

PINPOINTING FOOD SOURCES: OLFACTORY AND ANEMOTACTIC ORIENTATION IN DESERT ANTS, *CATAGLYPHIS FORTIS*

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Summary

Desert ants, *Cataglyphis fortis*, search for a repeatedly visited food source by employing a combined olfactory and anemotactic orientation strategy (in addition to their visually based path-integration scheme). This behaviour was investigated by video-tracking consecutive foraging trips of individually marked ants under a variety of experimental conditions, including manipulations of the olfactory and wind-detecting systems of the ants. If the wind blows from a constant direction, ants familiar with the feeding site follow outbound paths that lead them into an area 0.5–2.5 m downwind of the feeding station. Here, the ants apparently pick up odour plumes emanating from the food source and follow these by steering an upwind

course until they reach the feeder. If the food is removed, foragers usually concentrate their search movements within the area downwind of the feeding site. Only when the wind happens to subside or when tail-wind conditions prevail do the ants steer direct courses towards the food.

Elimination of olfactory input by clipping the antennal flagella, or of wind perception by immobilising the bases of the antennae, altered the foraging behaviour of the ants in ways that supported these interpretations. Ants with clipped flagella were never observed to collect food items.

Key words: desert ant, *Cataglyphis fortis*, olfaction, orientation, anemotaxis, foraging.

Introduction

In most ant species, olfactory cues are essential for orientation outside the nest, in the context of foraging, colony dispersal or adverse colony interactions. Pheromone trails lead foraging ants back and forth between areas rich in food and their nesting site. New trails are established by pioneer ants, while old ones are abandoned because the pheromone is less frequently renewed when the food supply declines. The ants are able to follow highly localised pheromone trails because of the sensitivity of their antennal olfactory organs, which signal minute differences in pheromone concentration towards the edge of the trail (Hangartner, 1967; Hölldobler and Wilson, 1990). Only specialised desert dwellers, such as *Cataglyphis* species, apparently dispense with olfactory orientation because of the small size and unpredictable distribution of most food items (with circuitous foraging trajectories and straight homebound paths, there is no need for recruitment) and the short-lived nature of pheromone trails under desert temperature conditions.

Instead, *Cataglyphis* species rely on remarkable 'computational' feats of navigation accomplished by dead-reckoning (path integration). In dead-reckoning, the distances covered and the angles steered during a foraging trip are integrated *en route*. The result of this integration provides the animal with a continuously updated home vector. Once a food item is encountered, this vector, sometimes more than 200 m long, leads the animal on a direct path back to its nesting site, i.e. to an area within a few centimetres of the nest entrance

(Wehner et al., 1983). In the well-studied *Cataglyphis* species, the angular components of movement are determined by using compass information based on light from the sky (Wehner, 1997), while distances are gauged, at least in part, by exploiting self-induced optic flow (Ronacher and Wehner, 1995). If available, landmark orientation complements this dead-reckoning strategy, particularly in areas close to the nesting and feeding sites or in cluttered environments encountered *en route* (Wehner et al., 1996).

Provided with this powerful visual navigation system, and lacking any pheromone trails, *Cataglyphis* spp. foragers might not use olfactory cues. But is this really so, or do the foragers use olfactory information to increase their chance of encountering food items that may well be odorous? We investigated this question by recording the foraging trips of *Cataglyphis fortis* ants to rich, repeatedly visited feeding stations. If a steady wind blows, as is usually the case in the desert habitats of these ants, *Cataglyphis fortis* appear to optimise their approach by steering to the area downwind of a familiar food source. Here, they pick up odour plumes emanating from the food and follow these by steering an upwind course until they reach the source. This interpretation of a combined olfactory and anemotactic orientation strategy is in agreement with the results of experiments in which the olfactory and wind-sense organs of foraging ants were manipulated (Wehner and Wolf, 1998).

Materials and methods

Training and test procedures

Experiments were carried out near the village of Maharès (34°30'N, 19°29'E), Tunisia, in June, July and August in 1996 and 1997. We selected nests of the formicine ant *Cataglyphis fortis* located on even desert ground devoid of any vegetation within at least 5 m of the nest entrance and for at least 20 m in the direction of the feeding site. Feeding stations were established 15 m from each nest. A small Petri dish (diameter 35 mm) was used as a feeder and was glued into the lid of a jar (diameter of lid 70 mm, height of rim 8 mm). This double-walled construction minimised spillage of food crumbs by wind or foraging ants. If food items were dislodged from the feeder by strong wind, these were readily discovered during test runs (which were then disregarded, see below). The jar itself was used as a lid for the feeder in test situations in which the feeder had to be removed without leaving an odour mark on the desert floor or presenting a distracting nearby odour source.

Small numbers of dry and sun-baked cookie crumbs, approximately 1.0–1.5 mm in diameter, were used as food items. These nutritiously poor food sources avoided long-range attraction of ants and thus reduced the number of foragers to be monitored at any one time. In addition, they probably mimicked the natural foraging situation more closely than very odorous food items.

In some experiments, the feeding site was surrounded by three artificial landmarks located at the edges of an equilateral triangle and placed at distances of 1 m from the feeding site. All three landmarks were black cylinders, measuring (diameter × height) 12.5 cm × 40 cm (front right cylinder, as seen from the nest), 20 cm × 40 cm (front left cylinder) and 12.5 cm × 20 cm (cylinder directly behind the feeding site). Tripod, camera and observer were positioned 5 m behind the feeder. They represented another landmark that was always present, but was probably less conspicuous than the cylinders because of their greater distance from it, the slender tripod legs (4 cm diameter) and camera body (12 cm × 30 cm × 50 cm, 154 cm above ground) and the light clothing of the observer. The camera arrangement was not used in pinpointing the feeding site, as indicated by the data presented in Fig. 9 (see Discussion).

Foraging ants that had discovered the feeding site were captured during their return to the nest and marked with a colour code. Their initial visit to the feeding site and at least 10 (often more than 20) subsequent visits were recorded. After the forager had become familiar with the feeding site ('training runs'), experimental changes were introduced ('test runs'). For example, the feeder was removed and the resulting search trajectory of the foraging ant was recorded. To keep the foragers motivated and to avoid possible extinction of memory traces acquired during the previous training procedure, the feeder was replaced at a moment when the ant was searching at a distance of at least 6 m from the feeder. In this way, the test runs were of different durations, but they always ended with the ant successfully acquiring a food item. Two

intervening training runs were allowed before the next test was made, except in cases of irreversible manipulation of the sensory systems of the ants.

Experimental manipulation of the wind- and odour-detecting systems of the ants

To prevent the foraging ants from perceiving wind (Wehner and Duelli, 1971), the bases of their antennae were immobilised by applying a drop of insect wax to the joints between the head capsule, scape, pedicel and flagellum (subsequently described as SCAP.IMM. animals). The wax was heated using a battery-powered soldering iron to just above its melting point. In each experimental animal, the successful immobilisation of both antennae was examined microscopically after the experiments had been completed. Data from ants with incompletely immobilised antennae were discarded. Olfactory input from the antennae was eliminated by clipping the funiculi, i.e. performing a cut within the pedicel segment with a pair of miniature scissors (subsequently described as FUN.CLIP. animals; in ants, the pedicel and flagellar joints form the funiculus of the antennae, only flagellar joints bear the olfactory sensilla). Again, the success of this operation was verified after completion of the experiments by examining the animals and the clipped antennal parts under a dissection microscope.

Video recording techniques

The walking trajectories of *Cataglyphis fortis* foragers visiting the feeding site were recorded using a video system (Panasonic camera WV-F350E; recorder AG-7450). Walking trajectories and foraging behaviour were recorded on the sound track and the video track of the tape, respectively (Wolf and Wehner, 1998). Using this recording system, the experimenter tried to keep the recorded ant in the centre of the field of view of the video camera. A zoom lens (7–105 mm) enabled the ant to be kept in focus at distances of more than 20 m. Details of the behaviour of the ants were discernible up to distances of 5 m. The angles by which the video camera was tilted (α in Fig. 1) and turned (β in Fig. 1) on its tripod during the tracking procedure were measured using two potentiometers (one for the turning angle, the other for the tilting angle), translated electronically into frequency codes (voltage/frequency converter VFC110; Burr-Brown) and stored on the two stereo sound tracks. Assuming a level and even desert floor, the position of the ant with respect to the video camera can then be computed by using these two angles and applying simple trigonometry.

The angular resolution of the tracking system, as defined by mechanical constraints and, primarily, by the analogue-to-digital conversion of the frequency code for computer-aided evaluation, is 0.1°. This corresponds to a (maximum) deviation of approximately 3 cm from the true position of the ant at a typical working distance of 5 m (the distance between the camera and the feeding station) and to a deviation of approximately 51 cm at a distance of 15 m. A realistic estimate

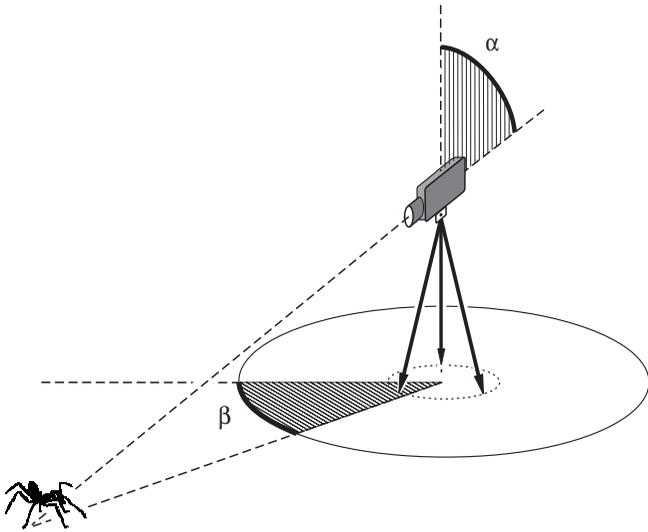


Fig. 1. Experimental arrangement for video-tracking desert ants, *Cataglyphis fortis*. While being filmed with a video camera, the ant is kept continuously in the centre of the field of view of the video camera. A zoom lens (7–105 mm) allows the animal to be observed for distances of 20 m or more, although walking trajectories may be recorded with acceptable precision (less than 20 cm deviation) only within a 10–15 m radius of the camera. The angles by which the video camera is tilted (α) and turned (β) on its tripod while tracking an ant are measured by two potentiometers (one for the turning angle, the other for the tilting angle), translated electronically into frequency codes and stored on the two stereo sound tracks of the video tape. The position of the ant with respect to the camera is later computed trigonometrically from these two angles.

must make allowance for the jitter introduced by video-tracking the fast-moving (up to 1 m s^{-1}) ants by hand. We estimated the accuracy of the recording method under field conditions by tracing a $1 \text{ m} \times 1 \text{ m}$ grid painted on the desert floor (e.g. Wehner et al., 1983) under worst-case conditions (wind $8\text{--}10 \text{ m s}^{-1}$; experiment performed at the end of a tiring day of field work; tracking straight lines is more demanding than tracking curved trajectories, which allow frequent change of muscle use). The mean deviation of the recorded trajectories from straight lines was $3.7 \pm 3.6 \text{ cm}$ (mean \pm s.d., $N=289$) at a working distance of 5 m and $20.0 \pm 16.6 \text{ cm}$ at a distance of 15 m. These values are comparable with an error of 15–20 cm estimated for manual recording on graph paper, which was employed in previous studies of *Cataglyphis bicolor* starting in the late 1960s (Wehner and Menzel, 1969). In addition, systematic errors occur as a result of factors such as uneven terrain, restrictions in the calibration of the electronic circuitry, etc. These errors proved to be more important than the jitter introduced by the tracing procedure and sometimes amounted to 27.0 cm at a working distance of 5 m and up to 38.9 cm at a distance of 15 m. It is important to note that these systematic errors, although distorting the representation of the desert floor, preserve relative distances in the immediate vicinity of the recorded trajectories as well as spatial relationships between the trajectories and objects such as the feeding station or

landmarks. In summary, and disregarding systematic errors that do not affect our interpretation of the results below, errors in the recorded trajectories were usually smaller than 20 cm, or 4%, in the present study.

The walking trajectories recorded on video tape were evaluated by first digitising the frequency-coded tilting and turning angles. Sample periods of 125 ms yielded eight coordinate pairs per second, which were transferred into an orthogonal coordinate system spread on the desert floor. Further evaluation was performed with custom-programmed routines (GEDIT 2.5 for Windows; MbasoSoft) on DOS and Macintosh computers. Video recordings of segments selected for further evaluation were viewed to assess the behaviour of the animals during foraging.

If an ant was lost to view from the camera for a short time, e.g. after disappearing behind landmarks or other obstacles, the corresponding segment of the tracking record was deleted from the data file before further computer-aided evaluation. The missing segment of the walking trajectory was approximated by a straight line connecting the points of disappearance and reappearance (see, for example, straight-line segments in Fig. 3B).

Results

A feeding station was established on open and level desert terrain at a distance of 15 m from a nest of *Cataglyphis fortis*. The video camera was positioned another 5 m past the feeder. This video system was used to record the walking trajectories of foragers as they approached the feeding site. The feeding site was supplied with food during training runs, but contained no food or other objects during test runs. At different nests, feeding sites were established in different compass directions. Since a fairly reliable southeastern wind blows in the desert habitat near Maharès (Wehner and Duelli, 1971), the direction of the wind differed with respect to the direction of the feeding site for the different nests used in this study.

Cataglyphis fortis foragers steer towards the leeward side of a familiar food source

A newly established feeding site was usually discovered by foraging ants roaming downwind of the feeder. The animals appeared to pick up odour plumes emanating from the food (dry biscuit crumbs) from distances of up to 3 m. They turned into the wind and approached the food source by steering an upwind course, often on a slightly zigzag path. Having discovered the source, where food was available *ad libitum*, the (individually marked) ants returned faithfully every 1.5–3 min to retrieve another biscuit crumb and did so for 3 h or more. Certainly, their initial approach was guided by the well-known path-integration system of *Cataglyphis* spp. (Müller and Wehner, 1988), but most ants did not steer directly towards the feeding site. Instead, they moved into an area 0.5–2.5 m downwind of the feeder. Here, they appeared to pick up the food odour and to follow it by steering an upwind course until they reached the food.

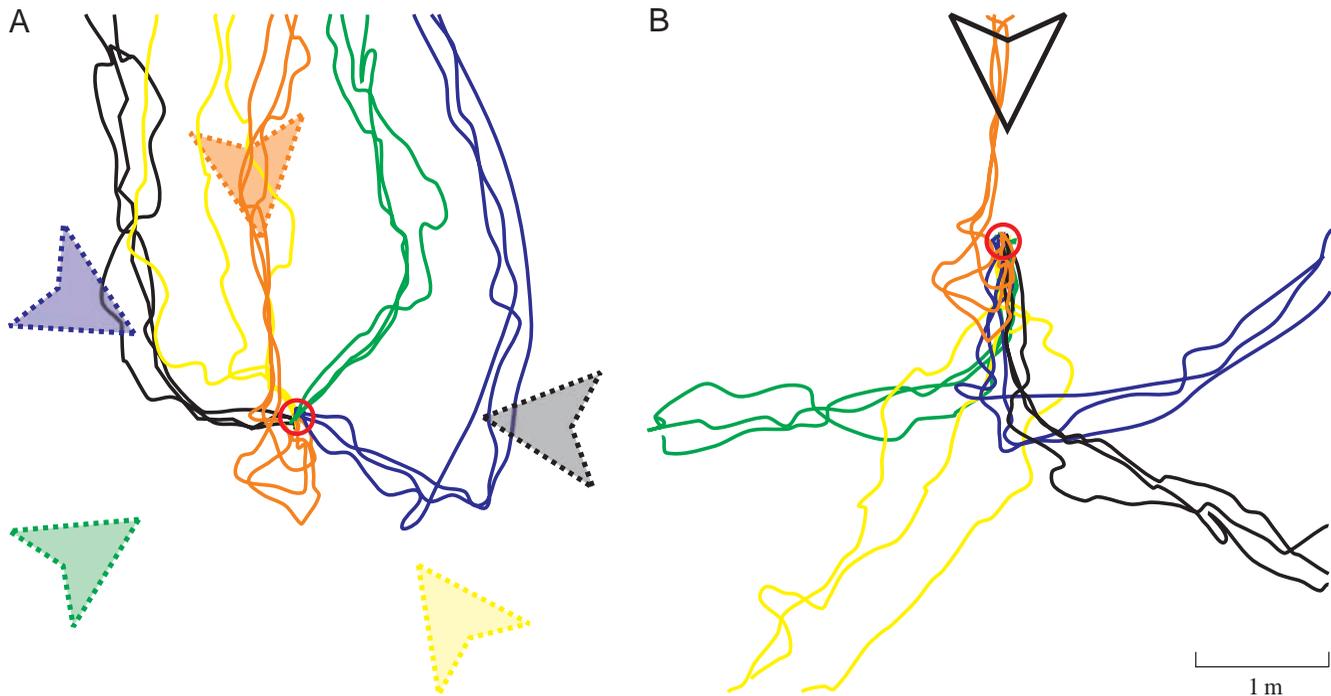


Fig. 2. *Cataglyphis fortis* ants approach food sources against the ambient wind direction. (A) Sample tracks (three tracks for each ant) are shown for five different foragers approaching feeders located 15 m from their nests. In this and the following figures, the feeding site is marked by a red circle (equivalent to a diameter of 25 cm on the scale of the desert floor; actual diameter of feeder 35 mm). The nests are not shown and are located beyond the upper margin of the figure exactly above the feeding site. The five foragers were from five different nests and exploited different feeders. Their walking trajectories are superimposed, taking nest and feeder positions as reference. Consequently, the angular difference between the ambient wind direction (always approximately eastsoutheast) and the initial approach directions of the ants varies. Tracks of individual ants are marked by different colours; corresponding wind directions for these ants are marked by arrowheads of the same colour. Note that one ant (orange trajectories) arrived from the nest under almost tail-wind conditions and walked past the feeder to make its final approach against the wind. (B) The same sample tracks as shown in A but arranged with reference to wind direction (rather than nest direction as in A). Wind direction is from the top (arrowhead). The ants arrive at the feeding area from various directions, but then coincide in their final upwind approach to the feeder.

The consistency of this orientation strategy becomes apparent if one compares data recorded at different nests and feeding sites and, therefore, under different ambient wind directions. Fig. 2 provides an illustrative example. Here, the walking trajectories of five different ants (three sample trajectories for each ant) are superimposed. The trajectories are arranged such that either the azimuth of the nesting site (the global approach direction of the ants; Fig. 2A) or the direction of the wind (Fig. 2B) is at the top of the figure. It is evident that all ants initially steered into the leeward side of the feeder, turned into the wind some 1–2 m downwind of the food and made their final approach against the wind.

When the food was removed during test runs, ants familiar with the feeding site concentrated their search to an area just downwind of the feeder, and they often showed a preference for walking cross-wind. This is illustrated for an individual forager in Fig. 3B. For comparison, typical search trajectories followed by the same ant during training are shown in Fig. 3A. In Fig. 3C, 19 search trajectories of eight ants (from five different nests) are superimposed, taking wind direction as a reference. Note that the ants were rewarded at the end of their search runs by replacing the feeder (at a moment when the ant

was searching at least 6 m from the feeding site). In addition, two normal training runs were interposed between any two test runs. If the feeder was not replaced, and if the ant's search thus remained unrewarded, the foragers extended their searches far beyond the vicinity of the feeding site, and during subsequent foraging trips examined the feeding site only superficially (compare the data in Fig. 8).

While searching, the ants exhibited two types of behaviour. When searching at some distance, usually more than 0.5 m from the feeding site, they followed smooth and only slightly circuitous paths, moving at a fairly constant speed. In the vicinity of the feeding site, they moved in short bursts separated by brief pauses (and sometimes turns), during which they whipped their antennae. This occurred even at the end of long-lasting (approximately 10 min) search episodes.

If the wind direction changed during the foraging period of an ant, the animal adjusted its initial approach to the feeding site accordingly (Fig. 4). In this way, the ant's final approach was always against the wind. The middle traces in Fig. 4 (medium blue) represent approaches to the feeding site against the wind. It is remarkable that in this situation, as in cross-wind conditions, there is a clear change between the initial approach,

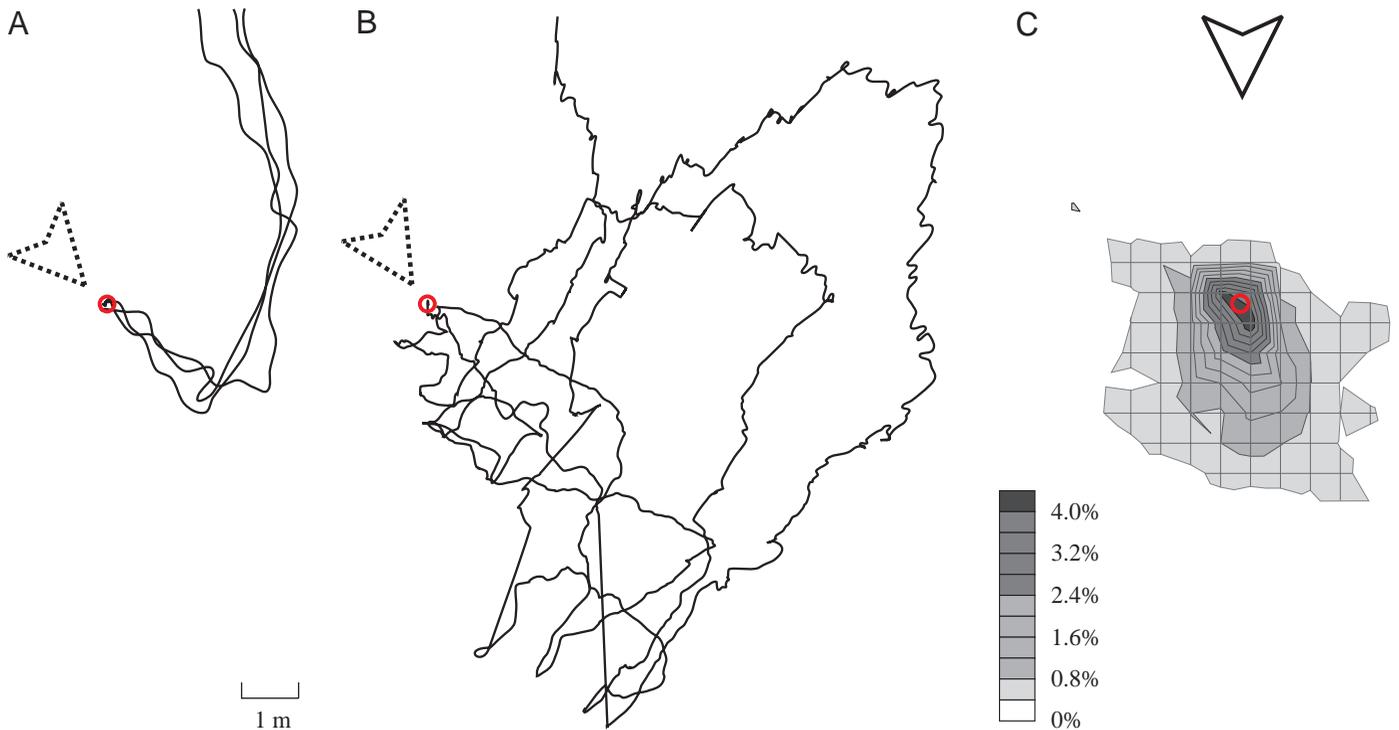


Fig. 3. *Cataglyphis fortis* foragers search mainly to the leeward side of a familiar food source. (A) Three sample trajectories recorded during training in one individual. Wind direction is indicated by the arrowhead. Further conventions as in Fig. 2. (B) Foraging trajectory of the same individual recorded during the test phase, i.e. with the food source removed. Note the tendency to walk cross-wind. (C) Search density plot computed from 19 trajectories (eight animals from five colonies). Wind direction was always from the top (arrowhead) for superposition and evaluation. Note the downwind skew of the search density distribution. Iso-density lines mark increments of 0.4% path length m^{-2} .

in this case slightly meandering, and the final approach, when the animal had presumably picked up the odour plume and followed a fairly straight upwind path (almost identical in the three samples shown).

It is interesting to note that many ants apparently use a similar orientation strategy in their final approach to the nest entrance, in particular when there are no landmarks nearby, such as the rubble mound that often surrounds the nest entrance. When returning from foraging trips, these animals steer 1–2 m to the leeward side of the nest, and there they appear to pick up odour cues emanating from the nest. In the present study, we have concentrated our experiments on the orientation strategy employed to locate food sources.

The initial approach to the feeding site is idiosyncratic and depends on previous experience

Despite the general consistency of the orientation strategy outlined above, individual ants exhibited remarkable idiosyncrasies in their ways of approaching the feeder. For example, the initial approach towards the feeding site was slightly different in individual foragers, even when individual variability was taken onto account. In Fig. 5, sample recordings are depicted for three ants belonging to the same nest and foraging at the same time of day, i.e. under the same wind conditions (three sample trajectories each). Two foragers (orange and blue traces) exhibited the typical pattern of an

initial leeward side approach and a final upwind path, with the latter being almost identical in the two ants. These two individuals started off from the nest in slightly different directions, however, which is still evident in the distal segments of the walking trajectories shown in Fig. 5. This difference in the outbound paths may be because, prior to establishment of the feeding station, the two ants exploited different segments of the nest environs.

The third forager was committed to a direct approach towards the feeding site (green traces). This unusual strategy appeared to result from the ant's first encounter with the feeder. In the morning, the wind had blown from southwest (roughly from the top of Fig. 5), so that the forager discovered the feeder under tailwind conditions and on an almost direct path when arriving from the nest. This was probably a chance encounter, not facilitated by olfactory cues. Later in the day, the direction of the wind changed to southeast. It was then that the walking trajectories shown in Fig. 5 were recorded. Unlike the animals shown in Fig. 4, this ant maintained its direct approach towards the feeding site despite the change in wind direction, which may be due to the absence of olfactory orientation cues during its initial visit. The animal sometimes missed the feeder by a few centimetres and had to search for a few seconds before finding the food.

This behaviour is distinctly different from the strategy adopted by one of the foragers recorded in Fig. 2 (orange

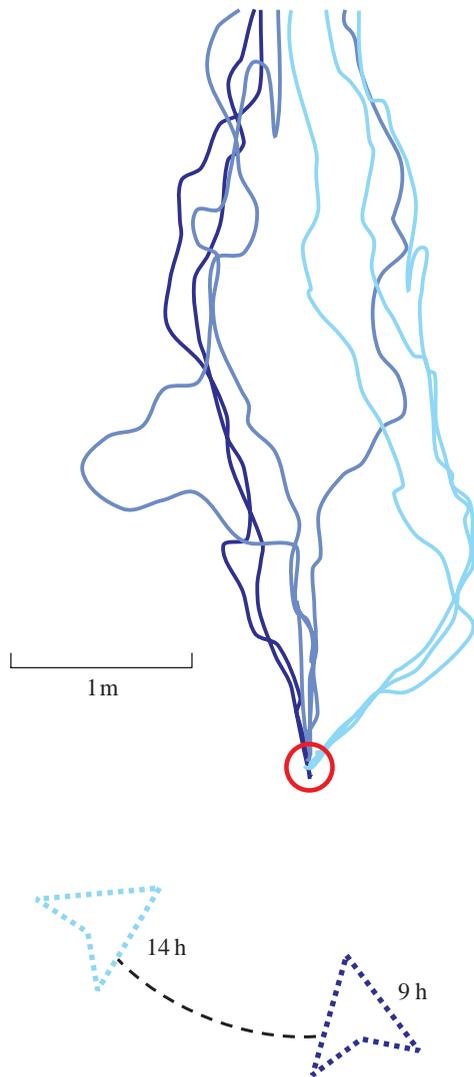


Fig. 4. Effect of short-term (hour-by-hour) shifts in wind direction on the approaches to a food source by an individual ant. The ant's approaches to the feeder were recorded at different times of the day (dark blue 09:00 h, medium blue 11:00 h; light blue 14:00 h). During the course of this particular day, the ambient wind direction shifted between 09:00 h and 14:00 h from east to east-southeast (arrowheads). The direction of the final approaches of the ant to the feeder shifted accordingly.

traces). Owing to near tailwind conditions, this animal, too, steered an almost direct course towards the feeder. However, it regularly walked past the feeder, 10–20 cm to the leeward side, and made its final approach using an upwind course, like most other ants. In this case, the animal's first encounter with the feeder had been under near crosswind conditions and, hence, had apparently been guided by olfactory cues. This is in contrast to the tailwind situation encountered by the ant described in the preceding paragraph and shown in Fig. 5 (green traces).

As indicated by these examples, the walking trajectories chosen by individual ants appeared to depend on previous experience and in particular on the conditions of their first

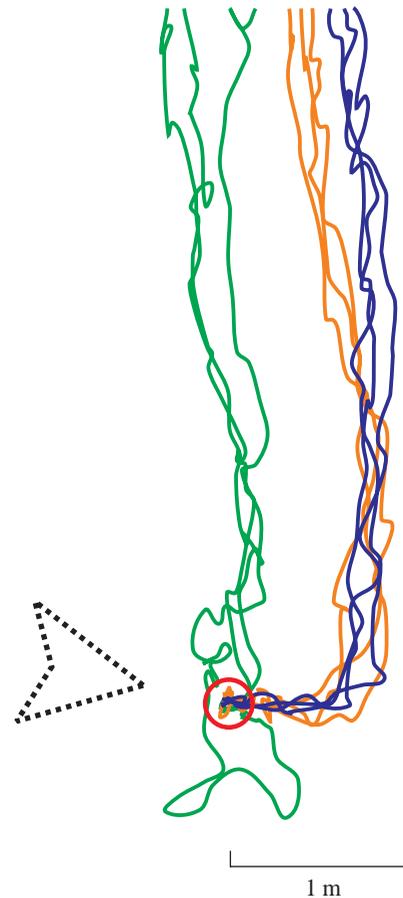


Fig. 5. Idiosyncratic approaches to a food source of different foragers. Three sample tracks each are shown for three different forager ants. The tracks of each individual are drawn in a different colour. All ants were from the same colony, foraged at the same time and had been familiar with the location of the feeder for more than 6 h. They approached the feeder along idiosyncratic paths. Note that one animal (green trajectories) chose a rather direct path, initially missing the feeder in one of the three approaches. Most other animals followed paths resembling those marked in orange and blue, i.e. they aimed towards the leeward side.

encounter with the feeding station. Even under typical circumstances (initial approach to the leeward side and final upwind approach), some fine-tuning of the walking trajectories was often observed during the subsequent few (the second to approximately the fifth) visits to the feeding station. This tuning consisted of a limited straightening and shortening of the foraging paths. Fig. 6A shows trajectories recorded during the second, third and fourth visits of a forager (the first visit had been a chance encounter from the far right of the figure). The animal always steered to the leeward side, but gradually decreased its sideways displacement from the feeder. After the fourth visit, the trajectories of subsequent approaches stayed fairly constant, with the initial segment leading the animal approximately 1 m to the leeward side of the food. If, as happened occasionally, the wind subsided, all ants after some time chose a direct path towards the feeder.

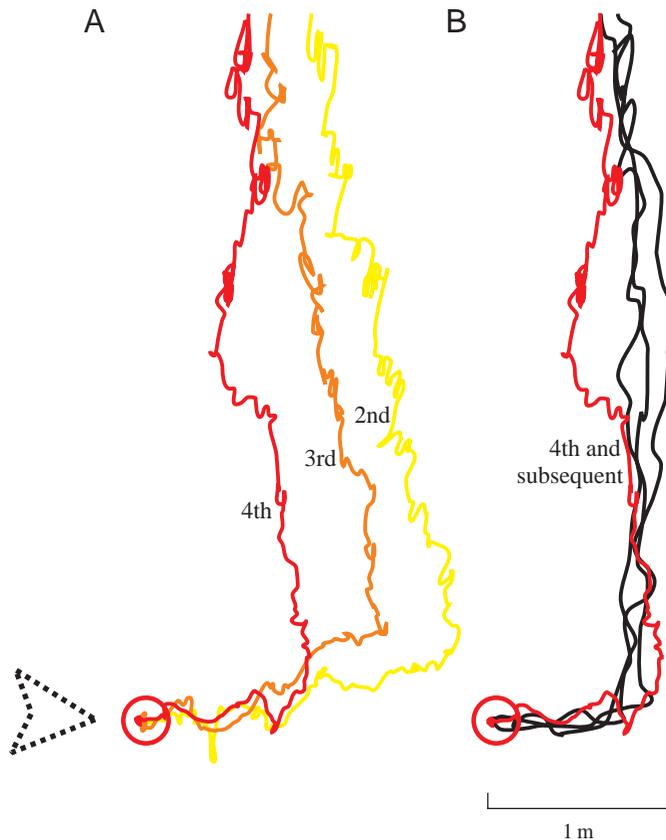


Fig. 6. With increasing numbers of visits to the same food source, *Cataglyphis fortis* tends to steer more closely towards the feeder. (A) The second to fourth trips of an individual forager are shown (the first visit was a chance encounter), recorded within approximately 30 min. (B) Later foraging trips, recorded up to 3 h later, remained close to the fourth path (red).

Manipulation of the wind-perception system compromises food localisation

The results described above suggest that individual *Cataglyphis fortis* ants employ a combined anemotactic and olfactory orientation strategy during their final approach to a food source. We tested this hypothesis further by manipulating the wind-sense organs and olfactory receptors of the ants.

Immobilising the proximal parts of both antennae, i.e. the joints between the head capsule, scape, pedicel and flagellum, abolishes wind perception (Gewecke, 1974). Ants that had their antennae immobilised in this way (SCAP.IMM. animals) resumed foraging a few hours after the operation and could continue to forage successfully for several days. Their performance, however, was impaired. Animals familiar with the feeding site prior to the operation started their foraging excursion by resuming their normal approach. As soon as they appeared to encounter the odour plume emanating from the food, they adopted a local search strategy that appeared to be independent of the distance from the feeder and the wind direction (Fig. 7, coloured traces). Locating the food therefore took much longer than for intact ants (controls; compare, for example, Fig. 3A and Fig. 3B). Over time, SCAP.IMM.



Fig. 7. Effect of preventing the ants from perceiving wind direction. Approaches to a food source of an ant that had had the joints of the pedicel and scape segments of its antennae immobilised (SCAP.IMM. animal) are shown. The number of each trip is indicated, and the trajectories are drawn in colours for trips performed within 20 min of the operation; foraging excursions indicated in black were performed more than 30 min after the operation (twelfth trip and later). Note that the animal started a search as soon as it arrived to the leeward side of the feeding site, irrespective of its distance from the feeder.

animals usually managed to approach the feeder directly (Fig. 7, black traces).

The foraging behaviour of ants with only one of their antennae immobilised was indistinguishable from that of intact animals (data not shown).

Removing olfactory input incapacitates Cataglyphis fortis foragers

Clipping the funiculi (pedicels and flagella) of both antennae eliminates olfactory input. Ants treated in this way (FUN.CLIP. animals) obviously remembered the location of the feeding site when they re-emerged from the nest 1 or 2 days after the operation, and they approached the feeding site in a more-or-less normal fashion (sometimes steering slightly to the leeward side). Having arrived in the vicinity of the feeder, they started to search

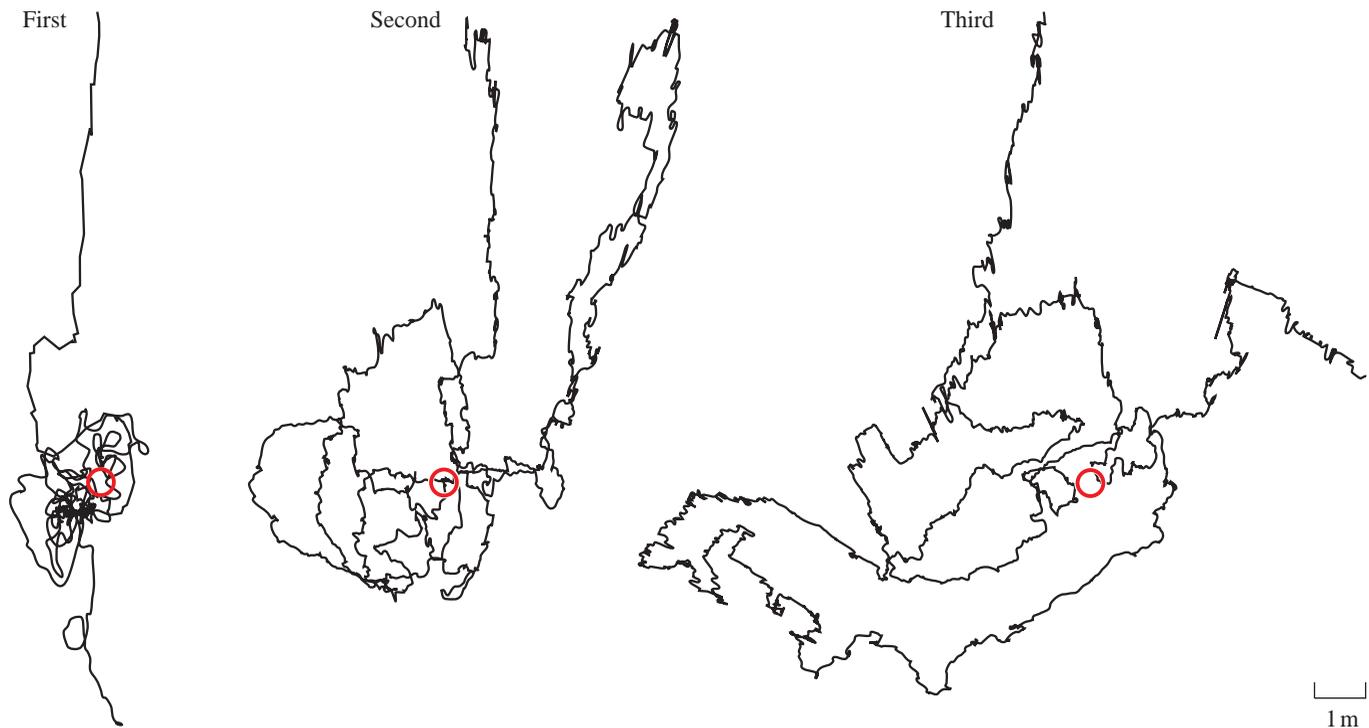


Fig. 8. Effect of preventing the ants from perceiving food odours (FUN.CLIP. animals). The animals were familiar with the feeding site before their olfactory apparatus had been eliminated (clipping both flagella, see Materials and methods). Perception of wind direction, though greatly impaired, was still present in these animals because part of the scape and pedicel segments remained. The figure depicts the first, second and third approaches to the feeding site after the operation. Note that the animal behaved in a similar manner to intact ants in situations in which the feeder had been removed (see Fig. 3B,C), even though the feeder was supplied with food in the present case.

for food (Fig. 8; first run), but did not exhibit the anemotactic orientation behaviour normally triggered by olfactory input. In fact, the FUN.CLIP. animals were never observed to collect food. If, in the course of their search, they came across the feeder, they often did not recognise the food; and if they did, they handled the food crumbs with their mouthparts for extended periods (up to 10 min) and eventually left the feeder without carrying food, only to resume their search. During subsequent foraging trips (Fig. 8; second and third runs), they no longer paid particular attention to the feeding site but performed extended, and always unsuccessful, search runs.

Upon encounters with nest-mates, the FUN.CLIP. animals sometimes exhibited aggressive behaviour, which is normally restricted to encounters with conspecifics from foreign colonies (Knaden and Wehner, 1998). Removal of just one antenna had only a minor, if any, effect on the foraging behaviour of the animals (data not shown).

Discussion

Recording technique

A video system was used to record the walking trajectories of *Cataglyphis fortis* ants during their visits to a familiar feeding site (Fig. 1). Once the software and hardware components had been calibrated, this system allowed rapid computer-aided evaluation of field data. For example, walking trajectories recorded during the day might be evaluated in the

evening, allowing further experiments based on these results to be planned. This is in contrast to the conventional recording of walking trajectories on graph paper. Data recorded in this way have to be digitised on a graphics pad, a procedure that, by comparison, is much more time-consuming. Manual recording also needs a reference frame, usually a 1 m×1 m grid painted on the desert floor. Video tracking can be applied without the need for such a reference system but is, however, limited to rather short distances from the camera. Beyond 10–15 m, the accuracy of the system deteriorates rapidly to below that achieved by the manual recording technique, which is approximately 20 cm. In addition, systematic errors introduced by, for instance, uneven desert terrain, may compromise accurate orthogonal representation (see Materials and methods).

While the walking trajectory is stored on the sound tracks of the video tape, the video track allows the behaviour of the animal to be recorded. The two different patterns of search behaviour observed in *Cataglyphis fortis* ants during test runs provide an example for such behavioural recordings. When searching at some distance from the feeding site, the walking trajectories are smooth, and the animals move at a rather steady pace. However, when the ants are searching close to the feeding site, they move in a series of bursts interrupted by pauses during which they whip their antennae. The latter behaviour may be interpreted as active probing for olfactory cues expected near the feeding site.

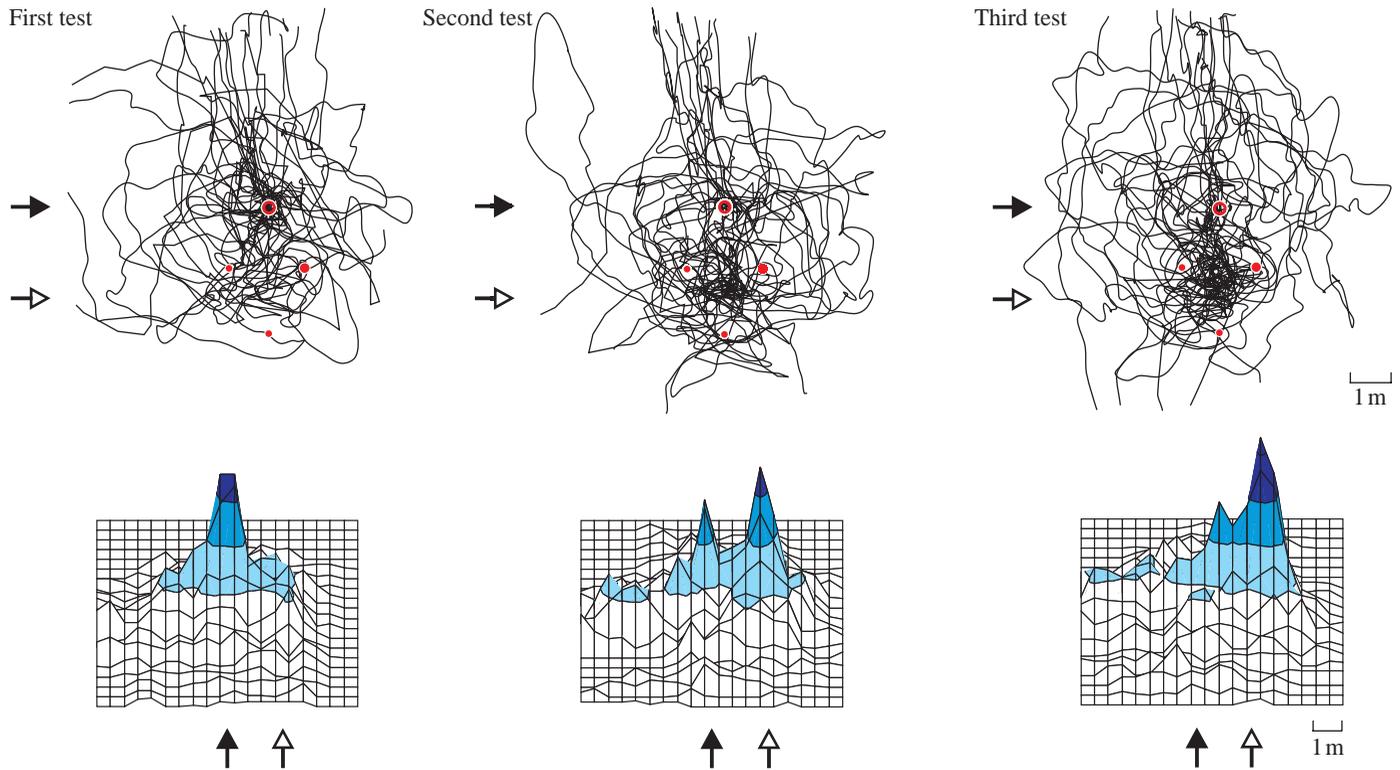


Fig. 9. Conflicting information provided by the path-integration and landmark-based navigation systems of the ants. Ants familiar with the feeding site were tested after the food source (open red circle) had been removed and after the set of familiar landmarks surrounding the feeder had been shifted from its original position by 2 m (filled red circles; in a direction away from the nest). The three data sets depict the superimposed search trajectories recorded during the first, second and third tests of six individuals from different colonies (two training runs were allowed between tests; see Materials and methods). Home direction is to the top. The graphs below each set of trajectories provide the search-density profiles calculated from the data given above. Graphs are seen in side view (compare arrows in upper and lower figures). Open and filled arrows mark the location of the feeder as indicated by the original and the displaced landmark arrays, respectively. Note the gradual shift in the search-density peak from the original location to the centre of the landmark array. Iso-density lines mark increments of 1% path length m^{-2} , and the white background corresponds to the 0–1% path length m^{-2} intervals.

Nevertheless, there is at least one drawback to the recording technique applied here. The camera system and observer are always in the same position with respect to feeding and nesting sites and, hence, by serving as landmarks, may confound the interpretation of the orientation strategies of the ants. This is of minor importance in the context of the olfactory and anemotactic orientation strategies treated in this account, but it might be a serious disadvantage if visually guided behaviour were being studied.

One set of experiments was designed to address the problem of competing landmark-based orientation and idiothetic orientation cues. During training, the feeder was surrounded by a set of landmarks. During test runs, the landmarks were moved 2 m away from the feeding site, in the direction opposite to that of the nest. Animals familiar with the feeding site from previous training visits clearly concentrated their search activity on the location indicated by their idiothetic orientation system, rather than on the location indicated by the landmarks (Fig. 9, first test). It was only during subsequent searches that the ants gradually shifted the focus of their search to the centre of the landmark array (Fig. 9, second and third tests). This shift occurred consistently in all the ants examined and highlights

the fact that experience and behavioural history are important variables in shaping the decision-making processes of the ant. It also indicates that landmark information is of minor importance during the first search run at a given location and compared with the olfactory cues discussed below.

Anemotactic–olfactory orientation strategy

The present results demonstrate that foragers of the desert ant *Cataglyphis fortis*, when visiting a familiar food source, use their dead-reckoning (path-integration) system to steer towards the leeward side of the feeder. Upon encountering the odour plume emanating from the food, they use a combination of anemotactic and olfactory cues to locate the food in the upwind direction (Fig. 2).

Several lines of evidence indicate that this strategy is a flexible and efficient means of quickly exploiting a plentiful food source (under natural conditions, this may be a larger carcass or fruit), e.g. when there is competition with members of neighbouring *Cataglyphis fortis* colonies. First, if the food is removed, foragers start searching within an area that is located downwind of the feeding site (Fig. 3) and do so in a rather systematic way, at least for the first few minutes. This

strategy ensures that areas characterised by the highest probability of encountering odour cues are searched first and most thoroughly. Second, ants adjust their initial approaches to changes in ambient wind direction (Fig. 4). They also seem to adjust their behaviour to wind speed by steering closer to the feeding site as wind speed increases (H. Wolf and R. Wehner; this is a preliminary observation and may be an adjustment to larger turbulences occurring at higher wind speeds). Third, during the initial four or five visits to a newly discovered food source, the ants appear to fine-tune their approach strategy. For instance, they adjust the distance at which they move into the downwind area of the feeder (Fig. 6). Finally, if a food item had accidentally been dislodged from the feeder, it was reliably retrieved during subsequent test runs, i.e. when the feeder had been removed. While this invalidated that test run, it confirmed the efficiency of the foraging strategy of the ants.

The experimental elimination of wind perception and olfactory input provides further proof of the orientation strategy outlined above. Immobilisation of the primary wind-sensitive structures of the antennae (in the SCAP.IMM. animals) interferes mainly with the final upwind approach of the ant (Fig. 7). Successful foraging is still possible, but it takes the ants much longer to locate the food. Some residual wind perception seemed to remain after the basal segments of both antennae had been immobilised with insect wax. This may have been due to incomplete immobilisation; e.g. a very thin layer of wax was applied, particularly at the pedicel–flagellum joint, to avoid interference with visual or olfactory inputs. Alternatively, wind sensors elsewhere on the body, e.g. filiform hairs on the antennal flagella or on the head capsule, may have provided wind information.

Elimination of olfactory input (in FUN.CLIP. animals) severely incapacitates the foraging ants (Fig. 8), and this is not due only to the missing olfactory signals, which normally trigger the ant's final upwind approach. In fact, the antennal flagella seem to be indispensable for both the localisation and recognition of food items. Foragers with clipped antennae sometimes handle food items with their mouthparts for long periods and hence clearly recognise the food substance by means of contact chemoreceptors. By closely observing intact foragers at the feeder, one realises that *Cataglyphis fortis* uses its antennae in contexts other than olfaction, contact chemoreception and wind detection. For example, the antennae apparently serve to size food items and to determine whether to carry a particular item to the nest. In the absence of antennal input, the food items might be misinterpreted as being solid structures that lack identifiable cues characterising them as food particles that might be carried home. In summary, failure to collect food items after the elimination of antennal input might result from the absence of the releasing signals essential for triggering this behaviour.

The main incentive for the ant's indirect (detour-like) approach to a food source and its use of odour cues appears to be the efficiency and reliability of the foraging process. This conclusion is illustrated by the fact that the few animals that

steered a direct course towards the feeder often missed it by a few centimetres. This usually happened under tailwind conditions or in still air. In these circumstances, the ants had to search, often rather lengthily, for the food items. Such search trajectories were almost always longer than the extra distance afforded by deviating towards the downwind area of a feeding site to pick up an olfactory food signal.

Because of the nature of the food odour cues, the olfactory orientation strategy used by *Cataglyphis fortis* ants, and described in the present account, is strikingly different from that exhibited by other species of ants when following pheromone trails (Hölldobler and Wilson, 1990). Instead, it bears a resemblance to the olfactory orientation studied thoroughly in several moths and butterflies (Kennedy, 1983). Males of many lepidopteran species approach conspecific females on the basis of the sex pheromones released into the air by the receptive females. In both ants and moths, the key elements are identical: olfactory cues serve to trigger anemotactic upwind locomotion. Moths do not fly (or walk, in the case of *Bombyx mori*) straight into the wind, but adopt an oblique upwind course. They frequently change from right to left oblique flight paths so that they increase their probability of remaining within an area filled with the odour (within the 'odour plume'). This behaviour is known as upwind counterturning (or casting if the animal has lost contact with the odour). The directional changes in the flight paths are triggered by the time structure of encounters with the odour (Kennedy, 1983; Willis and Arbas, 1997) or represent the output of an endogenous programme (Kaissling and Kramer, 1990; Kramer, 1992). The final upwind approaches of *Cataglyphis fortis* foragers often have a slight zigzag component and, in this respect, resemble the upwind counterturning behaviour described for moths within an odour plume. Anemotactic orientation and upwind courses elicited by odour stimuli in walking insects, although described for several species, have not yet been analysed in much detail (for a review, see Linsenmair 1973).

Spread of airborne substances near the desert floor

Close to the desert floor, the distribution and spread of airborne substances, such as odorants, must be different from those in open-air conditions. This is primarily due to turbulence and lower air speeds near the surface. It is important to know whether and to what extent the upwind orientation of the ant, as triggered by olfactory input is spatially related to the spreading pattern of odorants near the desert floor. We addressed this question by filling a feeder with a few drops of TiCl_4 , rather than with the usual biscuit-crumbs food items. In air, TiCl_4 develops into dense clouds of smoke carried away by ambient wind. The paths taken by the TiCl_4 plume were recorded by the video camera, digitised frame by frame and traced manually with the help of graphics software (CorelDraw). Fig. 10 shows the recorded spreading pattern of the smoke and, by inference, of the odorants normally released from the feeder. This procedure may slightly overestimate the air volume normally carrying odorants since TiCl_4 actively produces a (small) gas volume.

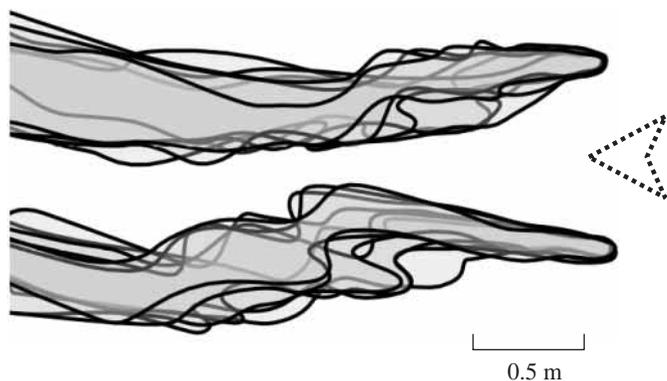


Fig. 10. Spread of a TiCl_4 smoke plume near the desert floor. The smoke plume emanating from a feeding station (right-hand narrow end of tracings, diameter 6.5 cm) was traced from video frames at 40 ms intervals. Twelve consecutive images of a smoke filament are shown in superimposed form, the six tracings taken between 0 and 240 ms at the top, the six tracings taken between 240 and 480 ms at the bottom. Wind speed was 4 m s^{-1} , and wind direction (arrowhead) was from the right.

The smoke filaments stayed close to the desert floor for distances of 3 m or more. Within that distance, they usually remained less than four times as wide as the smoke source, although occasional plume-like structures grew up to seven times as wide. The filaments undulated and formed small vortices, the size of these structures increasing with larger distances from the smoke source. At wind speeds of approximately 4 m s^{-1} , which corresponds to the conditions of most behavioural experiments reported here, most segments of a smoke filament stayed within an angular extent of $25\text{--}35^\circ$ downwind of the source. Occasional larger undulations or vortices covered 40° or a little more, particularly close to the feeder.

These data are in good agreement with the final upwind approach of the *Cataglyphis fortis* foragers (Fig. 11): most zigzag-like paths observed in the approach movements of the ant covered an angular range of $20\text{--}30^\circ$ downwind of the feeder, with some larger zigzags, which were more frequent close to the feeder, reaching 40° or a little more.

Ambient wind speed was always measured 1–1.5 m above the desert floor. When calculating the speed of isolated smoke pockets or eddies from the video recordings, lower velocity values were consistently obtained, ranging from approximately 2.5 to a maximum of 3.5 m s^{-1} . Vortices sometimes remained almost stationary for a few milliseconds. This indicates that the speed of travel of odorants near the desert floor is indeed reduced as a result of friction at the surface and the development of turbulence.

This investigation was carried out while H.W. was a Guest Professor at the Department of Zoology, University of Zurich, Switzerland. The project would have been impossible without the dedicated and excellent support of Hansjörg Baumann (electronic equipment and software routines), Helmut Heise (mechanical design), Evelyn Wacker (data evaluation) and

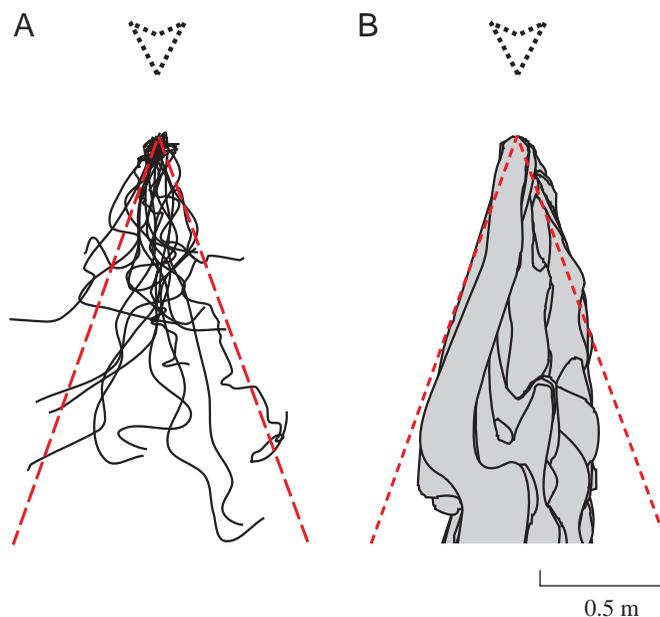


Fig. 11. Comparison of the final upwind approach of forager ants (A) and the spread of smoke plumes (B). Wind velocity was always approximately 4 m s^{-1} . (A) The final segments of 19 approaches to a feeder by eight ants (from five different colonies) are superimposed, taking wind direction (from the top, see arrowheads) and feeder location (top end of trajectories) as reference. (B) Spreading pattern of a TiCl_4 smoke plume emanating from the feeder (top end of tracings). The 25 images traced during a 1 s interval (compare Fig. 10) are superimposed. The average duration of the final upwind approach of the foragers (see A) was also approximately 1 s. An angle of 40° , marking the approximate angular extent of both phenomena, is indicated by broken red lines.

Ursula Menzi (graphical design of figures). Bärbel Herrnberger evaluated calibration data for the video tracking system, and Jessica Ausborn traced innumerable smoke filaments, such as the ones shown in Figs 10 and 11. Financial support was provided by a research grant from Schweizerischer Nationalfonds to R.W. (31-43317.95) and, during part of the project, by a Heisenberg fellowship of Deutsche Forschungsgemeinschaft to H.W. (Wo466).

References

- Gewecke, M.** (1974). The antennae of insects as air-current sense organs and their relationship to the control of flight. In *Experimental Analysis of Insect Behaviour* (ed. L. Barton Brown), pp. 100–113. Berlin: Springer.
- Hangartner, W.** (1967). Spezifität und Interaktivierung des Spurpheromons von *Lasius fuliginosus* Latr. und Orientierung der Arbeiterinnen im Duftfeld. *Z. Vergl. Physiol.* **57**, 103–136.
- Hölldobler, B. and Wilson, E. O.** (1990). *The Ants*. Harvard: Harvard University Press and Springer Verlag.
- Kaissling, K.-E. and Kramer, E.** (1990). Sensory basis of pheromone-mediated orientation in moths. *Verh. Dt. Zool. Ges.* **83**, 109–131.
- Kennedy, J. S.** (1983). Zigzagging and casting as a programmed response to wind-borne odour: A review. *Physiol. Ent.* **8**, 109–120.

- Knaden, M. and Wehner, R.** (1998). Intercolonial aggressiveness among foragers of the desert ant, *Cataglyphis fortis* (Hymenoptera: Formicidae). *Zoology* **101** (Suppl. 1), 28.
- Kramer, E.** (1992). Attractivity of pheromone surpassed by time-patterned application of non-pheromonal compounds. *J. Insect Behav.* **5**, 83–97.
- Linsenmair, K. E.** (1973). Die Windorientierung laufender Insekten. *Fortschr. Zool.* **21**, 59–79.
- Müller, M. and Wehner, R.** (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**, 5287–5290.
- Ronacher, B. and Wehner, R.** (1995). Desert ants *Cataglyphis fortis* use self-induced optic flow to measure distances travelled. *J. Comp. Physiol. A* **177**, 21–27.
- Wehner, R.** (1997). The ant's celestial compass system: spectral and polarization channels. In *Orientation and Communication in Arthropods* (ed. M. Lehrer), pp. 145–185. Basel: Birkhäuser.
- Wehner, R. and Duelli, P.** (1971). The spatial orientation of desert ants, *Cataglyphis bicolor*, before sunrise and after sunset. *Experientia* **27**, 1364–1366.
- Wehner, R., Harkness, R. D. and Schmid-Hempel, P.** (1983). Foraging strategies in individually searching ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Akad. Wiss. Lit.: Mainz, Math.-Naturwiss. Kl.* Stuttgart: Fischer.
- Wehner, R. and Menzel, R.** (1969). Homing in the ant *Cataglyphis bicolor*. *Science* **164**, 192–194.
- Wehner, R., Michel, B. and Antonsen, P.** (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129–140.
- Wehner, R. and Wolf, H.** (1998). Olfactory and anemotactic orientation towards food sources by desert ants, *Cataglyphis fortis*. In *Proceedings of the 26th Neurobiology Conference Göttingen* (ed. N. Elsner and R. Wehner), p. 23. Stuttgart: Thieme.
- Willis, M. A. and Arbas, E. A.** (1997). Active behavior and reflexive responses: Another perspective on odour-modulated locomotion. In *Insect Pheromone Research. New Directions* (ed. R. T. Cardé and A. K. Minks), pp. 304–319. New York: Chapman Hall.
- Wolf, H. and Wehner, R.** (1998). Video-tracking system for the two-dimensional recording of walking trajectories in desert ants (Genus *Cataglyphis*). In *Proceedings of the 26th Neurobiology Conference Göttingen* (ed. N. Elsner and R. Wehner), p. 22. Stuttgart: Thieme.