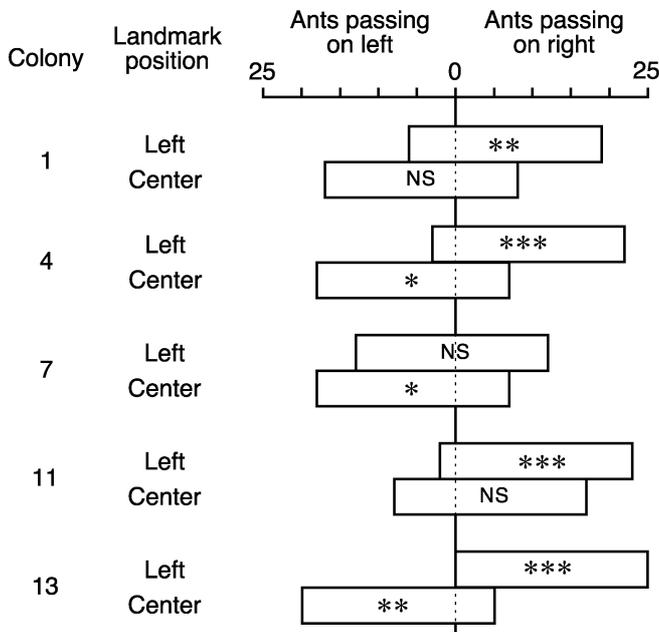


Figure 2. Results of Experiment 1, showing the number of paths in each colony passing to the left or right of the landmark, before and after it was shifted from the left side to the centre of the arena. G tests were used to detect significant departures from an equiprobable distribution between left and right sides (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, NS: not significant; $n = 25$ in each test)

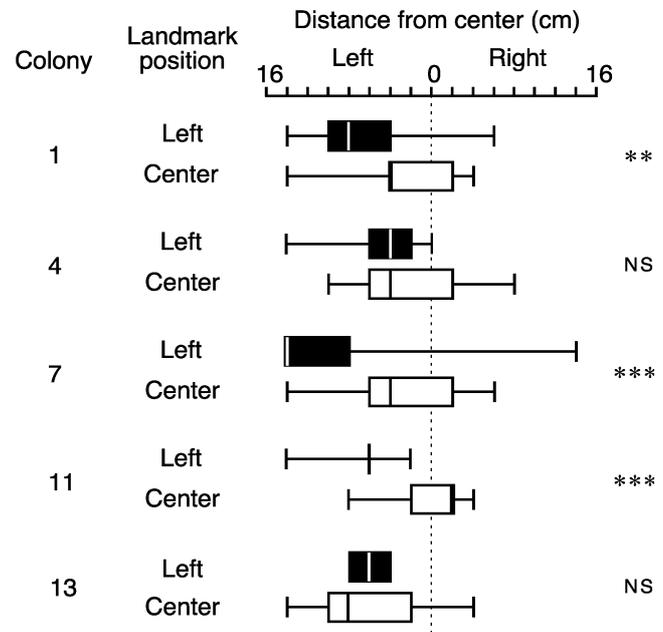


Figure 3. Results of Experiment 1, showing the positions at which paths crossed the row of grid squares halfway between the two nests. Data are given separately for each colony, before and after the landmark was shifted from the left side to the centre of the arena. Path positions were measured as the distance from the central column of grid squares in which the two nest entrances lay (see Fig. 1). In each plot, the box extends from the first to the third quartiles and is crossed by a vertical line at the median; brackets show the range of values. For each colony, the median positions before and after the landmark shift were compared by Wilcoxon's signed ranks test (**: $p < 0.01$, ***: $p < 0.001$, NS: not significant; $n = 25$ pairs in each test)

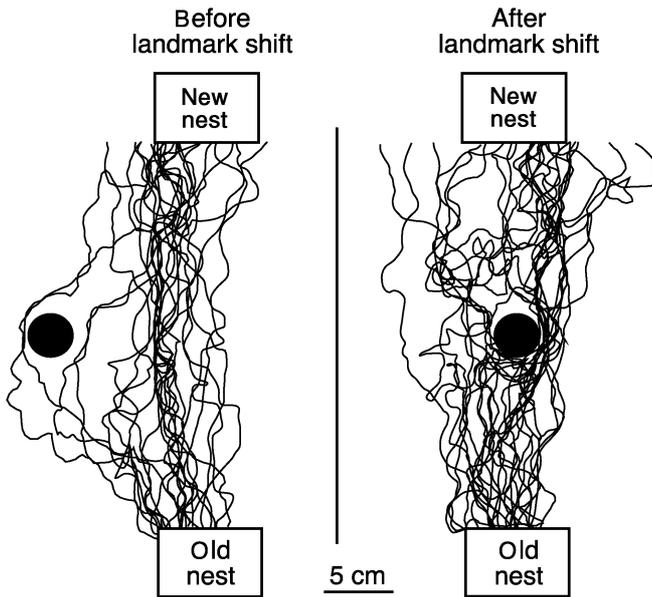


Figure 4. Results of Experiment 1, showing individual paths mapped before and after the landmark was shifted from the left side to the centre of the arena, during an emigration by Colony 11. The black circle shows the position of the landmark

shows the distribution of locations at which ants crossed the midline between the nests, before and after the landmark shift. When the landmark was on the left, all five colonies had median crossing points on the left side of the axis running between the old and new nests. After the landmark shift, three colonies showed a significant shift of the median crossing point toward the landmark's new location, and one other colony showed a non-significant shift in the same direction. Figure 4 shows the position of individual paths before and after the landmark shift, for a single emigration.

Before the landmark shift, a leftward bias was also evident in the points at which ants departed from the old nest, with 98 of 125 paths exiting on the left side. In contrast to the midline crossing points, departure locations showed no rightward shift after the landmark was moved (87 of 125 paths exited on the left side; G test of independence of exit point and landmark position: $G^2 = 5.0$, $df = 2$, $p = 0.08$).

Experiment 2: Aiming toward a beacon

The leftward bias evident in the first part of Experiment 1 suggests that ants treated the landmark as a beacon. Because the ants were always trained with the landmark on the left side, however, these results may instead reflect an unknown factor driving the ants toward the left. Hence, we performed another experiment in which the same colonies were trained with a landmark on the *right* side of the arena, and then subjected to a much larger shift in the landmark's position (Fig. 1B).

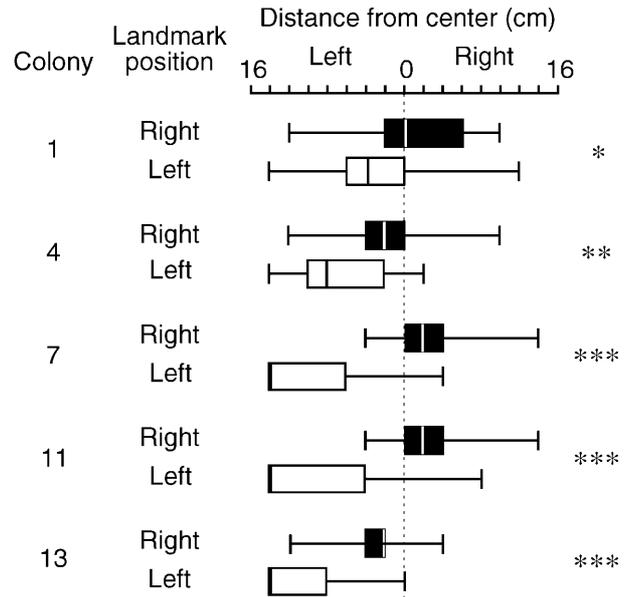


Figure 5. Results of Experiment 2, showing the positions at which paths crossed the row of grid squares halfway between the two nests. Data are given separately for each colony, before and after the landmark was shifted from the right side to the left side of the arena. See caption of Fig. 3 for further details

The results show that, when the landmark was on the right, ants crossed the midline with a consistent rightward bias, compared to their path locations in the first part of Experiment 1. Median path location differed by 8 ± 5 cm ($\bar{X} \pm SD$). In every colony, the path position was further to the right when the landmark was on the right (Fig. 5), than when the landmark was on the left (Fig. 3). This outcome differs significantly from a random distribution (Binomial test, 1-tailed: $n = 5$, $p < 0.05$). After the landmark was moved to the left side of the arena, the paths shifted leftward in all five colonies (Fig. 5), a significantly greater proportion than expected if the shift has no effect on path location (Binomial test, 1-tailed: $n = 5$, $p < 0.05$).

The path locations of individual ants varied widely (Fig. 6). Some ants aimed directly toward the landmark, closely approached it, and then changed their heading to the new nest. Others walked more or less directly toward the new nest throughout their journey, never coming near the landmark. Paths approaching within one grid square of the landmark were much more common after the landmark shift (81 of 125 paths) than before (12 of 125 paths) (G test of independence of closeness of approach and landmark position: $G^2 = 88.8$, $df = 1$, $p \ll 0.0001$).

Departure points also showed a significant dependence on landmark position. Only 36 out of 125 paths observed before the landmark shift departed from the left side of the nest. This increased to 78 paths out of 125 after the landmark was moved (G test of independence of exit point and landmark position: $G^2 = 31.5$, $df = 2$, $p \ll 0.0001$).

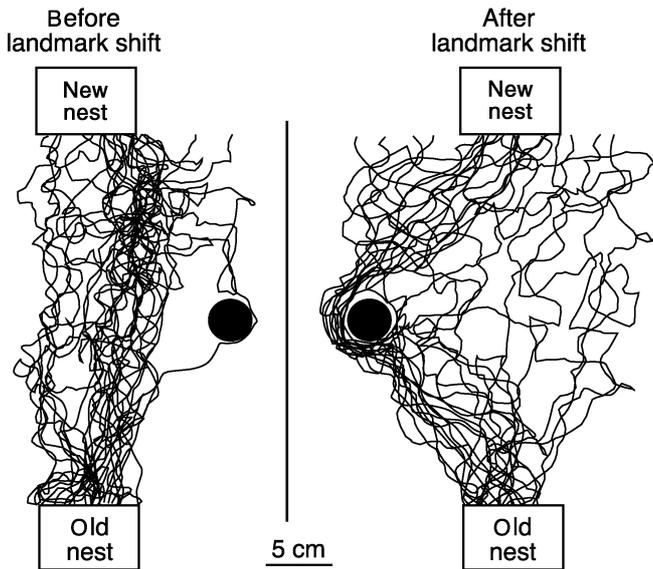


Figure 6. Results of Experiment 2, showing individual paths mapped before and after the landmark was shifted from the right side to the left side of the arena, during an emigration by Colony 11. The black circle shows the position of the landmark

Discussion

Our results show that emigrating workers of *Leptothorax albipennis* can make use of a prominent visual landmark when navigating between nests. We found that ants did not use the landmark in the simple way previously demonstrated for the desert ant *Cataglyphis* (Collett et al., 1992). That is, they did not adjust their course so that the landmark always lay on a particular side of the route. Instead, they treated the landmark as a beacon, veering toward it as they left the old nest and crossed the arena. As a result, their paths were consistently biased toward the side of the arena on which the landmark stood.

The influence of the landmark was most clearly seen in those ants that walked directly toward it, approaching within one grid square before heading toward the new nest (Figs. 4 and 6). The frequency of this behaviour increased significantly after the landmark was shifted in Experiment 2. At first, this increase appears to suggest that the landmark was not heeded by the ants during the first phase, but was only used afterwards, perhaps as a spontaneous response to the loss of substrate cues when the acetate carpet was removed. However, this is not consistent with the significant bias of paths toward the landmark even before it was shifted. In particular, paths were biased toward the landmark side in the first phases of both Experiments 1 and 2, when few ants directly approached the beacon. Indeed, when we re-analyzed the data for the first phase of each experiment, excluding all paths that approached within 1 grid square of the landmark, we still found a bias toward the landmark side in four cases, no difference in one case, and an average difference in median path location of 4 ± 3 cm ($\bar{X} \pm SD$). This suggests that even those ants whose paths did not aim directly at the beacon used it as a guide.

If ants use the landmark, even when they are not walking directly toward it, this suggests a relatively sophisticated visual navigational strategy. On such an oblique route, the ants must take into account changes in the appearance of the landmark as they move across the arena floor, and make continuous adjustments to their preferred orientation with respect to the landmark. Evidence for a similar strategy has been found in the wood ant *Formica rufa*, which appears to store a sequence of “snapshots” of a visual scene, so that it can adjust its path by moving so that its current view matches the appropriate memory from the sequence (Judd and Collett, 1998; Nicholson et al., 1999). It would be interesting to learn if *Leptothorax albipennis* uses a similar mechanism.

The landmark is unlikely to have been the only important navigational guide. In the first place, other visual cues may have been available, despite the arena’s relatively featureless appearance. Likewise, pheromonal cues were probably present, as indicated by the period of confusion that followed the removal of the acetate sheets carpeting the arena. For about 15 minutes, the ants wandered in winding paths over the arena floor and failed to reach the new nest. Similar confusion after an identical manipulation has been reported before in *L. albipennis* (Pratt et al., 2001), and is likely due to the loss of pheromonal cues deposited on the sheet by the ants themselves in the first part of the emigration. Indeed, the ants’ reliance on pheromones may account for part of the difference between their use of visual landmarks and that of *Cataglyphis*, which does not use pheromonal cues for navigation.

In addition to landmark guidance and pheromone cues, *Leptothorax* may also make use of path integration. It is not known if they can use celestial cues for compass information, and such cues were in any event not available in the lab. Some animals, however, can perform path integration using only internal proprioceptive and inertial cues (Seyfarth et al., 1982; Alyan and Jander, 1994; Mittelstaedt, 2000), and these ants conceivably have similar abilities.

The contribution of cues other than the experimental landmarks may account for the slight leftward tendency in the ants’ paths in Experiment 1, even after the landmark was shifted to the centre (Fig. 3). Such a tendency could be created by competing visual or other cues, and then reinforced by the laying of new orientation trails as the ants repeatedly travelled their new route. It is nonetheless clear that the landmark strongly influenced the route, and did so even more effectively in Experiment 2, when it was moved farther from its original position.

The abilities demonstrated here are accomplished with impressively small eyes, each one containing only about 60 ommatidia, compared to approximately 1000 and 6900 for *Cataglyphis* and *Apis mellifera*, respectively (Dade, 1977; Zollikofer et al., 1995). Because the spatial resolution of a compound eye is limited by the size and number of its ommatidia (Land, 1997), this implies low visual acuity in *Leptothorax*. That small numbers of ommatidia can guide complex visual navigation was already apparent from the ability of *Cataglyphis bicolor* to detect and navigate with polarization patterns in the sky, using only a 50-ommatidia region of

its eye (Wehner, 1982). The present results show that similarly minimal visual equipment can also guide navigation by landmarks, even in an ant thought to orient mostly with odour cues. Future work should focus both on further describing the visual abilities of these insects and on analyzing the interaction of visual and other cues.

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