

Navigating desert ants (*Cataglyphis fortis*) learn to alter their search patterns on their homebound journey

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Abstract. In navigating home, desert ants first run off a global vector estimated on their outbound journey, and then engage in systematic search consisting of ever-increasing loops interrupted by returns to the starting point of search. Desert ants (*Cataglyphis fortis*; Wehner, 1983) were trained to travel 6 m down a channel to a food source. Different groups of ants were trained to return home in another channel, from distances of 6 m (control), 9 m or 12 m. Ants at the feeder were then tested in a long test channel. The measure of where the ants first turned back on a test gave an estimate of the length of the global vector calculated on their outbound trip. The median distance of search on a 5-min test gave an estimate of the centre of the search pattern. Relative to controls, the experimental ants did not increase their estimated length of global vector, but changed their search patterns, searching on average further from the start than the controls. Tests of the outbound journey, however, revealed no differences between groups. Desert ants can learn to modify their search pattern based on experience.

Key words. Ants, learning, navigation, path integration, search.

Introduction

Many aspects of the navigational mechanisms of insects are known (see Wehner, 1992; Collett & Zeil, 1998; Cheng, 2000). Desert ants of the genus *Cataglyphis* compute their outbound vector as they travel in search of food (see Wehner *et al.*, 1996). After they have found food, the return journey consists of two phases: a vector phase and a search phase (Wehner & Srinivasan, 1981). The returning forager first runs off the vector computed *en route* (the global vector) or sometimes a series of vectors defined with respect to landmarks encountered *en route* (local vectors; Collett *et al.*, 1998). At the end of its vector run, the ant makes a sharp turn and commences a systematic search for its nest (Wehner & Srinivasan, 1981). This consists of ever-increasing spirals that return occasionally to the start of the search (Müller & Wehner, 1994).

Path integration requires learning. The experience on the most recent outbound journey must be used to chart the path home. The use of local vectors requires learning to use landmarks in particular contexts to chart a vector. Navigating desert ants can also learn from more than the current outbound journey. For example, experience over a number of trips can influence the global vector. Collett *et al.* (1999) reported re-calibration of the direction of the global vector. Ants (*Cataglyphis fortis*; Wehner, 1983) were trained to go from their nest to a food site along a constrained channel. They were then forced to return home along a different channel. They thus returned home in a different direction than 180° from the outbound direction. After four days of training, ants at the training feeder were tested on an open field. As reported for honeybees in a similar experimental paradigm (Otto, 1959), the direction of their homeward global vectors was modified, suggesting that the ants added a correction vector to their path integration system. Wehner *et al.* (2002) trained and tested *Cataglyphis fortis* under natural, unconstrained conditions (without channels). Their displacement manipulations showed that the calibration process is a flexible one and that under certain conditions (see also Wehner & Flatt, 1972), re-calibration does not occur at all.

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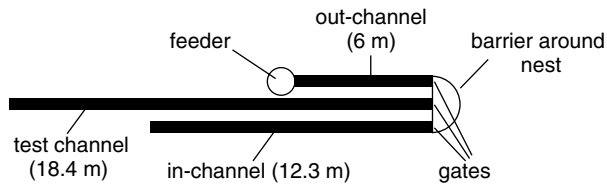


Fig. 1. Overhead view of the experimental apparatus (not to scale). A semicircular barrier was made around the nest entrance, with three gate-controlled channels (10 cm wide by 10 cm high) leading out from the enclosure. During training, ants were released into the out-channel to travel to a feeding site 6 m away. Captured ants returned home in the in-channel, travelling 6, 9 or 12 m back (different groups). Ants were occasionally released in the test-channel for tests.

Whereas Otto (1959), Collett *et al.* (1999) and Wehner *et al.* (2002) investigated the direction of the global vector, the present experiments investigated the distance component. Can the distance of the global vector be re-calibrated by suitable inducing experience, and do the ants modify their search pattern along the distance dimension? In this study, the focus was limited to one dimension by the use of constraining channels. Unlike the study of Collett *et al.* (1999), ants were tested in a constrained channel as well, so that the context in training and tests was identical to the ants.

In the experiments, ants walked down a channel to a food source 6 m from their nest (see Fig. 1). They were then offered food in another channel to carry home. Different ants were trained to run 6, 9 or 12 m home by being placed at different locations in the training channel. After training, they were tested in a long channel. The point at which an ant first turned back in the test channel gave an indication of the ant's estimate of the homeward global vector. The ants were also left to search for 5 min in the test channel. The central tendency of search was measured to assess possible biases in searching.

Materials and methods

Animals and set-up

One nest of ants, *Cataglyphis fortis*, was used in the experiments, and participating ants were painted for identification. The nest was located at a field site *c.* 5 km from Maharès, Tunisia. The terrain was sandy and flat, with scattered shrubs. Experimentation took place from July to early August 2001. Channels for the experiments were set up at *c.* 08.00 h each day, at a time when few foragers were active. Channels were dismantled typically between 16.00 and 17.00 h, when most foragers were again inactive. Experimentation was terminated in strong winds.

Figure 1 shows the set-up for the experiments. Surrounding the nest was a half circle of plastic material (80 cm long, 10 cm high) that prevented most of the ants from climbing over. The diameter of the half ring consisted of gates to three parallel channels: from an exiting ant's viewpoint an out-channel on the right, a test-channel in the middle, and

an in-channel on the left. Entrance to the channels was controlled by guillotine-styled plastic gates fitted into slots in aluminium connecting pieces.

Channels (10 cm wide, 10 cm high) were constructed of 1.5-m plywood pieces. Parallel channels were separated by 10 cm. The inner side-walls of the out- and in-channels were covered with tape to make them very difficult for ants to climb. The inner side-walls of the test channel were covered with tape in Experiment 2 but not in Experiment 1. (The reason for the difference was that in Experiment 1, tests ended with the first turn made by an ant, whereas in Experiment 2, the ants searched for 5 min inside the test channel. Thus, ants needed to be kept in the test channel in Experiment 2 but not in Experiment 1.) Segments of the channel walls were connected by grooved aluminium connecting pieces held down by screws stuck into the sand. Channels ran in the direction 153° from north. Measuring tapes beside the in-channel and test-channel allowed distance measurements. Sand piled outside the walls of channels prevented ants from crawling under the channel wall.

The out-channel led to food at 6 m distance (measured from the gate). Food consisted of a piece of watermelon, on the ground in Experiment 1 and in a sunken food trap (24 cm diameter, 8 cm deep) in Experiment 2. The wall of the trap was coated with fluon to prevent ants from escaping. The in-channel was eight segments long (12.3 m). The test-channel was 12 segments long (18.4 m). The in-channel and test-channel were both blocked at their furthest point from the nest, to prevent ants from escaping.

Procedure for Experiment 1

Throughout the experiment, the out-channel was left open. Ants arriving at the feeder were divided at random into two groups: experimental ($n = 18$) and control ($n = 19$). Experimental ants were captured individually from the watermelon at the feeder, painted, and then offered a small piece of biscuit 12 m from the gate in the in-channel. The ant was left to wander in the channel until it crossed the gate and found the nest; the gate was lifted as the ant approached it. A maximum of 45 min was set for the training trial. Control ants were offered a piece of biscuit at 6 m distance from the gate in the in-channel. The next time a painted ant arrived at the watermelon in the out-channel, it was captured for a test. On a test, the ant was offered a piece of biscuit in the test channel, 18.4 m from the gate. The test was ended when the ant turned back and travelled >20 cm, or when it climbed out of the channel; behaviours that indicate the start of a systematic search for the nest. The distance at which this turn was made, to the nearest 0.1 m, constituted the data recorded.

Procedure for Experiment 2

Ants were allocated to three groups: 6 m (control, $n = 20$), 9 m ($n = 18$) and 12 m ($n = 18$) groups. Each ant was trained

for five trials and then given three kinds of test, each test separated by one training trial. It typically took more than one day to run an ant, and the first trial of the day was always a training trial. On a training trial, the ant was captured from the food trap and offered a piece of biscuit in the in-channel. The three groups differed in the distance from the gate at the nest at which the ants were released: 6, 9 and 12 m. After an ant crossed a segment of the channel, its return was blocked by a piece of plastic. This served to speed up training in the 9 and 12 m groups and minimize the difference between groups in the duration of training runs.

The three tests were an in-test, a zero-vector-test, and an out-test, in that order. For an in-test, the ant was offered a piece of biscuit in the test-channel, 18.4 m from the gate at the nest. It was left to run in the channel for 5 min. Each turn of at least 20 cm was noted. For a zero-vector test, the ant was offered a piece of biscuit and released 6 m from the gate at the nest in the in-channel. When it reached the gate after its 6-m run (thus reducing its global vector to near zero), it was recaptured and released in the test-channel, 9.4 m from the gate at the nest (9 m from the start of the channel). Every turn of at least 20 cm made by the ant was noted. The zero-vector test provided an additional test to the in-test for examining the search pattern of the ants. After each of these tests, the ant was captured and released into the nest. For an out-test, the out-channel was blocked. An experimenter waited at the nest for the appearance of the to-be-tested (labelled) ant. When it emerged from the nest, the gate to the test channel was opened to let the ant run an outbound journey in search of the food source. The gate was closed after the ant entered the test-channel. Behaviour was observed for 5 min, and every turn of at least 20 cm noted.

Data analysis

Three dependent variables were analysed. Distances were all measured from the starting point of a test. For zero-vector-tests, 3 m were subtracted from the recorded tape measurements (ants started at the 9 m mark on the tape in the test-channel, but had already travelled 6 m). For out-tests, measurements were made from the gate to the test-channel. 'First turn' measured the distance at which the ant first turned back. First turns were only measured on in-tests and out-tests. 'Search median' measured the central tendency of the search for the nest (see Fig. 2). For in-tests and out-tests, the first leg of the run was discarded in calculating this variable. The first leg was the first 6 m of the run if the first turn exceeded 6 m; otherwise it was the run up to the first turn. On zero-vector tests, searching was tabulated from the time the ant was released into the test channel. These procedures made the calculation of search medians roughly comparable across test types. The turning points were then joined, and each division of 0.1 m tabulated. For example, for a stretch from 6.5 to 6.9 m, the distances 6.5, 6.6, 6.7, 6.8 and 6.9 m were tabulated. The median of the tabulated points constituted the search median. The spread of search was calculated by computing

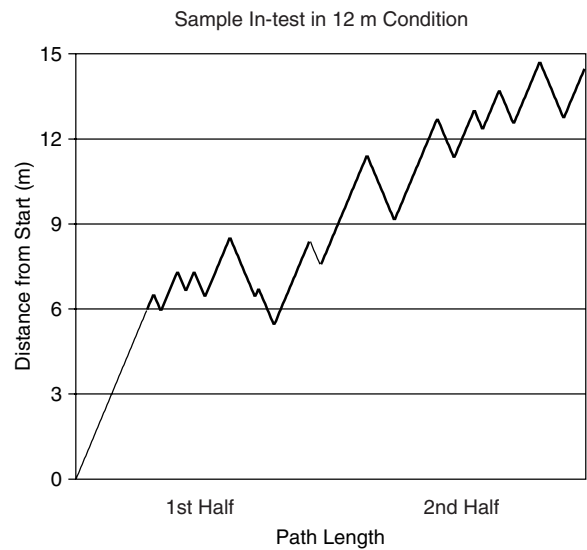


Fig. 2. Performance on a single 5-min in-test. The ant was released at one end of the test channel (0). Turns back and forth made by the ant are shown. The first turn made by the ant was at 6.5 m. The median distance of search was calculated for each half of the test (thickened lines). Halves were defined by number of turns rather than time; thus, each half contains 10 turns in the example. The middle segment (thin line) was not included in either half. The first 6 m of travel (thin line) was also not included in the calculation of medians. The median of a segment of search was calculated by tabulating in a spreadsheet every 0.1 m that the ant passed in either direction, and then finding the median of all points tabulated. Spread of search on each half of the test was measured as the distance between the 25th and 75th percentiles of search.

the 25th and 75th percentiles of search, and taking the distance between them. The patterns of results across conditions looked similar whether median, 25th percentile, or 75th percentile was used, indicating that the exact choice of a measure of central tendency was not crucial. The search medians and spreads on the two inbound tests (in-tests and zero-vector tests) were similar. The search medians and spreads were averaged across the two test types for each ant to compute single measures for inbound tests. To analyse differences across the duration of the test, however, each in-test and zero-vector test was divided into two halves. The division was by the number of turns (see Fig. 2). For out-tests, search medians were first examined in half tests, following the methods used on inbound tests. No differences across halves of tests were found, however, so that only data calculated from entire tests are reported as mean \pm SE. Statistical tests are considered significant at $\alpha = 0.05$.

Results

Inbound tests

Ants that were trained with different homebound distances after an outward trip of 6 m were given tests in

a long channel. For in-tests, an ant that had travelled to the feeder was captured and placed at the far end (from the nest) of the long test channel and allowed to run homeward. The distance at which it first turned back (first turn) was similar across conditions in both experiments. In Experiment 1, ants that were trained once to return 6 m (control condition) had similar first turns (mean = 6.1 ± 0.37 m) to ants trained to return 12 m (experimental condition, mean = 6.0 ± 0.43 m). An analysis of variance (ANOVA) confirmed that the condition effect was not significant. In Experiment 2, ants were trained five times to return 6, 9 or 12 m home. Distances of first turns were again similar across conditions (Fig. 3, leftmost column). The ANOVA revealed no significant effects. The ants as a whole, however, made their turns at a mean distance of 7.4 m, significantly longer than the outbound distance of 6 m. The 99% confidence interval of the mean of first turns in all groups combined exceeded 6 m.

On in-tests and zero-vector-tests in Experiment 2, ants were allowed to search in the test-channel for 5 min. The median distance of searches (search median) for the inbound tests combined (averaged, Fig. 3, second and third columns from left) showed that the experimental groups (9 and 12 m) searched on average further from the starting point than the control group (6 m), with the difference primarily in the second half of the search. A mixed ANOVA showed significant main effects of condition ($F = 5.27$) and half ($F = 63.69$), and a significant interaction

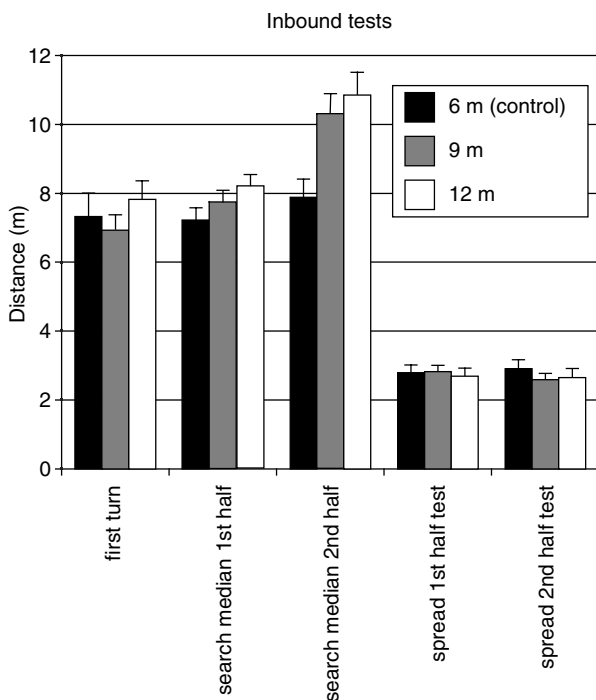


Fig. 3. Performance on inbound tests (mean \pm SE) in Experiment 2 after different return distances in training: 6 ($n = 20$), 9 ($n = 18$) or 12 m ($n = 18$). Search medians and spreads were averaged across the in-test and the zero-vector test for each ant. First turns were obtained from in-tests only.

of condition by half ($F = 7.34$). Analysing results from just the first halves of tests revealed no significant effects. Conditions differed significantly, however, on the second halves of tests ($F = 7.28$).

The spreads of search on inbound tests (measured by the distance between the 25th and 75th percentiles of the search distribution) were again averaged across in-tests and zero-vector tests, and computed separately for the two halves of tests. Spreads on inbound tests (Fig. 3, rightmost columns) were similar across conditions and halves of tests, with the mixed ANOVA not revealing any significant effects.

For each of the two halves of searches, the ants' first turns on in-tests were compared with their search medians (averaged across in-tests and zero-vector tests). The mixed ANOVA showed no significant effects for the first half of searches. For the second half of searches, significant main effects of condition ($F = 3.95$) and measure (first turn vs. search median, $F = 28.03$) were found, along with a significant condition by measure interaction ($F = 4.23$). Separate analyses for each condition revealed that control (6 m) animals had similar first turns and search medians, whereas the search medians of the experimental animals significantly exceeded their first turns ($F_s > 20$).

Search patterns

To examine search patterns further, each zero-vector test was divided into segments defined by turning points. A segment was defined as the length of run between two turning points. The midpoints of segments are plotted in Fig. 4, with

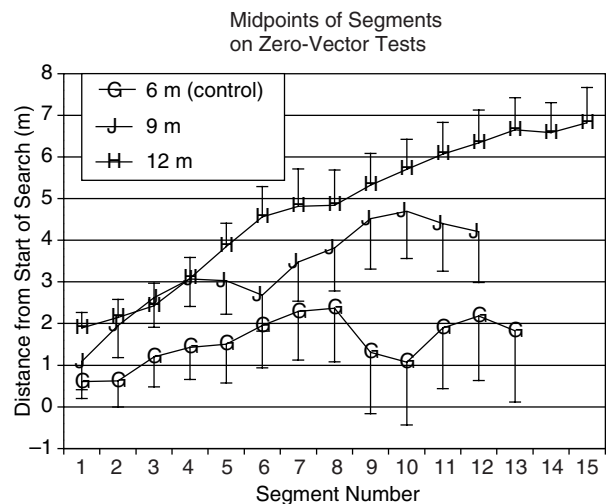


Fig. 4. The midpoints of segments of search on zero-vector tests (mean \pm SE) in Experiment 2. A segment was defined as the run between two turning points, with segment 1 being the run between the first and second turns. The point at which the ant was released into the test channel was not considered a turn. The y-axis measures distance from the start of the search, with positive being the direction toward the nest. Data points in each condition that contained 11 or more tests are shown.

segment 1 being the run between turn 1 and turn 2. The point at which an ant was released into the test channel was not considered a turn. The y axis is plotted with respect to the start of the search in the test channel, with positive numbers signifying the direction toward the nest. It can be seen that whereas midpoints of the search segments of control ants hovered near the start of the search throughout their searching, the experimental ants drifted gradually further from the starting point and toward the nest as searching proceeded. In addition, the increasing size of error bars across segments indicates that the search patterns became more variable across ants with time. Individual ants' search patterns resembled the mean, albeit with much more variability. A gradual drift was evident in many tests. The search patterns from in-tests (not shown) showed a similar pattern, although with smaller differences between the experimental conditions.

Outbound tests

Ants in Experiment 2 were also tested on their way out to the feeder (out-tests). First turns on out-tests (Fig. 5, left column) were similar across conditions, with the ANOVA revealing no significant effects. For out-tests as a whole, however, the first turns significantly exceeded the 6 m outbound distance to the feeder. The 99% confidence interval of the mean first turn in all groups combined exceeded 6 m. First turns on out-tests were also at a significantly greater distance than first turns on in-tests ($F=7.87$), the difference between in-tests and out-tests being similar across all three conditions (interaction of test type by condition non-significant).

For out-tests, search medians were also similar across conditions (Fig. 5, centre column), with the ANOVA failing to find any significant effects. On out-tests as a whole, however, the search medians significantly exceeded the 6 m

outbound distance to the feeder. The 99% confidence interval of the mean search median in all groups combined exceeded 6 m.

Search medians and first turns on out-tests were similar, with the ANOVA showing no significant effects. Spreads on out-tests (Fig. 5, right column) were also similar, with the ANOVA showing no significant effects.

Discussion

In these experiments, desert ants *Cataglyphis fortis* were offered a source of food 6 m down a channel from their nest. During training, they were released 6, 9 or 12 m (different groups) from the nest. The extra length on the homebound journey induces learning in the ants. The ants do not change the point at which they start their search for the nest. In two experiments, ants trained with different homebound distances made the first turn at similar distances. This means that the experimental ants do not re-calibrate the length of their global vector for the homebound journey. Another way to put this is that the length of global vector is based solely on outbound journeys, perhaps only on the most recent one. The experimental ants do, however, change their search pattern. Their search in the one-dimensional channel is characterized by a bias consistent with training experience: in the direction further from the starting point of the homeward run and toward the nest.

Collett *et al.* (1999) and Wehner *et al.* (2002) showed that the ants can re-calibrate the direction of their global homebound vector if, owing to the experimental manipulation, the direction of the inbound vector differs from the 180° reversal of the outbound vector. The present experiments show that the distance of the global vector is not re-calibrated if in the experiments the outbound and inbound distances differ. This negative finding, however, should be examined with some caution. It is always possible that the training procedures were not optimal for inducing distance re-calibration. For example, the difference between the inbound and outbound distances could have been too large.

The lack of distance re-calibration parallels findings on honeybees (Srinivasan *et al.*, 1997). Srinivasan *et al.* trained bees to enter a narrow channel for a reward of sugar water. The reward was set at a constant distance inside the channel. In these experiments, bees were found to use optic flow encountered while flying in the visually textured channel to estimate the distance they had flown. In one experiment, an extra piece of channel was added while a bee was feeding, so that distance into the channel (corresponding to the outbound journey to the food site) and distance out of the channel (corresponding to the homebound journey) differed. Tests on both outbound bees flying into the channel and homebound bees flying out of the channel showed that the distance flown was based solely on the distance experienced on the outbound journey. Only the first four turns were reported, so that it is unclear how the search pattern was affected by the discrepancy between homebound and outbound distances.

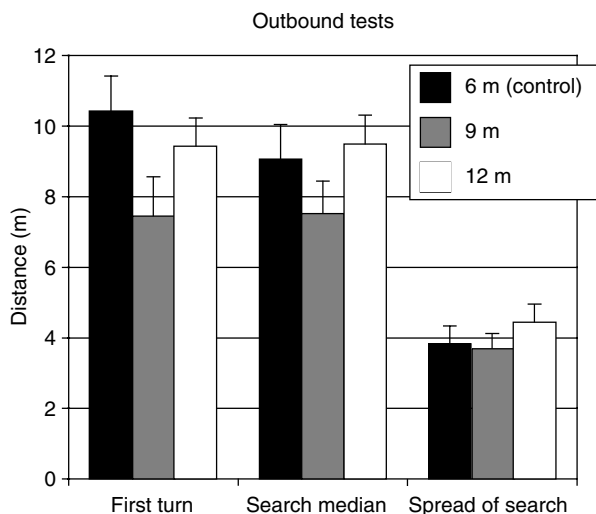


Fig. 5. Performance on outbound tests (out-tests, mean \pm SE) in Experiment 2 for the 6 ($n=16$), 9 ($n=17$) and 12 m ($n=17$) groups.

By contrast, the search pattern of the ants is appropriately modified by experience. The ants exhibit a significant search bias in the direction of the nest if the inbound training distance has been made larger than the outbound training distance. The bias unfolds gradually over the course of searching. One interpretation of these results is that the experimental ants learn an association between the context of searching and a direction of search. During training, searches only lead to finding the nest if they are in the direction toward the position of the nest. This might lead to a bias in the ants to move more in this direction. This bias is distributed across the entire search; the ants do not shift their centre of search by 3 or 6 m in one run.

On outbound tests, performance did not differ across conditions. This implies that the outbound vector is not re-calibrated on the basis of the homebound experience. The ants in all groups, however, overshot the 6 m nest-to-feeder distance. This behaviour matches foraging strategies of the ants under natural conditions. As their foraging lives proceed, the ants usually search in the same general direction (maintaining sector fidelity), but search further and further (Wehner *et al.*, 1983; Schmid-Hempel, 1984).

In the present study, the spread of search does not increase over the course of searching. Under natural search conditions, the ant generally searches further and further from the starting point of the search as the search goes on (Wehner & Srinivasan, 1981; Müller & Wehner, 1994). In the current experiment, however, searching is limited by the length of the test channel. Frequently, ants would search at the end of the test channel. This restriction of searching probably reduces the spread of searches, especially in the second halves of tests, thus leading to a lack of significant differences in spread across halves of tests.

One result for which no explanation is readily available is the difference in the distance of first turns between the two experiments. In particular, the distance of first turns is significantly longer than the training distance of 6 m in Experiment 2. Search behaviour of control ants in Experiment 2 also centres on a value greater than 6 m from the start of the run. Such overestimates in running off the global vector are not uncommon. It is unclear, however, whether differences in the experimental manipulations in the two experiments (one training trial vs. five training trials) might have contributed to this difference.

Finally, what function might be served by learning to modify the search pattern? In the course of navigation, desert ants may be blown off course by winds, which are typically from a similar direction over hours. Indeed, at our field site at Maharès, strong winds occasionally shut down our experimentation. Learning to bias homing behaviour might minimize the time needed to home after being blown off course by winds.

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