

## RESEARCH ARTICLE

# How to find home backwards? Navigation during rearward homing of *Cataglyphis fortis* desert ants

Sarah E. Pfeffer\* and Matthias Wittlinger

## ABSTRACT

*Cataglyphis* ants are renowned for their impressive navigation skills, which have been studied in numerous experiments during forward locomotion. However, the ants' navigational performance during backward homing when dragging large food loads has not been investigated until now. During backward locomotion, the odometer has to deal with unsteady motion and irregularities in inter-leg coordination. The legs' sensory feedback during backward walking is not just a simple reversal of the forward stepping movements: compared with forward homing, ants are facing towards the opposite direction during backward dragging. Hence, the compass system has to cope with a flipped celestial view (in terms of the polarization pattern and the position of the sun) and an inverted retinotopic image of the visual panorama and landmark environment. The same is true for wind and olfactory cues. In this study we analyze for the first time backward-homing ants and evaluate their navigational performance in channel and open field experiments. Backward-homing *Cataglyphis fortis* desert ants show remarkable similarities in the performance of homing compared with forward-walking ants. Despite the numerous challenges emerging for the navigational system during backward walking, we show that ants perform quite well in our experiments. Direction and distance gauging was comparable to that of the forward-walking control groups. Interestingly, we found that backward-homing ants often put down the food item and performed foodless search loops around the left food item. These search loops were mainly centred around the drop-off position (and not around the nest position), and increased in length the closer the ants came to their fictive nest site.

**KEY WORDS:** Navigation, Backward homing, *Cataglyphis* desert ants, Search behaviour, Food dragging

## INTRODUCTION

*Cataglyphis* desert ants occupy the ecological niche of a thermophilic scavenger (Wehner and Wehner, 2011). They do not recruit, but they search solitarily for single-load prey, especially dead arthropods that have succumbed to the prevailing harsh conditions. The food density is low in desert and desert-like environments, so *Cataglyphis* ants often have to cover long distances on meandering walks in the dry and hot habitat until they find food (Lenoir et al., 2009). They will grab the food and return immediately back to their nest by the direct path (beeline).

The homing *Cataglyphis* ant is guided mainly by path integration, which is a form of vector navigation that depends on angles steered and distance travelled (Wehner and Srinivasan, 2003). Specialized

ommatidia in the dorsal rim area of the ants' eye perceive the celestial e-vector pattern of polarized light (Wehner and Labhart, 2006), which provides the directional information of the vector. The distance information is most likely deduced from proprioceptive signals of the legs (Wittlinger et al., 2007; Steck et al., 2009; Wittlinger and Wolf, 2013). To a lesser extent, self-induced image flow can contribute to the odometer (Ronacher and Wehner, 1995). Besides vector navigation, several additional routines for orientation have been found in *Cataglyphis* (such as wind cues or visual, olfactory, tactile or even vibrational and magnetic landmarks), forming the ant's navigational toolkit (Wehner, 2009; Wolf and Wehner, 2005; Steck et al., 2011; Seidl and Wehner, 2006; Buehlmann et al., 2012).

*Cataglyphis* ants can carry loads of up to 200 mg, which is roughly 10 times their own body weight (Harkness and Wehner, 1977). If an ant finds a food item that is too large or heavy to be lifted up, it will drag the prey backwards towards the home nest. Whereas general walking and forward homing with a small food crumb is characterized by robust tripod coordination, the stepping pattern during backward dragging shows remarkable irregularities. Body and leg movements are unsteady and the inter-leg coordination is less tightly coupled (Pfeffer et al., 2016). Also, in terms of muscle activity and motor output, it seems that backward leg movements are not only a simple reversal of the forward motion sequence (Graham and Epstein, 1985). As the distance is most probably measured by sensory signals from the legs, one could assume that the stride integrator might be adversely affected. Compared with forward homing, which certainly makes up the majority of foraging trips, backward-homing ants have to deal with flipped environmental information. This affects several important input channels of the orientation and compass system: for example, polarization pattern, position of the sun, direction of the wind and diverse landmark cues.

In the present study, we attempt to gain insight into the navigational performance of backward-homing ants. In several paradigms, rearward-homing ants were examined according to their navigational abilities and were compared with forward-homing ants. We performed channel and field experiments to analyze the two components of vector navigation, distance and direction, separately and combined. In addition, we describe homing and search characteristics of backward-walking ants.

## MATERIAL AND METHODS

Our experiments were conducted with *Cataglyphis fortis* (Forel 1902) in its natural habitat of alluvial salt plains near Maharès, Tunisia (34.53°N, 10.54°E). All data were obtained during the summer months of 2013, 2014 and 2015. We presented the ants with a heavy food load to induce them to walk backwards (for details, see Pfeffer et al., 2016). Homing behaviour was examined in channel and open field experiments (see Fig. 1).

## Terminology

While the food load was dragged backwards, ants frequently dropped the load and performed a search behaviour around the left

Institute of Neurobiology, University of Ulm, Ulm D-89069, Germany.

\*Author for correspondence (sarah.pfeffer@alumni.uni-ulm.de)

 S.E.P., 0000-0003-1470-5055

item. We define these search trajectories as foodless search loops. To avoid confusion with the search behaviour occurring in the context of forward homing (which is never interrupted by breaks or food deposition), we call these search spirals search phases. The preceding straight part of the forward trajectory where vector ants ran off the internally stored vector is called the approach phase. Both parts of the forward trajectory are separated by the first conspicuous turning point (see below). This terminology is used throughout the paper. An example of backward and forward homing is illustrated in Fig. 2.

### Experimental procedure

To examine backward-homing ants and to compare them with forward-homing ants, we used channel and open field experiments. An overview of these two methods is given in Fig. 1, and the experiments are further described in the following sections.

#### Channel experiment

The ants were trained to forage at a feeder 10 m south of their nest entrance within a linear aluminium channel (sanded floor, U-shaped in cross-section, 7 cm high and 7 cm wide). The feeder offered many biscuit crumbs, each approximately 1.5 mm in diameter. An ant that had performed at least five trips to the food source (Fig. 1Ai, Fig. 3A) was caught and transferred to a test channel. This channel was positioned at some distance but aligned in parallel to the training channel. There, a large food item was presented and the ants were allowed to pull it in the direction of the fictive nest site (Fig. 1Aii, Fig. 3A). During the homeward path we recorded the extent of the foodless search loops and consecutive turning points as a one-dimensional nest search behaviour (Fig. 1Aiii). In channel experiments, we define the first turning point (1st TP) as the point at which a homing

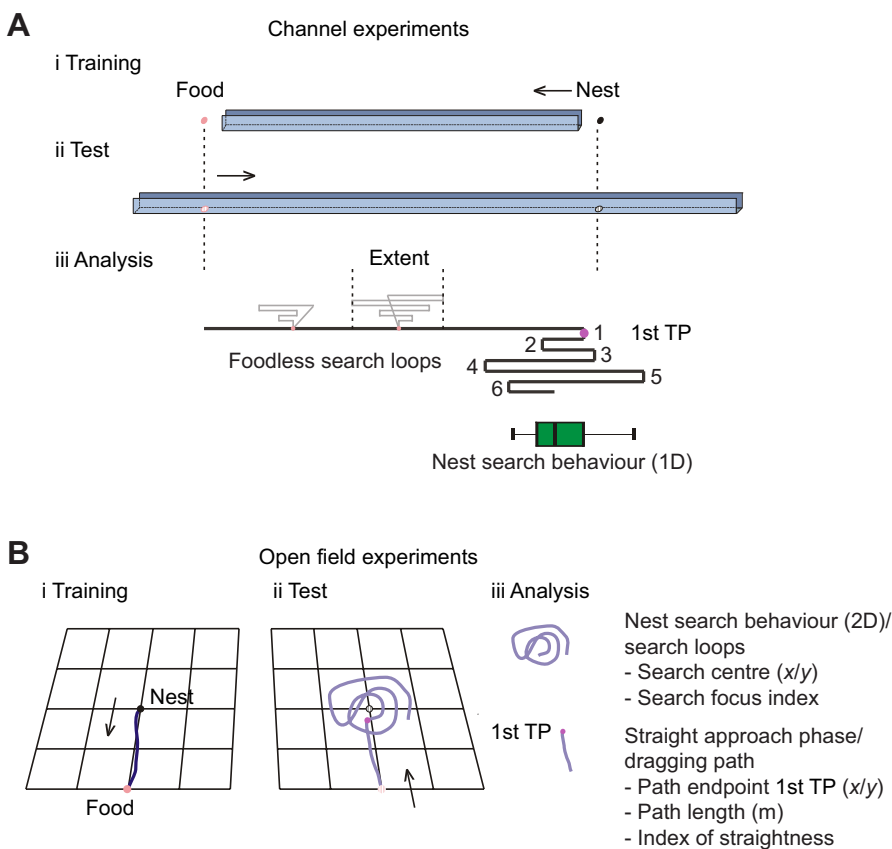
ant moved for the first time contrary to the running direction for at least 20 cm. The large food item was then replaced by a small food crumb, and we further recorded six consecutive turning points and calculated the corresponding median for comparison. The 1st TPs and the medians of one test group were used to generate box-and-whisker plots.

#### Field experiments

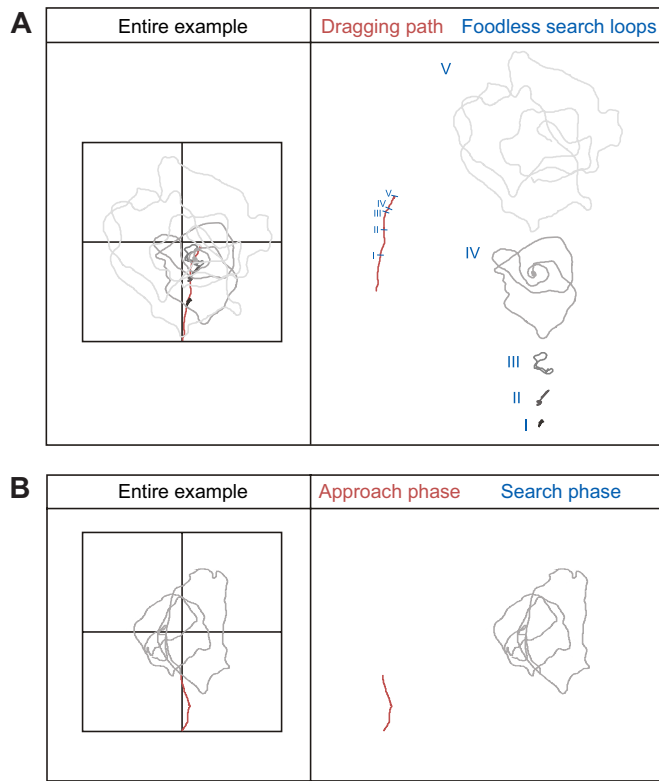
The ants were trained to visit a feeding site on an open field 10 m east of their nest entrance. An ant that had walked back and forth to the food source at least five times (Fig. 1Bi) was caught and transferred to a remote test field (20×20 m with 2×2 m grid cells). Walking trajectories were recorded on graph paper with an identical pattern of the test field (Fig. 1Bii). The forward-homing ants were tracked for 2.5 min. The backward-walking ants frequently put down the food item and performed foodless search loops that were recorded for 5 min maximum. To compare both types of searches appropriately, we considered only the first 20 m of the foodless search loops from the backward-walking ants and the first 20 m of the search phase from the forward-walking ants. Recorded trajectories were digitized with a graphics tablet (Wacom Intuos 3, Walcom Europe, Krefeld, Germany) for further analysis.

#### Data analysis

During backward homing, the ants frequently put down their food item and performed foodless search loops around the dropped load. For the analysis of the field trajectories we separated the food-dragging path from the foodless search loops. The food-dragging path is orientated straight towards the hypothetical nest site in all tested ants, while the foodless search loops are circular and much more meandering. We analyzed the forward control group in the same way and separated the straight approach phase from the loopy



**Fig. 1. Overview of the different methods used.** (A) Channel experiments and (B) open field experiments. For more details, see Materials and methods.

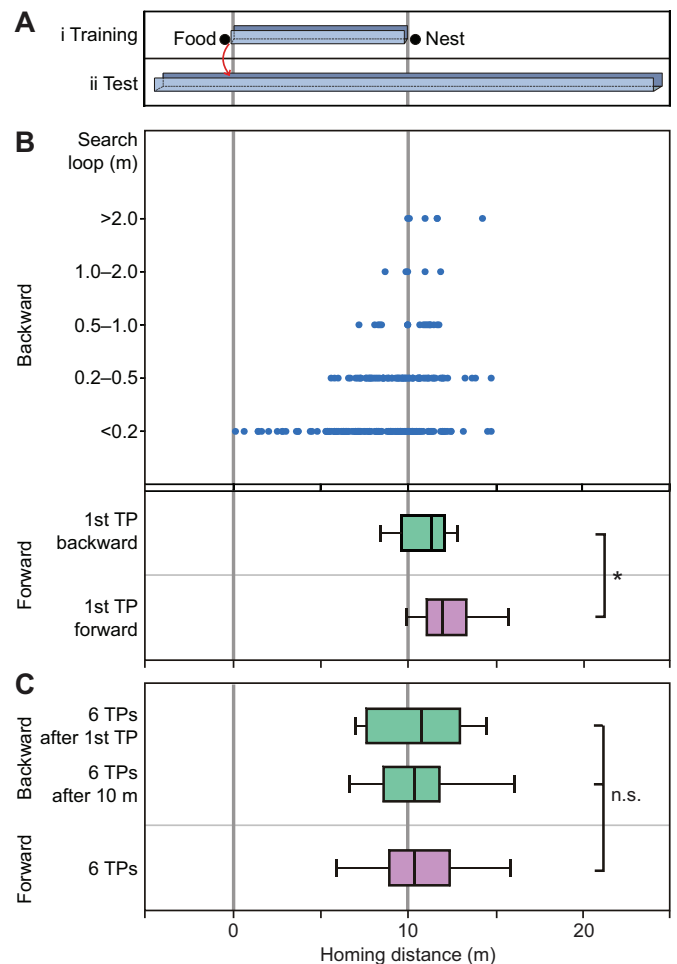


**Fig. 2. Example of open field backward and forward homing.** (A) Backward homing. During dragging, the ant frequently put down the food and performed foodless search loops (I–V). The recordings were stopped when the ants did not touch the left food item for 5 min (see foodless search loop V). (B) Forward homing. The straight approach phase was separated from the meandering search phase by means of the first turning point.

search phase (Fig. 1Aiii). Therefore, we used the criterion of the first conspicuous turning point, which has been applied to open field observations in earlier studies (e.g. Merkle et al., 2006) and is comparable to the first 180 deg U-turn in channel experiments (Ronacher and Wehner, 1995).

The 2D search trajectories of backward-homing ants were separated into the straight food-dragging path and the spiraling, foodless search loops. The 2D search trajectories of forward-homing ants were separated into a straight approach phase and a loopy search phase. To realize this separation we identified the 1st TP, which marks the end of the rather straight part and the beginning of search behaviour. The 1st TP marks the position of the run, where the ant started to deviate from its current path direction for at least 30 deg and did not revert to its previous path direction for at least 3 m. We applied the criterion at a minimum distance of 5 m to the release point to exclude occasional orientation behaviour at the beginning of the homing run.

The path endpoint is the last point of a respective trajectory and has  $x/y$  coordinates. The path length is the entire length of the trajectory and is measured in metres. The index of straightness can estimate the tortuosity of trajectories and is calculated as the division of the straight line distance by the actual length of the trajectory. The instantaneous index of straightness uses the same calculation method as the index of straightness. It does not refer to the entire trajectory but to different sections of it (see Fig. S3). The search centre is the median position of all  $x/y$  coordinates of the respective foodless search loop or search phase. The search focus index is a measure of whether the  $x/y$  data of the trajectory of a foodless search



**Fig. 3. Channel experiments: foodless search loops and odometer performance.** (A) Channel set-up. Ants were trained to visit a feeder a distance of 10 m from their nest (i). Ants were captured at the feeder and were transferred to our test channel, where we recorded their search behaviour (ii). The resulting data are shown below. (B) Foodless search loops during backward walks ( $n=18$ ). The extent of the foodless search loops is shown on the y-axis in categories from 0.2 m to more than 2 m. The point of release in the test channel is at 0 m; the fictive nest position is at 10 m. Each blue circle indicates a food-dropping point with the respective foodless search loop extent. Note that the closer the ants are to the fictive nest, the larger the foodless search loops get. Most tested ants also performed a sharp 180 deg turn when they reach their nest position. These first turning points (1st TPs) are shown as box-and-whisker plots ( $n=18$ ) and are compared with the 1st TPs of forward-homing ants ( $n=20$ ). The differences are statistically significant ( $t$ -test,  $P=0.020$ ). Box plots give the 10th, 25th, 50th, 75th and 90th percentile distributions (also applies to C). (C) Estimation of homing distance. Medians of six consecutive turning points (TPs) are illustrated as box-and-whisker plots. We analyzed six TPs (large food replaced with a small food crumb) after 10 m of backward dragging ( $n=20$ ), six TPs (large food replaced with a small food crumb) after the 1st TP during backward dragging ( $n=20$ ) and six TPs for forward-walking ants. No statistically significant difference was found (one-way ANOVA,  $P=0.947$ ).

loop are closer to its start position (food drop-off position) or to the actual goal (nest). We measured the median distance of all  $x/y$  data points to the start of the foodless search loop (A) as well as the median distance of all  $x/y$  data points to the goal position (B). If the quotient of A to B has a value of 1, the  $x/y$  data of the respective foodless search loop are distributed equally around the drop-off position and around the nest position. If the value is lower than 1, the  $x/y$  data points are distributed more around the drop-off position.

If the value is higher than 1, the  $x/y$  data points are distributed more around the nest position. For comparative reasons, we calculated the search focus index also for forward-homing ants. As a start position of the respective search phase we used the FTP, as the goal we used the nest position. For an illustrative explanation of the search focus index, see Fig. S1.

### Statistical analysis

We used SigmaPlot (Systat Software, San Jose, CA, USA) for statistical comparison and to generate box-and-whisker plots. For pairwise comparison of normally distributed data we applied the  $t$ -test, for non-normally distributed data the Mann–Whitney rank sum test ( $U$ -test). For a multiple comparison of normally distributed data we used the one-way ANOVA, for non-normally distributed data the ANOVA on ranks. Box-and-whisker plots show the median as the box centre, 25th and 75th percentiles as box margins and 10th and 90th percentiles as whiskers. To compare two scatter plots we used the  $t$ -test for regression coefficients. For circular statistics we applied the CircStat toolbox (Berens, 2009) for MATLAB.

## RESULTS

Are rearward-homing ants still able to navigate properly? To answer this question, we tested backward- and forward-homing ants in channel and open field experiments. The analysis of odometer and directional performance within several experimental paradigms will be described in the following section.

### Channel experiments

To investigate the odometer during rearward homing, *C. fortis* ants were offered a large food item that they had to drag backwards for a distance of 10 m within a channel set-up (Fig. 3A). During homing, backward dragging ants frequently put down their load and performed foodless search loops, back and forth around the food item. Eventually, the ants picked up the food load again and continued the homing path. For a quantitative investigation we recorded the position of the dropped food and the corresponding extent of the ant's foodless search loop (Fig. 3B). The foodless search loops became wider the closer the ants got to their nest.

All 26 ants observed dropped off the food load on their way home at some point and performed foodless search loops. However, some differences among the tested individuals emerged. Most ants (18/26) showed a sharp turn close to the hypothetical nest site and dragged the food into the opposite direction, comparable to the first conspicuous U-turn (1st TP) known as the beginning of search behaviour in forward-homing ants (Ronacher and Wehner, 1995). The 1st TPs recorded during backward locomotion were even slightly closer to the hypothetical nest site than the 1st TPs of forward-moving ants (see boxplots in Fig. 3B). Rarely (2/26), ants dragged the food item for a long distance that far exceeded their homing vector before they showed the 1st TP (distances of 33 and 25 m after the point of release; data points are extreme outliers and are not shown in the figure). Few ants (6/26) never performed a U-turn (1st TP). They only put down the load and ran back and forth around the dropped food but none attempted to resume dragging (the median position at which the ants finally dropped the food was at a distance of 14 m from the point of release; data not shown).

We tested the odometer performance of rearward-homing ants and compared it with that of forward-homing ants. Because the backward dragging ants did not show consecutive turning points (which is an established method of evaluating odometer ability), we

replaced the heavy load with a small food crumb after the 1st TP and in a different experiment after 10 m of backward dragging (Fig. 3C). Hence, turning points were performed as usual, and we were thus able to analyze the ants' odometer status. Our results show that rearward-homing ants were indeed able to estimate the homing distance correctly, with no statistical difference to forward-homing ants.

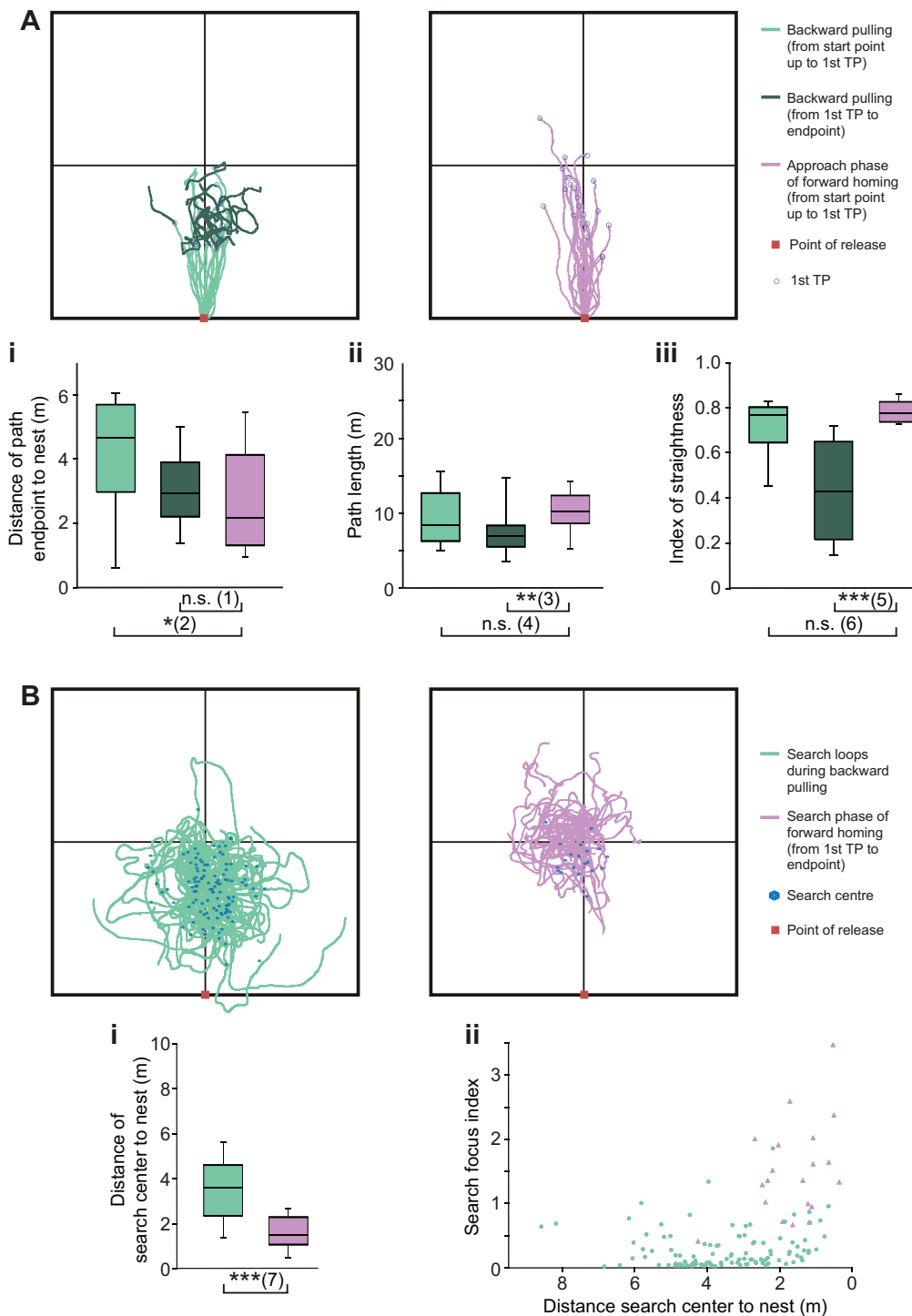
### Open field experiments

We further observed backward-homing ants in an open field experiment (see video uploaded to the Dryad Digital Repository). Some ants grasped the food item and started the homing journey immediately with reversed locomotion. Some ants were obviously motivated to drag the food item but were not able to hold it properly at first. They walked around it and probed for a suitable position to grasp and to drag the food. Although we did not quantify this, we did not observe any systematic initial body turns that could be interpreted as orientation behaviour (e.g. as is the case in dung beetles; Baird et al., 2012).

Remarkably, no ant moved in the incorrect direction, not even within the first few centimetres of homing. All ants at some point interrupted their straight homing path, laid down their food item and performed winding foodless search loops. For a better analysis, we separated the straight food-dragging path from the meandering, foodless search loops and compared these with the straight approach phase and the circular and winding search phase of forward-homing ants (Fig. 4).

Fig. 4A illustrates the superimposed trajectories of the backward food-dragging path to which the criterion of the 1st TP has been applied additionally (see Materials and methods). Thus, the backward dragging path was divided into a straight part (light green) and a subsequent meandering path (dark green). Both parts were compared with the approach phase (purple) of forward-homing ants. The straight backward path and the forward approach phase are comparable in length and straightness (Fig. 4Aii, iii). However, the endpoints of the straight part of backward dragging were farther away from the nest position than those of the forward approach phases. This is due to the slightly broader angular deviations (see Fig. 5), but the difference is not statistically significant. There is no difference between the endpoints of the entire backward trajectories and those of the forward approach phases (Fig. 4Ai). Hence, backward dragging is comparable to the approach phase of forward homing, although the final part of the backward course is more tortuous.

Fig. 4B shows the foodless search loops that emerged during backward homing on the left side and the forward search phases on the right side. The foodless search loops were performed along the entire backward dragging path. The early performed foodless search loops that were found in all runs emerged after approximately 3 m of backward dragging (which is 7 m away from the hypothetical nest site). They were small in extent and mostly represented only one short loop directed towards the hypothetical nest site. In contrast, the late performed foodless search loops that were in close vicinity of the hypothetical nest site were mostly longer in time and widely meandering, although small search loops still occurred when the homing vector approached its zero state. Because we have different search trajectories that vary in size and in their distance to the nest, we further analyzed the instantaneous index of straightness (see Fig. S3). Note that the foodless search loops covered primarily the area before the fictive nest site, whereas the search phases were centred more on the fictive nest site. This also becomes obvious regarding the position of the search centres. Their distances to the



**Fig. 4. Field experiments: comparison of backward and forward trajectories.** (A) Backward food-dragging path ( $n=20$ ) and forward straight approach phase ( $n=20$ ). Corresponding analyses (i–iii) are also shown. The backward dragging path was additionally separated into two phases according to the criterion of the first turning point (1st TP; as it was applied also for the forward walks). We plotted a  $20 \times 20$  m field site; the release point is marked by the red square, the intersection of the black lines in the middle of each plot marks the hypothetical nest site. Box plots give the 10th, 25th, 50th, 75th and 90th percentile distributions (also applies to Bi). (B) Foodless search loops and search phases. The search was restricted to a maximum length of 20 m. Corresponding analyses (i,ii) are also shown. Forward and backward search focus indices differ significantly from each other ( $t$ -test for regression coefficient,  $P < 0.05$ ). Statistical analysis: (1)  $t$ -test,  $P=0.273$ ; (2)  $t$ -test,  $P=0.021$ ; (3)  $U$ -test,  $P=0.262$ ; (4)  $U$ -test,  $P=0.002$ ; (5)  $U$ -test,  $P=0.250$ ; (6)  $U$ -test,  $P < 0.001$ ; (7)  $U$ -test,  $P < 0.001$ .

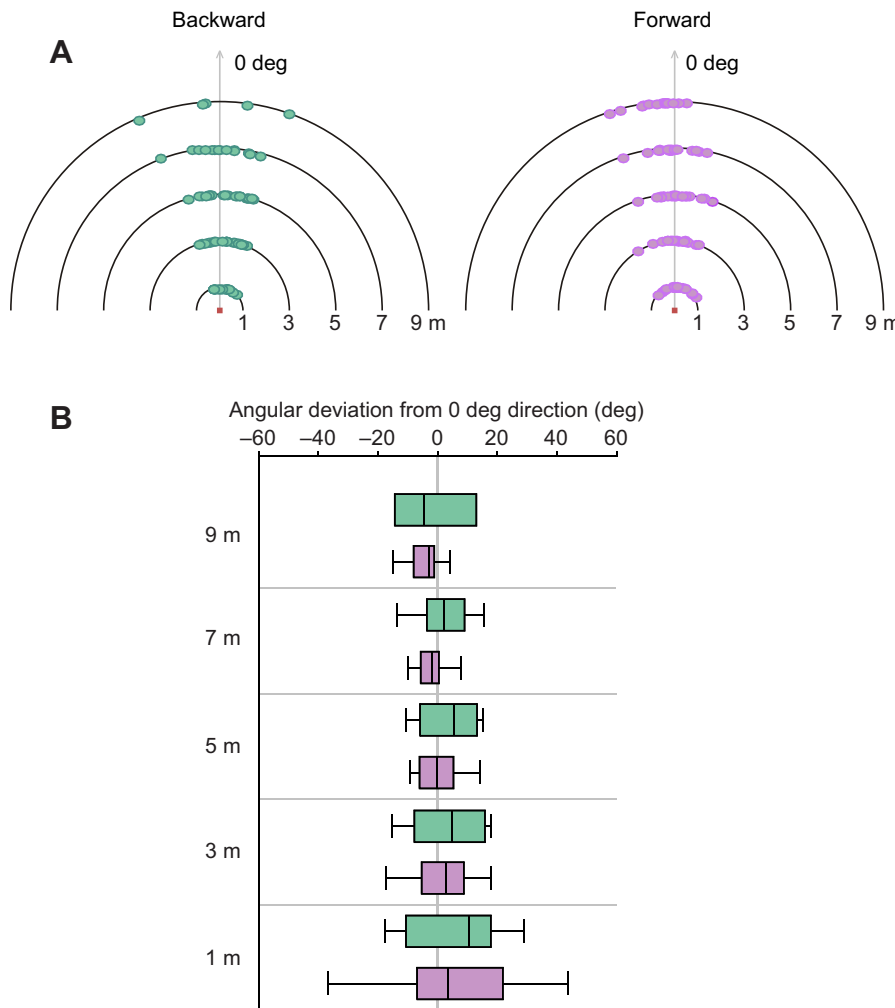
actual nest position were significantly smaller in forward walks than in foodless search loops (Fig. 4Bi).

We can analyze whether a respective foodless search loop is located closer to the food-dropping position (food focused) or closer to the fictive nest position (nest focused) by means of the search focus index (Fig. 4Bii). A value of 1.0 would mark exactly the middle position between the food-dropping position and the fictive nest site. A value that is higher than 1.0 indicates that the respective foodless search loop is closer to the nest site and vice versa (see Fig. S1). Our results show that most foodless search loops are food focused. The same analysis was performed for forward homing,

where the search focus index indicates whether the respective search phase is closer to the 1st TP or to the fictive nest position. Our data show that most search phases have higher values than 1.0 and are therefore nest focused.

#### Directional orientation

By means of the 2D trajectories in the open field experiments it was possible to evaluate the directional performance of our test groups (Fig. 5). Fig. 5A shows the position of the backward- and forward-homing ants after particular distances from the release point. The respective angular deviations from the homing direction (0 deg)



**Fig. 5. Directional performance.** (A) Angular distribution of backward ( $n=20$ ) and forward ( $n=20$ ) homing runs. The semicircles illustrate the different distances (1, 3, 5, 7 and 9 m) from the release point (red square). Each circle represents the first intersection point of a homing ant with the particular semicircle. The nest direction (0 deg) is marked as a grey arrow. (B) Angular deviation from the homing direction (0 deg) as box-and-whisker plots. Box plots give the 10th, 25th, 50th, 75th and 90th percentile distributions. Positive (negative) angles refer to an intersection point to the right (left) of the grey homing axis. The directionality of data could be proved by means of the Rayleigh test (all  $P<0.001$ ) and the V-test (all  $P<0.001$ ). All groups have a symmetrical distribution around the median (all  $P>0.05$ ). In a pairwise comparison of the forward and backward angular distributions (at each of 1, 3, 5, 7 and 9 m) by means of the Kuiper two-sample test, we could not find any statistically significant difference (all  $P>0.1$ ). The same was true for all absolute angular deviations (positive values, at each of 1, 3, 5, 7, 9 m, Kuiper two-sample test, all  $P>0.1$ ). The absolute angular error was calculated for each distance: 1 m (15, 20 deg), 3 m (12, 9 deg), 5 m (9, 7 deg), 7 m (7, 5 deg) and 9 m (12, 6 deg); the angles in brackets indicate first the backward, then the forward angular accuracy.

were calculated and are illustrated in Fig. 5B as box-and-whisker plots. The interquartile range ('box') is generally broader in the backward- than in the forward-homing group. None of the statistical pairwise comparisons reached a significant level.

## DISCUSSION

Desert ants *C. fortis* forage for dead arthropods during the hottest time of the day. When they find food that is too heavy and large to be lifted up, they will drag it backwards towards their home. Studies to date have not investigated how ants navigate towards their nest during backward locomotion. To answer this question, we compared the performance of backward- and forward-homing ants by means of channel and open field experiments.

### Odometer performance during backward walking

In general, our results suggest a slight underestimation of the odometer of rearward-homing ants compared with the forward-homing groups. In the channel experiments, the first turning point of backward dragging ants is performed before that of the forward-homing group. In the field experiments, we also see that the backward dragging behaviour ends before reaching the actual nest site. The endpoint is determined by our 5-min criterion of the foodless search loops. This tendency towards a shortening of the dragging paths might be due to the heavy load, which leads to a slower walking speed, an increased transport time and an increased thermal stress. This might induce a motivational shift from foraging

towards respite behaviour. It can be assumed that under heat stress, the food load becomes less important and therefore is dropped in order to discharge excess heat and to reach the nest the quickest way possible (Wehner and Wehner, 2011). Besides, if the food load is dropped near the nest site, the probability is high that at least a nest mate will find the left food item and, therefore, the endeavour was not in vain.

Although the backward dragging path is slightly shortened, it seems that the rearward-walking ants still estimate homing distances accurately. This is interesting, because the physiological basis of the odometer module was hitherto unclear (Wittlinger et al., 2007; Wittlinger and Wolf, 2013). Therefore, it was also difficult to predict *a priori* what influence the irregular stepping pattern would have on distance gauging (Pfeffer et al., 2016). It has been hypothesized that stride length might be deduced from stride frequency, because the relationship between these two parameters is relatively stable during forward walks (Bässler and Büschges, 1998). In a study in which ants had to walk over corrugated surfaces, a slight decoupling of the correlation of stride frequency to stride length has already been observed, which suggests that stride length is determined by sensory input of leg sense organs (Steck et al., 2009). This is also true for backward walking, where an even weaker correlation was found between stride length and stride frequency (see fig. S3 in Pfeffer et al., 2016). Despite the weak correlation between stride length and stride frequency, the efficiency of the stride integrator during backward homing comes close to that of forward homing. This

might indicate that the movement of each individual leg contributes separately to the odometer. Furthermore, for backward walking, leg motion and proprioceptive input is not just a simple reversal of forward movement, but the ants are still capable of estimating walking distance properly.

The role of optic flow in ant odometry is still unclear. Wobbly and unsteady movements of the body, and thus the head, might influence the perception of self-induced optic flow, which is thought to play a minor role in distance measurement (Ronacher and Wehner, 1995). Therefore, we tested rearward-homing ants with ventrally occluded eyes and compared this group with normal backward-homing ants (see Fig. S2). Nonetheless, we did not observe any difference between these two groups.

### Estimation of direction and the role of foodless search loops during backward homing

Our experiments show that the backward dragging paths have a tendency towards wider angular deviations from the homing vector than the forward control group. Although these deviations are consistent (during the different examined distances to the releasing point), they are minor and not statistically significant. The compass system predominantly relies on the polarized skylight, but can also use the position of the sun and a constant wind direction (Wehner, 2009; Wolf and Wehner, 2005). These visual and anemotactic cues are directionally reversed during backward dragging. Ants have a flipped sensory input while they are facing the opposite direction and not towards home as they would do in most of the foraging trips. That such a reversal can have impressive consequences has already been shown in the classical mirror experiment from Felix Santschi (Santschi, 1923; discussed in Wehner, 1990). He mirrored the sun onto the ants from the opposite direction while parts of the sky including the sun were shaded off; consequently, the ants changed their course to the opposite direction. The fact that backward homing did not have the same effect as in Santschi's experiment shows that the ants can adapt their compass to the reverted environment. In general, backward-homing ants show that polarization compass information, which is processed in the central complex (Homberg et al., 2011), has to be integrated in a context-dependent way. The path integrator therefore needs an internal representation of the direction of body movement (Seelig and Jayaraman, 2015).

The ants frequently interrupt their rearward homing, put down their large food item and search freely around it. Possible explanations as to why ants temporarily interrupt backward dragging and roam freely around the left food item might be respite behaviour, muscle fatigue or realigning of compass inputs. Another likely explanation for this behaviour is that the ants scan the panoramic scene with respect to the homing direction, which could be used for landmark guidance via snapshot matching or image difference function (Cartwright and Collett, 1987; Zeil et al., 2003; Philippides et al., 2011). Although ants have holoptic eyes and panoramic vision (Wehner et al., 2014), it is still important for them in backward walking to perceive the landmark scenery with the same visual field as during forward homing and not as a reversed image of it. Thus, one could assume that the rearward-homing ants might perform foodless search loops in order to align their ommatidial image according to visual memories of the true homing direction. Hence, if an ant has deviated from its homeward course it would be able to recalibrate its heading direction. And indeed, we observed several backward-homing ants to improve their dragging direction immediately after they had

performed a foodless search loop. Interestingly, during forward homing, ants are known to sometimes pirouette shortly on the spot in order to scan their environment (Wehner et al., 2014; Wystrach et al., 2014; Zeil et al., 2014).

Remarkable parallels (to ants' orientation during rearward homing) have been evolved in backward-rolling dung beetles (Baird et al., 2012). Just before rolling a new ball away from the dung pile, the beetles often perform a characteristic dance, where they climb on the ball and rotate about their vertical axis. In such a manner they can scan the sky in order to determine the direction of the subsequent rolling. While transporting the dung, the beetles frequently stop to perform further 'dances' on top of the ball, similar to ants that conduct foodless search loops on their homing route. Although there are striking similarities, the ants do not just rotate around their body axes, but cover a certain distance during their foodless search loops that increases with reduced vector length.

The closer the ants get to the hypothetical nest site with their vector approaching zero-state, the longer the path of the performed foodless search loops becomes. Contrary to the early emerging foodless search loops, the ants are scanning a wider area in spirals during the late performed loops. This behaviour strongly resembles the systematic search strategy (Müller and Wehner, 1994) shown in the search phase of our forward-homing ants. *Cataglyphis fortis* ants cannot see the nest entrance, which is only an inconspicuous hole in the desert floor, but they can recognize the familiar terrestrial signposts that are close to their nest. However, the main difference to the systematic search behaviour is that foodless search loops performed during backward homing are centred on the drop-off position of the food item, and not around the hypothetical nest site (as is the case during forward homing). This is remarkable because it seems that besides the nest position, the ants memorize another variable location, namely that of the dropped food load. It should be noted that we transferred the ants to a test field that was several hundred metres away from their original nest site, and hence did not offer any familiar landmark cues. During backward homing towards the actual nest site and in well-known terrain, it is likely that the ants would demonstrate an even better performance than our results already indicate, and that the extent of late foodless search loops might not be as pronounced as we show here.

### Acknowledgements

We express our gratitude to Harald Wolf for encouragement during the fieldwork and constructive feedback on the data evaluation. We would like to thank Ursula Seifert for her valuable help in organizing the field excursions and for editing the text. We are grateful to Verena Wahl for her valuable support during the fieldwork. We are much indebted to two anonymous referees for their valuable comments on an earlier version of the manuscript.

### Competing interests

The authors declare no competing or financial interests.

### Author contributions

The experiments were planned by S.E.P. and M.W., and carried out by M.W. and S.E.P. The data were analyzed by S.E.P. The manuscript was written by S.E.P. and M.W.

### Funding

The University of Ulm provided financial support and infrastructure.

### Data availability

Data are available from the authors on request. A video is available from the Dryad Digital Repository at <http://dx.doi.org/10.5061/dryad.8tk11>.

### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.137786.supplemental>

## References

- Baird, E., Byrne, M. J., Smolka, J., Warrant, E. J. and Dacke, M. (2012). The dung beetle dance: an orientation behaviour. *PLoS ONE* **7**, e30211.
- Bässler, U. and Büschges, A. (1998). Pattern generation for stick insect walking movements – multisensory control of a locomotor program. *Brain Res. Rev.* **27**, 65–88.
- Berens, P. (2009). CircStat: a MATLAB toolbox for circular statistics. *J. Stat. Softw.* **31**, 1–21.
- Buehlmann, C., Hansson, B. S. and Knaden, M. (2012). Desert ants learn vibration and magnetic landmarks. *PLoS ONE* **7**, e33117.
- Cartwright, B. A. and Collett, T. S. (1987). Landmark maps for honeybees. *Biol. Cybern.* **57**, 85–93.
- Graham, D. and Epstein, S. (1985). Behaviour and motor output for an insect walking on a slippery surface: II. Backward walking. *J. Exp. Biol.* **118**, 287–296.
- Harkness, R. D. and Wehner, R. (1977). *Cataglyphis*. *Endeavour* **1**, 115–121.
- Homborg, U., Heinze, S., Pfeiffer, K., Kinoshita, M. and El Jundi, B. (2011). Central neural coding of sky polarization in insects. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366**, 680–687.
- Lenoir, A., Aron, S., Cerda, X. and Hefetz, A. (2009). *Cataglyphis* desert ants: a good model for evolutionary biology in Darwin's anniversary year – a review. *Israel J. Entomol.* **39**, 1–32.
- Merkle, T., Knaden, M. and Wehner, R. (2006). Uncertainty about nest position influences systematic search strategies in desert ants. *J. Exp. Biol.* **209**, 3545–3549.
- Müller, M. and Wehner, R. (1994). The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. *J. Comp. Physiol. A* **175**, 525–530.
- Pfeffer, E. S., Wahl, V. L. and Wittlinger, M. (2016). How to find home backwards? Locomotion and inter-leg coordination during rearward walking of *Cataglyphis fortis* desert ants. *J. Exp. Biol.* **219**, 2110–2118.
- Philippides, A., Baddeley, B., Cheng, K. and Graham, P. (2011). How might ants use panoramic views for route navigation? *J. Exp. Biol.* **214**, 445–451.
- 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.
- Santschi, F. (1923). L'orientation sidérale des fourmis, et quelques considérations sur leurs différentes possibilités d'orientation. *Mém. Soc. Vaudoise Sci. Nat.* **4**, 137–175.
- Seelig, J. D. and Jayaraman, V. (2015). Neural dynamics for landmark orientation and angular path integration. *Nature* **521**, 186–191.
- Seidl, T. and Wehner, R. (2006). Visual and tactile learning of ground structures in desert ants. *J. Exp. Biol.* **209**, 3336–3344.
- Steck, K., Wittlinger, M. and Wolf, H. (2009). Estimation of homing distance in desert ants, *Cataglyphis fortis*, remains unaffected by disturbance of walking behaviour. *J. Exp. Biol.* **212**, 2893–2901.
- Steck, K., Hansson, B. S. and Knaden, M. (2011). Desert ants benefit from combining visual and olfactory landmarks. *J. Exp. Biol.* **214**, 1307–1312.
- Wehner, R. (1990). On the brink of introducing sensory ecology: Felix Santschi (1872–1940) – Tabib-en-Neml. *Behav. Ecol. Sociobiol.* **27**, 295–306.
- Wehner, R. (2009). The architecture of the desert ant's navigational toolkit (Hymenoptera: Formicidae). *Myrmecol News* **12**, 85–96.
- Wehner, R. and Labhart, T. (2006). Polarization vision. In *Invertebrate Vision* (ed. E. Warrant, D.-E. Nilsson), pp. 291–348. Cambridge: Cambridge University Press.
- Wehner, R. and Srinivasan, M. V. (2003). Path integration in insects. In *The Neurobiology of Spatial Behavior* (ed. K. K. Jeffrey), pp. 9–30. Oxford: Oxford University Press.
- Wehner, R. and Wehner, S. (2011). Parallel evolution of thermophilia: daily and seasonal foraging patterns of heat-adapted desert ants: *Cataglyphis* and *Ocymyrmex* species. *Physiol. Entomol.* **36**, 271–281.
- Wehner, R., Cheng, K. and Cruse, H. (2014). Visual Navigation Strategies in Insects: Lessons from Desert Ants. In *The New Visual Neurosciences* (ed. J. S. Werner, L. M. Chalupa), pp. 1153–1163. Cambridge, MA: MIT Press.
- Wittlinger, M. and Wolf, H. (2013). Homing distance in desert ants, *Cataglyphis fortis*, remains unaffected by disturbance of walking behaviour and visual input. *J. Physiol.* **107**, 130–136.
- Wittlinger, M., Wehner, R. and Wolf, H. (2007). The desert ant odometer: a stride integrator that accounts for stride length and walking speed. *J. Exp. Biol.* **210**, 198–207.
- Wolf, H. and Wehner, R. (2005). Desert ants compensate for navigation uncertainty. *J. Exp. Biol.* **208**, 4223–4230.
- Wystrach, A., Philippides, A., Aurejac, A., Cheng, K. and Graham, P. (2014). Visual scanning behaviours and their role in the navigation of the Australian desert ant *Melophorus bagoti*. *J. Comp. Physiol. A* **200**, 615–626.
- Zeil, J., Hofmann, M. I. and Chahl, J. S. (2003). Catchment areas of panoramic snapshots in outdoor scenes. *J. Optical Soc. Am. A* **20**, 450–469.
- Zeil, J., Narendra, A. and Stürzl, W. (2014). Looking and homing: how displaced ants decide where to go. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **369**, 20130034.