

RESEARCH ARTICLE

The choreography of learning walks in the Australian jack jumper ant *Myrmecia croslandi*

Piyankarie Jayatilaka, Trevor Murray, Ajay Narendra* and Jochen Zeil[‡]

ABSTRACT

We provide a detailed analysis of the learning walks performed by *Myrmecia croslandi* ants at the nest during which they acquire visual information on its location. Most learning walks of 12 individually marked naïve ants took place in the morning with a narrow time window separating the first two learning walks, which most often occurred on the same day. Naïve ants performed between two and seven walks over up to four consecutive days before heading out to forage. On subsequent walks, naïve ants tend to explore the area around the nest in new compass directions. During learning walks, ants move along arcs around the nest while performing oscillating scanning movements. In a regular temporal sequence, the ants' gaze oscillates between the nest direction and the direction pointing away from the nest. Ants thus experience a sequence of views roughly across the nest and away from the nest from systematically spaced vantage points around the nest. Further, we show that ants leaving the nest for a foraging trip often walk in an arc around the nest on the opposite side to the intended foraging direction, performing a scanning routine indistinguishable from that of a learning walk. These partial learning walks are triggered by disturbance around the nest and may help returning ants with reorienting when overshooting the nest, which they frequently do. We discuss what is known about learning walks in different ant species and their adaptive significance for acquiring robust navigational memories.

KEY WORDS: Learning walks, Homing, Visual navigation, Ants, Scene memories

INTRODUCTION

Ants, wasps and bees are central place foragers that always return to the nest after outbound journeys. In order to do this, a forager can employ path integration but must also form robust long-term visual memories of the nest and goal locations (reviewed by Zeil, 2012; Collett et al., 2013a). In the case of inexperienced foragers, these memories about the location of the nest or goal location are acquired through a highly structured process of learning during learning walks and learning flights (reviewed by Collett and Zeil, 2018). These visual memories are then used to guide the subsequent approach to the goal.

We are concerned here with the learning walks of pedestrian insects. Namibian desert ants, *Ocymyrmex robustior*, perform

learning walks when confronted with a new landmark around the nest (Müller and Wehner, 2010). The learning walks are spiral-like with well-choreographed rotations along the vertical body axis (Müller and Wehner, 2010). There are short stopping phases (~150 ms) during these rotations where individuals look back in the direction of the nest. From their perspective, the ants cannot see the nest, so these nest-directed turn-backs must be informed by the current state of their path integrator, and the suggestion is that the views across the nest are remembered at these moments (Graham et al., 2010; Müller and Wehner, 2010). Wood ants *Formica rufa* also engage in learning walks when they leave a newly discovered feeder and look back at landmarks associated with the feeder and not the goal itself (Nicholson et al., 1999). Backward turns where ants face the landmarks directly become less frequent as the ants become more familiar with the location and with increasing distance from the feeder (Nicholson et al., 1999). It should be noted here that in both published cases, the ants under investigation were already experienced foragers and performed learning in response to a new situation in their familiar environment.

The learning walks and flights around the nest of inexperienced foragers in their natural environment have only recently received more attention. These learning events in ants are characterized by an insect leaving the nest and returning to it repeatedly after walking in different compass directions close to the nest (Wehner et al., 2004; Muser et al., 2005; Stieb et al., 2012; Fleischmann et al., 2016, 2017, 2018a,b; Grob et al., 2017). On a different scale, the 'exploration flights' of naïve honeybees (Capaldi and Dyer, 1999; Capaldi et al., 2000; Degen et al., 2015) and bumblebees (Osborne et al., 2013; Woodgate et al., 2016) are very similar, in that successive flights cover different compass directions around the hive.

There are some interesting similarities and differences between the learning walks and the learning flights of insects. First, in both ants and flying insects, learning occurs on leaving the nest for the first time, as the first response to an altered visual environment (e.g. Nicholson et al., 1999; Müller and Wehner, 2010; Narendra and Ramirez-Esquivel, 2017), or whenever the insects had difficulties locating a goal during the previous approach (e.g. van Iersel and van den Assem, 1964; Zeil, 1993a). The more familiar an insect is with the goal location, the shorter and less frequent learning flights and walks become (e.g. Collett and Lehrer, 1993; Lehrer, 1993; Lehrer and Collett, 1994; Zeil et al., 1996; Nicholson et al., 1999; Müller and Wehner, 2010; Robert et al., 2018). In both cases, learning involves moving along arcs and loops around the goal while backing away from it (e.g. Zeil, 1993a; Collett and Lehrer, 1993; Lehrer, 1993; Lehrer and Collett, 1994; Collett, 1995; Nicholson et al., 1999; Müller and Wehner, 2010; Collett et al., 2013b; Philippides et al., 2013; Riabinina et al., 2014; Stürzl et al., 2016). In the case of ants, individuals repeatedly turn back to face the goal (Fleischmann et al., 2017, 2018a), whereas flying insects carefully control where they view the nest as they pivot around it during their learning flights (e.g. Zeil, 1993a; Riabinina et al., 2014; Stürzl et al., 2016).

Research School of Biology, The Australian National University, 46 Sullivans Creek Road, Canberra ACT2601, Australia.

*Present address: Department of Biological Sciences, Macquarie University, 205 Culloden Road, Sydney, NSW 2109, Australia.

[‡]Author for correspondence (jochen.zeil@anu.edu.au)

 P.J., 0000-0002-5562-545X; T.M., 0000-0002-5713-9797; A.N., 0000-0002-1286-5373; J.Z., 0000-0003-1822-6107

Received 24 May 2018; Accepted 12 August 2018

Here, we concentrate on the detailed spatio-temporal organization of the learning walks of *Myrmecia croslandi* ants at the nest site, with the aim of understanding how place learning is organized and controlled. Preliminary results have been documented briefly before (Jayatilaka et al., 2013; Jayatilaka, 2014).

MATERIALS AND METHODS

Study species

Myrmecia croslandi Taylor 1991 (the Australian jack jumper ant; Fig. 1A) are solitary foragers. They show no evidence of relying on recruitment or trail pheromones for finding food: they are

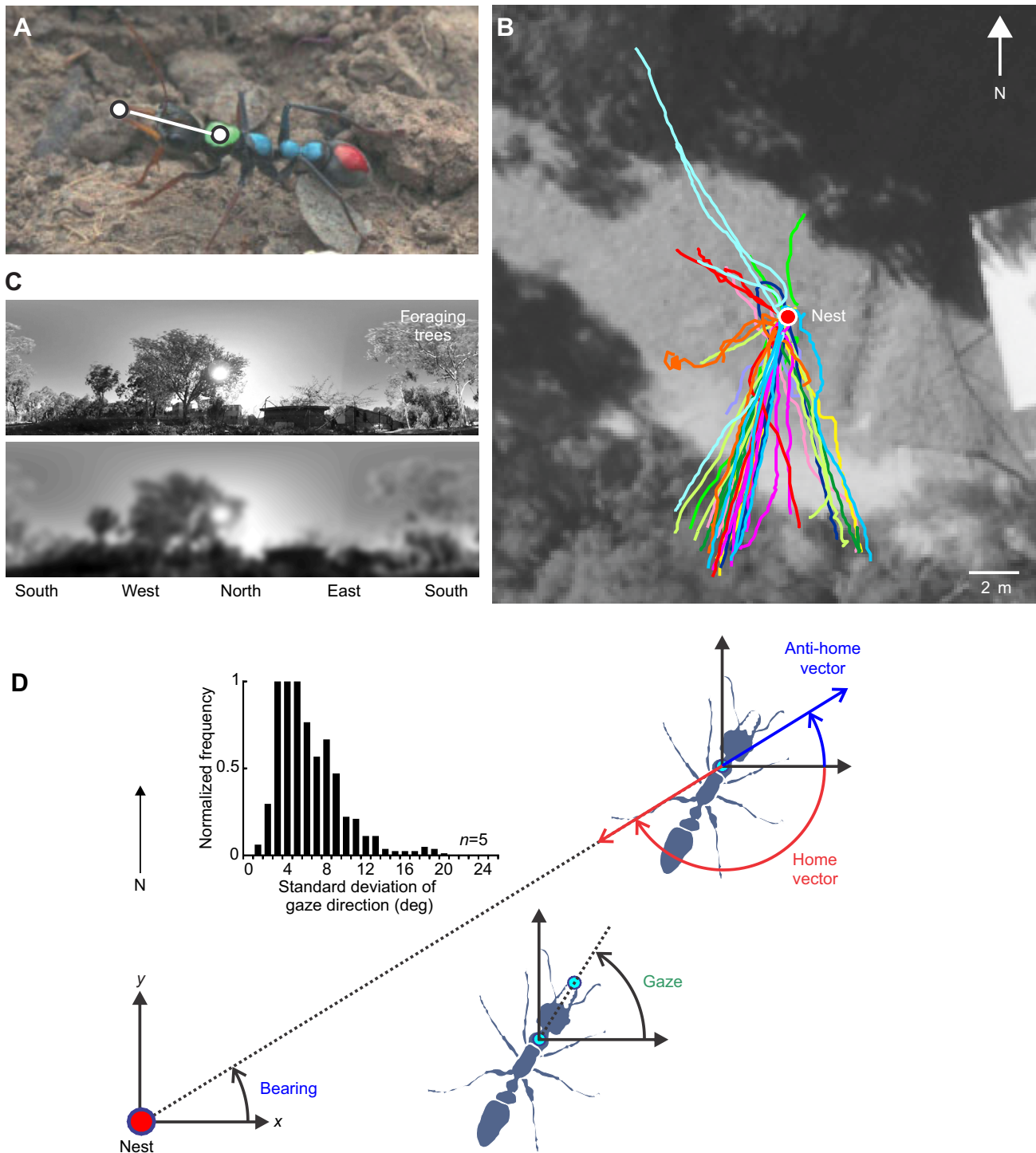


Fig. 1. Background and methods. (A) A marked forager of *Myrmecia croslandi* with white circles indicating the location of head and thorax coordinates extracted from video images. Note that this is not the resolution we achieved with video recordings (photo credit: Chloé Raderschall). (B) Outbound GPS tracks of the foraging paths of different ants at the focal nest. Each coloured line represents a different individual. Nest position is indicated by a red filled circle. Modified and expanded from Jayatilaka et al. (2014). (C) Panoramic view as seen from the nest, covering 38 deg of elevation above the horizon. Bottom image filtered with 3 deg full width at half maximum Gaussian to mimic average *M. croslandi* resolution. (D) Definition of variables. Inset histogram shows distribution of standard deviations of five independent measurements of gaze direction for a 22 s sequence of a learning walk. Results shown in Fig. 1A and D are reproduced in modified form from the PhD thesis of Piyanikar Jayatilaka (Jayatilaka, 2014).

seen individually hunting or climbing trees, they move along idiosyncratic paths and orient visually when displaced (Narendra et al., 2013; Jayatilaka et al., 2014). We studied one nest exclusively for data collection for this analysis. The nest is located at the Campus Field Station at the Australian National University in Canberra, Australia (35°16'49.87"S, 149°06'43.74"E). Workers of *M. croslandi* at this nest predominantly foraged on two *Eucalyptus* trees approximately 10 m southwest of the nest and hunted for insect prey on both these trees and on the ground (west and northwest of the nest; Fig. 1B,C), which they carry back to the nest (for details of the foraging ecology of this species, see Jayatilaka et al., 2011; Jayatilaka et al., 2014; for details of their navigational abilities, see Narendra et al., 2013; Zeil et al., 2014).

Recording

The nest was observed from October 2012 to October 2013. Data on the learning walks of inexperienced and individually identified ants were collected from October 2012 to November 2012. During this period, above-ground activity was high following cessation of foraging activity during the winter months (Jayatilaka et al., 2011). Before above-ground activity had completely resumed, we made regular checks on the nest towards the end of austral winter and beginning of spring (August, September and October), to ensure that recording was started when the nest first became active.

We observed the nest from 07:00 to 19:00 h on consecutive days. Sunrise time in 2012 from 7 October to 30 November varied from 06:32 to 05:42 h. All ants that left the nest ($n=74$) were individually marked with a water-soluble acrylic paint (Citadel Colours, France) using a four spot, three colour code system (Fig. 1A). Observations were carried out throughout the day, from when the first forager left the nest until no more ants left the nest. No observations were made on rainy and overcast days as pilot studies showed ants to be mostly inactive on overcast days and completely inactive on rainy days ($n=5$ days when no observations were made owing to unfavourable weather from October 2012 to November 2012). Learning walks were recorded in an area of 40×30 cm around the nest using a Canon HD Legria HFS 10 camera at 25 frames s⁻¹ with an image size of 1920×1280 pixels.

Twelve marked ants out of a total of 74 observed ants were selected at random and used to record learning walks and their complete foraging careers. These ants were marked as soon as they exited the nest for the first time in that season. A complete foraging career encompassed, for each individual, data from the time an individual: (1) first became active above-ground, (2) carried out learning walks, (3) departed the nest to forage for the first time (i.e. after ants had carried out several learning walks and travelled distances over 2 m from the nest) and (4) continued above-ground foraging activity (i.e. continued to forage over the following days after the first foraging trip had been recorded). Although we cannot be certain whether these marked ants had over-wintered, using the methods described above, we were able to ensure that the ants we observed had not been active in the current observation period prior to marking nor foraged in the last 6 months. In addition to video recording (see below), we also noted the daily timing of learning walks relative to sunrise time and determined for each individually marked ant the number of learning walks, the duration of each learning walk and, in cases where learning walks occurred over a single day, the time between learning walks.

The first three to five consecutive foraging trips of each ant were tracked by placing coloured flags behind her as she walked and by recording the flag trail with a differential GPS as described in detail

elsewhere (Narendra et al., 2013). Here, we only show the first foraging trip.

We recorded additional learning and homing walks of unidentified and most likely experienced forager ants at the same nest in April 2016 and January 2017 with a higher resolution camera (3840×2160 pixels, Sony FDR-AX100E) at 25 frames s⁻¹ that allowed us to film larger areas of 73×42 cm and 66×38 cm, and with a Panasonic DMC-FZ200 camera (1842×1036 pixels) at 100 frames s⁻¹ to investigate the details of fixation durations.

Description and analysis of learning walks

Video clips were first converted to JPEG or PNG image sequences using Final Cut Pro (Apple, Cupertino, CA, USA), Vegas Pro 13 (Sony Creative Software, Middleton, WI, USA) or QuickTimePro (Apple) and the x - y coordinates of the front of the head and the pronotum (Fig. 1D) were tracked manually frame by frame (40 ms or 10 ms inter-frame interval) with a custom-written MATLAB (MathWorks, Natick, MA, USA) program (Digilite, Robert Parker and Jan Hemmi, The Australian National University). From this, gaze direction could be reliably determined to within ±10 deg (see Fig. 1D, inset).

Using a scale object in the video images, x and y coordinates were converted to centimetres and, after coordinate transformations to make the nest the origin of the coordinate system and aligned with north, the bearing, gaze direction, retinal position of the nest, angular velocity and walking speed were determined using custom-written MATLAB programs (see Fig. 1D for definition of variables). Coordinates and derived variables were smoothed with a 3- or 11-point running average as indicated in the figure legends. Probability densities were determined with the *ksdensity* MATLAB function using a smoothing window of 9 deg for directional data. To document regularities across ants and learning walks, the probability densities of speed, angular velocity, scanning amplitudes and gaze directions for individual sequences were normalized to maximum, before means and standard errors (s.e.m.) were determined across samples.

RESULTS

Learning and other walks

There are broadly three kinds of ant movements close to the nest (Fig. 2A,B): the paths of ants engaged in nest excavation (digging paths), the paths of ants heading out to forage and returning from foraging (foraging paths), and learning walk paths. Digging and outgoing foraging paths are more or less straight, with digging paths characterized by immediate, but not necessarily direct, returns to the nest (blue paths in Fig. 2A and left panel of Fig. 2C). Learning walk paths form arcs or loops around the nest with ants entering the nest at the end of the walk (Fig. 2B). These differences are evident in the plots of distance to the nest versus path length that are shown in Fig. 2C and in the inset graphs, which are examples of bearing distributions of three individuals for each of the digging, foraging and learning walk paths. This illustrates that it is only during the learning walks that individual ants cover a wider range of bearings around the nest.

The occurrence and timing of learning walks

Learning walks are thus characterized by an ant leaving the nest and returning to it after walking in a loop close to the nest (Fig. 2B). As we will see later, however, learning ants move and turn in characteristic ways while moving along these paths, and experienced ants will sometimes also walk in an arc around the nest before heading out on a foraging excursion.

Most learning walks of the 12 identified naïve ants occurred between 2 and 6 h after sunrise ($n=30$ walks from $n=12$ ants;

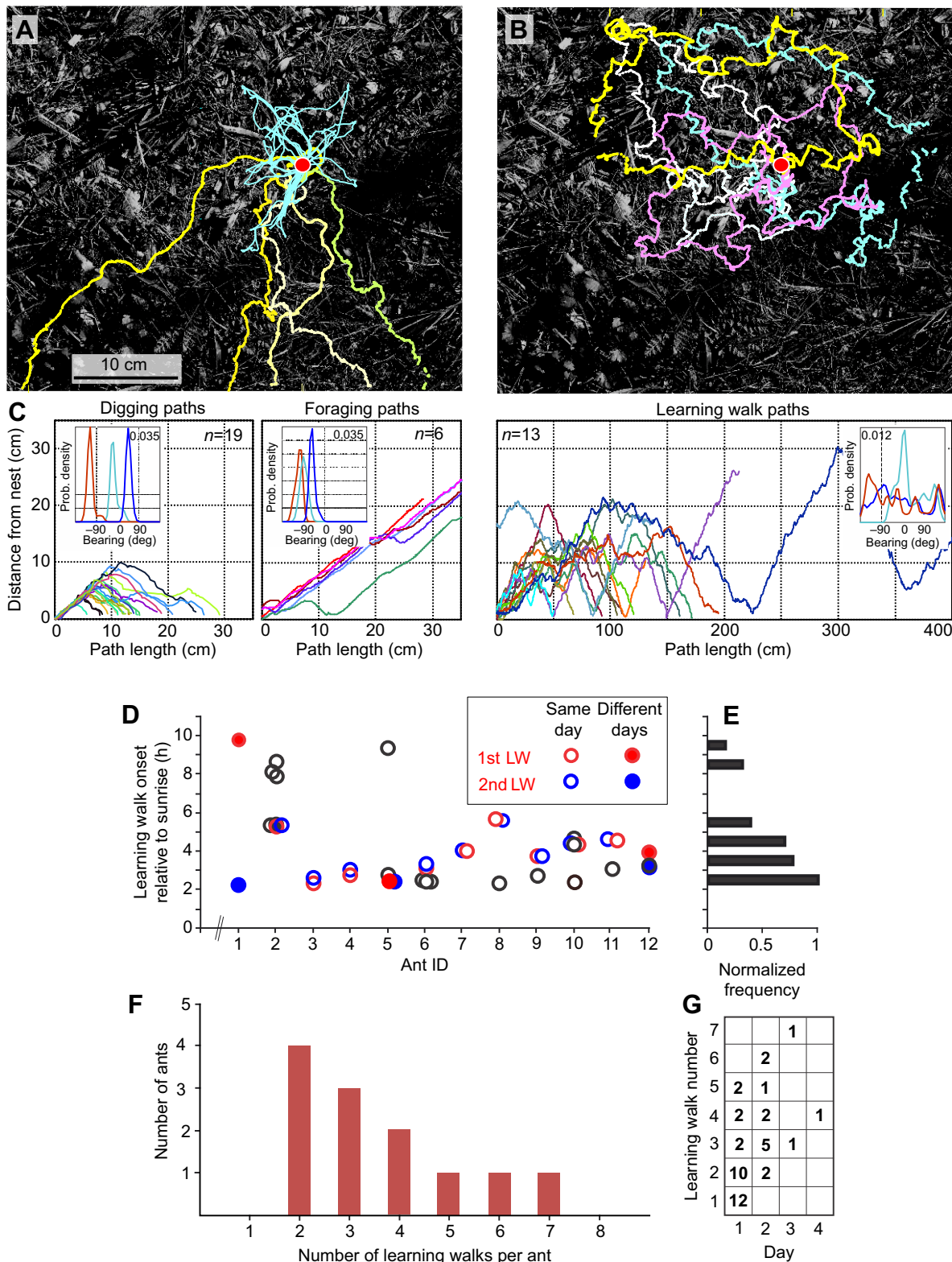


Fig. 2. The path characteristics, timing and number of learning walks. (A) Digging (blue) and foraging paths (yellow–green) of *M. croslandi*. Nest entrance marked by red dot. (B) Five learning walk paths at the same nest. (C) Distance from nest over path length for digging, foraging and learning walk paths. Number of paths is indicated within the panels. Note the different x-axis scales. Insets show bearing distributions for three ants for each path type. (D) Time of day at which learning walks were observed relative to sunrise for 12 individually identified ants. Red and blue open circles: first and second learning walk on same day; red and blue filled circles: first and second learning walk on different days; black open circles: all other learning walks. Overlapping symbols are slightly displaced laterally for clarity. (E) Histogram of the time of day learning walks were observed relative to sunrise time. (F) Number of learning walks per ant. (G) The distribution of successive learning walks over different days. Values indicate the total number of first, second, etc. learning walks that happened on the same day (day 1) or on subsequent days (days 2–3). Results shown in Fig. 2D–G are reproduced in modified form from the PhD thesis of Piyankarie Jayatilaka (Jayatilaka, 2014).

Fig. 2D,E), although some ants performed their walks much later in the afternoon, between 8 and 10 h after sunrise (e.g. ants 1, 2 and 5; Fig. 2D). First and second learning walks occurred in a narrow temporal window relative to sunrise always within 2 h of each other, even on separate days, with the exception of those of ant 1 (Fig. 2D, red and blue circles). When learning walks occurred on a single day, the time between them was highly variable, averaging 13.6 ± 33.6 min (mean \pm s.d., $n=12$ ants, range 0.5–164 min). Ants carried out between two and seven learning walks (Fig. 2F) over up to 4 days before starting to forage (Fig. 2G), although most ants performed learning walks over 2 days. There was no significant correlation between the duration and the number of learning walks (regression analysis, $P=0.28$, d.f.=41). Learning walks within the recording area (40×30 cm) had an average duration of 56.8 ± 49.3 s (mean \pm s.d., $n=12$ ants, range 12.4–225.9 s). Unfortunately, with the recording equipment available at the time, only a few learning walk paths were confined to the recording area around the nest (Fig. 3), which had to be kept small to be able to determine gaze directions. We estimate that ants covered an approximate maximum distance of 86 cm outside the field of view of the camera (judged by their average walking speed of 1.2 cm s^{-1} and time of exit from and subsequent entry into the recording area). Tracking of extended learning walks with differential GPS showed that they covered distances of up to 3 m away from the nest (data not shown).

Learning walk paths and bearings

Viewed across 12 ants, there was no consistent direction in which ants carried out their first learning walks (red paths in Fig. 3 and red distributions in Fig. 4) and these first walks were also not necessarily restricted to an area very close to the nest. However, successive learning walks of individual ants occurred in different compass directions around the nest (Fig. 4). Ants differed in the degree to which they covered directions around the nest relative to their first foraging trip (marked by long red line in inset histograms in Fig. 3). However, the group distribution showed no clear, preferred directions between ants (circular mean direction: -99 deg, vector length: 0.0135; Rayleigh $z=0.0103$; $P=1.0$). Note that all first foraging trips went south towards the colony's preferred foraging trees (see Fig. 1B), which may have provided guidance with their overhanging canopy.

The detailed choreography of learning walks

On a fine spatial and temporal scale, learning walk paths had a meandering structure (Figs 5 and 6) that was caused by very regular scanning movements of the head (gaze in Fig. 5B), which are supported by body movements (Fig. 5C). Ants oscillated between looking in the direction of the nest and in the opposite direction (see light blue line in Fig. 5B). In the example shown in Fig. 5 and in following figures, instances when an ant looked to within ± 10 deg of the nest are marked red (looking in the direction of the home vector) and instances when the ants looked to within ± 10 deg directly away from the nest (anti-home vector views) are marked dark blue. The ants' scanning movements oscillated between the nest direction (red line and red circles in Fig. 5B) and directions pointing directly away from the nest (dark blue line and dark blue circles in Fig. 5B), because scanning direction was reversed shortly before or after the ant encountered these directions (see oscillating time course of gaze direction; light blue line in Fig. 5B). This is also evident in the regular reversals of the angular gaze velocity shown in Fig. 5D. It is necessary to add one caveat in relation to this detailed analysis: we have to assume that the ant's home vector points at the nest directly, although we do not know when and where exactly the animals start path integrating at the beginning of these walks.

We note the following regularities in this learning walk and the further examples shown in Fig. 6: the ants walked relatively slowly ($< 3 \text{ cm s}^{-1}$; Fig. 5D) compared with foraging walks (Fig. 6B, top) and their angular velocity profile differed from that during foraging exits (Fig. 6B, bottom). Their scanning movements can be, but do not have to be, very regular, as documented by the periodic auto-correlations of the angular velocity time series for six walks in the left panel of Fig. 6C and the weak or absent periodicities for seven walks in the right panel of Fig. 6C. During part of their walks, however, some ants turned in the direction of the nest at very regular intervals (Fig. S1), encountering regularly spaced nest- and anti-nest directed views (Fig. S1A,B). Successive nest-directed viewing directions changed at a constant rate during such path segments, as documented for six examples shown in Fig. S1C. In general, the reversals of scanning direction were roughly linked to the moments in which the insects were aligned parallel to the home vector so that the ant's gaze direction oscillated between the direction of the home vector (marked by red circles in Figs 5B, 6A and Fig. S1B) and that pointing away from home (anti-home vector views marked by dark blue circles in Figs 5B, 6A and Fig. S1B). This was the case even during the initial path sections, when the ants predominantly looked away from the nest as they moved away from it (as indicated by their distance from the nest, black line Figs 5 and 6), and during their final return, when they predominantly looked in the nest direction.

If reversals of scanning direction are indeed associated with instances in which the ants are aligned parallel with the home vector, we would expect: (1) a decrease in angular velocity following nest or anti-nest view encounters; (2) scanning amplitudes between reversals of scanning direction to be approximately 180 deg; and (3) gaze directions relative to the nest at the moment of scanning direction reversal to show two peaks, one close to 0 deg (when the ants look in the direction of the nest) and one close to 180 deg (when the ants look away from the nest). We extracted these features from 13 walks for which we have complete paths, and found that the ants' angular velocity was particularly high when encountering nest and anti-nest views and did not significantly decrease following these encounters (Fig. 7A). Because this pattern may be dominated by nest and anti-nest views encountered during initial movements away from the nest and during the ants' return to the nest, we restricted this analysis to sections of walks between the first turn-back to the nest and the moment the ants began their return to the nest (inset Fig. 7A). Again, angular velocity was relatively high during these view encounters and there was no significant decrease of angular velocity following view encounters, most probably because reversals of scanning direction occurred at variable times before and after view encounters (see Figs 5 and 6). For the same reason, the scanning amplitude distribution has a broad peak between 90 and 180 deg (Fig. 7B) and the distribution of gaze directions relative to the nest direction at the moments in which scanning direction is reversed has three peaks at 20, 74 and 141 deg (Fig. 7C). Overall, the distribution of gaze directions relative to the nest broadly and quite uniformly covers all directions between nest and anti-nest views (Fig. 7D).

We also note that the ants did not linger (or 'fixate') when they were aligned parallel to the home vector, but rather swept through these alignments, in contrast to what has been described for desert ants (Müller and Wehner, 2010; Fleischmann et al., 2017, 2018a): at the moment of first alignment (time=0 in Fig. 7A), mean angular velocities were close to 150 deg s^{-1} , which is toward the higher end of the angular velocity distribution of learning walks (Fig. 6B, bottom).

High-speed video analysis confirmed that nest-directed views are not associated with prolonged fixations compared with fixations at

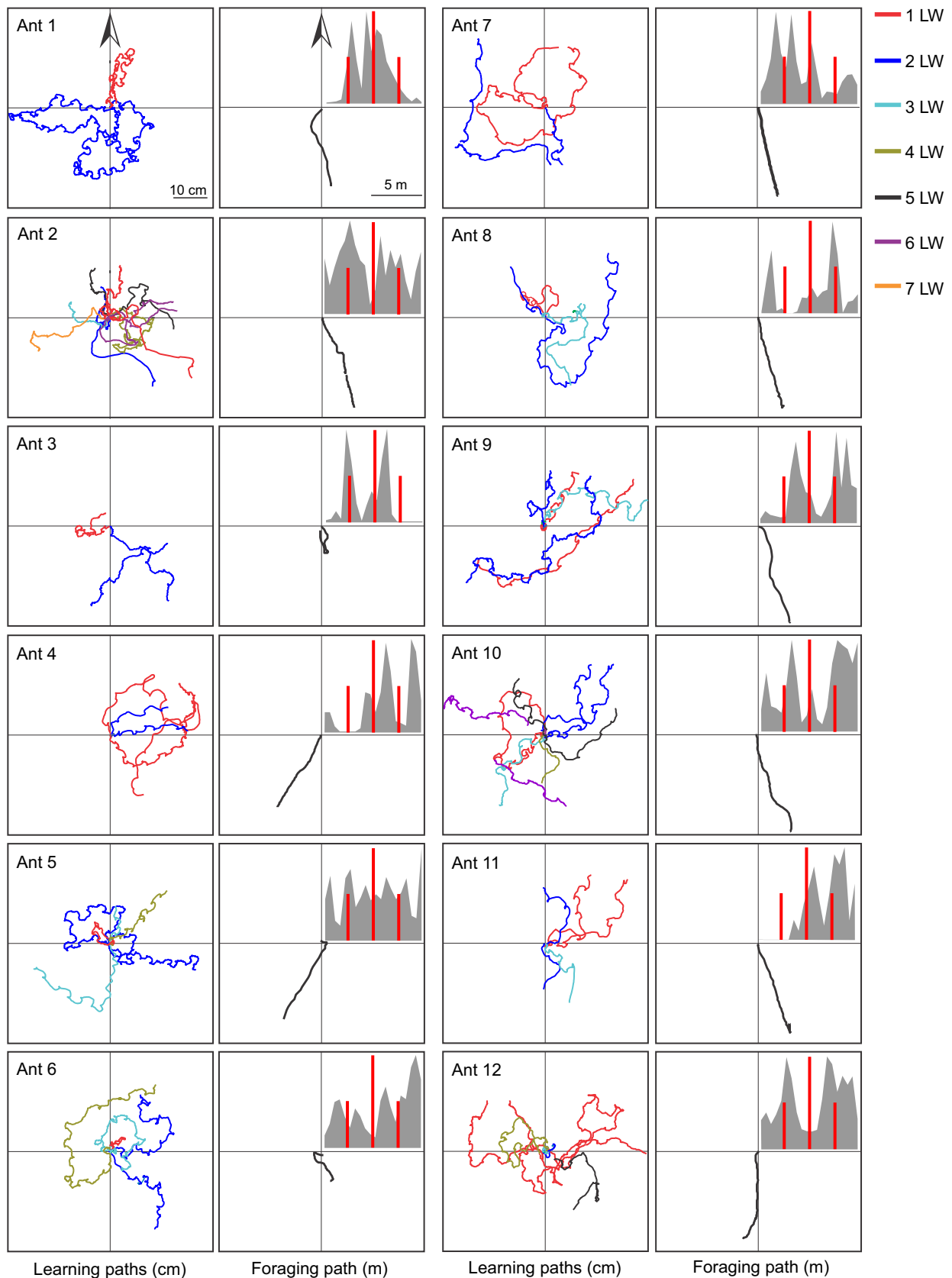


Fig. 3. Learning and foraging paths. All observed learning walk paths (columns 1 and 3) of 12 identified ants and the GPS path of their first foraging trip (columns 2 and 4). Note the differences in scales. The nest is in the centre of panels at the intersection of lines and north is indicated by the arrow. Successive learning walks (LW) are colour-coded as per the key on the right. Inset histograms show compass directions of all learning walk paths per ant relative to the direction of her first foraging trip (marked by a long vertical red line) normalized to the maximum. Shorter red lines mark the directions ± 90 deg relative to the foraging direction. Histogram x-axis ranges from -180 to 180 deg. Results shown in Fig. 3 are reproduced in modified form from the PhD thesis of Piyankarie Jayatilaka (Jayatilaka, 2014).

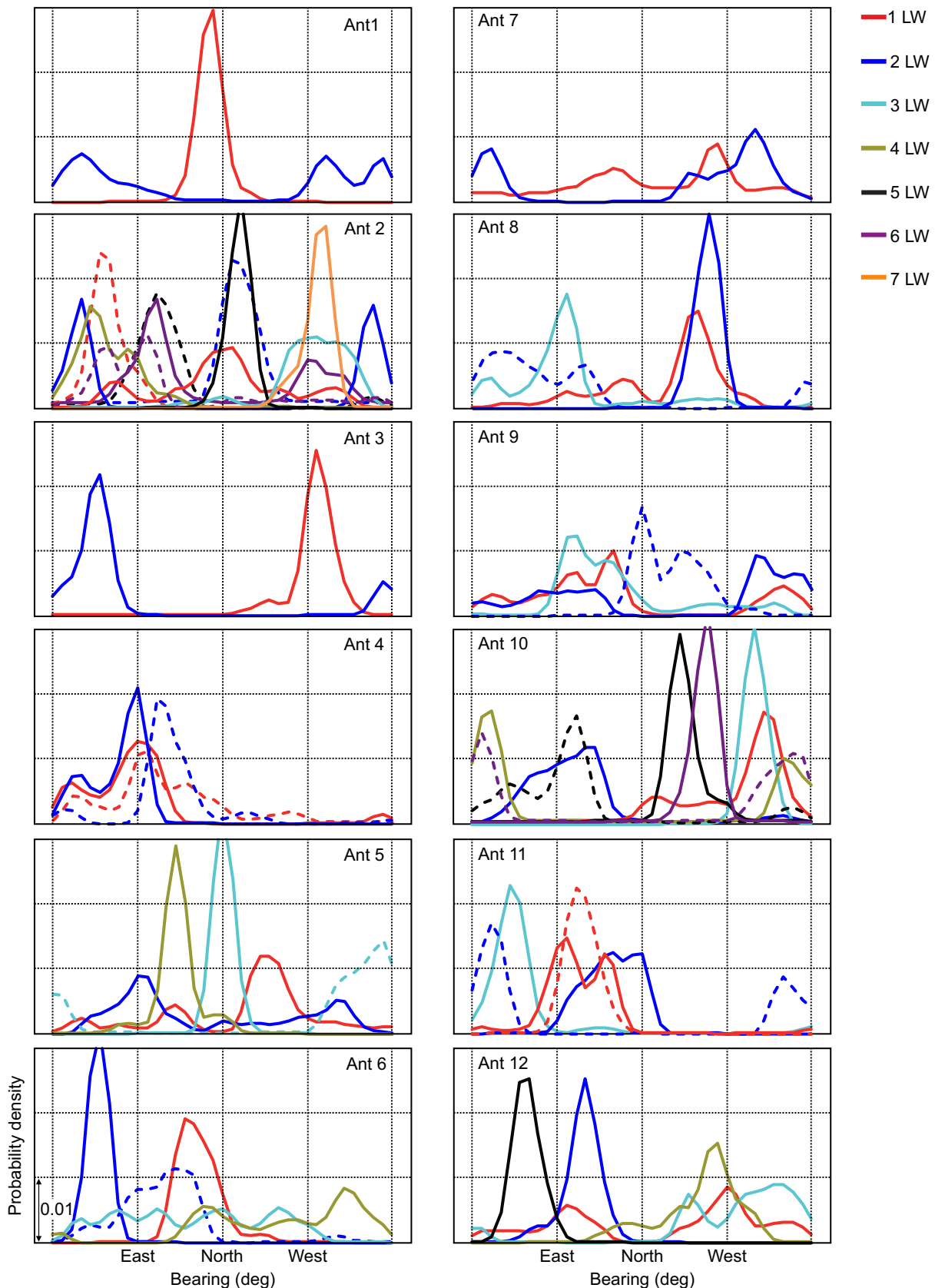


Fig. 4. The compass directions covered by successive learning walks. Shown are the probability density distributions of the frame-by-frame compass directions relative to north in which successive learning walks were made by 12 identified ants. Successive learning walks (LW) are colour-coded as per the key on the right. For walks that left the recording area, bearing distributions are shown separately for outbound (solid lines) and inbound legs (dashed lines). Bearings were determined at 40 ms intervals and distributions were determined with kernels of bandwidth of 10 deg. Results shown in Fig. 4 are reproduced in modified form from the PhD thesis of Piyankarie Jayatilaka (Jayatilaka, 2014).

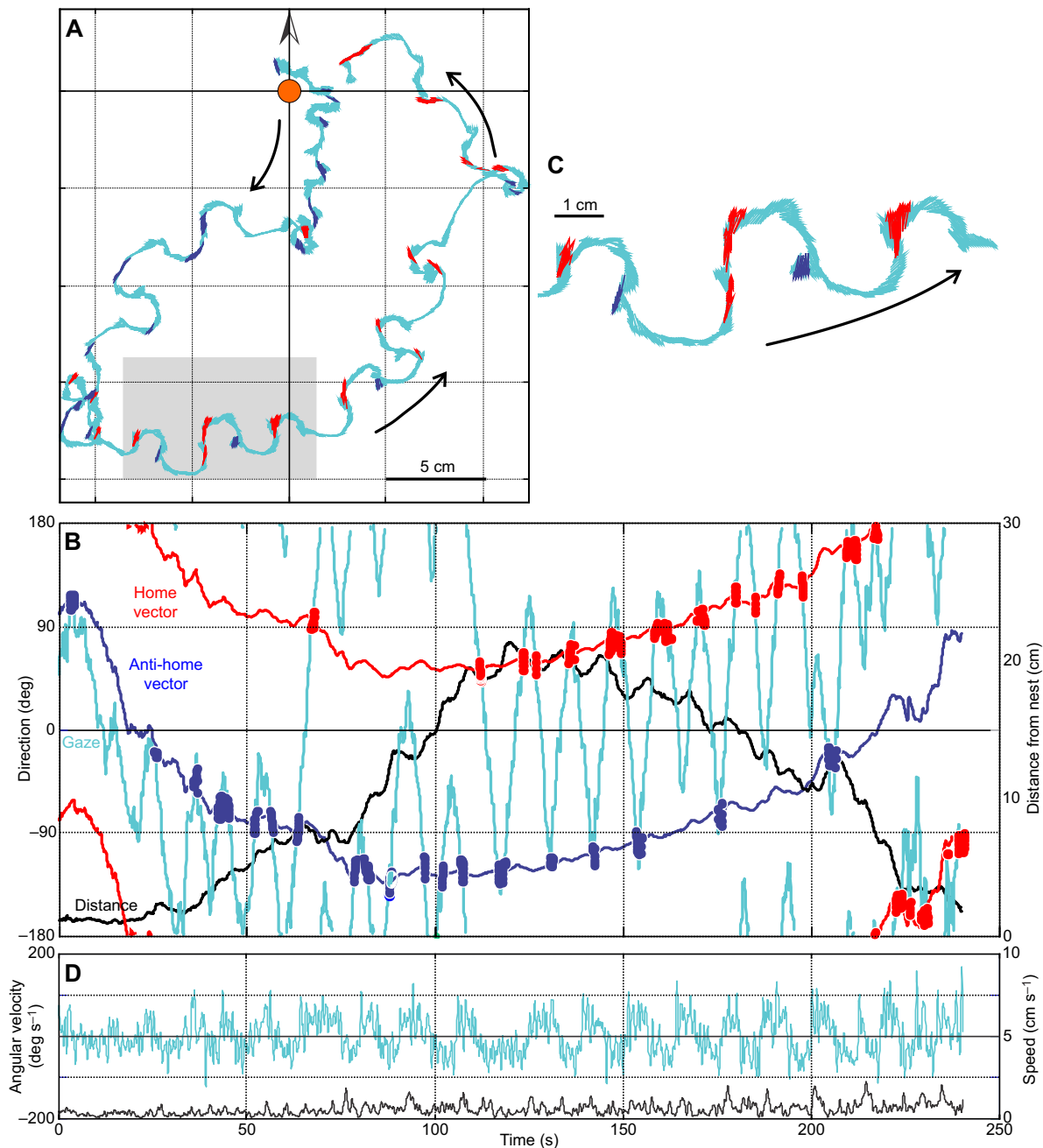


Fig. 5. The choreography of learning walks. (A) The initial loop of the second learning walk of ant 1. North is indicated by the arrowhead; the nest is marked by an orange circle; travel direction is indicated by black arrows. Light blue arrows show the gaze direction (head orientation) of the ant every 40 ms. Red and blue arrows mark the locations when the ant's head is oriented in the nest direction to within ± 10 deg (red) or in the opposite direction (blue). Grey shaded area marks the expanded view of the ant's path in C. (B) Time course of gaze direction (light blue) (north at 90 deg), the bearing relative to the nest (blue), the home vector direction (red) and the distance from the nest (black) for the learning walk loop shown in A. The gaze trace is labelled with a red circle whenever the ant looks within ± 10 deg in the nest (home vector) direction and blue circles when she looks in the opposite direction. Note that these instances are often followed by a reversal of scanning direction. (C) Detail of the ant's path as indicated by grey shaded area in A. Otherwise, conventions as in A. (D) Time course of the ant's angular velocity (light blue) and walking speed (black) for the same sequence. The ant does not appear to stop and 'fixate' the nest direction. x - y coordinates and derived variables were smoothed with an 11-point running average. Results shown in Fig. 5 are reproduced in modified form from the PhD thesis of Piyankarie Jayatilaka (Jayatilaka, 2014).

other times during learning walks (Fig. 7E, lower panel), with the exception of four instances of slightly longer fixations within 10–20 deg of the nest when fixation durations longer than 0.1 s were considered (Fig. 7E, top panel). Finally, the gaze directions of ants during their learning walks were not associated with specific panorama features: Fig. 7F shows the distribution of all gaze directions of ants (black lines) and of gaze directions when looking

into the nest direction (red lines) during seven learning walks filmed at 100 frames s^{-1} and 13 walks filmed at 25 frames s^{-1} together with the local panorama (top images) and the mean pixel values along vertical pixel columns (blue lines).

We conclude that during their learning walks, the ants experience a systematic sequence of views as they alternate between turning in the nest direction and turning away from the nest at different

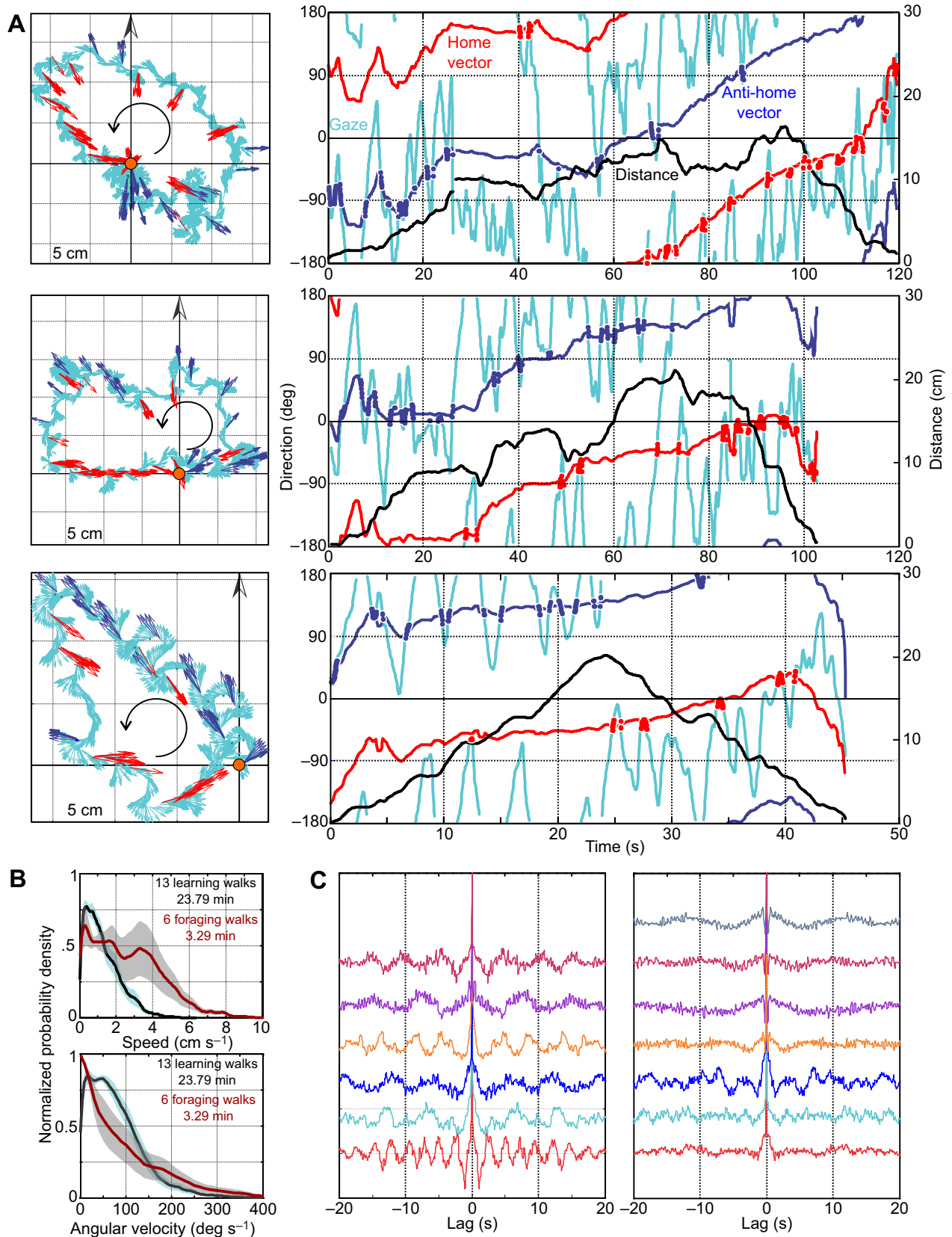


Fig. 6. The choreography of learning walks. (A) Three examples of full learning walk paths of three different ants (left panels) and the time course of gaze direction, bearing and distance from the nest (right panels). Otherwise, conventions as in Fig. 5. (B) Top: normalized distributions of walking speed during learning walks (black) and foraging walks (red). Shaded areas mark the s.e.m. Bottom: same for angular velocity. (C) Autocorrelation functions of the time course of the angular (gaze) velocity of ants (see Fig. 5D) during 13 learning walks. Correlation functions are displaced vertically for clarity and sorted into those with clear periodicities (left panel) and those that are less regularly modulated (right panel).

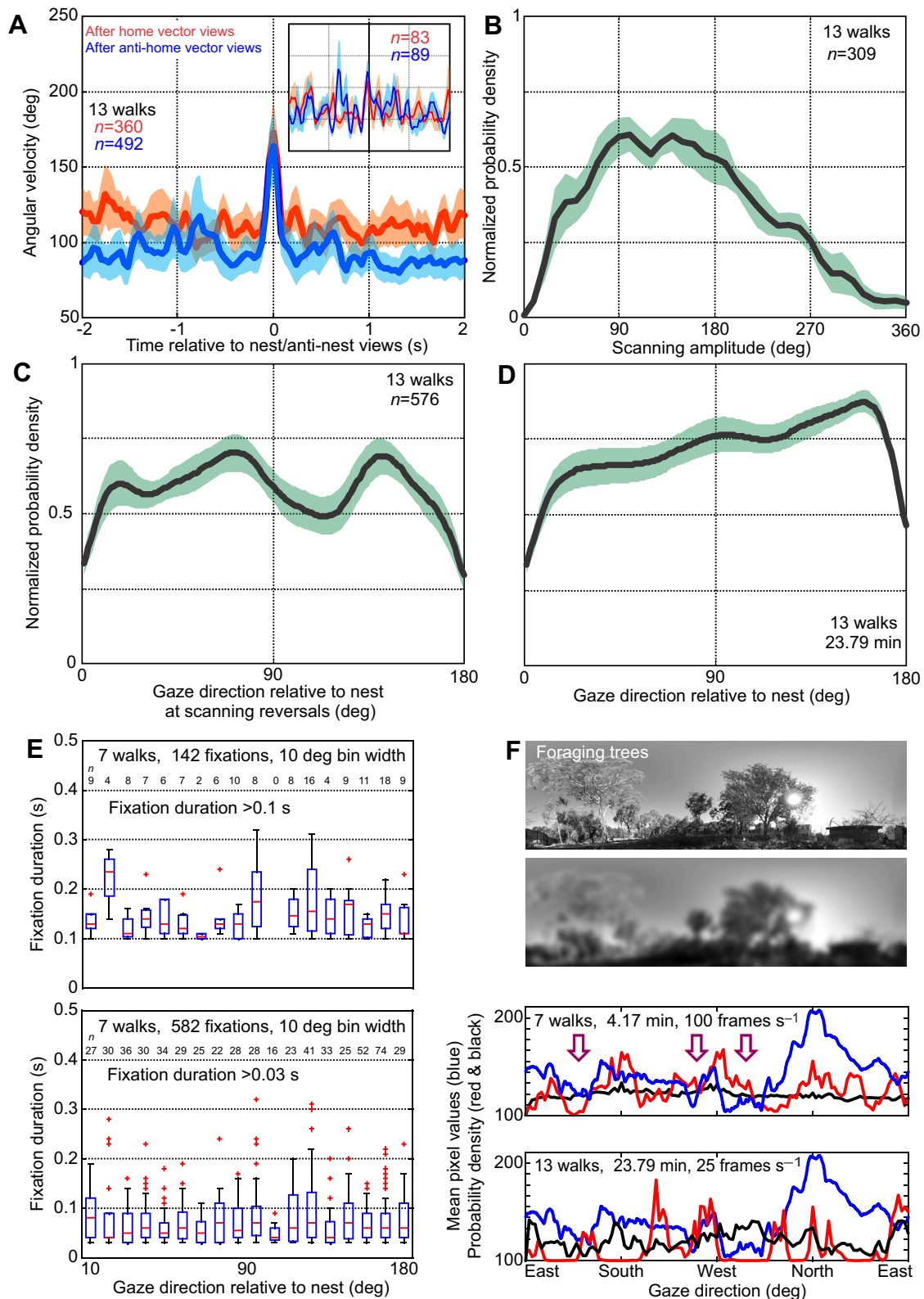


Fig. 7. See next page for legend.

compass bearings around the nest, and that this sequence must be guided by the state of the ants' path integrator (as shown by Müller and Wehner, 2010), because from their perspective, the ants cannot see the nest entrance. The ants' scanning movements oscillate between the nest and the anti-nest direction despite the fact that the

association between the reversals of scanning direction and the ants' alignment parallel to the home vector direction is rather weak overall (Fig. 7C), mainly because the strength of this association varies greatly throughout the execution of a learning walk (e.g. Figs 5, 6 and Fig. S1).

Fig. 7. The quantitative analysis of learning walks. (A) Mean angular velocity (thick lines) and s.e.m. (shaded area) over time 2 s before and 2 s after ants encountered the nest (home vector) direction (red) or the opposite direction (blue) during scanning movements. A total of 360 and 492 four-second segments after ants first looked within ± 10 deg of the nest or anti-nest direction were extracted from 13 learning walks. Individual distributions were normalized to maximum before averaging. Data were smoothed with a three-point running average. Inset shows the same for a subset of segments between the first turn-back and the moment the ants start returning to the nest. (B) Average distributions of scanning amplitudes between reversals of scanning direction during 13 learning walks. Individual distributions were normalized to maximum before averaging. Mean (thick black line) and s.e. (shaded area). Data were smoothed with a three-point running average. Seventeen out of 309 scanning amplitudes were larger than 360 deg. (C) Same for the absolute gaze direction of ants relative to the nest direction at the moments of reversal of scanning direction. Gaze directed at the nest at 0 deg and gaze directed away from the nest at 180 deg. Otherwise, procedures and conventions as in B. (D) Absolute gaze directions relative to the nest throughout 13 learning walks. (E) Fixation durations depending on gaze direction relative to the nest at zero (ignoring sign). Shown are box and whisker plots in 10 deg bins for 582 fixations during seven learning walks filmed at 100 frames s^{-1} with durations longer than 30 ms (bottom panel) and for 142 fixations out of the same sample with durations longer than 100 ms (top panel). Fixations are defined as consecutive sampling intervals where the angular velocity of gaze direction was smaller than 10 deg s^{-1} for periods longer than 0.03 s (bottom) and longer than 0.1 s (top). Numbers of fixations in each bin are shown. (F) Gaze directions during learning walks of *M. croslandi* and their relationship with the panorama as seen from the nest. Upper: panoramic views from the nest at camera resolution and filtered with a 3 deg full width at half maximum Gaussian. Lower: panorama brightness (blue lines; pixel values averaged across vertical pixel rows); probability density of all gaze directions (black lines); and probability density of gaze directions when ants look across the nest (red lines). Data are shown separately for seven learning walks filmed at 100 frames s^{-1} (top panel) and for 13 learning walks filmed at 25 frames s^{-1} . Locations of foraging trees are marked in the topmost panorama, and all major tree locations are marked by arrows in the topmost lower panel.

In addition to full learning walk loops, which are terminated by ants entering the nest, we also found that experienced foragers often performed a partial learning walk segment in an arc opposite to their intended foraging direction (Fig. 8A). Other ants left the nest during the same period of observation in much straighter paths (see Fig. 2A). We recorded these walks after several days of experimenting with foragers that were captured and subsequently released close to the nest. These partial re-learning segments are thus presumably triggered by disturbance experienced previously by individuals and exhibit a similar organization as the one we described for full learning walk loops (see bottom right panels Fig. 8A,B). However, in contrast to the learning walks of naïve ants, partial learning walks were immediately followed by a foraging excursion (indicated by large blue arrows in Fig. 8A).

Homing walks

Although it is attractive to suggest that ants memorize the scene around the nest whenever they are aligned parallel to the home vector, looking in (as suggested by previous work, e.g. Müller and Wehner, 2010; Graham et al., 2010; Fleischmann et al., 2017, 2018a) and opposite to the nest direction (as suggested, in addition, by our observations here), a way still has to be found to show that this is the case. One possible avenue would be to identify the navigational decisions made by homing ants, in relation to where they had been during their learning walks (e.g. Fleischmann et al., 2018b). Unfortunately, we did not collect data on the details of the homing paths of identified ants that would allow us to perform this analysis at this stage. However, the behaviour of homing ants in general suggests that such an analysis would be fruitful: homing ants perform regular scanning movements, which are of much

smaller amplitude compared with the scanning oscillations during learning walks (Fig. 9), but most importantly, in many cases, they do not approach the nest directly, but walk past it, before correcting their path. It will be interesting to see whether there is a relationship between the navigational corrections of homing ants and the locations they had occupied during learning, in particular those where they had been aligned parallel to the home vector.

DISCUSSION

Before going out on their first foraging excursion, *M. croslandi* ants perform two to seven learning walks around the nest over up to 4 days, as has recently also been described for the desert ant *Cataglyphis fortis* (Fleischmann et al., 2016). Most learning walks occurred between 2 and 6 h after sunrise, with the first two learning walks restricted to a narrow temporal window of 2 h when they occurred on the same day, but also when the first and second walk were performed on different days. Such temporal fidelity in the timing of learning walks may be attributed to the fact that most foragers exit this nest 4–6 h after sunrise (Jayatilaka et al., 2014).

Successive learning walk paths cover different compass bearings around the nest (see also Wehner et al., 2004; Muser et al., 2005; Stieb et al., 2012; Fleischmann et al., 2016), an observation that is strikingly similar to what has been documented for the sequence of learning flights in honeybees (Capaldi and Dyer, 1999; Capaldi et al., 2000; Degen et al., 2015) and bumblebees (Osborne et al., 2013; Woodgate et al., 2016). It is not clear at this stage whether insects choose successive directions randomly or whether they remember where they have been before and head in novel directions.

The learning walks of *M. croslandi* exhibit a distinct spatio-temporal organization with, at times, very regular scanning movements that lead to a series of systematically changing views toward and away from the nest from the perspective of different compass bearings. We found no evidence that the ants stop and fixate exactly when facing toward or away from the nest, nor that their gaze directions during learning walks are related to dominant visual features in the nest environment (Fig. 7E,F).

Although recent studies of the learning walks in *Cataglyphis* ants and an older study in *Formica* were not primarily concerned with investigating the full spatio-temporal dynamics of learning choreography, there are a number of interesting similarities and differences that emerge from a comparison between different ants.

A common observation in ant learning walks is that ants frequently turn back to look in the nest direction, a behavioural element called ‘pirouettes’ by Müller and Wehner (2010) and Fleischmann et al. (2017, 2018a,b). However, in contrast to *M. croslandi*, the desert ants *Ocymyrmex robustior* (Müller and Wehner, 2010), *Cataglyphis noda* and *C. aenescence* (Fleischmann et al., 2017, 2018a,b) stand still for 130 to 200 ms when facing the nest during these turn-backs, and wood ants walk a few centimetres back towards a feeder (Nicholson et al., 1999) or along a novel route (Graham and Collett, 2006). In addition, both *C. noda* and *C. fortis* frequently perform fast 360 deg turns on the spot (Fleischmann et al., 2017). We did observe such complete turns in *M. croslandi*, but at most two times during a learning walk (e.g. Figs 5 and 6). We document here that turn-backs in *M. croslandi* alternate with turns in the opposite direction, away from the nest, and it will be interesting to see whether this is also true for desert ants. It is clear, however, that directed turns during learning walks at the nest must be guided by path integration (Müller and Wehner, 2010), because from the ants’ perspective, they cannot see the nest entrance. Interestingly, the desert ant *C. noda* continues to be able to execute nest-directed turns when celestial compass cues are absent (Grob et al., 2017), but is unable to do so when the magnetic

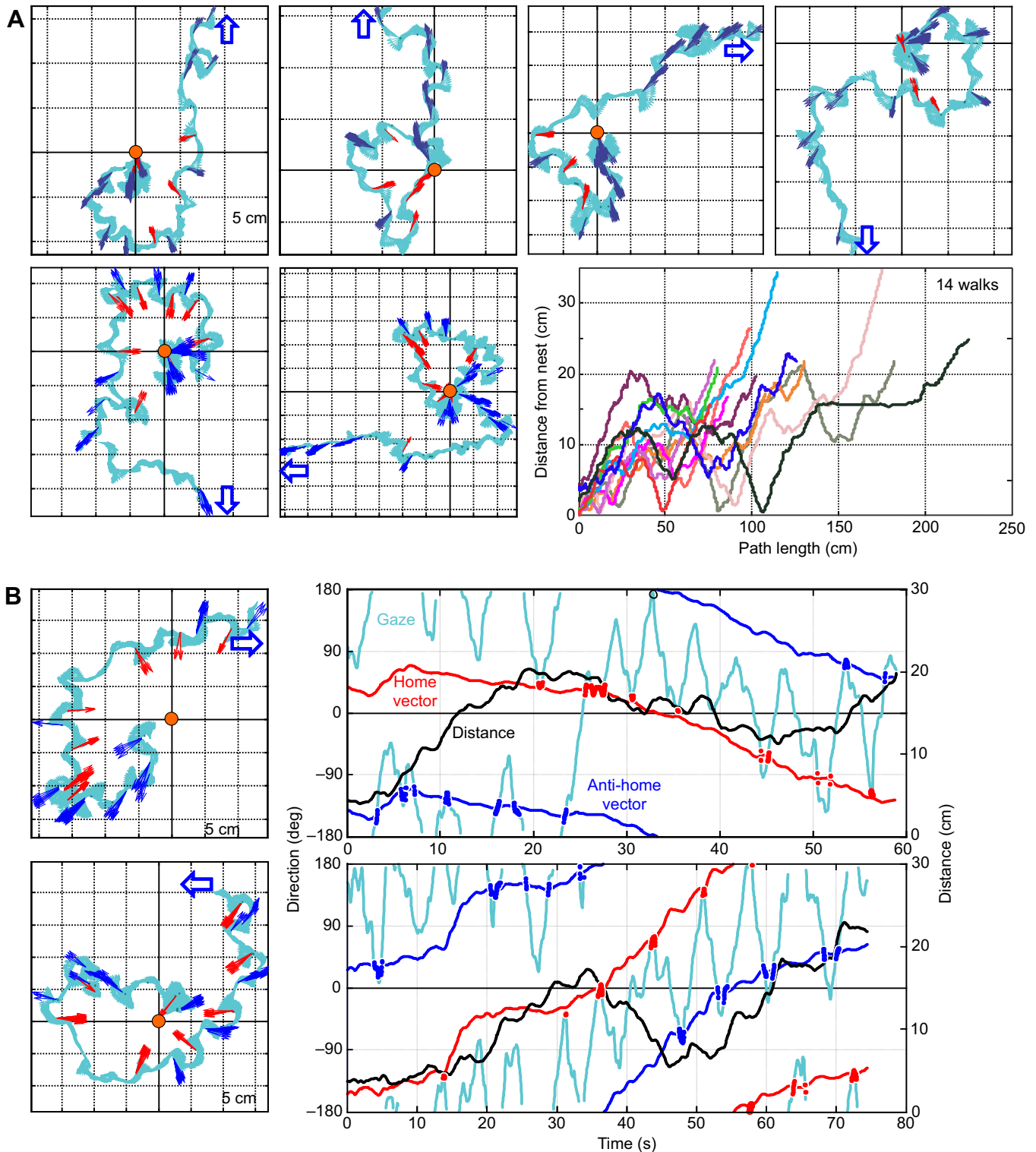


Fig. 8. Partial learning walk segments followed by foraging. (A) Six examples of partial learning walk segments performed by ants that subsequently leave for foraging in the directions indicated by the dark blue arrows. Gaze direction indicated by light blue arrows, instances when ants look back at the nest (at the intersection of thick black lines) to within ± 10 deg are marked by exaggerated red arrows and those when ants look away from the nest direction to within ± 10 deg by blue arrows. Bottom right panel: distance to nest over path length for 14 partial learning walks. All paths were recorded on a single day in April 2016. Otherwise conventions as before. (B) Two further partial departure segments, together with the time course of gaze (light blue), bearing (blue), home vector direction (red) and distance from the nest (black). Otherwise, conventions as in Fig. 5.

field is disturbed. When the magnetic field is rotated, they turn to 'virtual nest directions' as predicted by the extent of the rotation (Fleischmann et al., 2018a).

The learning walks (or exploration runs) of foragers exiting the nest for the first time, as they have now been described in *Melophorus bagoti* (Muser et al., 2005), *C. bicolor* (Wehner et al., 2004),

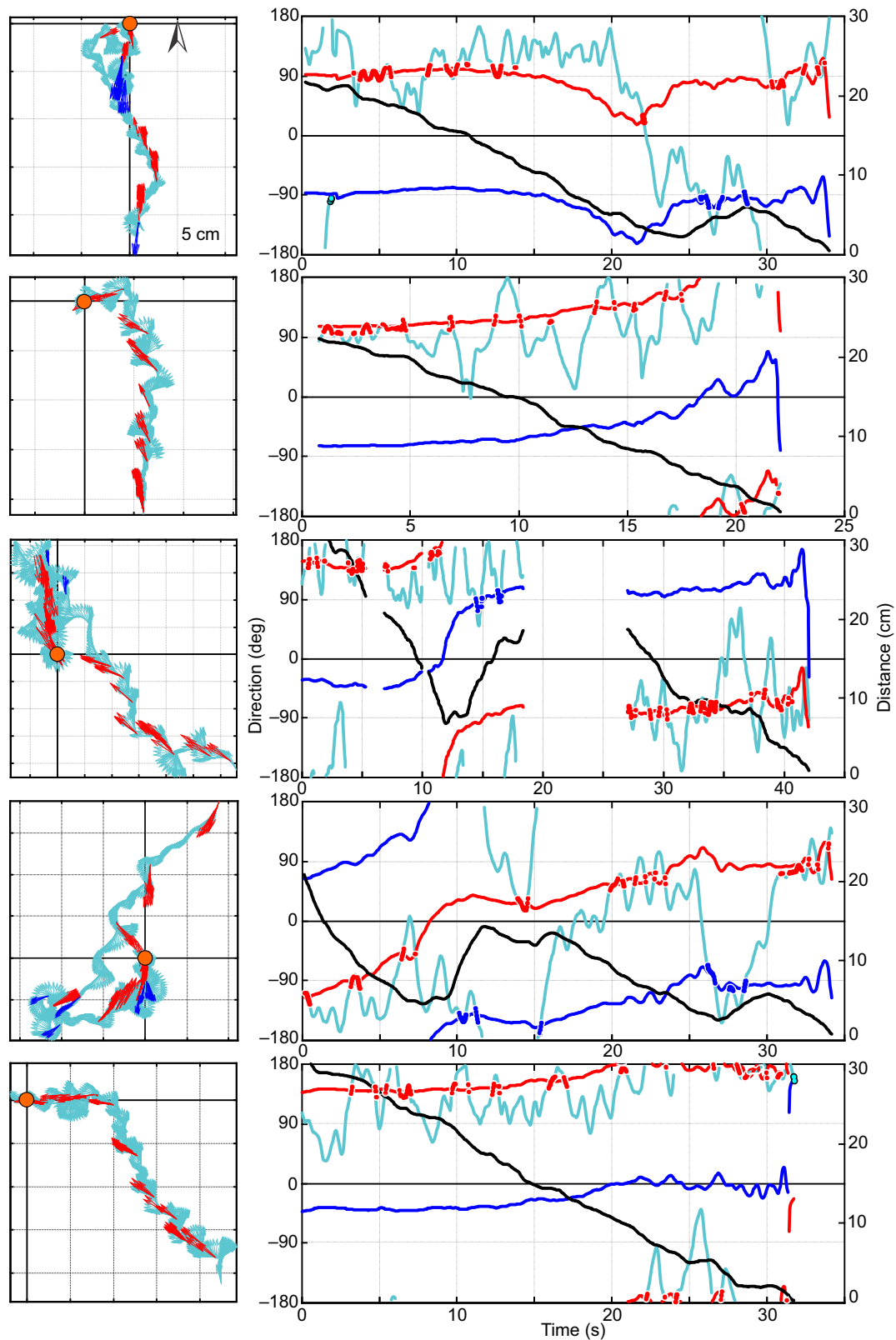


Fig. 9. The paths and scanning behaviour of ants returning to the nest. Conventions as in Fig. 5.

C. fortis, *C. noda*, *C. aenescens* (Fleischmann et al., 2016, 2017, 2018a,b) and *M. croslandi* (present study), all end with the ant entering the nest again and therefore are defined as ‘small-scale round trips around the nest entrance that preceded the foraging runs’

(Wehner et al., 2004). The re-learning walks performed by apparently experienced *M. croslandi* ants after they have encountered disturbance around the nest or had difficulties locating it previously (see also Müller and Wehner, 2010; Jayatilaka, 2014; Narendra and

Ramirez-Esquivel, 2017), differ from the learning walks of naïve ants by not ending with re-entry into the nest, but with the ants leaving the nest area to forage (Fig. 8; see also Müller and Wehner, 2010). Re-learning ants pivot around the nest in the direction opposite to the subsequent foraging direction, during which their scanning behaviour closely resembles that of the learning walks of naïve ants. Considering that homing ants often do not approach the nest directly, but make a number of corrective manoeuvres close to the nest, these partial learning walks followed by foraging may supply homing ants with a crescent of nest-directed and opposite views that protect them from getting lost when overshooting the nest location.

The function of learning walks

What happens during learning walks and what potential navigational information do they provide?

As has been demonstrated before with regard to the learning flights of bees and wasps (e.g. Opfinger, 1931; Becker, 1958; Tinbergen and Kruyt, 1938; Zeil, 1993b), the learning walks of ants are a prerequisite for subsequent homing success with the aid of the landmark panorama (Fleischmann et al., 2016, 2018b). Like *M. croslandi*, *C. fortis* ants also perform three to seven learning walks before heading out to forage, and the more learning walks they have performed at the nest that was surrounded by a landmark array, the

more closely they searched for the fictive nest position when released at an identical test array (Fleischmann et al., 2017). The trick appears to be the acquisition of nest-directed views from different compass directions, as first suggested by Graham et al. (2010) and modelled by Baddeley et al. (2012) and Dewar et al. (2014). We illustrate the navigational information provided by such views for the specific environment of the nest we studied (Fig. 10A). In addition, we suggest why it may be advantageous for ants to also learn views when facing away from the nest during learning walks (Fig. 10C).

Consider the case of a nest-directed panoramic snapshot taken 20 cm to the north of the nest, facing south (Fig. 10A): the orientation of this snapshot can be recovered by alignment matching up to 6 m away from the nest in this particular environment, because the rotational image difference function (rotIDF; yellow lines in Fig. 10B) comparing the reference view with the view seen 6 m north of the nest has a detectable minimum (bottom image, Fig. 10B). Approaching the nest from the north (dashed line, Fig. 10A), this minimum becomes more pronounced, flanked by increasingly steeper gradients, as the location of the reference image is approached (Fig. 10B). Over some distance, then, nest-directed snapshots provide information on nest direction even at locations an ant may never have visited before (Narendra et al., 2013; Stürzl

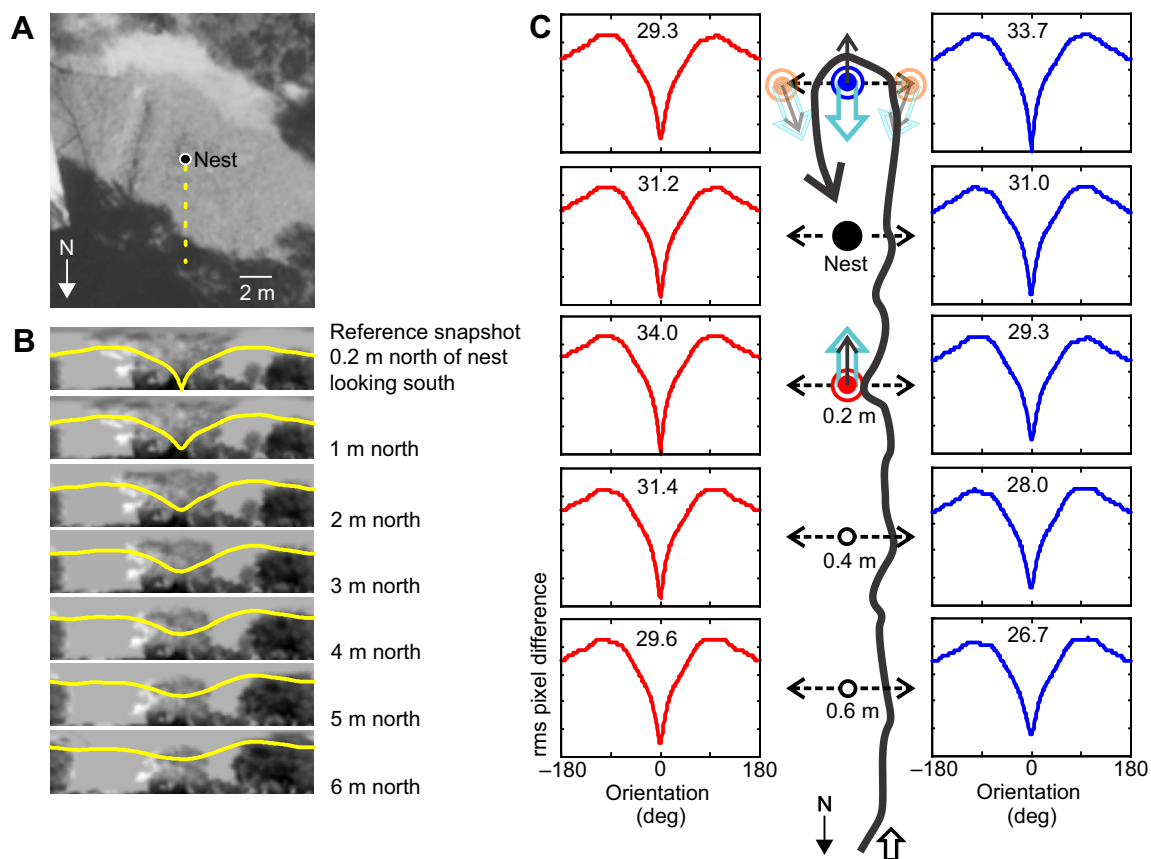


Fig. 10. The navigational information provided by panoramic views. (A) Aerial image of the nest area of *M. croslandi* involved in this study. Yellow dashed line marks a 6 m long transect from the north towards the nest. (B) The changing views experienced by an ant approaching the nest from the north along the path shown in A. Yellow lines superimposed on views at 1 m intervals show the rotational image difference function (rotIDF) generated by comparing a nest-directed reference snapshot assumed to be taken during a learning walk, 20 cm north of the nest (top view), with the views encountered 1 to 6 m north of the nest. (C) View guidance close to the nest (marked by black filled circle). The rotIDFs are shown at 0.2 m spacing for two snapshots: one nest-directed 0.2 m north of the nest (red, left panels) and one directed away from the nest 0.2 m south of the nest (blue, right panels). Thick black line shows a hypothetical path of a homing ant; black arrows indicate orientation of snapshots and light blue arrows the nest direction associated with each snapshot. Two nest-directed snapshot locations to the south of the nest are marked in pale orange and light blue. The panoramic images shown in A were used for calculating rotIDFs in A and B and were rendered in a 3D model of the nest environment and low-pass filtered to 3 deg resolution (see Murray and Zeil, 2017). See Discussion for details.

et al., 2015; Murray and Zeil, 2017). Following that direction, an ant would also potentially know how close to the nest she is if she monitored the minimum of the rotIDF as it progressively decreases (Fig. 10B). The area and the vantage points covered by learning walks thus determine the range over which an animal can detect where it currently is relative to the nest (Narendra et al., 2013; Dewar et al., 2014; Stürzl et al., 2015). This is potentially the reason why Fleischmann et al. (2018b) found that homing by landmark guidance is affected by the space ants had available for performing learning walks. Finally, we note that the effective range of guidance afforded by panoramic views also depends on the particular distribution of objects and on the visual structure of habitats (e.g. Stürzl and Zeil, 2007; Dewar et al., 2014; Murray and Zeil, 2017; Zahedi and Zeil, 2018).

As an ant approaches the nest (schematic black path in Fig. 10C), still under the guidance of the same nest-directed snapshot taken from a position 0.2 m north of the nest (marked red in Fig. 10C), a second snapshot taken 0.2 m south of the nest, but facing away from the nest (marked blue in Fig. 10C), will gain in ‘familiarity’ (*sensu* Baddeley et al., 2012) as the minimum of its rotIDF becomes smaller (blue curves in right panels, Fig. 10C). The navigational instruction the ant can derive from the northern snapshot when it has reached close to the location from which it was taken during a learning walk is to keep moving in the direction of the minimum of the rotIDF (red curves in left panels Fig. 10C, direction indicated by light blue arrows in the schematic), which is zero at that location, marking the most familiar of all the learning walk snapshots taken at different orientations and bearings. As the ant continues to move in that direction, small lateral displacements may take her past the nest entrance as shown in this example, which causes the southern snapshot to become more familiar. However, the instruction associated with that anti-nest snapshot is to turn 180 deg to face the nest entrance (indicated by light blue arrow attached to blue snapshot location in Fig. 10C). Note that this manoeuvre would align the ant with neighbouring nest-directed snapshots (marked pale orange in Fig. 10C) and therefore would redirect the ant towards the nest (see also the homing paths shown in Fig. 9).

These considerations suggest that there may be at least two reasons why *M. croslandi* ants (and possibly other species) systematically intersperse views that are nest-directed and views that are directed away from the nest: first, the latter may provide negative examples improving classification, as has been shown in machine learning and image classification (e.g. Kherfi et al., 2003; Baddeley et al., 2012); and second, if these views are more specifically associated with nest direction (not only learnt as negative examples), they can improve homing efficiency by aligning homing ants that are facing away from the nest with nest-directed views without the need for large-amplitude scanning movements. For instance, scanning movements with 180 deg amplitude would be needed to align the example ant shown in Fig. 10C that had overshoot the nest entrance with the nest-directed views south of the nest.

The question remains whether ants during their learning walks only store views when aligned parallel to the home vector. For desert ants, this suggestion is motivated by the observation that they stop and fixate when looking in the nest direction (Müller and Wehner, 2010; Fleischmann et al., 2017, 2018a) and for *M. croslandi* it is motivated by the observation that scanning direction tends to be reversed around the time the ants are aligned in either direction parallel to the home vector. Another hint comes from modelling studies, where the suggestion is made that alignment with

and the decreasing length of the home vector could be used as a reinforcement signal for learning views along routes (Ardin et al., 2016; Webb and Wystrach, 2016). However, so far, there is no evidence to reject the possibility that ants learn all the views they experience during their learning walks tagged with the home direction provided by their path integration system. When a homing ant was aligned with any of these views, each would contribute an instruction in which direction to move to pinpoint the nest, as suggested for homing wasps by Stürzl et al. (2016).

Outlook

Our detailed analysis of learning walks raises a number of intriguing questions regarding the acquisition, storage and use of views for homing. Why is place learning in central place foraging insects so distinctly choreographed in time and space? We suggest that the spatio-temporal pattern in these learning procedures reflects three aspects of navigation that are insufficiently understood: (1) what rules guide the (anticipatory) acquisition of information needed for successful homing; (2) how is the quality of information assessed during acquisition; and (3) considering that the transition from interior to the outside (when ants move from within the nest to the surface to carry out learning walks) triggers changes in the mushroom bodies of their brains (Stieb et al., 2012; Grob et al., 2017), what temporal organization of behaviour is required by the underlying neural processes to form stable memories, both at the time scale of seconds (e.g. Bittner et al., 2017) and at longer time scales for the formation of long-term memories (e.g. Hourcade et al., 2010; Falibene et al., 2015)? It is worth noting in this context that learning walks and learning flights constitute an unusual form of learning, with no obvious reinforcing or unconditional stimulus or associative context (except potentially path integration, see above), but with features resembling perceptual learning or recognition memory, which are thought to be involved in imprinting (e.g. Horn, 1998; McCabe, 2013). Finally, there is a need to investigate whether the systematic scanning between view directions parallel to the home vector is a common feature of ant learning walks, or an idiosyncrasy of *M. croslandi*. In any case, it raises interesting questions regarding the organization of navigation-relevant memories and leads to the prediction that if ants only memorize views when aligned parallel to the home vector during learning walks, they should execute 180 deg turns when missing the nest entrance during their approach to the nest. A prerequisite for answering these questions and testing these predictions will be a detailed comparison of gaze directions and navigational decisions during the learning walks of identified ants and during their subsequent homing paths, as it has been recently done for the learning and homing flights of honeybees, bumblebees and wasps (Dittmar et al., 2010; Hempel de Ibarra et al., 2009; Collett et al., 2013b; Stürzl et al., 2016).

Acknowledgements

We thank Chloé Raderschall, Animesh Agrawal and Teresa Iglesias for their help with field work and with data analysis. We are grateful to Hwan-Yin Joon from the Statistical Consulting Unit (SCU) at the ANU for his help with statistical data analysis. We thank Tom Collett, Pauline Fleischmann, Robin Grob, Wolfgang Rössler, Wolfgang Stürzl and Rüdiger Wehner for their comments on an early draft of the manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: P.J., A.N., J.Z.; Methodology: T.M., A.N., J.Z.; Software: T.M., J.Z.; Validation: P.J., J.Z.; Formal analysis: P.J., A.N., J.Z.; Investigation: P.J.,

T.M., J.Z.; Resources: A.N., J.Z.; Data curation: J.Z.; Writing - original draft: P.J., J.Z.; Writing - review & editing: P.J., T.M., A.N., J.Z.; Visualization: P.J., J.Z.; Supervision: A.N., J.Z.; Project administration: A.N., J.Z.; Funding acquisition: A.N., J.Z.

Funding

We acknowledge financial support from the Australian Research Council (ARC) Centre of Excellence Scheme (CE0561903), an ARC Discovery Early Career Award (DE120100019), an ARC Future Fellowship Award (FT140100221), ARC Discovery Project Grants (DP0986606, DP150101172) and The Hermon Slade Foundation (HSF 10/7).

Data availability

Data are available at FigShare: <https://doi.org/10.6084/m9.figshare.6972842.v1>. Requests for further information and for original video footage should be directed to and will be fulfilled by the corresponding author.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.185306.supplemental>

References

- Ardin, P., Peng, F., Mangan, M., Lagogiannis, K. and Webb, B.** (2016). Using an insect mushroom body circuit to encode route memory in complex natural environments. *PLoS Comput. Biol.* **12**, e1004683.
- Baddeley, B., Graham, P., Husbands, P. and Philippides, A.** (2012). A model of ant route navigation driven by scene familiarity. *PLoS Comp. Biol.* **8**, e1002336.
- Becker, L.** (1958). Untersuchungen über das Heimfindevermögen der Bienen. *Z. Vergl. Physiol.* **41**, 1-25.
- Bittner, K. C., Milstein, A. D., Grienberger, C., Romani, S. and Magee, J. C.** (2017). Behavioral time scale synaptic plasticity underlies CA1 place fields. *Science* **357**, 1033-1036.
- Capaldi, E. and Dyer, F. C.** (1999). The role of orientation flights on homing performance in honeybees. *J. Exp. Biol.* **202**, 1655-1666.
- Capaldi, E. A., Smith, A. D., Osborne, J. L., Fahrback, S. E., Farris, S. M., Reynolds, D. R., Edwards, A. S., Martin, A., Robinson, G. E., Poppy, G. M. et al.** (2000). Ontogeny of orientation flight in the honeybee revealed by harmonic radar. *Nature* **403**, 537-540.
- Collett, T. S.** (1995). Making learning easy: the acquisition of visual information during the orientation flights of social wasps. *J. Comp. Physiol. A* **177**, 737-747.
- Collett, T. S. and Lehrer, M.** (1993). Looking and learning: a spatial pattern in the orientation flight of the Wasp *Vespa vulgaris*. *Proc. Roy. Soc. B* **252**, 129-134.
- Collett, T. S. and Zeil, J.** (2018). Insect learning walks and flights. *Curr. Biol.* **28**, R952-R1008.
- Collett, M., Chittka, L. and Collett, T. S.** (2013a). Spatial memory in insect navigation. *Curr. Biol.* **23**, R789-R800.
- Collett, T. S., Hempel de Ibarra, N., Riabinina, O. and Philippides, A.** (2013b). Coordinating compass-based and nest-based flight directions during bumblebee learning and return flights. *J. Exp. Biol.* **216**, 1105-1113.
- Degen, J., Kirbach, A., Reiter, L., Lehmann, K., Norton, P., Storms, M., Koblofsky, M., Winter, S., Georgieva, P. B., Nguyen, H. et al.** (2015). Exploratory behaviour of honeybees during orientation flights. *Anim. Behav.* **102**, 45-57.
- Dewar, A. D. M., Philippides, A. and Graham, P.** (2014). What is the relationship between visual environment and the form of ant learning walks? An *in silico* investigation of insect navigation. *Adapt. Behav.* **22**, 163-179.
- Dittmar, L., Stürzl, W., Baird, E., Boeddeker, N. and Egelhaaf, M.** (2010). Goal seeking in honeybees: matching of optic flow snapshots? *J. Exp. Biol.* **213**, 2913-2923.
- Falibene, A., Roces, F. and Rössler, W.** (2015). Long-term avoidance memory formation is associated with a transient increase in mushroom body synaptic complexes in leaf-cutting ants. *Front. Behav. Neurosci.* **9**, 84.
- Fleischmann, P. N., Christian, M., Müller, V. L., Rössler, W. and Wehner, R.** (2016). Ontogeny of learning walks and the acquisition of landmark information in desert ants *Cataglyphis fortis*. *J. Exp. Biol.* **219**, 3137-3145.
- Fleischmann, P. N., Grob, R., Wehner, R. and Rössler, W.** (2017). Species-specific differences in the fine structure of learning walk elements in *Cataglyphis* ants. *J. Exp. Biol.* **220**, 2426-2435.
- Fleischmann, P. N., Grob, R., Müller, V. L., Wehner, R. and Rössler, W.** (2018a). The geomagnetic field is a compass cue in *Cataglyphis* ant navigation. *Curr. Biol.* **28**, 1440-1444.
- Fleischmann, P. N., Rössler, W. and Wehner, R.** (2018b). Early foraging life: spatial and temporal aspects of landmark learning in the ant *Cataglyphis noda*. *J. Comp. Physiol. A* <https://doi.org/10.1007/s00359-018-1260-6>.
- Graham, P. and Collett, T. S.** (2006). Bi-directional route learning in wood ants. *J. Exp. Biol.* **209**, 3677-3684.
- Graham, P., Philippides, A. and Badderley, B.** (2010). Animal cognition: multi-modal interactions in ant learning. *Curr. Biol.* **20**, R639-R640.
- Grob, R., Fleischmann, P. N., Grübel, K., Wehner, R. and Rössler, W.** (2017). The role of celestial compass information in *Cataglyphis* ants during learning walks and for neuroplasticity in the central complex and mushroom bodies. *Front. Behav. Neurosci.* **11**, 226.
- Hempel de Ibarra, N., Philippides, A., Riabinina, O. and Collett, T. S.** (2009). Preferred viewing directions of bumblebees (*Bombus terrestris* L.) when learning and approaching their nest site. *J. Exp. Biol.* **212**, 3193-3204.
- Horn, G.** (1998). Visual imprinting and the neural mechanisms of recognition memory. *Trends Neurosci.* **21**, 300-305.
- Hourcade, B., Muenz, T. S., Sandoz, J.-C., Rössler, W. and Devaud, J.-M.** (2010). Long-term memory leads to synaptic reorganization in the mushroom bodies: a memory trace in the insect brain? *J. Neurosci.* **30**, 6461-6465.
- Jayatilaka, P.** (2014). Individual foraging careers of the jack jumper ant, *Myrmecia croslandi*. PhD thesis, The Australian National University, Canberra, Australia. <http://hdl.handle.net/1885/13471>.
- Jayatilaka, P., Narendra, A., Reid, F. S., Cooper, P. and Zeil, J.** (2011). Different effects of temperature on foraging activity schedules in sympatric *Myrmecia* ants. *J. Exp. Biol.* **214**, 2730-2738.
- Jayatilaka, P., Raderschall, C., Zeil, J., and Narendra, A.** (2013). Learning to forage: the learning walks of Australian jack jumper ants. *Front. Physiol. Conference Abstract: Int. Conf. Invert. Vision*.
- Jayatilaka, P., Raderschall, A. C., Narendra, A. and Zeil, J.** (2014). Individual foraging patterns of the jack jumper ant *Myrmecia croslandi* (Hymenoptera: Formicidae). *Myrmecol. News* **19**, 75-83.
- Kherfi, M. L., Ziu, D. and Bernardi, A.** (2003). Combining positive and negative examples in relevance feedback for content-based image retrieval. *J. Vis. Comm. Image Represent.* **14**, 428-457.
- Lehrer, M.** (1993). Why do bees turn back and look? *J. Comp. Physiol. A* **172**, 549-563.
- Lehrer, M. and Collett, T. S.** (1994). Approaching and departing bees learn different cues to the distance of a landmark. *J. Comp. Physiol. A* **175**, 171-177.
- McCabe, B. J.** (2013). Imprinting. *WIREs Cogn. Sci.* **4**, 375-390.
- Müller, M. and Wehner, R.** (2010). Path integration provides a scaffold for landmark learning in desert ants. *Curr. Biol.* **20**, 1368-1371.
- Murray, T. and Zeil, J.** (2017). Quantifying navigational information: the catchment volumes of panoramic snapshots in outdoor scenes. *PLoS ONE* **12**, e0187226.
- Muser, B., Sommer, S., Wolf, H. and Wehner, R.** (2005). Foraging ecology of the thermophilic Australian desert ant *Melophorus bagoti*. *Austr. J. Zool.* **53**, 301-311.
- Narendra, A., Gourmaud, S. and Zeil, J.** (2013). Mapping the navigational knowledge of individually foraging ants, *Myrmecia croslandi*. *Proc. Roy. Soc. B* **280**, 20130683.
- Narendra, A. and Ramirez-Esquivel, F.** (2017). Subtle changes in the landmark panorama disrupts visual navigation in a nocturnal bull ant. *Phil. Trans. Roy. Soc. B* **372**, 20160068.
- Nicholson, D. J., Judd, S. P. D., Cartwright, B. A. and Collett, T. S.** (1999). Learning walks and landmark guidance in wood ants (*Formica rufa*). *J. Exp. Biol.* **202**, 1831-1838.
- Opfinger, E.** (1931). Über die Orientierung der Biene an der Futterquelle. *Z. Vergl. Physiol.* **15**, 431-487.
- Osborne, J. L., Smith, A., Clark, S. J., Reynolds, D. R., Barron, M. C., Lim, K. S. and Reynolds, A. M.** (2013). The ontogeny of bumblebee flight trajectories: from naive explorers to experienced foragers. *PLoS ONE* **8**, e78681.
- Philippides, A., Hempel de Ibarra, N., Riabinina, O. and Collett, T. S.** (2013). Bumblebee calligraphy: the design and control of flight motifs in the learning and return flights of *Bombus terrestris*. *J. Exp. Biol.* **216**, 1093-1104.
- Riabinina, O., Hempel de Ibarra, N., Philippides, A. and Collett, T. S.** (2014). Head movements and the optic flow generated during the learning flights of bumblebees. *J. Exp. Biol.* **217**, 2633-2642.
- Robert, T., Frasnelli, E., Hempel de Ibarra, N. and Collett, T. S.** (2018). Variations on a theme: bumblebee learning flights from the nest and from flowers. *J. Exp. Biol.* **221**, jeb172601.
- Stieb, S. M., Hellwig, A., Wehner, R. and Rössler, W.** (2012). Visual aspects affect both behavioral and neuronal aspects in the individual life history of the desert ant *Cataglyphis fortis*. *Dev. Neurobiol.* **72**, 729-742.
- Stürzl, W. and Zeil, J.** (2007). Depth, contrast and view-based homing in outdoor scenes. *Biol. Cybernet.* **96**, 519-531.
- Stürzl, W., Mair, E., Grixa, I., Narendra, A. and Zeil, J.** (2015). Three-dimensional models of natural environments and the mapping of navigational information. *J. Comp. Physiol. A* **201**, 563-584.
- Stürzl, W., Zeil, J., Boeddeker, N. and Hemmi, J. M.** (2016). How wasps acquire and use views for homing. *Curr. Biol.* **26**, 470-482.
- Tinbergen, N. and Kruyt, W.** (1938). Über die Orientierung des Bienenwolfes (*Philanthus triangulum* Fabr.) III. Die Bevorzugung bestimmter Wegmarken. *Z. Vergl. Physiol.* **25**, 292-334.
- Van Iersel, J. J. A. and Van den Assem, J.** (1964). Aspects of orientation in the digger wasp *Bombix rostrata*. *J. Anim. Behav.* **1** Suppl., 145-162.
- Webb, B. and Wystrach, A.** (2016). Neural mechanisms of insect navigation. *Curr. Opin. Insect Sci.* **15**, 27-39.

- Wehner, R., Meier, C. and Zoliker, C.** (2004). The ontogeny of foraging behaviour in desert ants, *Cataglyphis bicolor*. *Ecol. Entomol.* **29**, 240-250.
- Woodgate, J. L., Makinson, J. C., Lim, K. S., Reynolds, A. M. and Chittka, L.** (2016). Life-long radar tracking of bumblebees. *PLoS ONE* **11**, e0160333.
- Zahedi, M. S. and Zeil, J.** (2018). Fractal dimension and the navigational information provided by natural scenes. *PLoS ONE* **13**, e0196227.
- Zeil, J.** (1993a). Orientation flights of solitary wasps (*Cerceris*; Sphecidae; Hymenoptera). *J. Comp. Physiol. A* **172**, 189-205.
- Zeil, J.** (1993b). Orientation flights of solitary wasps (*Cerceris*; Sphecidae; Hymenoptera): II. Similarities between orientation and return flights and the use of motion parallax. *J. Comp. Physiol. A* **172**, 209-224.
- Zeil, J.** (2012). Visual homing—an insect perspective. *Curr. Opin. Neurobiol.* **22**, 285-293.
- Zeil, J., Kelber, A. and Voss, R.** (1996). Structure and function of learning flights in bees and wasps. *J. Exp. Biol.* **199**, 245-252.
- Zeil, J., Narendra, A. and Stürzl, W.** (2014). Looking and homing: how displaced ants decide where to go. *Philos. Trans. R. Soc. B* **369**, 20130034.

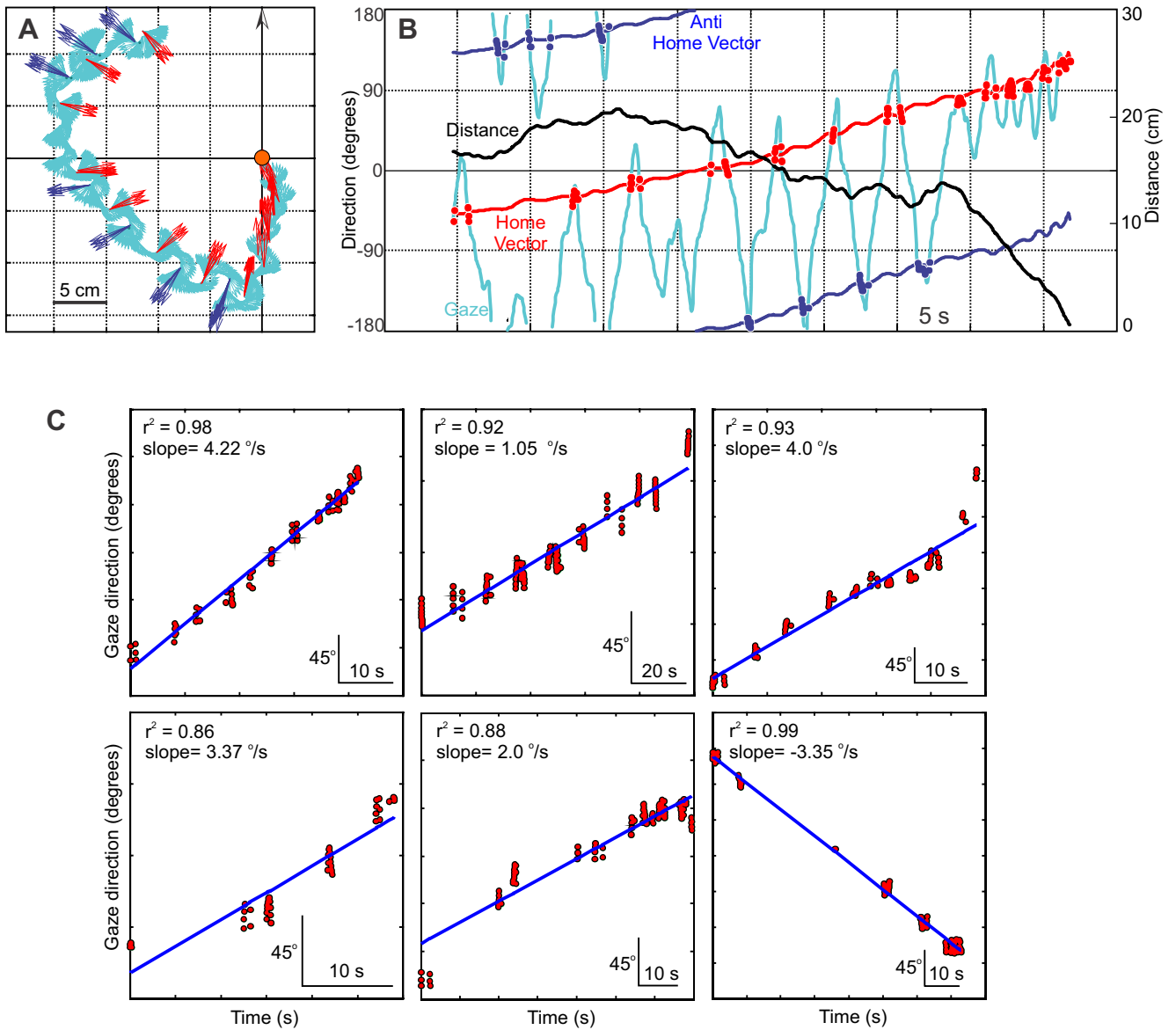


Fig. S1. The choreography of learning walks. (A) The return leg of a learning walk. (B) Time course of variables during the same sequence. Otherwise conventions as before. (C) Six examples of the gaze direction of ants during periods of regular scanning when looking in the nest direction plotted over time (extracted from gaze time courses such as the one shown in (B)). Blue line is the regression line with r^2 and slope indicated.