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Current Biology 24, 1–5, May 5, 2014 ©2014 Elsevier Ltd All rights reserved http://dx.doi.org/10.1016/j.cub.2014.02.056

Report

Desert Ants Locate Food by Combining High Sensitivity to Food Odors with Extensive Crosswind Runs

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Summary

Desert ants feeding on dead arthropods forage for food items that are distributed unpredictably in space and time in the food-scarce terrain of the Saharan salt pans [1]. Scavengers of the genus *Cataglyphis* forage individually and do not lay pheromone trails [2]. They rely primarily on path integration [3] for navigation and, in addition, use visual [4] and olfactory cues [5–7]. While most studies have focused on the navigational mechanisms of ants targeting a familiar place like the nest or a learned feeding site, little is known about how ants locate food in their natural environment. Here we show that *Cataglyphis fortis* is highly sensitive to and attracted by food odors, especially the necromone linoleic acid, enabling them to locate tiny arthropods over several meters in distance. Furthermore, during the search for food, ants use extensive crosswind walks that increase the chances of localizing food plumes. By combining high sensitivity toward food odors with crosswind runs, the ants efficiently screen the desert for food and hence reduce the time spent foraging in their harsh desert environment.

Results and Discussion

We tracked foraging ants from nests at the edge of a salt pan using GPS. During foraging trips, the ants covered distances of up to 1,238 m (n = 73 ants from three nests; walking distances of complete trips ranged from 32 to 1,238 m; median walking distance, 348 m; maximal distance away from nest, 356 m; see Figure 1A and Figure S1A available online), and around half of the ants successfully found food. The maximum journey length described here is much longer than any *Cataglyphis* run reported before (see, e.g., [8]). In their heterogeneous habitat, paths were not uniformly distributed, as in more homogenous environments [9–11]. Nests were at the edge of the salt pan, and ants restricted their foraging to the salt pan itself.

To investigate the food-locating capabilities of *Cataglyphis fortis*, we placed individual dead crickets (size, 5 mm) in the salt pan (at a range of distances up to 100 m from the edge of the salt pan where the nests were located) and measured the time before ants discovered them. The crickets were located on average in less than 4 min (n = 61; all crickets were detected; mean detection time, 3:26 min; maximal detection time, 14:01 min). How do ants manage to detect food so quickly?

Plume Following

While tracking ants on a test field, we observed that they approached a given food item only after passing it downwind and encountering the odor plume emanating from the dead insect (n = 54 ants; see Figure 1B). Ants that passed the food item upwind did not approach, even when only a few centimeters away. In these conditions, food approach seems to be exclusively driven by olfaction.

To investigate the functional reach of a food plume, we attached a dead insect to a stick and placed it upwind of foraging ants at varying distances (n = 93 ants; see Figure S1Bi; further details are available in the Supplemental Experimental Procedures). The number of ants responding decreased with increasing distance to the food item (Figure S1Bii; n = 85 ants; Pearson's linear correlation coefficient, r = −0.87). The distance at which 50% of the ants responded was 3.3 m, and the maximal response was 5.9 m (Figure S1B). We conclude that ants detect tiny food items by means of olfaction over distances of several meters. Following an odor plume to its source is a widespread orientation strategy for locating resources of interest, such as a feeding site, a mating partner, or a host, and is found in animals as diverse as fruit flies [12, 13], moths [14–18], cockroaches [19], desert ants [6, 7], fish [20], and birds [21].

How Do Ants Locate a Plume?

During plume following, some insects are known to respond to plume loss with casting flights in which they travel perpendicular to the wind (see, e.g., [12–18]). Only a few studies have investigated how animals initially find odor plumes and whether they also do so by moving crosswind. Male gypsy moths searching for mates do not pay attention to wind direction [22], and tsetse flies preferably head downwind when searching for an odor plume [23]. On a larger scale, wandering albatrosses perform long crosswind flights when foraging [21]. How do ants scan the desert efficiently for prey so that they limit their exposure to potential predation and the heat of the desert [24, 25]?

While tracking ants, we observed individuals taking long crosswind walks interrupted by short upwind segments (about 2 m), when ants pinpointed some kind of organic material that was probed and either rejected or picked up and brought back to the nest (Figure 2; see also Movie S1). To further explore this search behavior, we stationed ourselves in the salt pan and tracked paths of a random selection of foraging ants while simultaneously recording wind direction (n = 24 ants; Figure 3A, black paths). For the first 10 m of the path, the mean walking directions are shown in Figure 3B (outer circle). The wind direction was rather constant during these recordings (Rayleigh test, $Z = 18.5$; $p < 0.05$; Figure 3B, inner circle). For each of these ants, we looked at the directions of the path relative to the wind at 1 s intervals (see Figure 3C). Twenty-three out of 24 runs showed a significant directional bias relative to the wind (Rayleigh test, $p < 0.05$). Figure 3D (outer circle) shows the mean direction of these paths relative to wind direction. The ants exhibited a median deviation of 27.5° from a crosswind direction, and significantly more paths were within a 30° crosswind sector than would be expected for random heading directions (n = 24 ants; Chi-square test, $\chi^2 = 7.5$; $p < 0.05$). With this deviation from crosswind, the area of desert screened is close to optimal (Figure S2A). We conclude that

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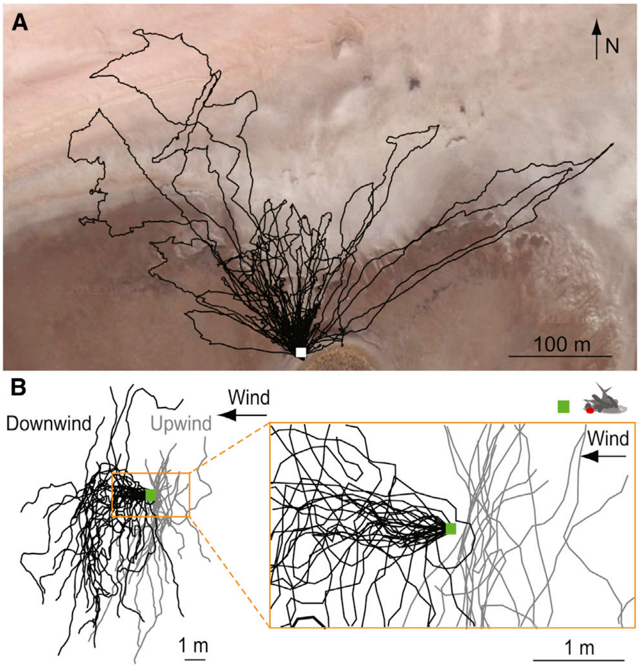

Figure 1. Desert Ants Locate Food Items by Means of Olfaction

(A) Foraging paths of food-searching ants ($n = 39$ ants; white square, nest position; for paths of neighboring nests, see Figure S1A).

(B) Olfactory-guided food approach. Thirty out of 37 (81%) of the ants that passed downwind of a food item (green square) approached it (black trajectories; $n = 37$ ants). Gray trajectories depict ants that passed the food upwind and never approached the food item ($n = 17$ ants; none of the ants approached food). Ants encountering the odor plume (i.e., passing the food downwind) pinpointed the food item significantly more often than ants not encountering the food plume (Fisher's exact test, $p < 0.05$).

See also Figure S1.

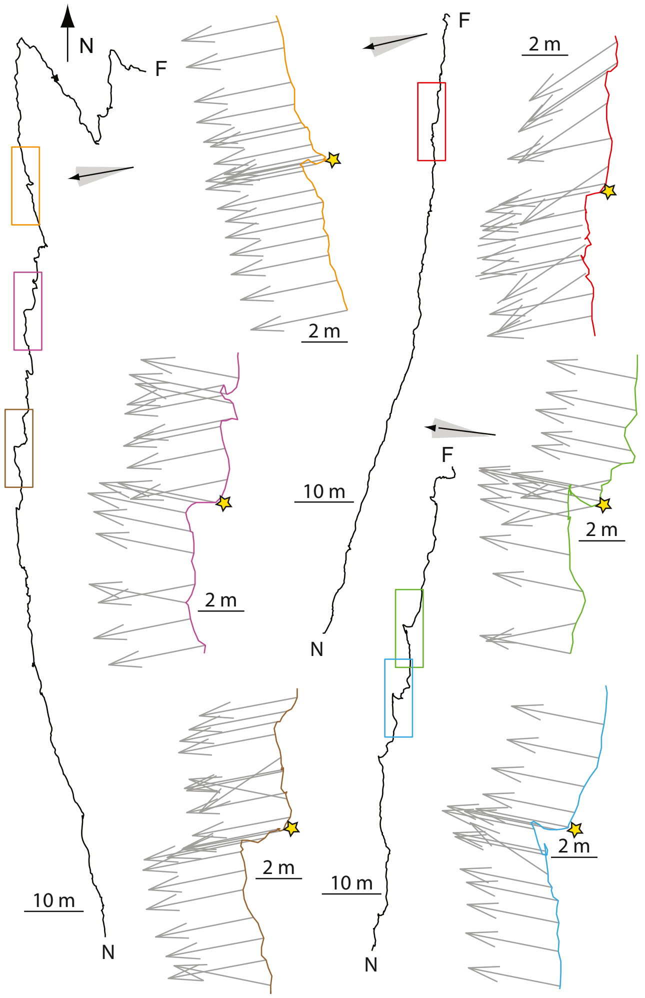

Figure 2. Transitions from Crosswind to Upwind Movements

Food search of three individuals shown in Figure 1A. N, nest; F, food. Wind direction for full runs is shown as mean direction ± circular SD. Crosswind walks were interrupted by short upwind segments (about 2 m). After probing and refusing a potential food item (marked with stars), the ants switched to crosswind again. Transitions between crosswind and upwind are color coded and shown in detail. Arrows depict wind direction measured every second but, for clarity, shown every 3 s only. See also Movie S1.

the ants do not search randomly for food, but rather adopt directions close to crosswind.

A commonly reported aspect of ant navigation is that individuals show sector fidelity. After initially adopting arbitrary directions when naive, individuals tend to focus their search within a restricted area where they previously have been successful [9–11]. By encoding and integrating information about direction and distance, foraging ants return to a familiar feeding site using path integration [26, 27]. However, ants retain the necessary flexibility to find food that is unpredictably distributed by responding to food plumes independently of whether they are close to the previously visited food site [28] and the tendency to search beyond that position when food is not encountered [27, 29]. As different individuals visit different sectors, the whole area surrounding the nest can be exploited. At first glance, this may seem to be at odds with maximizing the amount of crosswind walking, which depends on current wind direction. We found that when leaving the nest, ants initially chose directions that were not structured relative to the wind direction (inner circle in Figure 3D; $n = 52$ ants; Chi-square test, $\chi^2 = 0.1$; $p > 0.05$), but were significantly directed toward the salt pan (Rayleigh test, $Z = 42.4$; $p < 0.05$; brown paths in Figure 3A and outer circle in Figure 3E). The wind direction was uniformly distributed in all directions (Rayleigh test, $Z = 0.7$; $p > 0.05$; Figure 3E, inner circle). The walking directions relative to wind directions (shown in Figure 3D; see also Figure S2B) were significantly different between the path segments far away from the nest and the initial path segments (Chi-square test, $\chi^2 = 31.9$; $p < 0.05$). The two groups also differed significantly regarding their direction relative to geographic north (Mardia-Watson-Wheeler test, $W = 15.9$; $p < 0.05$; outer circles in Figures 3B and 3E; see also Figure 3A). Thus, our data are consistent with outbound runs that have two components: ants initially head back to a previously visited foraging area and then increase their probability of locating a food item by adopting crosswind directions.

Theoretical work may explain how optimal course headings relate to wind conditions [30–32]. Crosswind casting might be the best strategy to search for plumes in steady wind, but can be the worst for locating a plume when the wind shifts by more than 60° [32]. Indeed, for *Drosophila*, it has been reported that search is optimized by adaptation of flight headings to wind conditions [33]. Under steady wind, flies screen the environment for odor plumes by flying crosswind, whereas under changing wind, upwind flights are preferred. In the natural

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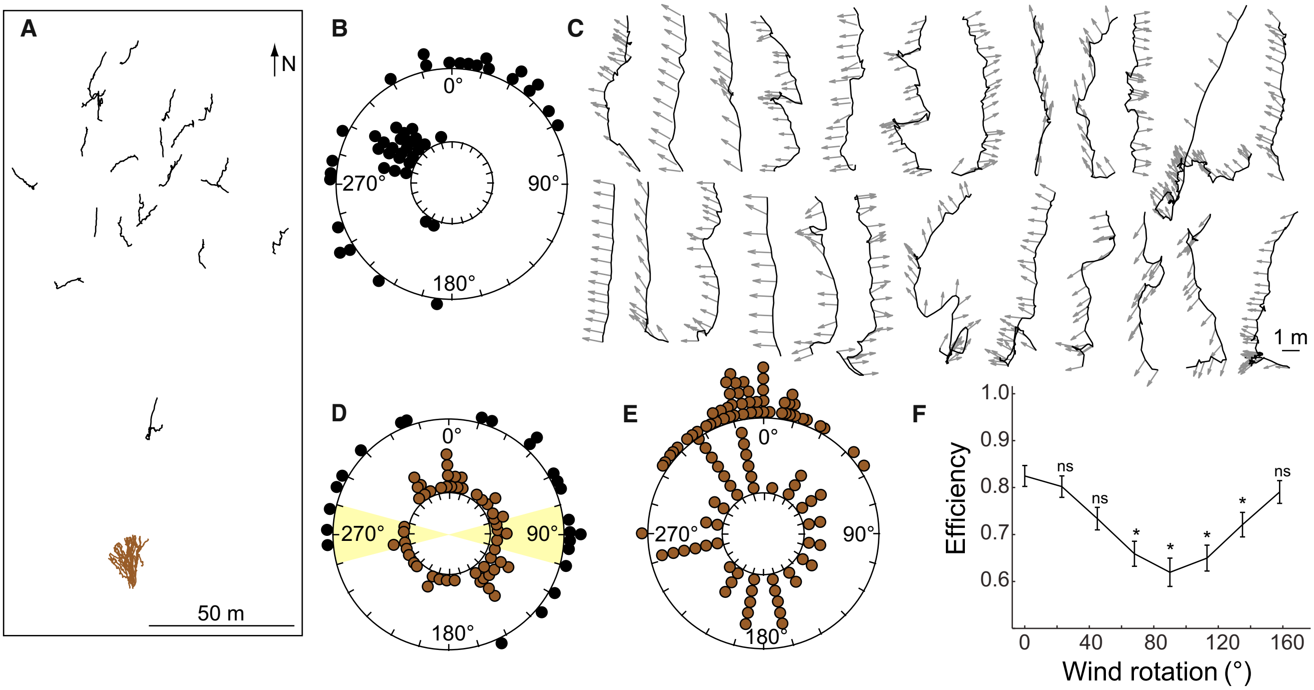

Figure 3. Ants Undertake Extensive Crosswind Movements

(A) Beeline segments (10 m) from 24 foraging ants recorded far away from the nest (black paths) and from 52 ants leaving the nest (brown paths).

(B) Mean wind (inner circle) and walking directions (outer circle) of the black trajectories shown in (A). Each circle depicts the mean angle for one ant (n = 24 ants).

(C) Food-search trajectories from 24 foraging ants (black paths) shown in (A) each with a beeline distance of 10 m. Start, lower end; end, upper end. Gray arrows depict wind direction measured every second but, for clarity, shown every 3 s only.

(D) Direction of ant trajectories relative to wind direction. Each circle depicts the mean direction relative to wind of one ant's path. Crosswind directions are 90° and 270°; 0° and 180° are downwind and upwind, respectively. The outer circle shows the preferred walking direction relative to wind from ants tracked when approximately 100 m away from the nest (n = 24 ants; see black trajectories in A and also B and C). Significantly more paths were within a 30° crosswind sector than would be expected for random heading directions (Chi-square test, $\chi^2 = 7.5$, $p < 0.05$). The inner circle shows the walking direction relative to wind from ants tracked in the initial phase when leaving the nest (n = 52 ants; see brown trajectories in A and data in E). Ants do not favor crosswind directions (Chi-square test, $\chi^2 = 0.1$, $p > 0.05$).

(E) Mean wind (inner circle) and walking (outer circle) directions of the brown trajectories shown in (A). Each circle depicts mean angle of one ant (n = 52 ants).

(F) Efficiency of search path (based on trajectories from C) as a function of wind direction. A value of 1 on the y axis is perfect efficiency where a 1 m section of path would screen 3.3 m^2 of desert given a food-detection distance of 3.3 m (see Figure S1B). Efficiency was calculated for the true wind profile (0°) and rotated versions of the true wind profile. Error bars indicate the SEM. Kruskal-Wallis test and Dunn's multiple comparison tests were used to compare efficiency to the baseline with 0° rotation (H = 58.4; *p < 0.05; ns, not significant).

See also Figure S2.

habitat of *Cataglyphis fortis*, there is usually a steady wind blowing in a rather constant direction [34]. Indeed, the median change in wind direction experienced by individual ants during a run was 45° (data shown in Figure 3, black paths; n = 24 ants). Only two out of 24 ants had to deal with changes of more than 60°. To determine whether under these conditions moving crosswind is a good search strategy, we examined the efficiency of that strategy given the ants' behavior. Assuming that ants can detect food that is 3.3 m away in the upwind direction (Figure S1B), the greatest possible area scanned during a meter's run is 3.3 m^2. We show that, on average, the area scanned by the ants is 2.7 m^2, giving an efficiency of 0.82 (2.7 m^2/3.3 m^2). This value drops significantly if we repeat the calculations with the path rotated relative to the actual wind (Figure 3F). We conclude that ants can screen the salt pan efficiently for prey by moving crosswind.

Food Odors

What are the chemical compounds that elicit plume following and facilitate the location of food items? Numerous chemical compounds have been labeled as necromones because they induce necrophoric or necrophobic behavior in insects. Most necromones are fatty acids that are widely present in insect cuticles [35]. In social insects such as ants or honeybees, necromones provoke the removal of the corpses of dead nest mates, thereby reducing the risk of contagion [36–39]. Isopods, cockroaches, or springtails exhibit similar self-preservation by avoiding shelters containing the odors of dead conspecifics [40–42]. Necrophoresis is reported to be triggered by decomposition products such as fatty acids (e.g., linoleic acid and oleic acid; see, e.g., [39]), although it is also possible that the absence of chemical compounds associated with life, rather than the increase in decomposition products postmortem, can provoke necrophoric behavior [43].

To date, most studies have focused on necrophoric or necrophobic behavior, and little is known about the role of necromones in foraging (see e.g., [44] for oleic acid). We tested ants' responses to a range of compounds known to be released by dead insects (see references above) to see which evoked plume following. We followed foraging ants until they started to run crosswind and then presented a test odor upwind. We defined the odor as attractive if it caused the ant to

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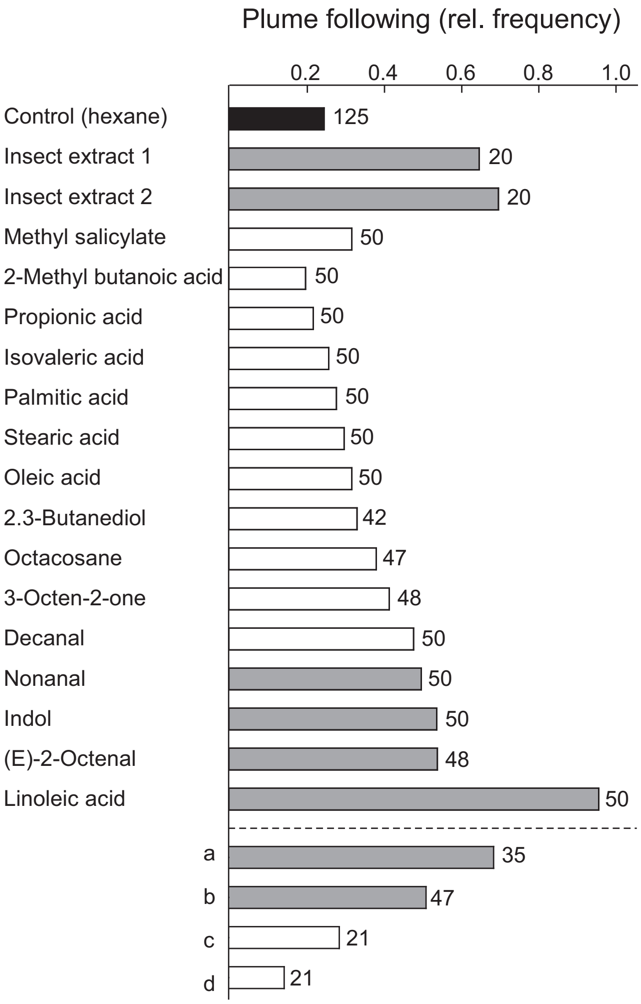

Figure 4. Odorants Used for Food Detection

Frequency of elicited plume following in response to insect extracts and single odorants diluted in hexane and used in doses of 0.4 mg. Control is hexane alone. Additional doses for linoleic acid were as follows: 2 µg (a), 0.2 µg (b), 20 ng (c) and 2 ng (d). Sample sizes are shown next to bars. Fisher's exact tests with Bonferroni correction revealed differences between tested odorants and/or extracts and solvent control: $p < 0.05$ (gray bars), $p > 0.05$ (white bars). See also Figure S3.

turn upwind significantly more often than did the solvent alone. We found that the whole-body extracts of dead insects and four of the 15 tested odorants provoked plume following (Figure 4). Three of these odorants attracted about half of the tested ants, while linoleic acid turned out to be the most attractive odorant tested, with 48 of 50 ants turning upwind. Linoleic acid has a vapor pressure (8.68×10^{-7} mm Hg at 25°C) that is eight orders of magnitude lower than that of other described insect attractants, like ethyl acetate (89 mm Hg at 24°C) or ethanol (65 mm Hg at 27°C). However, despite its extremely low volatility, the attractiveness of linoleic acid persisted when the doses were reduced from 0.4 mg to 0.2 µg (Figure 4). We conclude that ants are highly sensitive to linoleic acid and most likely use this compound as a key odorant when detecting food. Because odor blends are usually more attractive than their constituent compounds [45, 46], it was surprising that the ants displayed the strongest response to linoleic acid alone. Perhaps as it is a stable long-chained fatty acid with low volatility, linoleic acid provides a persistent stimulus under the thermal conditions of the salt pan, thus having a key role in food detection.

Recently, we have shown that path-integration information outweighs olfactory information for homing *C. fortis* ants, who will follow a CO_2 plume to a nest only when the path integrator indicates that they are close to home [6]. This is crucial, as homing ants will pass neighboring nests that smell like home but must not be diverted to these foreign nests [6]. We now asked whether linoleic acid attracts ants even when they are on their way home or whether all olfactory responses are damped in homing ants. We exposed homing ants—that had already found a food item—to linoleic acid, and more than 50% of the ants (12 out of 22 homing ants) exhibited plume-following behavior. Analyses of the food items carried by responding and nonresponding ants revealed that the size of the carried food item governed the ant's willingness to respond to the odor. Ants carrying large items neglected the plume and continued homing (median dry weight of items, 4×10^{-3} g), whereas ants with small items followed the plume (median weight, 4×10^{-4} g; Mann-Whitney test, $U = 25$, $p < 0.05$; see Figure S3). We do not know whether ants made their decision, to follow the plume or not, based on an evaluation of the value of their food item or whether large items smell stronger and mask the linoleic acid plume. However, regardless of the causation, this behavior, together with the ants' high sensitivity to food odors and their structured search paths is likely part of the secret to the success of this *Cataglyphis* species in the harsh environment of the Tunisian salt pans.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, three figures, and one movie and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.02.056.

Acknowledgments

This study was supported financially by the Max Planck Society. We thank G. Lutze, T. Retzke, R. Huber, and I. Liebetrau for help in the field and Emily Wheeler for editorial assistance. We also thank Tom Collett for his valuable comments on the manuscript. We gratefully acknowledge the three anonymous reviewers for their helpful comments on the manuscript.

Received: October 10, 2013
Revised: February 4, 2014
Accepted: February 26, 2014
Published: April 10, 2014

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