

RESEARCH ARTICLE

Route learning during tandem running in the rock ant *Temnothorax albipennis*

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ABSTRACT

Many animals use information from conspecifics to change their behavior in adaptive ways. When a rock ant, *Temnothorax albipennis*, finds food, she returns to her colony and uses a method called tandem running to lead nestmates, one at a time, from the nest to the food. In this way, naive ants can learn the location of a food source. Less clear is whether they also learn navigational cues that guide them from nest to food, although this is often assumed. We tested this idea by tracing the routes of individually marked ants as they followed tandem runs to a feeder, returned to the nest, and later traveled independently back to the food. Our results show, for the first time, that tandem run followers learn specific routes from their leaders. Independent journeys back to the food source were significantly more similar to the routes on which the ants had been led, compared with the routes taken by other tandem runs. In contrast, the homeward journey did not resemble the tandem run route. These results are consistent with followers memorizing visual cues during the tandem run that are useful for recapitulating the outward journey, but not as effective when facing in the opposite direction on the homeward journey. We further showed that foraging routes improved through individual experience over multiple trips but not through the social transfer of route information via tandem running. We discuss our findings in relation to social learning and integration of individual and social information in ants.

KEY WORDS: Social learning, Teaching, Navigation, Foraging

INTRODUCTION

Many species, from invertebrates to vertebrates, engage in social learning, meaning that they change their behavior based on information obtained from others (Heyes, 1994; Hoppitt and Laland, 2013; Kendal et al., 2018; Laland, 2004). For example, if chimpanzees are given a straw and a box of juice with a small hole, they typically try various inefficient methods to drink the juice, such as dipping the straw in and licking it. As soon as one chimpanzee in the group ‘correctly’ uses the straw (i.e. sucking the juice out of the box), others imitate and start drinking much more efficiently (Yamamoto et al., 2013). Likewise, when red-winged blackbirds observe that conspecifics become ill after eating certain food, they avoid the food and the consequent illness without having to experience it (Mason and Reidinger, 1982). Social learning is an

important ability because it allows animals to avoid costly trial and error and take ‘shortcuts’ to improve their performance (Hoppitt and Laland, 2013).

Although vertebrates have received more attention, eusocial insects, such as ants, bees and termites, are also well known to use social learning (Leadbeater and Chittka, 2007, 2009; Grüter et al., 2010; Grüter and Leadbeater, 2014; Leadbeater and Dawson, 2017). These insects use a wide variety of signaling mechanisms to share information about the location of valuable resources. For example, when a *Temnothorax* ant finds food, she goes back to her colony and starts recruiting nestmates using a method called tandem running, in which she slowly leads a single follower at a time to the food source (Franklin, 2014; Möglich et al., 1974) (Fig. 1). Tandem run recruitment is known to help the colony to share the location of valuable food sources and enhance its exploitation of them. As a consequence, they can adaptively allocate foragers across sources of different quality (Shaffer et al., 2013).

It is generally assumed that a tandem run follower learns not only the location of a food resource but also how to get there (e.g. Franks and Richardson, 2006). That is, the follower is thought to learn a specific path from home to destination, most likely guided by visual landmarks along the route (Bowens et al., 2013). However, this assumption has not been empirically supported. In fact, published data appear to suggest that followers do not learn the route from their leaders (Franklin, 2014). For example, Franks and Richardson (2006) tracked the paths taken by tandem followers when they returned from the target back to the old nest. These paths were shorter than the routes on which they were led, suggesting they were different. Another study showed that when followers later led their own tandem runs, they also did not use the route on which they had been led (Franklin and Franks, 2012). These studies cannot be considered definitive tests, because they had either a small sample size or little variance of individual routes. Thus, they lacked statistical power to conclusively reject the hypothesis of route learning during tandem recruitment.

In this study, we tested whether the follower learns a route from the leader during tandem running, including two principal modifications of previous studies. First, we used a larger experimental arena and supplied it with many visual and tactile landmarks. This gave us larger variation in individual routes, thus increasing our ability to detect consistent differences in the routes taken by different ants. Second, we measured route similarity using a more precise method originally developed to detect route stereotypy in homing pigeons over repeated releases from the same site (Guilford and Biro, 2014; Meade et al., 2005). In this method, route similarity is calculated as the average of nearest distances between points on the two routes. Using these approaches, we tested whether a tandem run follower subsequently uses a route more similar to the one on which she was led, compared with those of other tandem runs in the same foraging bout. Additionally, we

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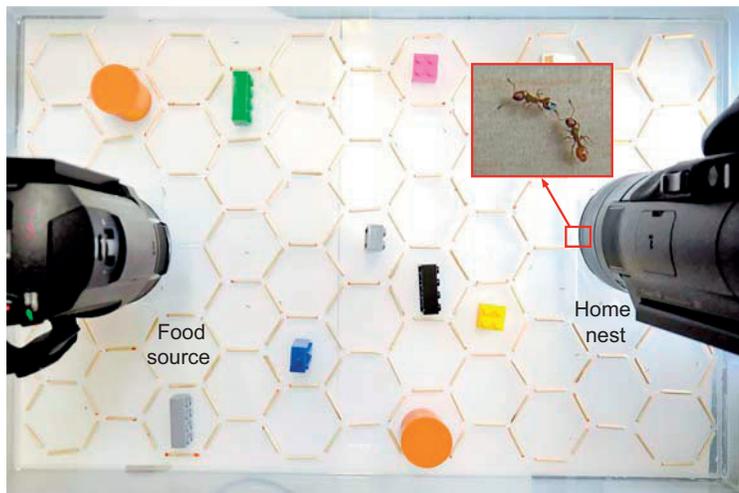


Fig. 1. An image of the whole arena from the 'arena' camera. The inset image shows a tandem-running pair of painted *T. albipennis*, with the leader on the left and the follower on the right, from the 'home nest' camera.

tested whether subsequent trips of followers were more efficient (i.e. shorter) than their first trip. Finally, because some tandem run leaders recruited multiple times, we tested whether they showed route fidelity (i.e. taking similar routes in every tandem run) and whether they improved their route efficiency over tandem run trips.

MATERIALS AND METHODS

Subjects

We collected five colonies of the rock ant, *Temnothorax albipennis* Curtis 1854, from the Isle of Portland in Weymouth, UK (50° 32'51.131"N, 2°26'3.555"W). All colonies had one queen, with worker populations ranging from 105 to 140 (mean 120) and brood populations ranging from 28 to 53 (mean 38). Each colony was housed in a standard nest, which was composed of glass microscope slides (50×75 mm) above and below a balsa wood slat. A circular cavity (38 mm diameter) was cut through the middle of the slat, and an

entrance tunnel was cut on the side (see Sasaki et al., 2015, for details). Each nest was stored in a plastic box (11×11 cm) with the sides coated in Fluon to prevent the ants from escaping. All colonies were provided with a water-filled plastic tube capped with cotton and an agar-based diet (Bhatkar and Whitcomb, 1970) that was refreshed weekly.

Procedure

The foraging experiment was conducted in a box arena (30×50 cm) with walls coated in Fluon. Because *Temnothorax* ants use proximate landmark cues during foraging (McLeman et al., 2002), the arena was enriched with objects of various sizes and shapes (Fig. 2). Furthermore, because these ants tend to walk along edges (Pratt et al., 2001), the arena floor was provided with a hexagonal array of short rods to discourage ants from walking along the arena walls (Fig. 2) and to provide more route variations. We placed a home nest at one side of the arena and, immediately after

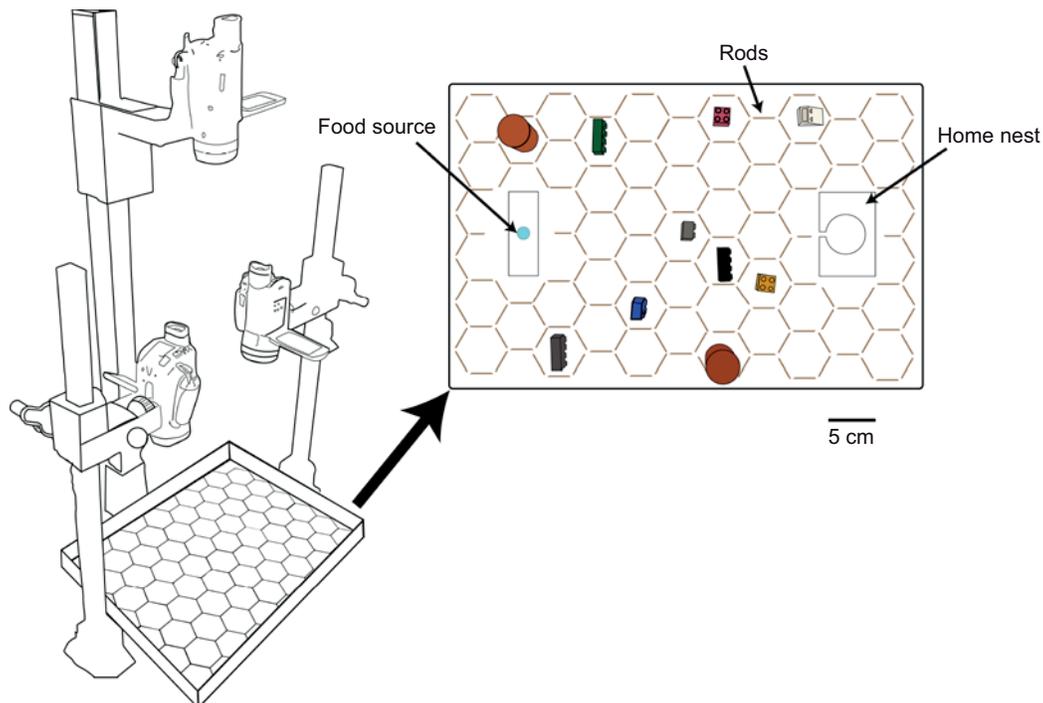


Fig. 2. Experimental setup. A home nest was placed at one side of the arena and a food source (0.8 mol l⁻¹ sugar solution) on the opposite side. Foraging behavior was recorded by three 4k cameras. One camera took in the whole arena, and the other two obtained closer views of the food source and home nest. In the arena, a hexagonal pattern of short rods provided tactile guides, and objects of various sizes and shapes served as visual cues.

that, a food source on the opposite side, at a distance of 30 cm. The feeder consisted of a glass depression slide (25×75 mm) provided with 0.2 ml of 0.8 mol l⁻¹ sugar solution. This concentration was selected because *Temnothorax* ants typically show a strong recruitment effort (i.e. many tandem runs) towards it (Shaffer et al., 2013).

For individual tracking, each ant was first anesthetized using carbon dioxide and then painted with distinctive color patterns on the head, thorax and gaster using Tamiya acrylic paints. This procedure usually took less than 5 min, and painted ants typically started moving normally again within a few minutes. Each foraging bout was recorded by three 4k cameras (Sony FDR-AX100E), one for the home, one for the food source and one for the whole arena (Fig. 2). We filmed each bout for 3 h although over 80% of tandem running occurred in the first 1.5 h.

To motivate ants to forage, colonies were not fed for 2 weeks prior to the foraging bouts (Shaffer et al., 2013). Each colony was tested only once. Before each bout, the arena was cleaned with ethanol to remove all chemical marks.

Analysis

The total of five foraging bouts (one for each colony) provided 95 tandem runs led by 28 independent leaders. Of these tandem runs, 74 were successful (i.e. the leader and the follower reached the feeder without breaking up). Although some of the unsuccessful tandem run followers still reached the food source on their own (9 out of 21), as in a previous study (Pratt, 2008), we focused only on the successful ones to eliminate the possibility of individual route learning after the breakup. Nineteen of the successful tandem runs were led by former followers. That is, after a tandem run, the follower herself became a tandem run leader and recruited a nestmate from home to the food source. We did not consider these as ‘new’ tandem runs but instead as subsequent trips by the followers (see below for details). Therefore, we had 55 distinct followers (led by 26 distinct leaders) for testing route learning during tandem running.

We manually traced each tandem run route by identifying the position of the leader’s gaster every second, using ImageJ2 software (Rueden et al., 2017). We also traced the next two trips made by the follower: its homeward trip (from the food source to home) and its

outward trip (from home back to the food source). The trace position was identical if the ant did not move during this interval, which occurred in 6.8% of all sampled positions (the average duration of a ‘pause’ was 2.0 s and the maximum duration was 37 s). For each follower path, we measured its similarity to the path on which it had been led, by calculating the mean distance from each point on the follower’s route to the nearest point on the tandem run route (see Guilford and Biro, 2014, for details). Thus, if the same point was sampled multiple times because of a pause, it was included only once in the analysis. To test the robustness of this method to sampling frequency, we repeated the analyses but sampled only one data point every 5 s. These results showed similar patterns to those seen when analyzing the full dataset (i.e. one data point per second) (Fig. S1).

To detect route learning during tandem running, we conducted a permutation test of the null hypothesis that each follower’s path is no more similar to its corresponding tandem run path than to a randomly chosen tandem run path. We first generated a single index of path similarity by taking the average of all the observed pairwise path similarities across the experiment. We then generated 1000 simulated datasets in which each follower path was paired with a randomly chosen tandem run path from the same foraging trial. For each simulated dataset, we calculated the same index of path similarity as in the real data. This gave us the distribution of similarity indices expected if the null hypothesis is true. If instead the follower learned a route from the leader during tandem running, we expected the observed index to be lower than the values predicted by the null hypothesis. We therefore calculated a one-tailed *P*-value from the proportion of simulated index values that were lower than the observed value. We carried out this test separately for the two types of follower trip (homeward and outward).

We designed our permutation test to avoid being misled by route similarities caused by factors other than learning. One such factor is orientation via pheromone trails, and tandem leaders in this species are known to deposit a pheromone during the run (Basari et al., 2014). If this pheromone produces lasting orientation trails, then a permutation test would not be able to distinguish path similarities due to shared trails from similarities due to route learning. To prevent this problem, our simulated datasets

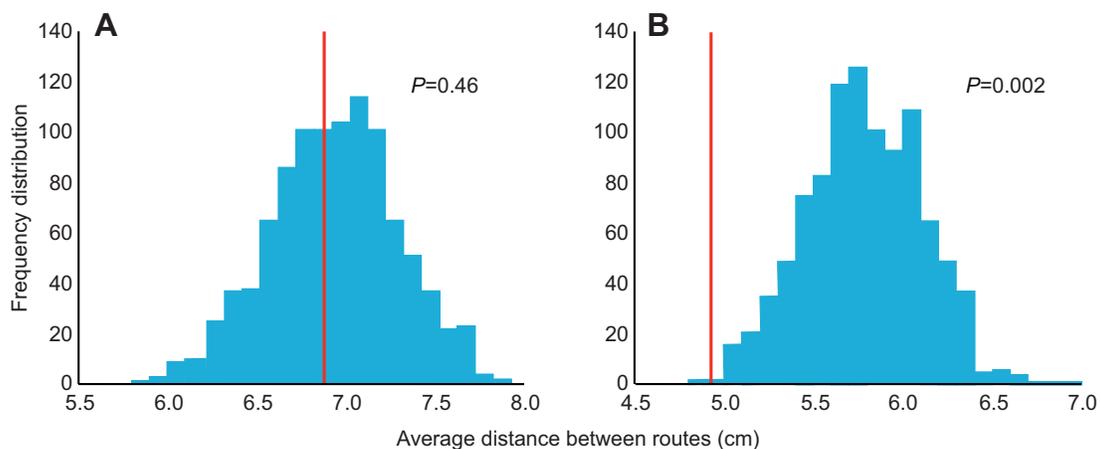


Fig. 3. Results of permutation tests comparing tandem routes with the routes taken by followers. (A) Homeward trips; (B) outward trips. In each plot, the red line shows the observed average difference between tandem paths and follower paths. The blue bars show the distribution of the same measure for 1000 simulated datasets in which tandem paths were randomly paired with follower paths. Each *P*-value gives the proportion of simulations with smaller average distances than the observed value.

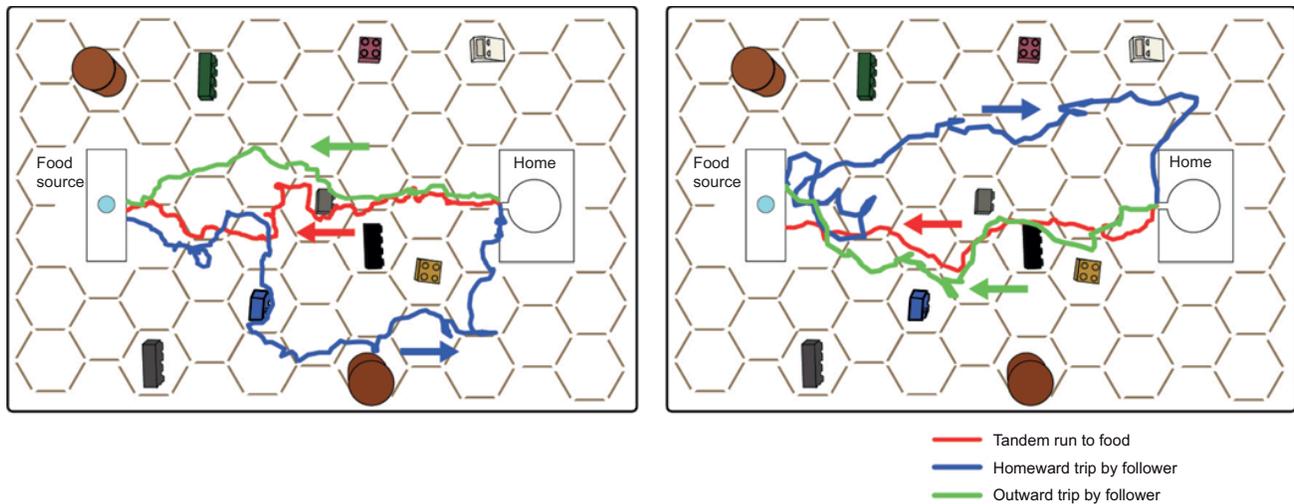


Fig. 4. Examples of foraging trips. The tandem-running pair first went to the food source from the home nest (red). The follower walked alone back to the nest (blue) and then returned to the food source (green). Arrows indicate the direction of each trip.

randomized pairs within each colony's trial instead of across trials. In addition, we performed another permutation test of the existence of colony-specific foraging routes. For this test, we first measured the average route similarity among all pairwise combinations of tandem-running paths within trials. We then compared this value with the distribution of the same value generated from 1000 randomizations of these pairs across trials. If colony-specific routes existed as a result of pheromone trails, the tandem run routes should be more similar within trials than across trials.

Fifteen tandem run leaders recruited more than once (mean 2.9 times, maximum 5 times), allowing us to test whether these leaders used consistent routes over multiple tandem runs. To do so, we used a permutation test similar to the one described above. We measured similarity between each leader's first route and each of her subsequent routes and took the average of these measures over all leaders. We then compared this value with the same measure taken in each of 1000 randomizations in which we shuffled the pairs within each trial.

We tested for improved performance with experience by focusing on ants that led more than one tandem run, regressing tandem run path length against the run's position in the leader's sequence of runs. We first normalized the data using a log transformation (base 10) and then fitted a linear mixed model with tandem run length as a fixed variable and ant ID as a random variable. If leaders improve their routes, we expected lengths to become shorter over multiple trips. We also compared tandem run path lengths with the lengths of the followers' subsequent homeward and outward trips using the Friedman–Nemenyi test, a *post hoc* test for repeated measurements.

Pairwise path similarities were calculated using Matlab (R2018b). We measured distances between paths only in the plane of the arena floor, and so did not account for a few instances in which ants climbed onto landmark objects. In these cases, path distances were somewhat underestimated. We used R (3.5.3) for all statistical tests, including the 'lme4' and 'PMCMRplus' packages for the linear mixed model and the Friedman–Nemenyi test, respectively.

Ethical statement

This work complied with relevant regulations and laws of the University of Oxford and the UK, where the work was conducted.

RESULTS

Ants learn foraging routes during tandem running

The permutation tests showed that the followers' homeward trips were no more similar to the tandem paths they had been led on than were randomly paired paths (Fig. 3A; $P=0.46$). However, their subsequent outward trips back to the food were significantly more like their tandem routes than were the random pairs (Fig. 3B; $P<0.01$). These results indicate that the follower learned a foraging route from her leader during tandem running and used this information when she returned from home to the food source, but not when she walked from the food source back to home. Examples of foraging trips are shown in Fig. 4.

We found no evidence for colony-level idiosyncrasy of tandem paths. That is, paths within each colony's trial were no more similar to each other than they were to paths in other colonies' trials (Fig. 5). This suggests that colonies did not develop pheromone trails for foraging. Fig. 6 shows all of the paths observed in each trial.

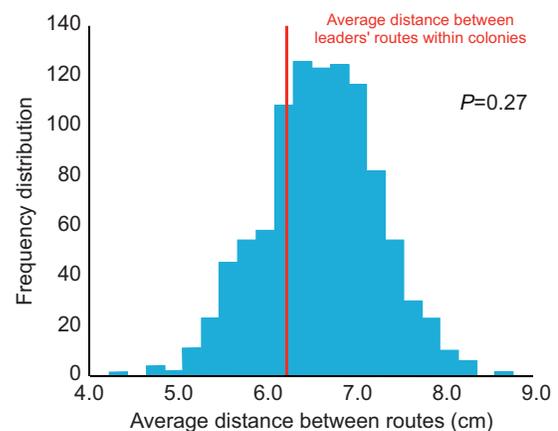


Fig. 5. Result of a permutation test for colony-specific foraging routes.

The red line shows the average path difference for all pairwise combinations of tandem running paths within each colony's foraging trial. The blue bars show the same measurement for 1000 simulated datasets in which tandem paths were paired across trials. The P -value gives the proportion of simulations that have smaller average distances than the observed value.

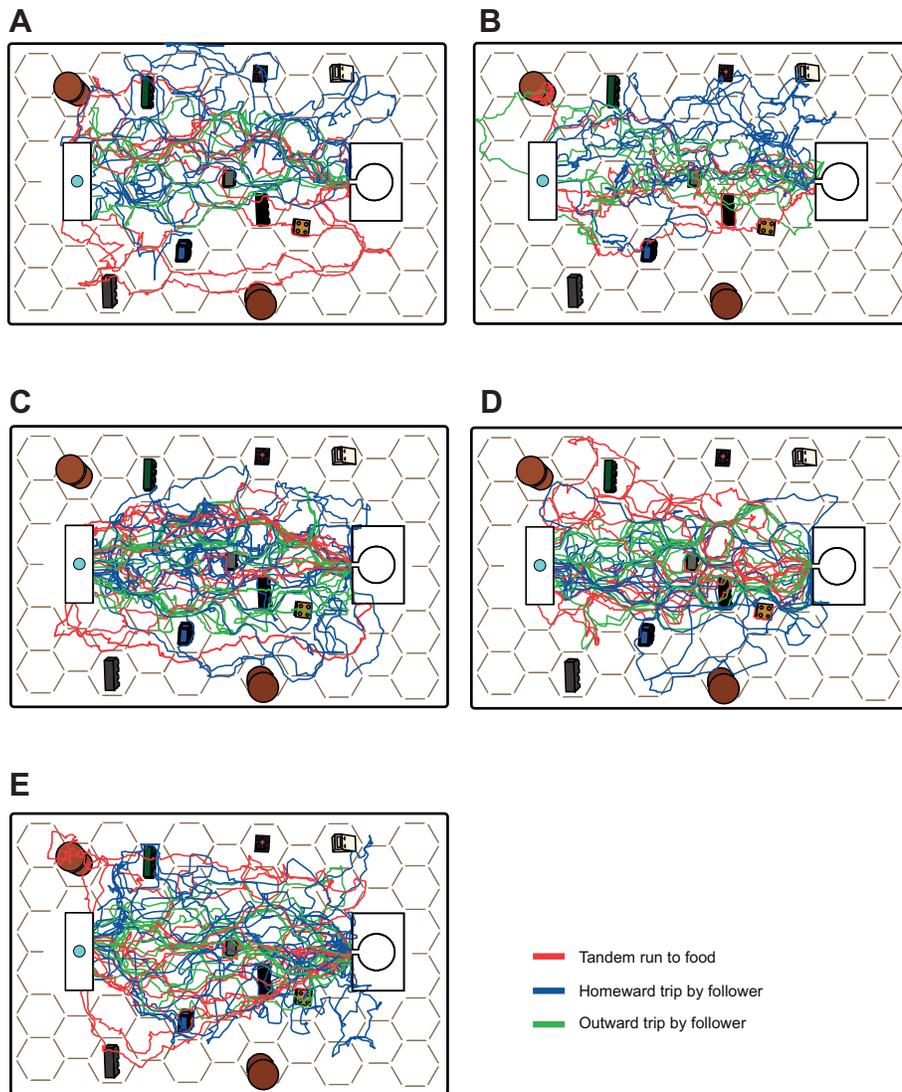


Fig. 6. Travel paths for each colony. We observed 8, 6, 16, 12 and 13 tandem runs for colonies A, B, C, D and E, respectively.

Tandem leaders have individual-specific routes but improve them with experience

The permutation test showed that repeated routes by the same tandem leader were significantly more similar to each other than to the routes of other leaders (Fig. 7A), indicating that leaders used individual-specific routes. Furthermore, tandem run path lengths overall became significantly shorter over successive trips (linear mixed model: $t=-3.43$, d.f.=39.6, $P<0.01$; Fig. 7B). Because only one ant led five runs, the data point of the 5th trip was not included in the regression analysis.

Followers' homeward trips are longer than their outward trips back to the food

Followers' return routes back to the nest were significantly longer than the tandem runs that brought them to the food (Fig. 8; Friedman–Nemenyi test: $P<0.01$). The homeward trips were also significantly longer than the subsequent outward routes back to the food. The outward trips and tandem runs were not statistically different from each other ($P=0.28$). This lack of difference was true both for the 19 outward trips in which the former followers led tandem runs to the food source ($P=0.99$) and for the other 36 in which they walked on their own ($P=0.35$).

DISCUSSION

Although tandem followers are often assumed to learn the route on which they are led, this has not been experimentally demonstrated before this study. We found that a tandem follower, when later returning on her own to the food source, used a route similar to the one she was led on. This contrasts with an earlier finding that followers which later led their own tandem runs did not use the route on which they had been led (Franklin and Franks, 2012). We speculate that this difference stems from lower variation among routes in the earlier study. We departed from earlier methods by deploying an array of local landmarks and tactile cues designed to create alternative pathways from home to feeder. Our use of a larger separation between home and target may also have encouraged route variation. Greater variation in tandem paths gives more statistical power to detect associations between those paths and the subsequent trips of followers. Recent results reinforce our finding of route learning; genes related to learning and memory are up-regulated in tandem run followers of two other *Temnothorax* species (Alleman et al., 2019).

Interestingly, when the follower returned home from the food source, she did not use the route that the leader had shown to her during tandem running, a result that is consistent with earlier

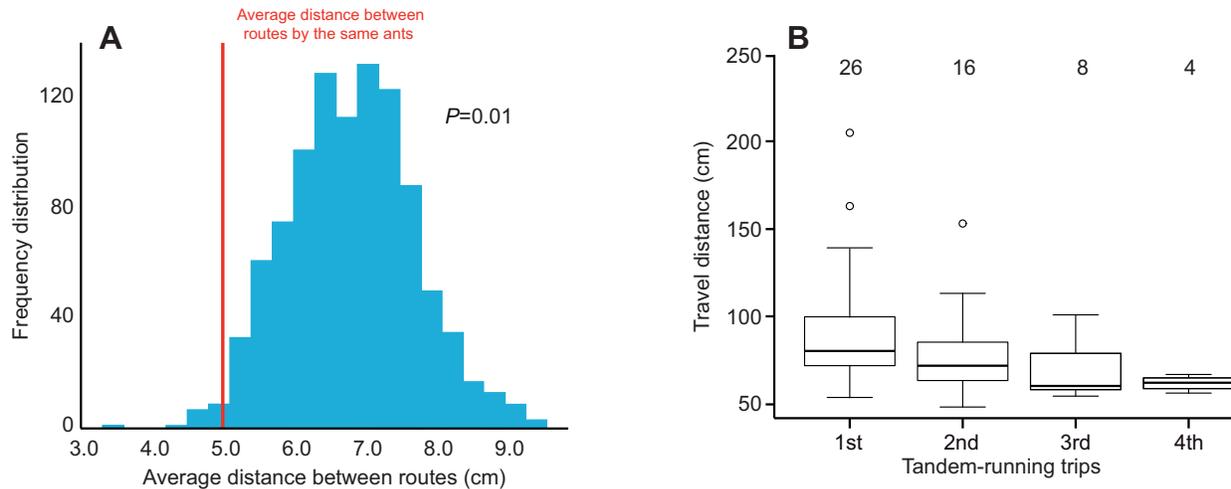


Fig. 7. Leaders use individual-specific routes and improve them over trips. (A) Results of a permutation test for route fidelity in tandem run leaders. The red line represents the average distance between tandem run routes led by the same leader. The blue bars show the distribution of the same measure for 1000 simulated datasets in which these pairs of routes were shuffled within trials. The P -value gives the proportion of simulations with smaller average distances than the observed value. (B) Tandem run distances plotted against the run's position in the leader's sequence of runs. Sample sizes are given above each boxplot. Because only one ant led five runs, this data point was omitted from the graph. Each box extends between the lower and upper quartiles, a horizontal line within the box indicates the median, and whiskers show the range of the data (up to $1.5\times$ interquartile range); circles are outliers.

findings (Franks and Richardson, 2006). Why did the follower use the learned route for one direction but not for the other? Past research actually showed a similar pattern; red honey ants, *Melophorus bagoti*, traveling between home and a food source use different routes for outward and homeward trips (Wehner et al., 2006). We hypothesize that the tandem run follower uses a 'view-based matching' navigational strategy (Cartwright and Collett, 1983; Cheng, 1986). Insects, including many ants, are known to navigate by memorizing images of landmarks and panoramic views (Wystrach and Beugnon, 2009; Wystrach et al., 2011). They later retrace the learned route by matching their current view with the

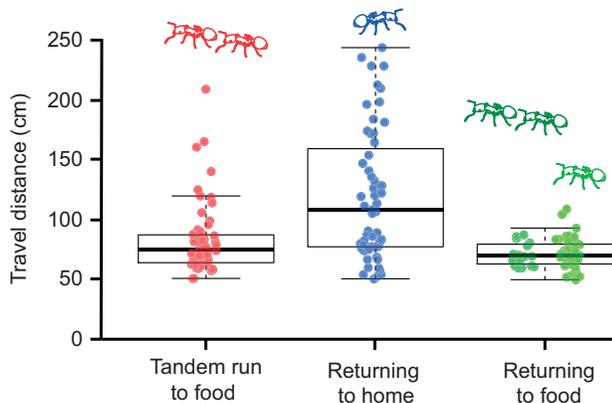


Fig. 8. Travel distances of followers. The tandem run route (red) was significantly shorter than the homeward route from the food source to the nest (blue) ($P<0.01$). The third trip (green), returning to the food source from home, was also significantly shorter than the homeward trip. This third trip was shorter on average than the tandem run, but not significantly so ($P=0.28$). Followers returning to the food sometimes led tandem runs themselves (dark green) and sometimes did not (light green). There was no significant difference between the length of either type of return trip and that of the original tandem runs ($P=0.99$ and $P=0.35$, respectively). Scatterplots show individual data points. For box plots, each box extends between the lower and upper quartiles, a horizontal line within the box indicates the median, and whiskers show the range of the data (up to $1.5\times$ interquartile range).

memorized images. This strategy works well, except when the subject views its surroundings from a different position, as in our study, where the homeward-bound ant walked in the opposite direction from the tandem run in which she had learned the route. This hypothesis is supported by the longer travel distance for the homeward trip than for the outward trip – the follower might have difficulties returning home because the view-based matching strategy did not work well. Note that the followers were probably not completely lost on the way back home because they all were still able to head in the right direction when they left the food source (Fig. 6). They might achieve this by remembering home-directed landmarks (e.g. the wall behind the home nest), as a previous ant study showed (Zeil et al., 2014).

We primarily focused on route learning during tandem runs, but ants can also learn routes during other phases of foraging or scouting. For example, they may learn routes even when they are searching for food. This 'latent learning' – learning routes without reinforcement, such as food – has been found in a few species of ants (Collett et al., 2006), but it is still an open question for many ant species, including *T. albipennis*. Furthermore, during a migration, *T. albipennis* ants physically transport nestmates one by one from home to a new nest site. In this method, called 'social carrying' (Möglich and Hölldobler, 1974), the recruiter carries the transportee curled back over her body so that the transportee faces down. Because of the posture of the transportee and the high walking speed of the transporter (approximately 3 times faster than tandem runs), it is often assumed that transportees of *Temnothorax* ants do not learn routes during this recruitment (e.g. Pratt, 2005). However, a recent study showed that transportees of the desert ant *Cataglyphis* can measure travel distance using optic flow during social carrying (Pfeffer and Wittlinger, 2016). Future work should directly examine what navigational strategies *Temnothorax* ants use in different contexts and how these strategies affect their route finding.

A recent study of *T. albipennis* showed that leaders lay a pheromone trail during tandem running and suggested that colony members develop a route by following the pheromone (Basari et al., 2014). However, our data indicate that foragers within a trial did not use similar routes, as would be expected if they are using a shared

pheromone trail (Morgan, 2009). Rather than form a lasting orientation guide, the leader's trail may instead help to maintain the tandem pair's bond by making it easier for a separated follower to reunite with her leader. (Basari et al., 2014; Hoelldobler and Traniello, 1980; Möglich et al., 1974; Traniello and Hoelldobler, 1984). But, we cannot rule out the possibility that leaders lay short-lived orientation trails. This is because our permutation test for colony-specific foraging routes (Fig. 5) can reject only the existence of a single pheromone trail shared by all foragers, as might be expected with longer-lived pheromones. Short-lived pheromones could instead create multiple routes during a foraging bout, each one used only by the leader that created it and by her follower. Against this possibility, the ants in our study did not tightly recapitulate their own routes, which they should do if they follow individual-specific pheromone trails (Basari et al., 2014). In short, the potential role of trail pheromones remains unclear, and a fuller understanding of the degree to which followers use them during and after tandem running must await future studies.

Ants took relatively inefficient routes, both during tandem runs and in the follower's subsequent trips. The shortest route was 49 cm, but most routes were longer than 60 cm, twice as long as the straight-line distance between home and feeder. This inefficiency was probably the result of the ants' tendency to walk along objects, such as the rods and landmark cues (McLeman et al., 2002; Pratt et al., 2001) (Fig. 6).

Route efficiency was low overall, but it improved with individual experience (Fig. 7B); recruiters tended to use shorter routes over repeated trips. In contrast, route efficiency did not improve via social transmission (Fig. 8). That is, when a follower later led a tandem run, she did not use a shorter path than the one her leader initially 'taught' her. Our finding is not consistent with a previous study that showed improvement of foraging routes via tandem running (Franks and Richardson, 2006). One possibility for this difference is that the followers in the previous experiment had greater opportunity to acquire individual information. In that experiment, after the initial tandem run, followers were allowed to travel between the home nest and the food source before they started recruiting nestmates. In our study, in contrast, we always measured the followers' first return trip to the food source, regardless of whether it was a tandem running trip or a solo trip, so that they did not have an opportunity to acquire route information individually after the initial tandem run. In fact, the previous study showed that followers which did not make individual trips before initiating tandem running did not improve routes socially (Franks and Richardson, 2006). Thus, the relationship between individual and social learning of routes remains unclear. Future research should investigate how groups integrate individual and social information, as previous studies have suggested in ants (Czaczkes et al., 2011; Stroeymeyt et al., 2017) and in other social animals (Enquist et al., 2007; Kameda and Nakanishi, 2003; Krause and Ruxton, 2002; Rendell et al., 2010; Rogers, 1988; Sumpter, 2010). Individual and collective route finding offers an especially promising context in which to pursue this investigation.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: T.S., S.P.; Methodology: T.S., L.D., B.T., T.M., S.P.; Validation: T.S.; Formal analysis: T.S., S.P.; Investigation: T.S., L.D., B.T., T.M.; Resources: T.S., S.P.; Data curation: T.S.; Writing - original draft: T.S., L.D., B.T., T.M., S.P.; Visualization: T.S.; Supervision: T.S.; Project administration: T.S.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.221408.supplemental>

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