Review

Traveling in clutter: Navigation in the Central Australian desert ant *Melophorus bagoti*

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A B S T R A C T

The Central Australian desert ant *Melophorus bagoti* is the most thermophilic ant on the continent. It comes out to forage during the hottest part of the day in the summer months. The ant shares a cluttered, plant-filled habitat with other arthropods and uses a range of navigational strategies. We review recent studies on this species concerning its use of habitual routes, distant landmarks, landmarks around the nest, and path integration, which is keeping track of the distance and direction traveled from one's starting point. Functional predictions concerning the acquisition, retention, and integration of memories of distances and of landmarks are also reviewed, illuminating the behavioral ecology of spatial cognition.

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1. Introduction

The Central Australian desert ant *Melophorus bagoti* (Fig. 1) is the most thermophilic (heat loving) ant on the Australian continent (Christian and Morton, 1992). Its common name is the red honey ant because of the presence of a worker caste called 'honeypots' that store liquid food in their gaster. The aboriginal people have given it a number of nicknames in the course of history, such as *ituny ituny* (which translates as "sun sun"; Conway, 1992). More recently, these ants have been called Furnace ants since they forage during the hot periods of the day (Andersen, 2002). The semi-arid habitat in which the ants typically live is cluttered with plants (Fig. 1), making available many landmarks usable for navigation. The physical habitat is shared with many other arthropods, but *M. bagoti* alone specializes in foraging in the heat of the day, when the ground temperature exceeds 50 °C. It thus carves out a temporal niche that few animals would utilize.

The study of *M. bagoti* is still in its infancy, earnest research on its navigation having begun after the turn of the 21st century. This contrasts with the large amount of published work on the neuroethology of visually guided behavior in the Saharan "racehorse ant" *Cataglyphis* (Wehner, 1994a), which in the last few decades has become a model system for the study of ant navigation in general (Wehner, 1982, 2003). *Cataglyphis* might well be the North African

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Fig. 1. The Central Australian desert ant *M. bagoti* (left) in its semi arid tussock-rich habitat (right). Photos by Ajay Narendra.

counterpart of the Australian *Melophorus*. In fact, Wehner (1987) has put forward the hypothesis that in each true desert of the world one genus of ant has filled the ecological niche of a "thermophilic scavenger": *Cataglyphis* in the North African and Asian deserts, *Ocymyrmex* in the deserts of southern Africa, *Melophorus* in Australia, and *Dorymyrmex* in the South American Atacama. While the ecological role of the latter genus has still to be established, enough evidence has now accumulated for the parallel-evolution scenario to hold true for the three genera *Cataglyphis* (Wehner et al., 1992), *Ocymyrmex* (Marsh, 1985; Wehner, 1987; R. Wehner, S. Wehner, D. Weibel, N. Blaser, A. Furrer, work in progress) and *Melophorus* (Christian and Morton, 1992; Wehner et al., 2003). These genera constitute a group of ecologically equivalent taxa, each characterizing a particular desert area of our planet. Hence they provide us with a unique opportunity to compare their systems of navigation. Similar among the studied species of the three genera are the facts that all ants forage solitarily during the hotter part of the day, that they search for spatially unpredictable food items, and that they employ visual (celestial and earth-bound) information during foraging trips. These three genera are ecologically equivalent taxa that face similar foraging challenges, with individually foraging ants relying little or not at all on pheromones having to locate food sources whose distribution is unpredictable. They comprise a unique system in which the relative importance of different navigational strategies can be tested. Furthermore, the visual complexity of the different deserts differs from being featureless to landmark-rich, making it interesting to compare navigational techniques used in different habitats.

In this review we draw together a number of published findings on navigation in *M. bagoti*. The ant's primary means of navigation is to follow set routes through its plant-filled habitat. When homing in the absence of familiar route cues, *M. bagoti* uses distant landmarks to locate the nest. Once it is close to the nest, however, it uses visual landmarks associated with the nest for pinpointing the tiny entrance to the nest. The ant also path integrates, i.e., keeps track of the straight-line distance and direction from the start of the journey. When confronted with unfamiliar contexts, it uses path integration. We review here differences in the functioning of the path integrator between the Australian and the North African desert ants. Finally, the ant's ability to acquire, retain and integrate memories of distance and visual information will be discussed, illuminating the behavioral ecology of cognition.

2. Route following

If a feeder is set at a constant location with respect to a nest, ants foraging in its general direction (sector) may well find the feeder. Once the ant finds food, typically a crumb of cookie, the forager becomes motivated to run home, and will chart its way back. Foragers may travel back and forth between the nest and

feeder numerous times. When they do so, they tend to follow similar routes each time (Fig. 2; Kohler and Wehner, 2005; Muser et al., 2005). Outbound routes are often different from homebound routes (see Fig. 7B in Wehner, 2003). Barriers may be set up to induce the ants to travel different routes outbound and homebound (Wehner et al., 2006). If a homebound ant that has almost reached home is displaced back to somewhere on its homebound route, it recognizes where it is and homes readily (Kohler and Wehner, 2005). Furthermore, Wehner et al. (2006) have shown that if a homebound ant is displaced somewhere on its outbound route, it fails to recognize the route home, even if it has traveled the same outbound route many times. They conclude that ants use familiar landmarks as one-way signposts rather than link them to one another to form some sort of a cognitive map (for signpost memories versus cognitive maps, see also Collett and Collett, 2002).
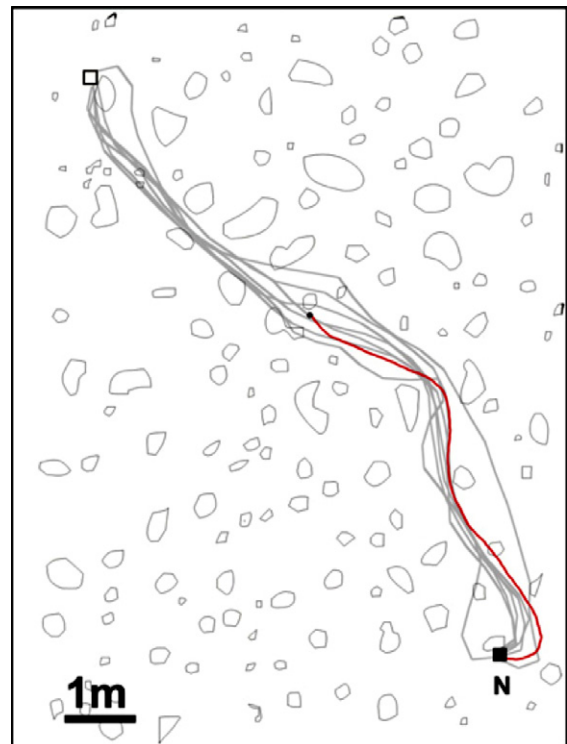

Fig. 2. Stereotypical routes home. The gray lines show the homebound paths of one *M. bagoti* ant traveling between a provisioned feeder and its nest. The red line shows its path home when it was displaced to approximately the middle of its route after it had almost completed its homebound journey. The unfilled polygons show the locations of tussocks. Reproduced from Kohler and Wehner, (2005) Fig. 6, Copyright (2005), with permission from Elsevier.

M. bagoti can also learn multiple routes (Sommer et al., 2008). Ants that arrived at a feeder were forced to travel through a channel, thus making a detour before heading their way home. After learning one such detour route, they were then trained to take one or two different detours in succession. Tests revealed that the ants retained memories of all the routes that they had learned.

Ants can also be trained to forage through a corridor of experimentally provided landmarks along a straight route. This manipulation results in trained ants traveling very straight paths home (Narendra, 2007b). After sufficient training (~300 runs), it turns out that the landmarks en route are not necessary. Even if they are removed, trained ants still home readily. But their paths are less straight. The landmarks thus help the ants to travel home more efficiently.

The route-following behavior of *M. bagoti* is what one might expect of an ant living in a cluttered habitat with many landmarks along routes, both distant and near. Many questions remain about route following. To use the landmarks en route appropriately, they must be identified. How is this done, when many tussocks are small and similar looking, especially to an animal whose visual system is not particularly acute? Other cues such as familiar context and the distance traveled probably influence how a landmark is identified. Evidence for the importance of familiar context in these ants came from the same study in which ants were trained to a feeder in a well-defined corridor of landmarks (Narendra, 2007b). Trained ants in the presence of these route-marks reached the nest successfully in the familiar training field. When the familiar landmark corridor was provided for the ants in an unfamiliar context, however, they traveled only on average half the distance toward the nest before beginning to search. Thus familiar visual cues presented in an unfamiliar context were not sufficient to lead the ants toward the (fictive) nest. Landmarks may also be identified by the distance traveled since the start of the journey, derived from path integration. But the information gained from path integration is not necessary for identifying a route. This is demonstrated by the success of displaced ants who have run most the way home and then are placed at an arbitrary point along the route (Kohler and Wehner, 2005). The use of distant landmarks to give a 'ball park' estimate of one's location might well help distinguish which landmark is which. Whether and how distant landmarks are linked to nearby landmarks remains to be investigated.

3. Distant landmarks

Evidence at hand suggests strongly that distant landmarks are used for homing, although we know little of what the information consists of. Evidence came from the already described study in which ants were trained to use a corridor of landmarks placed between their nest and a feeder 20 m away (Narendra, 2007b). Another set of manipulations displaced ants sideways from the feeder (Fig. 3). With small displacements of 1.5 or 3 m, the displaced foragers generally found their way back to the corridor of landmarks, and then headed down the corridor home. Indeed, with small displacements away from their habitual routes, Kohler and Wehner (2005) also found that the ants tended to find their route again and then follow it home. With a larger displacement of 10 m sideways, however, the ants generally did not find the route (Narendra, 2007b; Fig. 3). Their initial orientation, measured at half a meter distance from the release point, was toward the nest. Thereafter, they headed in a direction intermediate between the nest direction and the direction parallel to the corridor. This latter direction would be the compass direction home had the ants not been displaced. The direction of travel thus seemed to be a compromise between the dictates of the sky compass and the dictates of some distant landmarks surrounding the nest. After about half the distance home on average, the ants engaged in some systematic searching, turning in loops. Although some ants then found the landmark corridor and headed home by their usual route, many ants came out of the search loops and headed toward the nest, providing further evidence for the use of distant landmarks.

The use of distant landmarks has been found in wood ants as well (Fukushi, 2001; Fukushi and Wehner, 2004). Fukushi and Wehner (2004) found the homing paths of wood ants displaced by different amounts converging toward a distant location. But it is not clear what distant cues are being used. Future research needs to address what cues in the panorama are used. Are the cues truly panoramic, or are landmarks in certain directions, perhaps those straight behind the nest from the viewpoint of the feeder, most important? Are all elevations of visual information equally important? Both displacement experiments in natural terrain and experiments providing artificial landmarks can be revealing.

4. Landmarks around the nest

Landmarks around a target location are used by many animals in pinpointing a goal; well studied systems include rats (Cheng, 1986; Suzuki et al., 1980; review: Cheng and Newcombe, 2005), pigeons (Cheng, 1988, 1989; Spetch and Edwards, 1988; review: Cheng et al., 2006b), ants (Nicholson et al., 1999; Wehner et al., 1996; Wehner and Räber, 1979), wasps (Zeil et al., 1996), and honeybees (Cartwright and Collett, 1982, 1983; reviews: Cheng, 2000, 2006; Collett and Collett, 2002; Collett and Zeil, 1998). A basic strategy to demonstrate landmark-based searching is to train an animal to find a goal surrounded by landmarks, and then displace the landmarks on a test. The use of landmarks is demonstrated if the test animal searches at the target location suggested by the landmarks (Tinbergen, 1932). An early study on *C. fortis* has shown that they use prominent visual features to pinpoint a goal (Wehner and Räber, 1979; see also Wehner et al., 1996). Ants were trained to return from the feeder to the nest. The location of the nest was enhanced by placing either two or three black cylinders around the nest. A trained ant on its homebound journey that had almost reached the nest was captured and transferred to a distant test field on which the same landmark set-up was provided. The reason for using these zero-vector ants was to remove path integration as a possible competing navigational mechanism. When the path integrated vector reads zero, then path integration no longer provides useful information for navigation, and the ant must rely on searching behavior. The ants searched at the expected location according to the landmarks, with peak density of search in the center of the landmark array. If in the test situation the landmarks appeared at double the training distance, however, the search peak in the center of the landmark array broke down. But it reappeared when the landmarks placed at twice the training distance were twice the training size, so that the retinal image was the same as in the training situation.

The same strategy was used recently to examine the use of landmarks by *M. bagoti* (Narendra et al., 2007b). Four cylinders were placed around the nest, and the ants were trained to run between a feeder and home repeatedly. Transformation tests were given to the ants to examine how the experimental landmarks were encoded. Well-trained ants were tested, as zero-vector ants, on a distant test field as usual, with different arrays of landmarks set up (Fig. 4). The control test replicated the landmark set-up used in training, and showed again that the ants searched mostly at the center where the nest would be expected (the fictive nest location). One transformation matched the visual appearance of the landmark array from the viewpoint of the fictive nest, while doubling the landmark-
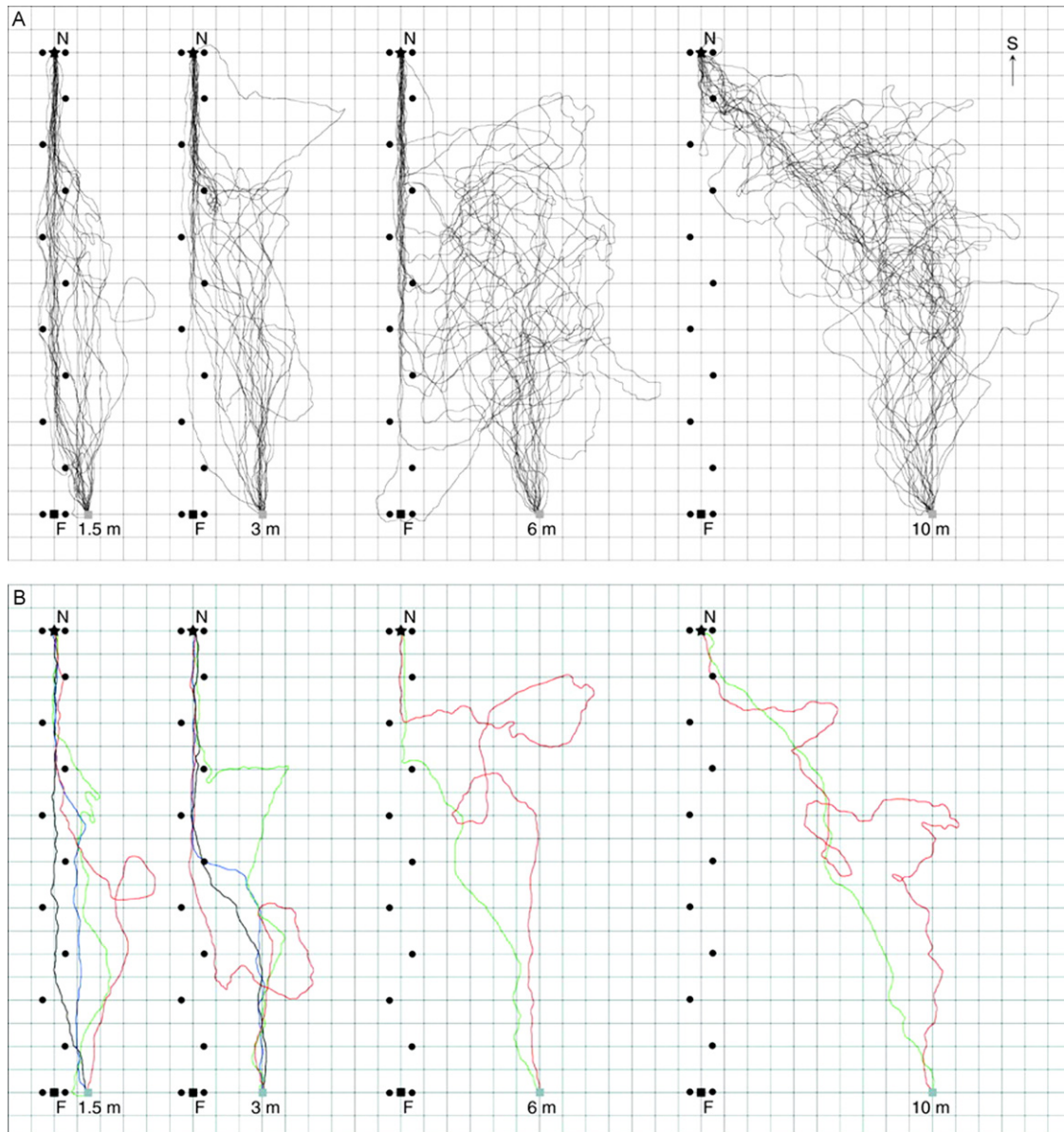
Fig. 3. Trajectories of homing ants following a sideways displacement. Ants were trained to travel through a corridor of landmarks (black cylinders shown as black circles) between their nest N and a feeder F. Well trained ants were displaced from the feeder sideways 1.5 m ($N = 21$), 3 m ($N = 20$), 6 m ($N = 18$) and 10 m ($N = 21$). (A) shows all trajectories of ants displaced sideways. (B) shows example paths of ants that had zero turns (black), one turn (blue), no loops (green) and $\geq$ one loop (red). Grid size is 1 m². With 10 m displacements, many ants headed in the direction of the nest after traveling some distance parallel to the landmark corridor. Reproduced with permission of the Company of Biologists from Narendra (2007b, Fig. 3).

landmark distances (as previously done in *Cataglyphis*, see above). This was accomplished by doubling the heights and widths of the landmarks in addition to doubling the inter-landmark distances. On this test, the ants also searched at a high density around the fictive nest. Performance did not differ significantly from the control condition. In a third test, inter-landmark distances were doubled, but the size of the landmarks did not change and remained the same as that used during training. At the fictive nest then, the array looked too small. The ants failed to search much around the fictive nest on this test. They tended to approach a landmark (something that they did on the other tests as well), and then travel the training landmark-nest distance toward the diagonally opposite landmark. After that distance was traversed, the ant searched briefly, but then gave up, since the match with the expected view was too poor. Some ants eventually tried to home in again, either approaching from the same landmark or from a different landmark.

Matching thus seems to be 'snapshot' like. But the snapshot differs from those used by honeybees (Cartwright and Collett, 1982, 1983). The bees would accept a match in the expanded array even if the landmark sizes were not expanded, with the landmarks identical to those used in training. Thus, as long as landmarks were found in the right directions from the fictive goal, the bees were satisfied. *M. bagoti* would not accept the mismatch in landmark sizes even if the landmarks were at the correct directions from the fictive goal. *M. bagoti*'s landmark matching strategy resembles to some extent that used by wood ants (*Formica rufa*; Nicholson et al., 1999), which also show a tendency to approach salient landmarks (Graham et al., 2003). Wood ants too would not accept a mismatch in landmark sizes. But the subsidiary processes differ. Wood ants would typically move toward a single landmark until its size matched to that encountered during training. And then they move so as to match the other landmarks. Unfortunately, in
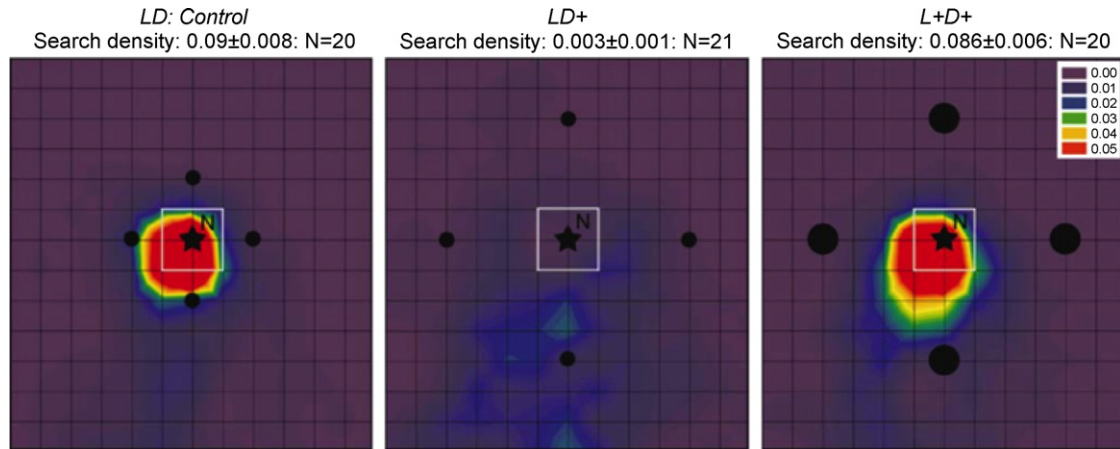
Fig. 4. Search density profiles of trained ants tested with different landmark configurations. The training configuration was replicated in the control test. In LD+, inter-landmark distances were doubled, but the landmarks were the same size as in training. In L+D+, inter-landmark distances were doubled, as were the height and diameter of the landmarks. The fictive nest position N is at the center of the four cylinders (filled circles). Release point is 2 m away from the fictive nest and not shown here. Search patterns were superimposed on a common starting point, although the ants started at different locations in physical space. An area of 0.5 m × 0.5 m (white square) around the nest denotes the area where search density (means ± S.E.M.) was measured. Grid size is 0.25 m × 0.25 m. Reproduced from Narendra et al. (2007b) Fig. 4, Copyright 2007, with kind permission of Springer Science+Business Media.

the expanded array, the match would never be good; when one landmark is the right size, the visual sizes of the others would be wrong, as would the directions of two of the other landmarks. *M. bagoti* tends to start from a landmark, and travel a vector from the landmark to search for a match. On failing to find a good match, it gives up, sometimes to try again from another landmark. This is also what *Cataglyphis* has been demonstrated to do (Möller, 2001).

5. Path integration

Path integration is a useful, indeed sometimes essential navigational strategy when cues to one's position from landmarks are missing or imprecise. For some *Cataglyphis* ants that inhabit landmark-sparse environments such as the open salt pans or the Saharan Desert, path integration is the dominant and often crucial navigational tool (Wehner, 2003). To path integrate, an animal needs to keep track of the straight-line distance and direction home as it meanders on its foraging journey. The directional estimates are derived from a celestial compass encoding the direction of the sun or especially the pattern of polarized light in the sky (Rossel and Wehner, 1986; Wehner, 1994b; Wehner and Müller, 2006), and the distance estimates are derived by some form of step counting (Wittlinger et al., 2006, 2007). This amounts to calculating a vector home as one travels (Hartmann and Wehner, 1995; Müller and Wehner, 1988). When the time comes to head home, the vector is 'run off' to chart a more or less straight line home. Given the inevitable inaccuracies in the vector calculations (Cheung et al., 2007), the vector points to somewhere in the vicinity of the nest, but usually not to the nest itself. Path integration is thus accompanied by a systematic search after the vector is run off (Wehner and Srinivasan, 1981; Wehner and Wehner, 1986; Müller and Wehner, 1994). The mechanisms of path integration in insects have been thoroughly reviewed (Collett and Collett, 2000; Wehner, 1992; Wehner and Srinivasan, 2003), and will not be detailed again here.

Evidence for path integration comes from experiments in which animals at a feeder are displaced to a distant test field where all familiar landmarks are absent. If the homing animal still runs in the compass direction from feeder to home, then path integration

is implicated. In *M. bagoti*, two separate studies have done this, and found that homebound directions are concentrated around the feeder-to-home direction (Narendra, 2007a; Wehner et al., 2006). In Narendra's (2007a) study, an additional interesting finding was that ants that traveled longer outbound distances were more accurate in determining their compass direction, showing less scatter as a group. The reasons for this are unclear. The stereotypical routes that the ants follow, on outbound as well as homebound trips (Kohler and Wehner, 2005) might provide a clue. It is possible (but not demonstrated as yet) that information along the route becomes associated with compass direction. Perhaps a longer outbound trip along a familiar route benefits directional estimation in that a longer trip has more route information available for associating with compass direction. Interestingly, recent analogous evidence on honeybees shows that they report the direction to a food source more accurately in their waggle dances with increasing nest-to-feeder distance (Gardner et al., 2008).

In an open salt-pan habitat, *Cataglyphis fortis* ants path integrate approximately the full outbound distance before making a sharp turn and beginning a systematic search for the nest (Merkle et al., 2006; Wehner and Srinivasan, 1981). Merkle et al. trained ants to feeders at 5, 10, and 20 m distances from the nest. Trained ants were displaced to a distant test field from the feeder and allowed to run with some food. The endpoints of the run home were unsystematically scattered around the fictive nest location (see their Fig. 2). In the only study that measured the distance path integrated by *M. bagoti*, ants that were displaced to a distant test field ran on average about 44% of the outbound distance, much shorter than the estimated feeder-to-home distance, before engaging in systematic search (Narendra, 2007a). Different outbound distances from 6 to 35 m were tested, and the average proportion of distance path integrated was very similar at all distances (Fig. 5). This underrunning was not due to an underestimation. In an artificial set-up in which outbound and homebound cues were made similar, the ants ran approximately 100% of the outbound distance before searching. In this artificial set-up, ants were forced to travel down narrow white channels, 10 cm wide and 10 cm high, outbound and homebound. The cues were thus similar on the outbound and homebound journeys. Most likely, ants in an unfamiliar habitat run only a part of the estimated distance home, and then search for cues to their familiar homebound route. This again conforms with earlier findings in *Cataglyphis bicolor* (e.g., Burkhalter, 1972).
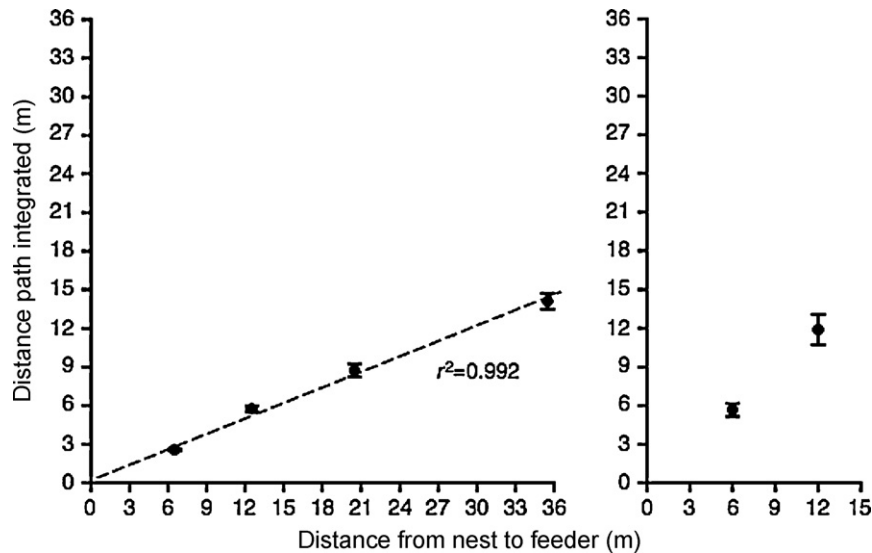
Fig. 5. Context specific path integration in desert ants. (A) Distance path-integrated (means ± S.E.M.) by ants at nest-feeder distances of 6 m (*N* = 128), 12 m (*N* = 80), 20 m (*N* = 40) and 35 m (*N* = 40) after being displaced to unfamiliar territory in the open field. The ants ran on average about 44% of the outbound distance before starting to search. (B) Distance traveled by ants in channels (means ± S.E.M.) with an outbound distance of 6 m (*N* = 24) and 12 m (*N* = 24). Homebound and outbound environments were very similar in the channels. The ants ran on average about 97% of the outbound distance before starting to search. Reproduced with permission of the Company of Biologists from Narendra (2007a, Fig. 2).

6. Behavioral ecology of spatial cognition

The channel set-up is convenient for studying odometry, or the estimate of distance traveled. The set-up controls surrounding cues, and facilitates the measurement of distances. A long channel can be used to test the ants, and a tape measure is used to observe the turning points as the ants turn back and forth in search of the nest in the essentially one-dimensional channel. Functional predictions about performance on odometry can be tested using the set-up. These are interesting because they are quite different from intuitive expectations of learning and memory.

An intuitive expectation is that memory accumulates gradually with experience; it would take a number of trials to learn. Path integration, on the other hand, needs to function well the first time and every time. Failure of path integration on the first trip would typically mean not getting home and thus not surviving. We would thus expect the performance of odometry not to improve much with repeated training. And indeed, *M. bagoti* ants that have run six trips home at the same distance do not estimate the outbound distance any better than ants with one trip home, as measured by the scatter (variance) found in a group of ants with the same training conditions (Narendra et al., 2007a).

This group measure of scatter is quite sensitive, as another prediction shows. The odometric distance need not be remembered for long. A trip is usually over within an hour. Odometric memory is certainly unlikely to be needed the next day. We can predict a significant decay of odometric memory in 24 h, as measured by a significantly larger variance in a group of ants delayed for 24 h, compared with immediately tested ants. And empirical evidence confirms the prediction (Narendra et al., 2007a; see also Ziegler and Wehner, 1997, for *C. fortis*).

A third prediction concerns integration of experiences, or actually the lack thereof. An intuitive expectation about memory is that an animal should integrate over multiple experiences to form a memory. After a memory is formed, it should take several trials of a new experience to alter the memory. Old memories should interfere with new learning, the well known phenomenon of proactive interference. The function of path integration, on the other hand, is to calculate the distance and direction traveled on the current trip.

Earlier trips should be made irrelevant, 'wiped clean' from the brain. One would expect no integration of earlier experiences, unlike a 'traditional' memory. This can be tested by training ants to travel repeatedly (5 trials) to one distance (e.g., 6 m) to the feeder, and then testing them on a critical trial after they have traveled a different distance to the feeder (e.g., 12 m). In the example, one would expect the repetitive training of 5 previous 6 m trips not to figure in the odometry at all on the current trip. The distance estimated should not differ from those of ants that have traveled 12 m outbound on their only trip to the feeder (i.e., without previous trips at a different outbound distance). And empirical evidence confirms this prediction (Narendra et al., 2007a).

This suite of memory properties is perhaps unusual, but the confirmation of these properties shows the powers of functional predictions. The 'specs' for different memory systems might well have evolved to be tuned to their functions. Our predictions are made for the system of path integration in general, not that of *M. bagoti* in particular, and other path-integrating insects might be expected to show these properties as well. Similar experiments on the North African ant *C. fortis* confirm the same suite of predictions (Cheng et al., 2006a).

The behavioral ecology of memories for landmarks around the nest, concerning acquisition and retention, have also been examined (Narendra et al., 2007b). Functional predictions concerning landmark learning are quite different from those concerning odometry. Learning would not be one-trial, or based solely on the last encounter with the landmarks. Landmark learning is prone to errors, and we would expect a more gradual learning process, certainly not one-trial learning. For a short-lived animal, however, we would expect quite quick learning, within a few trials. Retention, on the other hand, should be long, for the lifetime of the animal. For a short-lived animal, landmarks are highly probable to be stable for its lifetime, and landmarks around the nest can be used for homing time and again. Once learned, it makes functional sense to hold on to the memory.

The findings support the predictions a good deal, but not completely (Narendra et al., 2007b). Acquisition was indeed not one-trial. After two trials of training (two trips homebound to the nest), there was little sign of learning, as measured by significant

amounts of searching at the test field around the fictive nest. It took 15 trials of training to see significant improvements above this control level. To complicate matters, ants learned best when the training was spread over two or more days, and the test was on the third day or later. This last finding needs further investigation as days of training was not a controlled variable.

In accounting for these acquisition data, it should be kept in mind that tests were done in a distant test field, with the landmarks around the nest set up. This field would be missing other landmarks surrounding the nest that the ants might be sensitive to, including distant landmarks. These contextual cues have been shown to be important in insect navigation (Cheng, 2006; Collett and Collett, 2002; Collett et al., 2003). What Narendra et al. were testing was the use of the experimental landmarks in isolation. In addition, the ants could be using naturally occurring landmarks before the experimental landmarks were introduced, and these landmarks might block the learning of the 'new' experimental landmarks. That is, if prior natural landmarks were used before training began, then the experimental landmarks were redundant additional cues. In conditioning, such cues may well be blocked (classical conditioning in rats: Kamin, 1969; landmark-based search in honeybees: Cheng and Spetch, 2001). Whatever the explanation for the slow learning, it was well confirmed that learning took more than one trial, in contrast to odometric estimates.

The prediction concerning retention was confirmed. After two days of training, the ants could remember the landmarks around the nest even after 8 days of delay. The ants still searched extensively where the nest should have been. Furthermore, memories for natural landmark-based routes persisted for at least 5 days of delay with visual deprivation (Sommer et al., 2008). Natural foraging half-life has been estimated at around 4 days (Muser et al., 2005). The landmark memories probably last a lifetime once learned, as they do in *C. fortis* (Ziegler and Wehner, 1997).

7. Concluding remarks

The recent studies of navigation in the Central Australian desert ant have revealed a suite of strategies that is used by many insects. Like many insects, *M. bagoti* uses path integration, and landmarks around the goal and along the route. All these strategies have been much studied. Other strategies used by *M. bagoti* have been less studied. Chief among these is the use of distant landmarks, implicated in wood ants as well (Fukushi, 2001; Fukushi and Wehner, 2004). What an ant uses by way of distant landmarks remains to be investigated. This topic is likely to lead to interesting comparisons with other animals. After all, the cluttered semi-arid environment inhabited by *M. bagoti* is more akin to the habitats of intermediate levels of 'clutter' in which many animals dwell. This includes constructed and more natural human habitats. *M. bagoti* provides an excellent model for this topic. It has strong motivation to home repeatedly when carrying proffered food, making it a co-operative subject. It lives in varied environments, making it possible to study the effects of natural variation in habitat. And it travels over a manageably small scale; 6 m, for example, is a realistic foraging distance (Muser et al., 2005). At that scale, it is possible to construct artificial panoramas in which to let the ants forage. Given the usefulness of biomimetic adaptations in robotics (Franz and Mallot, 2000; Webb, 2000), this study is sure to benefit the engineering of robots that can navigate outdoors in human-constructed environments (see, e.g., the robot Sahabot 2, which mimicked the landmark navigation behavior of *Cataglyphis*; Lambrinos et al., 2000).

Some interesting twists have also been found in path integration. In unfamiliar surrounds, *M. bagoti* does not run off the entire estimated outbound distance in path integration, but only part of

the way (for *Cataglyphis bicolor*, see Burkhalter, 1972). Is this an innate propensity, a species-specific difference from, e.g., *C. fortis*, which lives in an open salt-pan habitat, or does it come from acquired experience in navigating cluttered habitats? Studying the occasional *M. bagoti* nest in sparse and open environments can prove revealing in this regard.

More generally, the study of navigation in this species can combine functional and mechanistic questions in a program of field experimentation. Such a program of research can study the animal in its natural habitats, and over scales of travel that it naturally engages in. Comparative cognition may benefit from more of this naturalistic and integrative approach, an approach espoused by the scientist to whom this issue is dedicated (Shettleworth, 1998).

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