How flexible is the systematic search behaviour of desert ants?

Tobias Merkle [a],[*], Rüdiger Wehner [b],[1]

[a] *Theoretical Biology, IZMB, University of Bonn, Germany*
[b] *Institute of Zoology and Brain Research Institute, University of Zürich, Switzerland*

ARTICLE INFO

Foraging desert ants, *Cataglyphis fortis*, rely on path integration for navigation. If the path integrator has not led them to the exact position of the point of departure, the nest entrance, they start a systematic search for the nest. Previous studies have shown that the longer the preceding outbound run has been the less confidence an ant has in its path integrator. This lower confidence is expressed by wider search loops. In this study, we investigated whether additional cues influence the systematic search patterns of desert ants. We captured ants that were trained to a feeder, either at different points during their inbound journeys or when they were about to enter the nest. They were then transferred to an unfamiliar test area, within which their paths were recorded. Most of the ants captured along their inbound path reeled off the remaining part of their runs and then commenced their nest search, whereas those captured at the nest entrance started searching for the nest entrance immediately. The latter group of ants had far narrower search patterns than ants that were captured during their inbound runs, irrespective of search path length (20, 40 or 50 m). This indicates that the ants' systematic search behaviour is more flexible than assumed hitherto. We compare the results with two previous studies and discuss different potential cues that ants could use to adapt their search patterns.
© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Foraging desert ants, *Cataglyphis fortis*, do not make use of chemical trails to return to their nest after foraging. Instead, they use a strategy called path integration, that is, they sum the directions steered and the distances covered during all their movements (reviewed in Wehner 2003; Wehner & Srinivasan 2003; Merkle et al. 2006b). This process provides them with a home vector which leads back to the nest on a fairly straight path, thereby minimizing the danger of falling prey to heat, desiccation, spiders or robber flies (Harkness & Wehner 1977; Schmid-Hempel & Schmid-Hempel 1984). In addition, the ants use landmark information, when available, to readjust their bearings (e.g. Wehner & Räber 1979; Collett et al. 1998; Wehner 2003). However, since the natural habitat of *C. fortis* rarely provides them with conspicuous landmark information, in most cases they rely exclusively upon the information provided by their path integrator.

Since the path integrator is error prone (Wehner & Wehner 1986; Müller & Wehner 1988; Merkle et al. 2006a; Merkle & Wehner, 2009), an ant, having reeled off its home vector, does not necessarily arrive precisely at the nest entrance. If it cannot detect the nest entrance at the position where it should be according to the path integrator, it begins to search for the nest in a systematic way. Several studies have examined and described the systematic search behaviour of *Cataglyphis* (Wehner & Srinivasan 1981; Wehner & Wehner 1986; Müller & Wehner 1994). These studies showed that the ants perform loops whose size increases with increasing duration of the search. At regular intervals, they return to the spot where they commenced the systematic search pattern, that is, the location at which the nest is supposed to be according to the path integrator. The systematic search patterns can be described as a Gaussian probability density function (Wehner & Srinivasan 1981): the higher the probability of finding the nest at one particular spot (considering the position indicated by the path integrator), the more intensely this area is explored by the ants. The end point of the home run (where the nest should be) is searched with the highest intensity, with the search intensity gradually decreasing the further an ant departs from it.

Although the geometrical shape of the systematic search seems to be a predetermined routine, the extension of its loops is not. This extension is adaptive (Merkle et al. 2006a; see also Figure 3.35 in Wehner 1992) and can be modified to a certain extent. The longer the foraging excursion has been (and therefore the more errors have accumulated, see Merkle et al. 2006a), the wider are the ants' search loops from the beginning of the search. Although the ants still search in the same manner, their search patterns have changed. The systematic search pattern thus reflects the ants' confidence in

* Correspondence and present address: T. Merkle, Centre for Visual Sciences, Research School of Biological Sciences, The Australian National University, Canberra, ACT 2601, Australia.
  E-mail address: tobias.merkle@anu.edu.au (T. Merkle).
[1] R. Wehner is at the Institute of Zoology and Brain Research Institute, University of Zürich, 8057 Zürich, Switzerland.

their path integrator, and this confidence decreases with increasing foraging length. Studies on the systematic search of desert isopods found a similar relationship between length of the foraging path and the systematic search pattern (Hoffmann 1983); also, desert ants adapt their approaches to familiar feeding sites to the nest–feeder distances (Wolf & Wehner 2005).

Taken together, the studies cited above give us a first glimpse into how desert ants and isopods deal with their uncertainty concerning the accuracy of their path integrator. This uncertainty is an inherent feature of their navigational system, and as such the ants cannot measure its amount. As errors add up during foraging excursions (Merkle et al. 2006a), a successful strategy to account for this is to adjust the search extension to the length of the preceding foraging excursion. The same argument also explains why desert ants adapt their approaches to a feeding site to the distance between nest and feeder.

However, as the ants cannot measure the exact amount of their uncertainty, it is likely that they make use of all available cues to decrease it. Therefore, (1) we addressed the question of whether the spatial extension of the systematic search, which represents the uncertainty as experienced by the ants, is exclusively determined by the distance travelled or whether it can be recalibrated by additional cues and (2) we examined the robustness of such cues under natural conditions. We trained ants to travel between their nest and a feeder and captured them after they had reeled off different portions of their inbound runs in the familiar training area. The ants were then released in an unknown test area. If cues other than the total foraging distance influenced the ants' search patterns, we would expect differences in the spatial layouts of the search patterns of ants that had covered different portions of their home runs in their familiar training area, even though all ants had covered the same overall distance before beginning their search. If, in contrast, the shape of the search is mainly or even exclusively determined by the length of the foraging trip, all ants should show similar search extensions, since the distance they had covered during foraging and homing was the same in all experimental set-ups. Comparing the systematic searches at different stages should give us an idea of how robust these cues are.

METHODS

The experiments were performed with desert ants in a salt pan close to the village Maharès in southern Tunisia (34°32′N, 10°32′E) in July and August 2004 and in June 2005. All tested ants belonged to the same colony. No obvious landmarks were found around the nest entrance or within the further visual range of the foraging ants. Temperatures and wind speeds were fairly constant throughout the experiments.

Experimental Set-up and Test Procedure

A feeder that contained small biscuit crumbs was set up 20 m south of the nest (Fig. 1a). Ants that had encountered the feeder were captured at the latter and marked with a colour code. They were then released at the feeder where they picked up a biscuit crumb and returned to the nest. They were tested after at least another full day of foraging.

During the test, the ants were allowed to take a food crumb from the feeder and head for the nest before being captured. They were captured by means of a plastic ring (diameter 15 cm) either after having covered a distance of 10 m, that is, 50% of the total distance (20 m) between feeder and nest (termed 50%-in ants, $N = 50$; Fig. 1a), after a distance of 15 m, that is, they still had to run 25% of the total distance (25%-in ants, $N = 50$; Fig. 1a), or shortly before entering the nest (0%-in ants, $N = 50$; Fig. 1a).

The ants were then put into a film container and transferred to a test area. This transfer usually took about 1 min. The test area had a white grid painted on the desert ground (painted with wall paint, mesh width 1 m, size either 20×30 m or 20×20 m). The lines of the grid were approximately 5 mm thick; lines of that thickness do not affect the ants' navigational performances (T. Merkle & R. Wehner, personal observation). The test area was about 70 m away from the nest, and the two areas were separated by a sand mound (height approximately 0.6 m). No obvious landmarks were found in the test area. The ants were released after they had picked up a small biscuit crumb (on most occasions, they lost the biscuit they had taken at the feeder during the transfer to the test area).
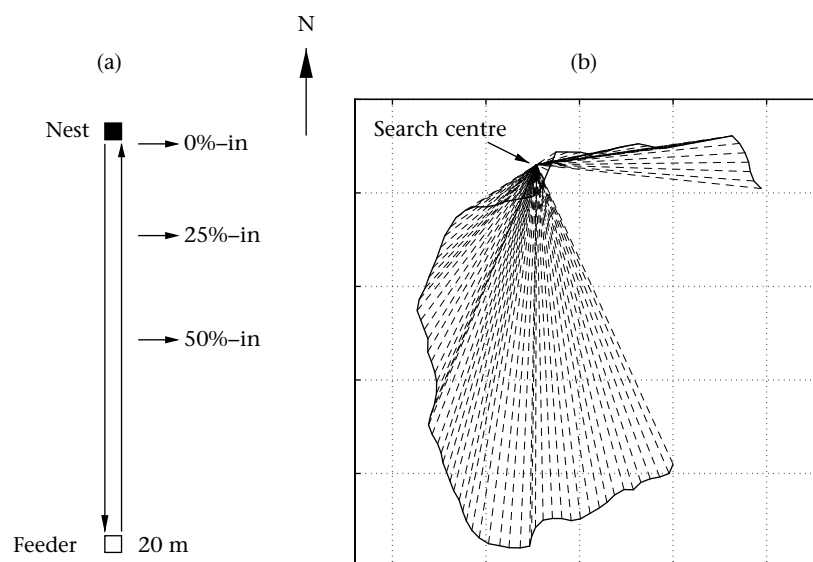

Figure 1. (a) Experimental set-up. Ants were trained to a feeder located 20 m south of their nest. During the test, the ants were captured on their inbound runs and then transferred to a remote test area. This was done after the ants still had to cover either 50% (50%-in ants) or 25% (25%-in ants) of their inbound runs, or had already reached the nest entrance (0%-in ants). (b) The first 5 m of the systematic search of a 50%-in ant. The centre of the search and the distances of all recorded points from this centre (indicated by dashed lines) are shown. The search centre was defined by the median X and Y values of the entire search. The median values of all distances to the search centre during the first 20, 40 or 50 m search lengths were used as the values describing the systematic search extensions (for more details, see text). Mesh width of grid: 0.5 m.

We recorded their paths for 5 min by drawing them on graph paper that contained the same grid with a scale of 1:100. Each ant was tested only once in one particular condition and excluded from further tests.

Data Analysis

The recorded paths were digitized using a graphics tablet and GEDIT Graphics Editor and Run Analyser (Antonsen 1995).

The 50%-in ants reeled off their home vectors and then switched to their systematic search program. The 0%-in ants, as expected, immediately started their systematic search program. Of the 50 25%-in ants, 17 (34%) also started with the systematic search, thereby skipping the reeling off of the home vector. The criterion for deciding which 25%-in ants started their systematic search programs immediately was that these ants did not run at least 2 m towards their nest (north) during the first 5 m of their runs; that is, they started performing loops after being captured instead of showing a directional preference towards the position of the nest, which indicates an immediate start of the systematic search program. Since it cannot be ruled out that these ants were somehow influenced by the transfer, we did not consider their systematic search patterns for the analysis, so that only 33 of the 25%-in ants were included in the analysis.

To determine the switch from home run to systematic search program in the 50%-in and the 25%-in ants that did not start searching for the nest immediately after being released, we applied the criterion that we had established during previous studies (Merkle et al. 2006a; Merkle & Wehner 2009).

For all ants that still had to reel off their home vectors (all 50%-in ants and 33 of the 25%-in ants), the home vectors and the systematic searches were digitized separately. In this study only the systematic searches are presented. To test whether the ants' systematic search extensions varied, we first calculated the centre of the systematic search for each ant as the median position of all points measured throughout the systematic search of that particular ant (Fig. 1b). Then, to judge the width of the search distribution, we computed the distance from this centre to each of the recorded points of the search (the average distance between two successive points was approximately 5 cm, owing to the recording procedure). Finally, we computed the median of all those distances between the search centre and all points for each ant (Fig. 1b).

To test whether possible differences vanish after searching for a longer time in the remote test area, we applied this procedure three times for each ant: after its overall search length had reached 20, 40 or 50 m. Multiple comparisons were conducted between the three groups (50%-in, 25%-in and 0%-in ants) for each search length (20, 40, 50 m) by using the Kruskal–Wallis one-way analysis of variance. When this analysis proved significant, we tested for differences between single groups by means of Tukey's post hoc test.

Ants whose searches did not reach the required search length (20, 40, or 50 m) during the time they were recorded were excluded from the respective analysis. All ants in all groups covered 20 m during their searches. However, two individuals of the 50%-in ants did not reach search lengths of 40 m and six did not reach 50 m. In the 25%-in ants the corresponding numbers were one (40 m) and seven (50 m) individuals, whereas all 0%-in ants reached a distance of 40 m and only one of them failed to cover 50 m.

RESULTS

When the systematic search patterns during the first 20 m were compared, the 0%-in ants differed markedly from the 50%-in and the 25%-in ants (Fig. 2a). Whereas the median distance between the
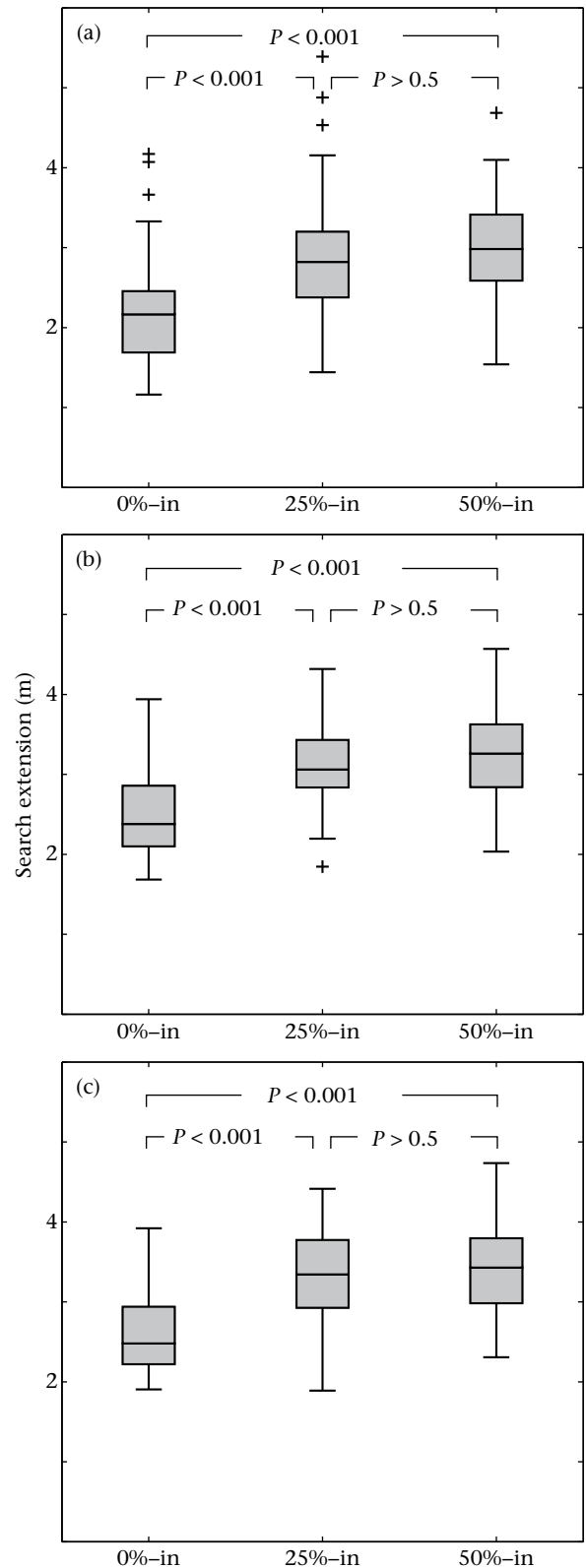

Figure 2. Search extensions during the first (a) 20 m, (b) 40 m and (c) 50 m for 0%-in, 25%-in and 50%-in ants. Box plots give medians, 25- and 75% quartiles, whiskers and outliers (+). The whiskers display either the minimum and maximum data values (if there are no outliers) or extend to a maximum of 1.5 times the interquartile range (if there are outliers). Kruskal–Wallis tests comparing the three groups: all *P*s <0.001. *P* values indicate results of Tukey's post hoc tests.
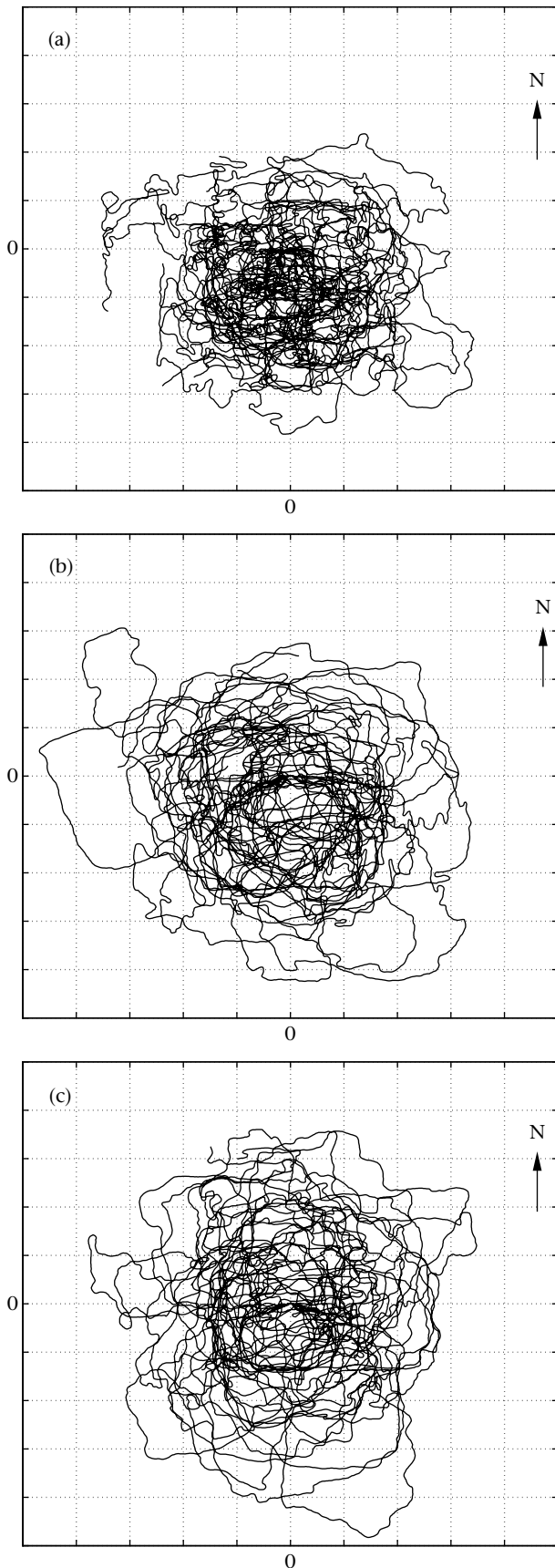
Figure 3. Search paths of 20 randomly chosen (a) 0%-in, (b) 25%-in and (c) ants 50%-in. Searches were cut at a length of 50 m. Start of all searches was at 0/0. Mesh width of grid: 2 m.

search centre and all path positions in 0%-in ants was 2.16 m ($N = 50$), it was 2.82 m in 25%-in ants ($N = 33$) and 2.98 m in 50%-in ants ($N = 50$; see Fig. 2a for results of Kruskal–Wallis test and Tukey's post hoc tests between the different groups).

The situation after 40 m of the search path had been covered was similar to that after 20 m (Fig. 2b). The 0%-in ants that had been captured just when they were about to enter their nest still showed significantly smaller search loops (median distance between centre and path points of 2.38 m, $N = 50$) than both 25%-in and 50%-in ants (3.06 m, $N = 32$, and 3.26 m, $N = 48$, respectively). Again, the 50%-in and 25%-in ants behaved similarly with regard to their search extensions (Fig. 2b).

After 50 m the result was the same as that obtained after 20 and 40 m: 0%-in ants showed narrow search patterns (median distance = 2.48 m, $N = 49$), whereas the search loops of both 25%-in and 50%-in ants were much wider (3.34 m, $N = 26$ and 3.43 m, $N = 44$, respectively; Figs. 2c, 3). As after 20 m and 40 m, the extensions shown by the latter two groups were similar.

DISCUSSION

In the present study we explored whether the systematic search patterns of desert ants, indicating the confidence the ants have in their path integrator, depend predominantly on the length of the preceding foraging excursion or are influenced by additional cues. To answer this question we compared the search patterns of ants trained to a feeder 20 m south of the nest. These ants were displaced to an unfamiliar test area after they had already covered parts of their inbound runs. We then compared the extensions of their systematic search patterns at different stages.

The search patterns of two groups (50%-in and 25%-in ants) differed markedly from the patterns shown by 0%-in ants, irrespective of the search path length (20, 40 or 50 m). Ants of the latter group that had returned from a 20 m distance and had temporarily reached the real vicinity of the nest where they could have experienced familiar nest site cues showed far smaller extensions of their search patterns. Thus, these individuals somehow had more confidence in the nest position as indicated by the path integrator and their searches were influenced not only by the distance covered during foraging but also by other factors. Both 50%-in ants and 25%-in ants that had never reached the vicinity of the nest were obviously not as certain about the nest position as the 0%-in ants; also, both groups that were captured and transferred during the inbound run differed only slightly in their search extensions.

We compared the data presented here with two earlier studies (Merkle et al. 2006a; Merkle & Wehner 2008). Both studies were conducted with ants of the same nest in 2004 and 2005. In the first study (Merkle et al. 2006a), one group of ants had also been trained to a feeder 20 m south of the nest, but during the test the individuals were captured at the feeder and transferred to the test area. Since we had used a different method to determine the extensions of the systematic search patterns, we recalculated the values for these ants (which would be called 100%-in ants according to the definition given above) with the method used here (see Methods). The fact that these 100%-in ants had greater search extensions not only when compared to the 0%-in ants in this study, but also when compared to the 50%-in and 25%-in ants (Table 1), indicates that ants that were allowed to reel off only parts of their home runs in their familiar training area have an increased confidence in their path integrator which is expressed by a reduction in the size of their search loops. Hence, these ants' searches were also influenced by other factors in addition to the foraging length.

In another study (Merkle & Wehner 2008) we had trained one group of ants to a feeder 10 m south of their nest. In the critical test situation, the ants were captured immediately after leaving the nest

Table 1
Search extensions of ants captured either at the feeder or after leaving the nest

	Search length		
	20 m	40 m	50 m
100%-in ants (Merkle et al. 2006a)			
N	50	50	50
Median (m)	3.22	3.72	4.03
Quartile range (m)	2.90–4.05	3.41–4.36	3.56–4.30
100%-out ants (Merkle & Wehner 2008)			
N	20	20	20
Median (m)	1.07	1.43	1.60
Quartile range (m)	0.79–1.68	1.09–1.84	1.20–2.00

The search extensions of ants that were trained to 20 m, captured at the feeder and then transferred to a test field (100%-in ants) and ants that were trained to 10 m, captured at the nest when they were about to start foraging, and then transferred to a test field (100%-out ants). Regarding the latter group, only ants that did not start foraging are given (for more details, see Discussion). The search patterns of both groups of ants were presented in previous studies (Merkle et al. 2006a and Merkle & Wehner 2008) and were recalculated to allow comparisons with the data of the present study.

(100%-out ants), that is, they had reset their path integrator to zero (see Knaden & Wehner 2005b), and then transferred to the test area. Since foraging desert ants are very sensitive to any disturbances during their outbound runs (Merkle & Wehner 2008), 80% of these ants did not start foraging, but immediately searched for the nest instead. Their search extensions (Table 1) were extremely small, even far smaller than the smallest search extensions in the present study, of the 0%-in ants. This suggests that the temporary vicinity of the nest entrance, although it has an effect on the systematic search patterns of desert ants, does not recalibrate the search pattern in the same manner as entering the nest does. The path integrator itself is only set to zero when an ant has entered the nest and cannot be reset even by landmarks defining the location of the nest entrance (Collett et al. 2003; Knaden & Wehner 2005a).

Our current results show that there are additional cues other than the length of outbound and inbound runs that influence the ants' systematic search patterns. It is possible that some cues acquired on the familiar route back to the nest within the training area increased the ants' confidence in the nest position. In addition, the results indicate that these route cues are either more frequent in the vicinity of the nest, or more salient to the ants, or that they are accumulated throughout the home run. In both cases, 0%-in ants would show the narrowest search patterns. However, if these cues are accumulated throughout the home run, this effect seems to be nonlinear, since otherwise we would expect larger differences between 50%-in and 25%-in ants. Since the 50%-in ants showed smaller search extensions than the 100%-in ants from our previous study on systematic search (Merkle et al. 2006a), desert ants obviously acquire such cues throughout the home runs. An alternative explanation is that the ants simply trust these cues more when they are closer to the nest, that is, when their path integrator has reached a lower stage. This interpretation is backed by the comparison with the 0%-out ants from our previous study: there the ants had been in the nest, so we could be sure that the path integrator had been reset. That could explain why these ants showed extremely narrow search patterns, even when compared with the 0%-in ants from the current study and strongly suggests that the acquisition of additional cues is linked to the state of the path integrator.

The cues used by the ants could be soil conditions (Seidl & Wehner 2006; Merkle 2009), horizon landmarks or the presence of nestmates. Whether the ants make use of such cues, whatever they are, and whether they also affect the path integrator, remains elusive.

An alternative explanation for our results could be that distance travelled in unfamiliar terrain during the home run or the distance travelled before an unforeseen event happens influences the systematic search patterns rather than the initial distance in familiar terrain. If the ants only consider that distance for the determination of their uncertainty and this value is not influenced by the systematic search itself, that is, it stays constant as soon as the home vector is reeled off, we would expect the search patterns we actually found. Moreover, it could be that the ants simply reset their uncertainty value when an unforeseen event happens as, in our case, being captured during the home run and transferred to the test field.

If, in contrast, the ants take both the distance travelled in unfamiliar terrain during the home run and the systematic search into account, the search patterns of all three groups should become more and more similar, since the relative differences in distance travelled in the unfamiliar terrain become more similar for all groups the longer the ants have been searching in the test area. This was not the case and, therefore, we can rule out this explanation.

Desert ants have to find their nest in the shortest possible time. An adaptive strategy to achieve this is to adjust the systematic search pattern according to the length of the preceding foraging run (Figure 3.35 in Wehner 1992; Merkle et al. 2006a), thereby taking into account that the probability of missing the nest increases with the length of the foraging run. However, since this strategy relies mainly on the growing uncertainty about the error proneness of the path integrator, it is not the ultimate solution. Therefore, it is very plausible that the ants make use of cues that might be helpful in providing them with an estimate of whether or not the position indicated by the path integrator is correct. Future experiments should investigate whether such cues exist, what exactly they are, and if and how they interact with the path integrator.

This study shows yet again the astonishing adaptiveness of the systematic search mechanism of desert ants which, depending on the situation, does not depend only on the length of the foraging trip.

References

Antonsen, N. 1995. *MbasaSoft GEDIT for Windows.* v. 2.5. Zürich: Institute of Zoology, University of Zürich.

Collett, M., Collett, T. S., Bisch, S. & Wehner, R. 1998. Local and global vectors in desert ant navigation. *Nature,* **394**, 269–272.

Collett, M., Collett, T. S., Chameron, S. & Wehner, R. 2003. Do familiar landmarks reset the global path integration of desert ants? *Journal of Experimental Biology,* **206**, 877–882.

Harkness, R. D. & Wehner, R. 1977. Cataglyphis. *Endeavour,* **11**, 115–121.

Hoffmann, G. 1983. The search behaviour of the desert isopod *Hemilepistus reaumuri* as compared with a systematic search. *Behavioral Ecology and Sociobiology,* **13**, 93–106.

Knaden, M. & Wehner, R. 2005a. Nest mark orientation in desert ants *Cataglyphis*: what does it do to the path integrator? *Animal Behaviour,* **7**, 1349–1354.

Knaden, M. & Wehner, R. 2005b. Ant navigation: resetting the path integrator. *Journal of Experimental Biology,* **209**, 26–31.

Merkle, T. 2009. Surface structure helps desert ants return to known feeding sites. *Communicative and Integrative Biology,* **2**, 27–28.

Merkle, T. & Wehner, R. 2008. Landmark guidance and vector navigation in outbound desert ants. *Journal of Experimental Biology,* **211**, 3370–3377.

Merkle, T. & Wehner, R. 2009. Repeated training does not improve the path integrator in desert ants. *Behavioral Ecology and Sociobiology,* **63**, 391–402.

Merkle, T., Knaden, M. & Wehner, R. 2006a. Uncertainty about nest position influences systematic search strategies in desert ants. *Journal of Experimental Biology,* **209**, 3545–3549.

Merkle, T., Rost, M. & Alt, W. 2006b. Egocentric path integration models and their application to desert arthropods. *Journal of Theoretical Biology*, **240**, 385–399.

Müller, M. & Wehner, R. 1988. Path integration in desert ants *Cataglyphis fortis. Proceedings of the National Academy of Sciences, U.S.A.*, **85**, 5287–5290.

Müller, M. & Wehner, R. 1994. The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis. Journal of Comparative Physiology A*, **175**, 525–530.

Schmid-Hempel, P. & Schmid-Hempel, R. 1984. Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Insectes Sociaux*, **31**, 345–360.

Seidl, T. & Wehner, R. 2006. Visual and tactile learning of ground structures in desert ants. *Journal of Experimental Biology*, **209**, 3336–3344.

Wehner, R. 1992. Arthropods. In: *Animal Homing* (Ed. by F. Papi), pp. 45–144. London: Chapman & Hall.

Wehner, R. 2003. Desert ant navigation: how miniature brains solve complex tasks. *Journal of Comparative Physiology A*, **189**, 579–588.

Wehner, R. & Räber, F. 1979. Visual spatial memory in desert ants, *Cataglyphis bicolour* (Hymenoptera, Formicidae). *Experientia*, **35**, 1568–1571.

Wehner, R. & Srinivasan, M. V. 1981. Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *Journal of Comparative Physiology A*, **142**, 315–338.

Wehner, R. & Srinivasan, M. V. 2003. Path integration in insects. In: *The Neurobiology of Spatial Behaviour* (Ed. by K. J. Jeffery), pp. 9–30. Oxford: Oxford University Press.

Wehner, R. & Wehner, S. 1986. Path integration in desert ants: approaching a long-standing puzzle in insect navigation. *Monitore Zoologico Italiano*, **20**, 309–331.

Wolf, H. & Wehner, R. 2005. Desert ants compensate for navigation uncertainty. *Journal of Experimental Biology*, **208**, 4223–4230.