Desert ants compensate for navigation uncertainty

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Summary

During foraging trips, desert ants *Cataglyphis fortis* do not rely only on their well-studied path integration system, they also use olfactory cues when approaching a familiar food source. When a wind is blowing from a constant direction, as is characteristic of their desert habitat, the ants do not approach the feeder directly. They rather steer some distance downwind of the food source to pick up odour filaments emanating from the food. They follow this odour trail upwind, and find the source quickly and reliably.

This approach behaviour was examined in more detail in order to identify the underlying orientation strategy. First, the ants may employ a 'goal expansion strategy', using odour spread as a spatially limited indicator for the presence of food. In that case, the distance steered downwind of the feeder should be determined by the range of the odour plume (and, for instance, wind speed). It should be independent of the distance between nest and feeder. Second, the ants may apply an 'error compensation strategy', using odour filaments as a guideline towards the food source. Steering downwind by a margin just exceeding their maximum navigation error will lead the ants safely across the odour guide. In that case, the distance steered downwind of the feeder should increase more or less linearly with the nest–feeder distance.

Our results unambiguously support the second strategy. When feeders were established at distances of 5–75 m from the nest, the distances steered downwind of the food increased from 0.7 m to 3.4 m in a linear fashion. This result was independent of wind speed or wind direction. It translates into an ant's estimate of its navigation error within a range of 3° to 8°.

Key words: insect, *Cataglyphis fortis*, navigation, uncertainty, error compensation.

Introduction

Navigation, and especially dead reckoning by path integration, is inevitably prone to both cumulative and systematic errors (e.g. Wehner and Wehner, 1986; Müller and Wehner, 1988). This is due to inaccuracies in both direction and distance measurements, resulting in any navigation target being surrounded by an area of uncertainty within which the target may be found (Fig. 6). This holds true for animal as well as human navigation, and indeed for modern electronic navigation aids, although the latter are on a much smaller scale.

Humans have developed a number of strategies to deal with navigation errors (Gladwin, 1975; Lewis, 1994). The old seafarers, for example, often would not reach their destination to within eyesight because of navigation errors. When travelling towards a coast without distinctive landmarks, upon sighting the shore the sailors would not know whether to turn left or right to reach their goal. The solution to this problem was to steer to one side of the intended course by a margin (just) exceeding the maximum navigation error to be expected from previous experience (of course, both the correct course and the maximum navigation error had to be known from previous visits and experience). This 'error compensation strategy' leads the vessel to one side of the destination, and upon reaching the coast the navigator will know where to turn to reach the goal.

A second strategy was used by Polynesians until recent times. In the vast Pacific Ocean, small islands were difficult to locate to within eyesight without extensive searching. Navigators relied on secondary long-range indicators of the presence of land, for instance, wave patterns, clouds or sea bird behaviour. This 'goal expansion strategy' restricted the search space considerably and reduced the effort to find small islands. It is unknown whether or not animals employ similar strategies to deal with navigation errors.

Desert ants, *Cataglyphis fortis*, achieve remarkable orientation feats. Foraging trips may lead a worker ant more than 100 m – or roughly 10 000 times its body length – away from the nest entrance. Upon encountering a prey item, the ant returns to the inconspicuous nest entrance on an almost straight path, relying exclusively on its path integration system, as its salt pan habitat is almost devoid of landmarks (for reviews see Wehner, 1992, 1996). Despite such impressive orientation performance, navigation errors may prevent the animals from

directly encountering their nest entrance, which is often just a couple of centimetres in diameter. Desert ants possess a number of strategies to deal with these navigation errors and other uncertainties. For example, if they miss their nest entrance upon returning from a foraging trip, they perform a systematic search centred on the assumed location of the nest entrance (Müller and Wehner, 1994). The ants also employ their path integration system for relocating previously visited places, in particular, reliable food sources (e.g. Wolf and Wehner, 2000). However, when visiting a familiar food source, the ants do not only rely on path integration but also use olfactory and anemotactic cues (Wolf and Wehner, 2000; see also Linsenmair, 1973). When a constant wind is blowing, as is characteristic of their desert habitat, the ants do not approach the feeder directly. Rather, they steer some distance downwind of the food source, and when they pick up the odour filaments emanating from the food, they follow this odour trail upwind towards the goal (see Fig. 1). This strategy avoids lengthy searches in the case of small food sources.

We have examined the ants' downwind approach behaviour in more detail in order to identify the underlying orientation strategy. As outlined above for human navigation, the ants may employ a 'goal expansion strategy', using odour spread as a spatially limited indicator for the presence of food. In this case, the distance steered downwind of the feeder should be determined by the range of the odour plume, and thus by parameters influencing plume shape and size, such as wind speed and wind direction. Consequently, the downwind approach should be independent of the distance between nest and feeder (Fig. 1, broken lines). Alternatively, the ants may apply an 'error compensation strategy' by using the odour filaments as a guideline towards the food source. Steering downwind by a margin just exceeding the expected maximum navigation error will lead the ants safely across the odour guide and prevent them from missing even small food sources. In that case, the distance steered downwind of the feeder should increase more or less linearly with nest–feeder distance,

reflecting the ant's assessment of its maximum angular range of navigation uncertainty (Fig. 1, solid line).

Materials and methods

Experiments were carried out near the Tunisian village Maharès (34°30′N, 19°29′E) during the months of July and August in the years 2002 and 2004. A nest of *Cataglyphis fortis* Forel 1902 was selected, the surroundings of which were devoid of vegetation and other landmarks for at least 20 m in all directions, and for 100 m to the north.

Training of *Cataglyphis* to feeding sites was according to standard procedures. In short, feeders were established at distances of 5 m, 10 m, 20 m, 40 m, 50 m, 60 m or 75 m to the north of the ant nest. Initially, and in order to attract the ants to the feeding site, a trail of biscuit crumbs was laid out towards the feeder. The feeder consisted of a Petri dish, 3 cm in diameter, glued into the lid of a jar, 7 cm in diameter. This arrangement prevented food items from being blown out of the feeder and thus contaminating the desert surroundings. Furthermore, it allowed removal of the feeder without leaving an odour mark on the desert floor. The feeder was filled with biscuit crumbs of selected size (sieved to roughly 2 mm diameter). This promoted rapid and frequent visits to the feeder since the crumbs were small enough to be easily carried by foragers, and it reduced the number of (too small and lightweight) crumbs blown out of the feeder. For some experiments, ants were marked individually with a colour code (small dots of automobile varnish applied with insect pins to thorax and gaster).

Concentric circles were drawn around the feeding sites to facilitate recording of the ants' approach trajectories (indicated in Fig. 1). We noted the distance from the feeder at which the ants picked up the odour filaments and changed their courses, often quite abruptly, from a roughly tangential approach downwind of the feeder to a slightly zigzagging course directed upwind towards the feeding site (indicated as zigzag lines in

Fig. 1. 'Goal expansion' and 'error compensation' strategies. Feeders (F) were surrounded by target circles painted on the desert floor, as shown for three nest–feeder distances D. The target circles were used for recording the ants' downwind approach distances d. The ants' approach towards the feeder may be governed by two alternate strategies: expectation according to the 'error compensation strategy' (solid line) and expectations according to the 'goal expansion strategy' (dashed lines; for details see text). Downwind angle α is indicated for comparison with d; at 20 m nest–feeder distance, a schematic distribution of approach distances is illustrated, typical of, although narrower than, those recorded in the present experiments (compare Fig. 4).
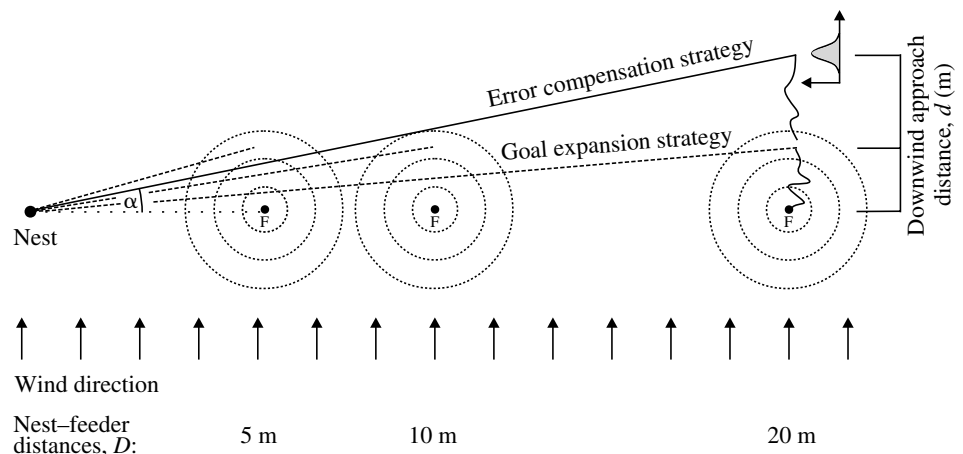
Fig. 1). Along with this 'downwind distance', termed *d*, we recorded the nest–feeder distance, the date and time of day, wind direction, wind speed and animal identification in those cases where the ants had been marked individually.

Ants change, and presumably optimise, their approach trajectory during their initial visits to a familiar feeding site (see for example fig. 6 in Wolf and Wehner, 2000). We, therefore, waited for at least 1 day after the ants had been trained to a new feeding site before we started to record their approach trajectories. It was at least partly because of this gradual optimisation of approach trajectories that the variance of the recorded downwind approach distances was almost as large for any given individual ant as it was for different individuals (when comparing their mean values). Therefore, we used all measurements of downwind approach distances, irrespective of whether or not individual ants had contributed more than one measurement, but did so only for the construction of distribution diagrams (Fig. 4). For statistical analyses of significance levels and regression lines (e.g. Fig. 5) we first averaged the values obtained for any given individual and used the resulting mean values for further (second order) statistical analyses. Hence, in all statistical treatments, each ant contributed just a single datum point. Since unmarked ants could not be differentiated they were regarded as a single individual for the purpose of statistics. For our data set, this treatment reduced the significance level of regression analyses and was thus regarded as conservative. This was due to the (sometimes greatly) reduced number of individuals (*N*), even though the variance of several individuals was thus collapsed into a single datum. Statistical analyses were performed according to Sachs (1992) and Sokal and Rohlf (1995). In the text below, *N* signifies the number of animals, and *n* the number of measurements made.

Results

When approaching a familiar feeding site, desert ants usually do not steer a direct course toward the goal – as would be expected from exclusive use of their path integrator – but rather steer some distance downwind of the food source (Fig. 1). This strategy leads them across the odour plume emanating from the food and enables them to find even small food items rapidly (Wolf and Wehner, 2000). We used this downwind approach to test the underlying orientation strategy, in particular, to differentiate between the 'goal expansion' and the 'error compensation' strategies, as outlined in the Introduction (see also Fig. 1). We therefore examined the downwind distance of the ants' approach, hereafter referred to as *d* (Fig. 1). We were especially interested whether *d* depended on parameters that affect odour spread, such as wind speed and turbulence, or on parameters that reflect navigation uncertainty, such as the nest–feeder distance.

Wind speed

First, we examined the dependency of *d* on wind speed (Fig. 2). In the Tunisian desert near Maharès, wind speeds
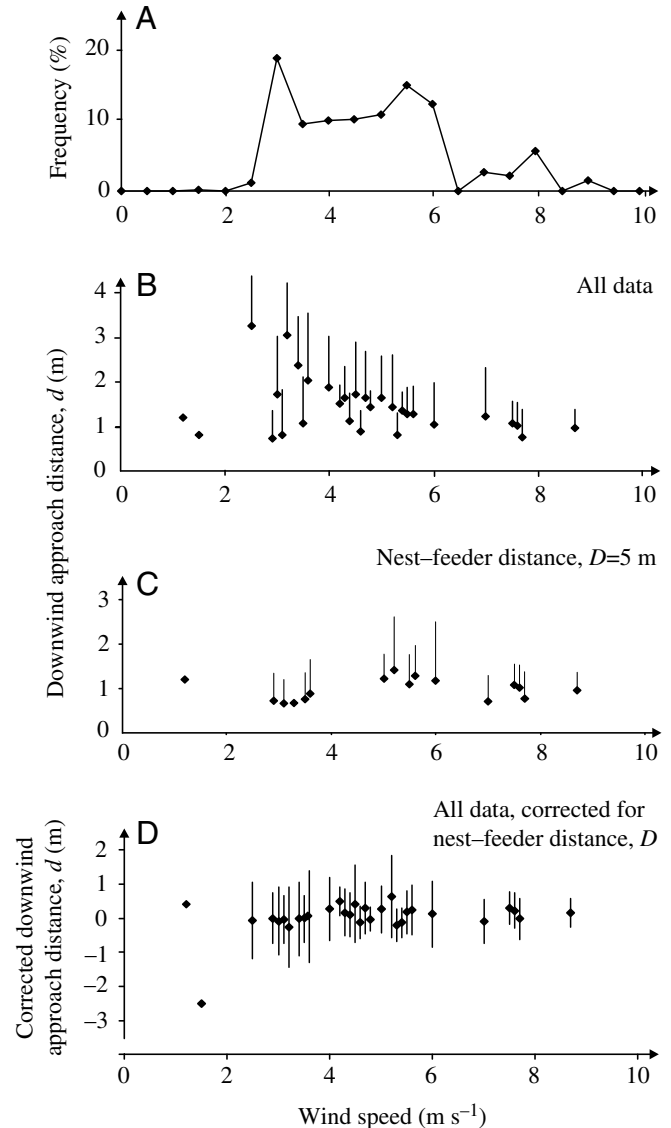

Fig. 2. Relationship between downwind approach distance *d* and wind speed. (A) The distribution of wind speeds in the desert near Maharès (bin width 0.5 m s^{-1}; recordings (*n*=1961) taken between ca. 08:00 h and 16:00 h, between 19 August and 5 September 2002, and 22 June and 3 July 2004). (B,C) The relationship between wind speed (bin width 0.1 m s^{-1}) and downwind approach distance *d*. In B, data from all experiments are pooled; in C only data recorded for the 5 m nest–feeder distance are shown. (D) The pooled data from all experiments, as in B, but the individual values were corrected for the dependency of *d* on nest–feeder distance *D*, effectively eliminating any bias introduced by this dependency into the relationship between wind speed and *d*. Values are means ± S.D. (D), +1 S.D. (B,C).

usually range from 3 to 6 m s^{-1} (Fig. 2A). Lower wind speeds occur regularly in the early morning, though mostly before *Cataglyphis* starts to forage. At wind speeds around 8 m s^{-1} locomotion of the ants becomes noticeably impaired, and towards 9 m s^{-1} the ants quit foraging.

Fig. 2B illustrates that *d* depends on wind speed only marginally, if at all. When data for all nest–feeder distances

and all wind speeds are pooled, there is a small but significant negative slope of the resulting graph (–0.17, different from 0 with $P<0.001$; $r^2=0.0625$). This means that at higher wind speeds, the ants appear to steer closer to the feeding site, presumably as the result of a smaller range of the odour plume and more turbulent air flow under these conditions.

However, the different wind speeds were not evenly spread among the different nest–feeder distances. In fact, the lower range of wind speeds prevailed during experiments where nest–feeder distances of 5 m and 10 m were examined. Considering the dependency of the downwind approach on nest–feeder distance (see below), this may have skewed the relationship depicted in Fig. 2B. We therefore analysed the data for the different nest–feeder distances separately. Fig. 2C shows the data sample collected for the 5 m nest–feeder distance. This experiment happened to cover the broadest range of wind speeds (1.2–8.7 m s^{-1}), although there was no dependency of d on wind speed (slope=0.02, not different from 0 with $P>0.1$; $r^2=0.0025$).

This observation prompted us to perform an analysis of covariance (ANCOVA; see Sokal and Rohlf, 1995) to differentiate the dependency of d on wind speed from that on nest–feeder distance, D (see Fig. 5). Fig. 2D shows the same data set as Fig. 2B – pooled observations from all experiments – but the data were now corrected for the dependency of d on D. It is immediately evident that the small negative slope visible in Fig. 2B has disappeared completely, and no dependency of d on wind speed is discernible. Not surprisingly, therefore, the analysis of covariance did not yield a significant correlation either ($P>0.1$; $r^2=0.0144$).

We also tried to examine the influence of wind turbulence. A dense row of pebbles was arranged perpendicular to the prevailing wind direction just downwind of the feeding site. This should significantly alter turbulence close to the desert floor (see also fig. 10 in Wolf and Wehner, 2000) and downwind of the feeder. Initially, the ants did not appear to alter their downwind approach after this manipulation. However, they quickly recognized the pebbles as landmarks and approached the end of the pebble row that was closest to the nest. This prevented any meaningful continuation of this experiment.

Wind direction

In our experimental area, wind patterns are remarkably reliable during the summer. Eastern winds prevail at daytime, as illustrated in Fig. 3A. Changes in wind direction in the morning and late evening (Wehner and Duelli, 1971) are mostly irrelevant for the strictly diurnal *Cataglyphis* foragers. It is mostly during unusual weather conditions, such as sand storms, that strong winds blow from other directions during the day. However, *Cataglyphis* does not forage under most of these conditions, that is, either under completely overcast skies or at wind speeds exceeding 9 m s^{-1}.

The distance d did not depend in any notable way on wind direction. The best-fit regression line follows the term $y=0.0006x+0.755$ (slope not significantly different from 0,
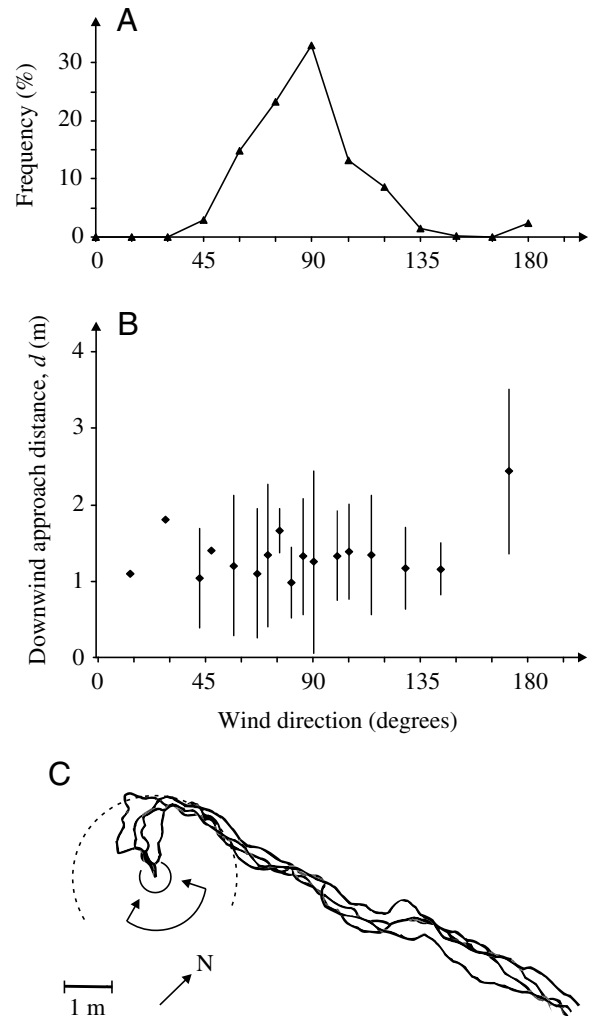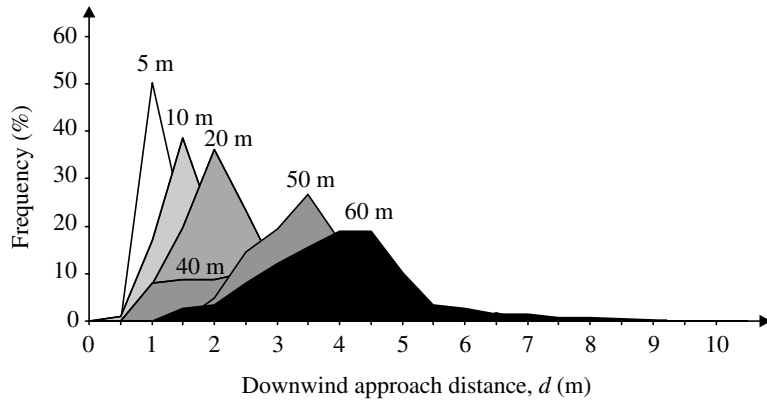

Fig. 3. Relationship between downwind approach distance d, and wind direction. (A) The distribution of wind directions in the desert near Maharès (bin width 15°, east is at 90°; recording times as in Fig. 2A; wind directions above 180° were not observed during the present experiments). (B) The relationship between wind direction and d; values are means ± 1 s.D. (C) Four approaches of an individually marked ant to a feeding site are superimposed (actual feeder was just 30 mm in diameter; its location is indicated by a 67 cm circle centred on the feeding site). As indicated by arrows, wind directions were slightly different from one approach to the next. The ant's final approaches were always against the wind. The broken circle centred on the feeder has a radius of 1.75 m.

$P>0.1$; $r^2=0.0324$). This was true for the data pooled from all nest–feeder distances (Fig. 3B), as well as for the separate evaluation of the different nest–feeder distances.

Details of the ants' approach trajectories may contribute to the independence of d from wind direction. The ants approach a familiar feeding station on idiosyncratic though more or less linear paths and aim at a lateral (downwind) distance d that has probably been established in the course of previous visits (Wolf and Wehner, 2000). If the animals have not encountered the food odour until they have reached a position where the

Fig. 4. Distribution of downwind approach distances *d*, for different nest–feeder distances *D*. The histograms illustrate the distributions recorded at the nest–feeder distances given above the bin peaks (bin widths 0.5 m). Different histograms are distinguished by different shadings. For the different nest–feeder distances *D*, the numbers of recordings (*n*) and ant individuals (*N*) were as follows: *D*=5 m, *n*=747, *N*>21; *D*=10 m, *n*=420, *N*>24; *D*=20 m, *n*=668, *N*>29; *D*=40 m, *n*=127, *N*>8; *D*=50 m, *n*=41, *N*>11; *D*=60 m, *n*=165, *N*>10; *D*=75 m, *n*=6, *N*=3. Half widths of the distributions correspond to angles of 8.8° for *D*=5 m, 5.8° for *D*=10 m, 3.8° for *D*=20 m, 5.2° for *D*=40 m, 2.0° for *D*=50 m and 2.4° for *D*=60 m.

feeder is roughly perpendicular to their approach path, they often adopt a curved trajectory, centred, more or less, on the feeder (Fig. 3C; see also fig. 2 in Wolf and Wehner, 2000). Hence, during the last part of their downwind approach, the ants may keep an almost constant distance to the feeder until they pick up the odour trail.

Nest–feeder distance

Different feeding sites were established at distances of 5 m to 75 m from the nest (see Fig. 1). Beyond a distance of about 20 m it became increasingly difficult to train ants to the feeder. There were two reasons for this. First, the animals were reluctant to travel such large distances at all. Instead, they searched for and exploited other food items, such as small insect carcasses, on the way. Beyond 40 m this was often true even if the ants had been familiar with the feeding site. The risk of experimental animals being eaten by predators also increased noticeably with larger nest–feeder distances. Second, ants from neighbouring nests inevitably discovered the feeding stations, where they often proved more numerous and competitively superior. As a consequence, the number of observations gradually declined towards larger nest–feeder distances. In the course of a week, only three ants could be trained to a nest–feeder distance of 75 m, and they visited the feeder just six times.

The distributions of *d* values observed at the different feeding sites are presented, in histogram form, in Fig. 4. First, it is immediately apparent that the peak values (as well as the means) of the distributions consistently increase with increasing nest–feeder distances, *D*. On average, the ants' feeder approach distance, *d*, was larger the farther away from the nest the feeder was located. The corresponding relationship between downwind approach and nest–feeder distance is shown in Fig. 5A. This relationship proved linear with high significance. The best-fit regression line follows the term $d=0.046D+0.56$ (values in metres; slope different from 0 with $P<0.0001$, $r^2=0.7225$, $t=13.31$). This translates into downwind angles steered by the ants when approaching the feeder of 3° to 8°.

This angular range of 3° to 8° results from the intercept (offset) of 0.56 m in the above equation. When the regression line is shifted down the ordinate to intersect it at zero, the
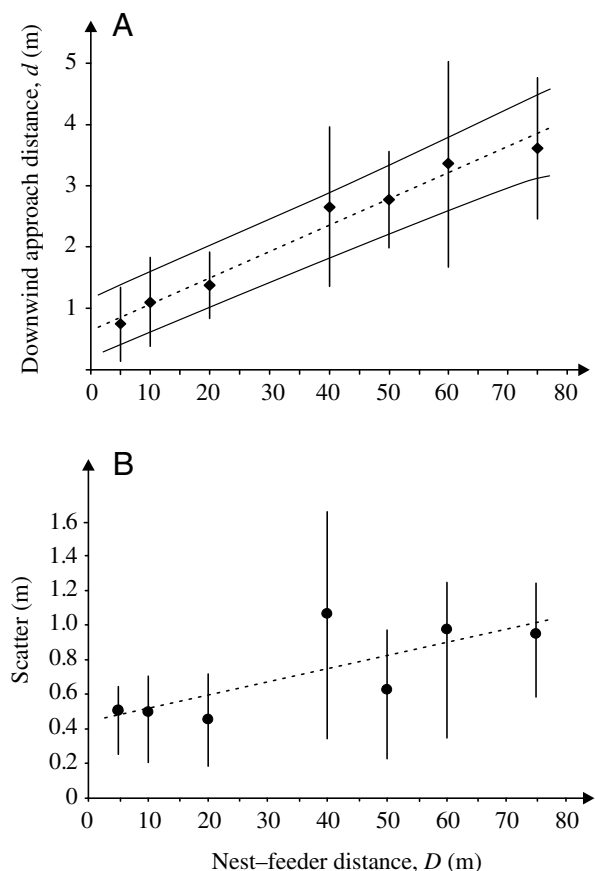

Fig. 5. (A) Relationship between downwind approach distance *d* and nest–feeder distance *D*. Same data set as in Fig. 4. Dotted line indicates the best-fit regression ($d=0.4D+0.56$), thin lines mark 95% confidence intervals. Measurements for each individual were pooled before calculating means, S.D. and regression line. (B) Relationship between the scatter of the downwind approach distance *d* and the nest–feeder distance *D*. Same data set as in A and Fig. 4. The dotted line indicates a trend line (scatter$_d$=0.008D+0.443, values in m; a regression line was not constructed since the data points were not normally distributed, because the scatter was calculated as absolute values of the difference between *d* and the mean of *d*). 25% and 75% percentiles are given. The values for 40 m nest–feeder distance showed unusually high scatter, as a result of the experimental conditions; see text.

resulting downwind angles average 3.0° over all nest–feeder distances (values for the actual feeders are 1.6° at 5 m, 3.1° at 10 m, 2.4° at 20 m, 3.1° at 40 m, 2.6° at 50 m, 2.7° at 60 m and 2.3° at 75 m).

Second, the distributions of d values becomes broader and the peak values lower, the larger the nest–feeder distances are. This is evident in Fig. 4, and is also indicated by the standard deviations depicted in Fig. 5A. This observation seems to indicate that the ants' navigation uncertainty increases with increasing distance of the goal. We therefore analysed the scatter of d in some more detail. Scatter values were calculated as the difference between a given measurement of downwind approach distance, d, and the mean of all d values for the particular nest–feeder distance, D (taken as absolutes; this measure is closely related to the standard deviation). This was done for the same data set as in Fig. 4, that is, for the pooled data from all trials (see Materials and methods; examining within-animal and between-animal scatter separately yielded similar results, not shown). Fig. 5B shows the relationship between the scatter of d and the nest–feeder distance, D. A trend line follows the term: $scatter_d = 0.008D + 0.443$. A regression line was not determined since the data points are not normally distributed, partly because of the calculation procedure mentioned above. The angles subtended by the half-widths of the distributions decline from 9° to 2° as the nest–feeder distances increase from 5 m to 60 m (inset in Fig. 1 illustrates the distribution of approach distances in the experimental setting). These values agree surprisingly well with the downwind approach angles mentioned above. The scatter for the 40 m nest–feeder distance is exceptionally high, perhaps because of one particular experimental situation: just before this feeding site was established in 2002, a thunderstorm moistened the soil to a degree that the desert floor became slippery even for the ants. The soil took more than two weeks to dry to its previous surface structure.

Third, despite somewhat different conditions between the various experiments, the results were remarkably consistent. The particular situation for the 40 m nest–feeder distance has just been mentioned, and the large scatter in this experiment was the only notable exception to the otherwise observed consistency. Data for the 5 m, 10 m and 20 m nest–feeder distances were also collected in 2002 but with dry and sunny weather throughout. Nest-feeder distances of 50 m and beyond were examined in 2004.

Finally, the numbers of animals contributing to the distributions were quite different, ranging from more than 29 to three individuals (for detailed data see legend of Fig. 4).

Discussion

When approaching a familiar feeding site, desert ants usually do not rely exclusively on their path integration system. When a constant wind is blowing, the animals do not follow a direct course toward the goal but rather steer some distance downwind of the food source. This strategy leads them across the odour plume emanating from the food, and enables the ants to locate even small food items rapidly (Wolf and Wehner, 2000). Otherwise such small food items (e.g. insect carcasses) might well be missed because of the inaccuracies inherent in the ants' path integration system (Wehner and Wehner, 1986; Müller and Wehner, 1988).

We used this downwind approach behaviour to examine the orientation strategy employed by the ants. In particular, we wanted to differentiate between the 'goal expansion' and the 'error compensation' strategies outlined in the Introduction (see Fig. 1). The major finding of the present study is the clear linear relationship between the downwind distance, d, steered by the ants when approaching a familiar feeder and the distance, D, between nest and feeding site (Fig. 5A). This is clear proof that *Cataglyphis fortis* ants employ an 'error compensation' strategy. Significant contribution of a 'goal expansion' strategy can be ruled out since the ants' behaviour – the downwind approach distance, d – is independent of parameters affecting odour spread, such as wind speed (Fig. 2), turbulence or wind direction (Fig. 3). This is the first demonstration of the use of an 'error compensation' strategy in animal navigation, whereas both 'error compensation' and 'goal expansion' strategies are well-documented in human navigation (Gladwin, 1975; Lewis, 1994).

In detail, the range of 3° to 8° that the ants have been observed to steer downwind of the direct course to the feeder might be interpreted as the ants' own assessment of their navigation uncertainty (see Introduction). This holds true when assuming that the animals optimise their approach under time and energy constraints. The optimal downwind angle should just exceed the ants' navigation uncertainty: a smaller angle, on the one hand, may occasionally lead the animals into the area upwind of the food source, that is, past the range of the odour plume. This would necessitate intensive searching for the food target. A larger downwind angle, on the other hand, would result in unnecessarily long approach trajectories.

For the sake of illustration let us assume that in the ant's path integrator, the target (feeding site) is surrounded by a range of uncertainty (Fig. 6, grey area). This uncertainty range has a directional (angular) and a distance (linear) component. And while these uncertainty components are most probably symmetrical with regard to the goal, the search space produced by this uncertainty range is polarised with respect to either component. This is due to (i) the wind carrying the food odour in one direction only (polarisation of the angular component), and (ii) foraging ants acquire strong sector selectivity, that is, they eventually restrict their foraging to a narrow sector of their nest surroundings within which they acquire and use landmark-based route integration (linear component) (Wehner, 1987; Wehner et al., 2004). To reduce search time, the foraging ant should take advantage of this asymmetry by heading towards the segment of search space (grey area in Fig. 6) that contains maximal information. In the case of the angular component, this is the downwind area (as described in the present account), and in the case of the linear component, this is the area closer to the starting point (the nest) and familiar to the ant by previously acquired landmark information. As to the latter
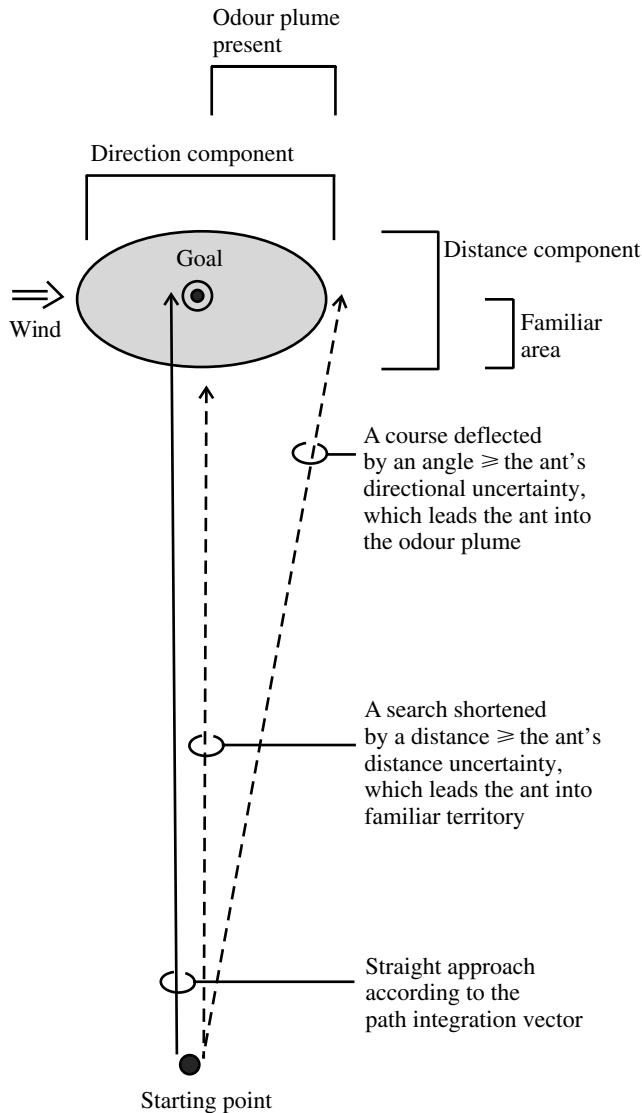
Fig. 6. Schematic illustration of the significance of the ants' 'error compensation strategy'. The goal (feeder) is surrounded by an uncertainty range (grey area). This uncertainty range has a directional (angular) and a distance (linear) component. For details and rationale see text.

aspect, it has indeed been observed that ants foraging within narrow linear channels search within a near-target range that is closer to the starting point rather than centred on the target itself (Sommer and Wehner, 2004).

Is this interpretation realistic? Indeed, are there other, preferably independent, ways to determine the ants' navigation uncertainty? There are several factors that indicate that it is realistic. First, the width of distributions of *d* values (Fig. 4, scatter of approach distances in Fig. 5B). The scatter of *d* values for a particular feeding site may be interpreted as a direct measure of the ants' navigation uncertainty, whatever the underlying causes (such as genuine navigation constraints of the ants, substrate structure, obstacles, etc.). Conspicuously, and in support of the above interpretation, the half widths of

the distributions were in the range of 2° to 9° (see inset in Fig. 1 for an illustration of distribution of *d* values; regression line in Fig. 5B corresponds to 1–5°).

Second, the search density distributions of foragers returning to the nest vary with their return distances. This has been demonstrated in experiments where ants are intercepted on their return from an artificial feeder and relocated to unfamiliar territory where they search for the nest entrance (e.g. Müller and Wehner, 1994). The widths of the search density profiles should reflect the expected navigation error since, at least initially, the ants should concentrate their search on the area predicted by their assumed navigation uncertainty. Nest-feeder distances of 0 m, 5 m, 15 m and 50 m were examined in previous studies (L. Bernasconi, Y. Nieuwlands and R.W., unpublished data; see also fig. 3.35 in Wehner, 1992). At a distance of 0 m (the animals were caught on their return right at the nest entrance) the half width of the search density profile was about 2.2 m. This may correspond to the intercept of 0.56 m in the equation describing the relationship of *d* on nest–feeder distance (see Fig. 5A). When this offset is subtracted from the (re-evaluated) half widths of the search density distributions observed at 5 m, 15 m and 50 m, the corresponding error angles are 6°, 7° and 3°, respectively. These values are indeed in the range to be expected if the ants' downwind angle reflected navigation uncertainty.

Third, the standard deviations of *Cataglyphis*' actual return paths, as reported in previous publications. Müller and Wehner (1988) investigated systematic navigation errors that occur when unilateral turns are imposed on the ants during their outbound journey. These systematic errors shed light on the underlying orientation algorithm that may in itself provide an idea about navigation uncertainty (below). What is of interest in the present context is the angular scatter of the return paths. Müller and Wehner (1988; fig. 2B therein) provide standard deviations superimposed onto the systematic navigation errors. These deviations average 9° (range 3° to 20°) if the ants can use polarised skylight as a compass cue but have no landmarks to support orientation. This is again close to the uncertainty angles mentioned above.

Fourth, the angular navigation errors to be predicted from the path integration algorithm just mentioned (Müller and Wehner, 1988) are difficult to determine in the context of realistic foraging situations. The errors produced during turns usually cancel out in the course of a foraging trip since right and left hand (or rather, tarsus) turns occur with almost equal frequency (Wehner and Wehner, 1990). The lower range of systematic errors, associated with imposed turns of 60° to 90°, is between 6° and 9° (fig. 2 in Müller and Wehner, 1988).

In summary, the published data that allow a comparison with the present results support the interpretation that the downwind approach of *Cataglyphis* foragers actually reflects the ants' own assessment of their navigation uncertainty.

At present, the question of how the ants acquire a measure of navigation uncertainty cannot be answered conclusively. It appears, however, that the downwind approach is optimised in the course of the initial few visits of a feeding site. The

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approach trajectory of individual ants often moves closer to the feeder during these initial visits and stays fairly constant later on (fig. 6 in Wolf and Wehner, 2000). This observation indicates that learning is involved in the adjustment of the approach trajectory, although the criteria that govern learning and therefore may define an optimal strategy remain unclear.

In conclusion, the results of the present study are in full accord with the assumption that foraging ants employ an 'error compensation strategy'. That is, the animals are informed about the spatial extent and asymmetric structure of the uncertainty range surrounding their goal. Also, the ants adjust the angular and linear component of their goal-directed (outbound) vector in such a way that they hit that sector of the predicted uncertainty range that contains most navigational information.

The 'error compensation strategy' employed by *Cataglyphis* ants is just one element in a suite of behaviours used to deal with navigation uncertainty. The systematic search initiated when the entrance is missed upon return to the nest has already been mentioned (Introduction; Wehner and Srinivasan, 1981; Müller and Wehner, 1994). Similarly, when a feeding site is missed, a comparable search is performed, although this one is centred on an area downwind of the food target (Wolf and Wehner, 2000). It will be interesting to examine, in future studies, whether *Cataglyphis* is able to quantitatively adapt its strategies in dealing with navigation uncertainties to the environmental situation, such as terrain familiarity or odour spread.

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