Collective decision making in a heterogeneous environment: *Lasius niger* colonies preferentially forage at easy to learn locations

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Many ants forage in complex environments and use a combination of trail pheromone information and route memory to navigate between food sources and the nest. Previous research has shown that foraging routes differ in how easily they are learned. In particular, it is easier to learn feeding locations that are reached by repeating (e.g. left—left or right—right) than alternating choices (left—right or right—left) along a route with two T-bifurcations. This raises the hypothesis that the learnability of the feeding sites may influence overall colony foraging patterns. We studied this in the mass-recruiting ant *Lasius niger*. We used mazes with two T-bifurcations, and allowed colonies to exploit two equidistant food sources that differed in how easily their locations were learned. In experiment 1, learnability was manipulated by using repeating versus alternating routes from nest to feeder. In experiment 2, we added visual land-marks along the route to one food source. Our results suggest that colonies preferentially exploited the feeding site that was easier to learn. This was the case even if the more difficult to learn feeding site was discovered first. Furthermore, we show that these preferences were at least partly caused by lower error rates (experiment 1) and greater foraging speeds (experiment 2) of foragers visiting the more easily learned feeder locations. Our results indicate that the learnability of feeding sites is an important factor influencing collective foraging patterns of ant colonies under more natural conditions, given that in natural environments foragers often face multiple bifurcations on their way to food sources.

Many ants use pheromone trails to recruit nestmate workers to valuable resources (reviewed in Czaczkes, Grüter, & Ratnieks, 2015; Detrain & Deneubourg, 2008; Hölldobler & Wilson, 1990). Recruitment allows a colony to quickly exploit and dominate newly discovered resources (Detrain & Deneubourg, 2008; Lanan, 2014). Because trail pheromones create positive feedback, the relative amount of pheromone on alternative routes affects forager allocation among different food patches (Beckers, Deneubourg, Goss, & Pasteels, 1990; Grüter, Czaczkes, & Ratnieks, 2011; Hangartner, 1969; von Thienen, Metzler, Choe, & Witte, 2014; reviewed in Czaczkes et al., 2015). The amount of pheromone on routes to different food sources may differ because of the temporal sequence of discovery (Beckers et al., 1990), differences in route length (Beckers, Deneubourg, & Goss, 1992b; Devigne & Detrain, 2006; Dussutour, Beekman, Nicolis, & Meyer, 2009), differences in food quality (De Biseau, Deneubourg, & Pasteels, 1991; Portha,

Deneubourg, & Detrain, 2002), differences in food volume (Mailleux, Deneubourg, & Detrain, 2000) or random fluctuations (Detrain & Deneubourg, 2008).

Individual foragers of many pheromone-laying ant species can also learn the route to a feeding site over multiple visits (reviewed in Collett, Chittka, & Collett, 2013; Collett, Graham, & Durier, 2003). Route learning can lead to improved accuracy or foraging speed or both (Aron, Beckers, Deneubourg, & Pasteels, 1993; Collett et al., 2013, 2003; Czaczkes, Grüter, Jones, & Ratnieks, 2011; Grüter et al., 2011). Thus, in many ants social pheromone information and individual memory combine to affect route choices at bifurcations or travelling speed on straight sections of a trail (Aron et al., 1993; Czaczkes, Grüter, Ellis, Wood, & Ratnieks, 2013; Czaczkes et al., 2011; Grüter et al., 2011; Harrison, Fewell, Stiller, & Breed, 1989; Hölldobler, 1976; Traniello & Robson, 1995). The use of social (pheromone) versus private (memory) information is probably not fixed, but varies between species and depends on factors such as previous foraging experience or the strength of the pheromone trail (Aron et al., 1993; Grüter et al., 2011; Grüter & Leadbeater, 2014).

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Natural trail systems tend to be more complex (e.g. Hölldobler, 1976; Lanan, 2014) than the single bifurcation T- and Y-mazes that are frequently used in laboratory experiments to study collective foraging in ants (e.g. Aron et al., 1993; Dussutour et al., 2009; Grüter et al., 2011; but see e.g. Reid, Sumpter, & Beekman, 2011). The complexity of many natural foraging environments, such as along the ground or up a tree, poses a challenge for an ant trying to navigate in this environment because more information needs be stored to learn the route and navigational mistakes become more likely (Czaczkes, Grüter, Ellis, et al., 2013). A recent study showed that some routes are more difficult to learn than others: foragers of the mass-recruiting ant *Lasius niger* make more mistakes when learning an alternating route (left—right; LR/right—left; RL) leading from the nest to a feeder in a doubly bifurcating maze than when learning a repeating route (LL/RR) of the same overall length and with feeders of equal quality (Czaczkes, Grüter, Ellis, et al., 2013). A possible explanation for this is that navigation by image matching (Collett, 2009; Collett et al., 2013) might be more difficult on some routes than on others (Czaczkes, Grüter, Ellis, et al., 2013). However, the learning curves in Czaczkes, Grüter, Ellis, et al. (2013) (their Fig. 2) were obtained by studying individually foraging ants, and social interactions (e.g. collisions or pheromones) on the trail were prevented. Thus, it remains unclear whether and how colony foraging patterns in freely foraging colonies are affected by the learnability of foraging routes.

We hypothesized that colonies of *L. niger* will preferentially exploit food sources that are easier to learn. We tested this in two ways. In experiment 1, variation in learnability of foraging routes was created by offering one food source at the end of a repeating route (LL/RR) and a second, equidistant and with equal quality food, at the end of an alternating route (LR/RL; see also Czaczkes, Grüter, Ellis, et al., 2013). In experiment 2, we provided prominent visual landmarks along the route to one of the two feeders in order to aid in visual learning. Furthermore, we recorded the foraging decisions of individually marked ants and measured foraging speed to explore whether the presence of landmarks along a route affects choice accuracy and speed of foragers.

METHODS

Study Species

We studied six *L. niger* colonies collected on the University of Sussex campus (U.K.) and 10 collected on the University of Lausanne campus (Switzerland). All colonies had ca. 1000 workers, small amounts of brood and were queenless. Queenless colonies are commonly used in foraging experiments (e.g. Dussutour, Deneubourg, & Fourcassié, 2005; Evison, Petchey, Beckerman, & Ratnieks, 2008; Grüter et al., 2011; Mailleux, Buffin, Detrain, & Deneubourg, 2010). Colonies were kept in plastic boxes (40 × 30 cm and 20 cm high). The bottom of each plastic box was covered with a layer of plaster of Paris. Each box contained a circular plaster nestbox (14 cm diameter, 2 cm high). We fed the colonies three times per week with a food mixture made from honey, raw egg and agar (see Bhatkar & Whitcomb, 1970) and once per week with fruit flies, *Drosophila melanogaster*. Colonies were starved for 4—5 days prior to a trial in order to achieve uniform high motivation for foraging. Water was provided ad libitum. All experiments were performed in a room that had both natural light coming from windows and artificial room lights. The walls and the ceiling were bright and the room contained different kinds of laboratory equipment that ants can use as visual landmarks (Evison et al., 2008). The room temperature was 20—22 °C.

Experimental Procedure

Experiment 1a: simultaneously introduced food sources

As in Czaczkes, Grüter, Ellis, et al. (2013) we tested colonies using a double bifurcation maze to create a foraging trail system with four end points (LL, LR, RR and RL; Fig. 1). The maze was covered with white printer paper. In experiment 1a, syrup feeders were introduced simultaneously at two end points and colonies could freely exploit them for the next 60 min. Feeders offered 1 M sucrose solution ad libitum and were large enough to avoid crowding effects (Grüter et al., 2012). At the beginning of a trial, the box containing a colony was connected to the maze with a paper bridge (Fig. 1). We performed two trials per colony: in one trial, feeders were placed at LL and LR and in the second, at RR and RL. Trials were separated by 1 week and performed in different locations to avoid interference from visual memories from previous trials. The ants at each feeder were counted every 2 min. The first three ants reaching the feeders were individually marked and their subsequent foraging decisions recorded at specified 'decision lines' (Fig. 1). Additionally, we observed the decisions of the first 10 naïve ants entering the maze to test whether they had a preference for a particular feeder location. Because some ants returned to the nest without finding a feeder we recorded the decisions of 103, rather than 120, ants (six colonies, two trials/colony and 10 ants/trial).

Experiment 1b: delayed introduction of the easier to learn source

In experiment 1b, colonies were initially offered only the alternating feeder (LR or RL) until at least three foragers laid pheromone on the final route branch (grey section, Fig. 1) leading to it. Pheromone deposition in *L. niger* is a characteristic behaviour that is easy to observe (Beckers, Deneubourg, & Goss, 1992a; Czaczkes, Grüter & Ratnieks, 2013; Grüter et al., 2011). Pheromone deposited by three ants is enough to cause a preference for the marked branch at a T-bifurcation (Grüter et al., 2011). Only then was the second feeder introduced (LL or RR). We again performed two trials per colony: in one trial, the feeder positions were LL and LR and in the second, RR and RL.

Experiment 2: individual learning

The same double bifurcation maze was used. Since the effect of landmarks on the learnability of a difficult to learn route (LR or RL) has not yet been studied, we first performed learning trials with marked ants (Czaczkes, Grüter, Ellis, et al., 2013). Landmarks (3 × 14 cm pieces of yellow or blue printer paper with horizontal or vertical stripes; half of the trials were performed with yellow and half with blue landmarks) were placed at the feeder position and next to the first bifurcation at around 1 cm from the maze (see Fig. 1). We chose blue and yellow for our landmarks because these colours are easily discriminated by ants (Cammaerts & Cammaerts, 2009). Owing to their proximity and relative size, these colourful landmarks are likely to be particularly useful for navigation by image matching (Collett et al., 2013). As a control, we also trained ants without the landmarks.

To start a learning trial, the maze was connected to the colony's box using a paper bridge. Once the first ant had found the feeder, the other ants were removed from the maze and put back in the colony. The feeding ant was marked with a dot of acrylic paint on her abdomen and allowed to make four more visits to the feeder. No other ant was allowed to enter the maze during a learning trial. After a test ant had returned to the nest we temporarily closed the maze and replaced all the pieces of printer paper on the maze with fresh pieces to remove any pheromone information (as in Czaczkes, Grüter, Ellis, et al., 2013). We recorded three types of data: (1) the decisions of the test ant for each trip to the feeder (decision lines in Fig. 1; an ant was considered to have made a correct decision if she
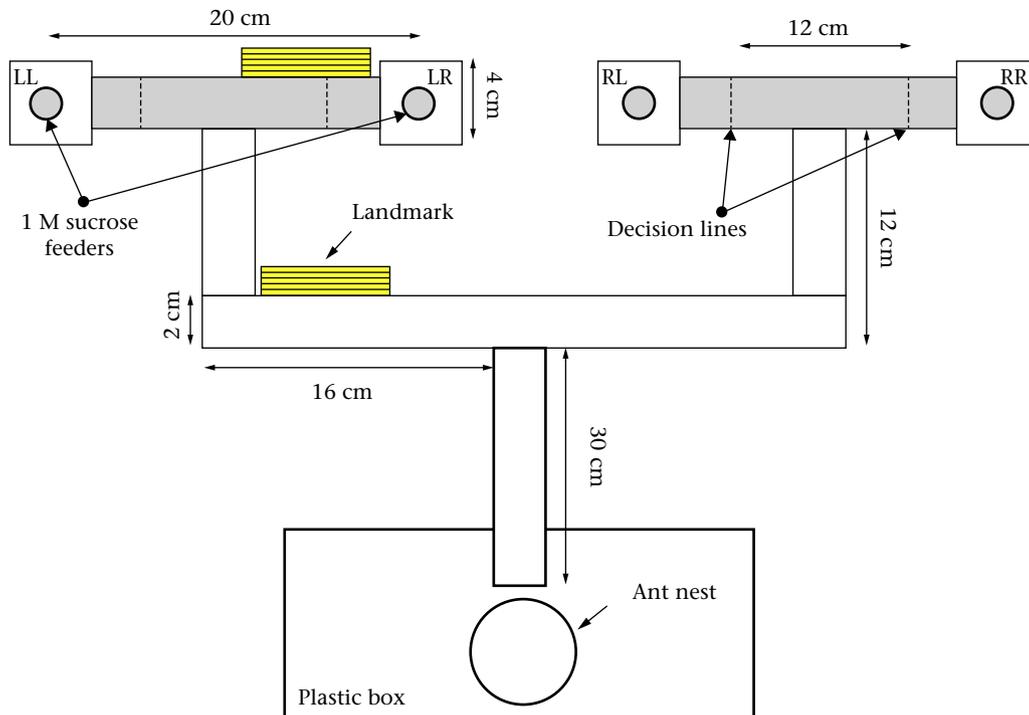
Figure 1. Double bifurcation maze. Pheromone depositions were recorded on the grey area of the trail system. Ants were considered to have chosen a feeder position when they crossed the relevant decision line (dashed lines). Each section of the maze was covered in printer paper, which could be replaced to remove any pheromone on the maze surface. LL: left−left, ants reaching this feeder had to turn left at both bifurcations; LR: left−right; etc. The landmarks for experiment 2 were yellow with horizontal stripes or blue with vertical stripes (3 × 14 cm long). For each trial two landmarks of identical colour were used; there was a gap of 1−2 cm between the maze and the landmark to prevent ants from walking on the landmarks.

chose the branch leading to the feeder); (2) the total time to make the five trips; and (3) the number of pheromone-depositing behaviours made on the branch leading to the feeder (grey section, Fig. 1). Test ants were removed from their colony to prevent the same ant being tested twice. We tested 72 ants in total, 12 from each of six colonies (48 with landmarks, 24 without landmarks). Each ant was tested at only one feeder location. Half were trained at the LR feeder and half at the RL feeder.

Experiment 2: collective foraging

Syrup feeders were simultaneously placed at the two alternating positions (LR and RL). Only one of the two routes to these feeders was given landmarks ('landmark feeder'). Colonies were allowed to forage freely for 60 min. We recorded the number of ants at each feeder every 2 min. We tested 10 colonies and performed two trials per colony. In one trial landmarks were placed at the LR position, and in the other at the RL position. Trials were separated by at least 1 week and performed in different locations in the laboratory to avoid interference from visual memories from previous trials.

Ethical Note

No licences or permits were required for this research. During experiments the ants were not restricted in their normal behaviour.

Statistical Analysis

We used linear (LME) and generalized (GLMM) mixed-effect models in R 3.1 (R Core Team, 2013). We included colony and trial as hierarchically nested random effects to control for the nonindependence of data points from the same colony and the same trial (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Proportional data in experiments 1 and 2 (proportion of ants foraging at the two alternative food sources) were arcsine transformed (Zar, 2010) and analysed with LMEs. We analysed collective foraging from minutes 15−60 to exclude the initial build-up period. Foraging was usually well underway after 15 min (Appendix Fig. A1). GLMMs with binomial and Poisson distributions were used to analyse the individual learning experiment. For model selection we used the protocol proposed by Zuur et al. (2009, chapter 5). We first explored the best structure of the random components and then the significance of the fixed effects. Significance of interactions (experiment 1: 'route'∗'time'; experiment 2: 'landmarks'∗'time') between two predictors was tested by comparing the model containing the interaction and the model without the interaction with likelihood ratio tests (LRT; Zuur et al., 2009). Nonsignificant interactions ($P > 0.05$) were removed for the final model. Descriptive statistics are given as mean ± SD or median [first quartile, third quartile].

RESULTS

Experiment 1: Collective Foraging

Naïve ants showed no preference for LL or RR (32 versus 37; $\chi^2_1 = 0.36$, $P = 0.55$). However, there was an initial preference of naïve ants for the repeating (LL/RR) versus alternating routes (LR/RL; 69 versus 34 ants; chi-square test: $\chi^2_1 = 11.9$, $P < 0.001$). In experiment 1a, colonies strongly preferred feeders at repeating end points (80.2 ± 8.5% of foragers from minutes 15−60, $N = 6$ colonies) over alternating bifurcations (LME: $t = 42.5$, $P < 0.0001$; 'time': $t = 0.26$, $P = 0.79$; 'route-type'∗'time': $t = 0.67$, $P = 0.41$; Fig. 2a).

Experiment 1b showed that colonies preferentially exploited the repeating feeders even if alternating feeders were discovered first and the branch to alternating feeders was marked by pheromone (LME: $t = 16.4$, $P < 0.0001$; 'time': $t = -2.06$, $P = 0.04$; 'route-type'*'time': LRT = 14.9, $P = 0.0001$; Fig. 2b). From minutes 15–60, $85.2 \pm 2.5\%$ ($N = 6$ colonies) of foragers visited the repeating feeder. The significant interaction suggests that the preference for the repeating feeder became stronger with time (Fig. 2b).
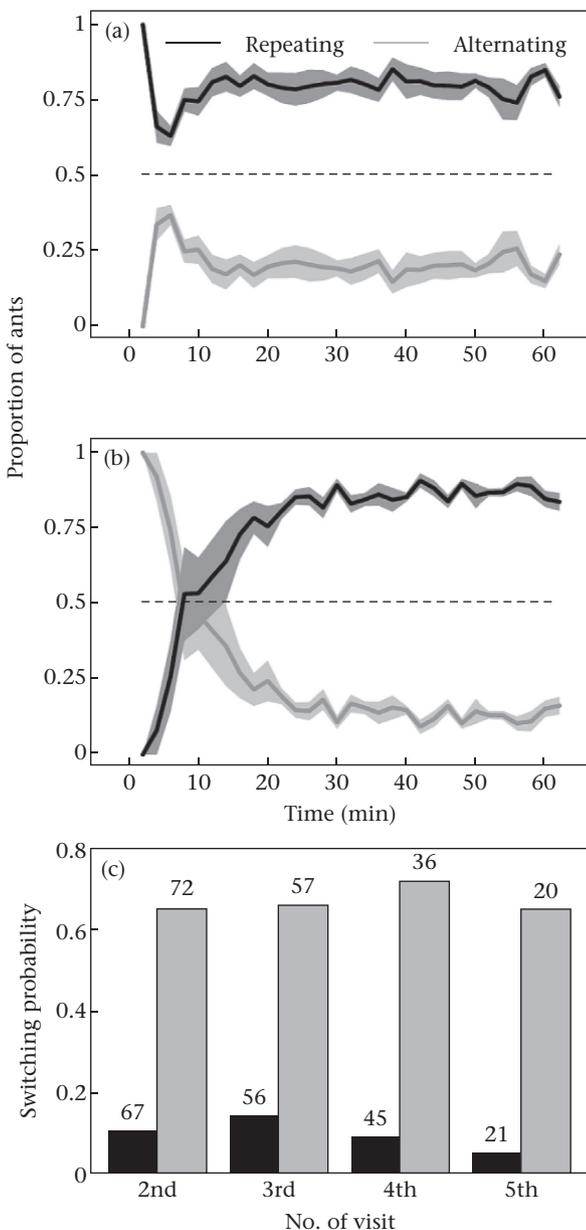
Figure 2. Experiment 1. (a) Proportions of ants exploiting the feeders at the end of repeating (LL/RR; black) versus alternating routes (LR/RL; grey) during the 60 min of observation. The line represents the mean of six colonies. The grey areas indicate the SEM. (b) The proportion of ants exploiting the feeders at the end of a repeating (LL/RR; black) versus an alternating route (LR/RL; grey) during the 60 min of observation of experiment 1b. (c) The proportion of individually marked ants making a feeder choice that differed from their first visit. Black bars show ants that initially chose the repeating feeder and changed their choice to the alternating feeder. Grey bars shows ants that initially chose the alternating feeder and changed their choice to the repeating feeder. Thus, the first visit is used as reference. The numbers above bars indicate the sample sizes.

Marked ants that initially visited the alternating branch feeders were more likely to switch to the repeating feeders on their second foraging trip than vice versa (47 of 72 versus 7 of 67 ants making a mistake; chi-square test: $\chi^2_1 = 41.6$, $P < 0.001$; Fig. 1c). The proportion of ants that visited a feeder that was different from the one visited on their first trip remained constant during later visits (Fig. 2c).

### Experiment 2: Individual Learning

We found a positive relationship between the number of previous visits to the feeder and the probability of choosing the correct route (GLMM: $z = 4.8$, $P < 0.0001$), but no effect of landmark presence ($z = -0.58$, $P = 0.58$; 'landmarks'*'visit': LRT = 0.07, $P = 0.79$; Fig. 3a). However, we did find that the presence of landmarks reduced the time it took ants to visit the feeder five times by 20% (37.5 min [30, 45] versus 30.0 min [25, 40]; GLMM: $z = 2.28$, $P = 0.023$; Fig. 3b). Next, we tested whether the number of previous visits and the presence of landmarks affected the probability of laying pheromone when returning to the nest. There was a positive effect of visit number on pheromone deposition probability (binomial GLMM: 'visit': $z = 5.4$, $P < 0.0001$; Fig. 3c), but no effect of landmark presence ('landmarks': $z = 0.53$, $P = 0.60$; 'landmarks'*'visit': LRT = 4.41, $P = 0.04$). When including only ants that deposited pheromone we found a positive relationship between the number of previous visits and the number of pheromone depositions (Poisson GLMM: $z = 3.9$, $P < 0.0001$), but again no effect of landmark presence ($z = -1.58$, $P = 0.11$; 'landmarks'*'visit': LRT = 0.12, $P = 0.73$). We then analysed pheromone deposition during the outward journey and found a positive effect of visit number on pheromone deposition probability (binomial GLMM: 'visit': $z = 5.2$, $P < 0.0001$; Fig. 3c), but no effect of landmark presence ('landmarks': $z = 0.19$, $P = 0.85$; 'landmarks'*'visit': LRT = 0.36, $P = 0.55$). Neither visit number nor landmark presence affected the pheromone deposition rate when considering only ants that deposited pheromone (Poisson GLMM: 'visit': $z = 0.28$, $P = 0.78$; 'landmarks': $z = -0.90$, $P = 0.37$; 'landmarks'*'visit': LRT = 0.06, $P = 0.81$).

Experiment 2: Collective Foraging

The proportion of ants foraging at the landmark feeder during minutes 15–60 was $63 \pm 25\%$ ($N = 10$ colonies; Fig. 3d). A model using 'landmark' and 'time' as predictors showed that a significantly larger proportion of ants visited the landmark feeder (LME: $t = 10.5$, $P < 0.0001$; 'time': $t = 0.02$, $P = 0.98$; 'landmarks'*'time': LRT = 0.74, $P = 0.39$).

DISCUSSION

Our results strongly suggest that location learnability has a significant effect on colony choice between two alternative food sources. In experiment 1, the more easily learned feeder location was visited by more ants even if the alternative feeder was discovered first and the route to the latter was marked with pheromone (Fig. 2b). The observation that individual ants lay more pheromone when foraging at an alternating branch feeder position (Czaczkes, Grüter, Ellis, et al., 2013) is further evidence that trail pheromones are unlikely to explain why colonies quickly switched to the repeating branch feeder. However, the pheromone trail leading to the alternating feeder was relatively week (deposited by three ants) and it remains to be seen whether a much stronger pheromone trail could prevent a switch to the easier to learn feeder location. The rapid establishment of a preference for the easier to learn route is probably caused by a combination of three factors.
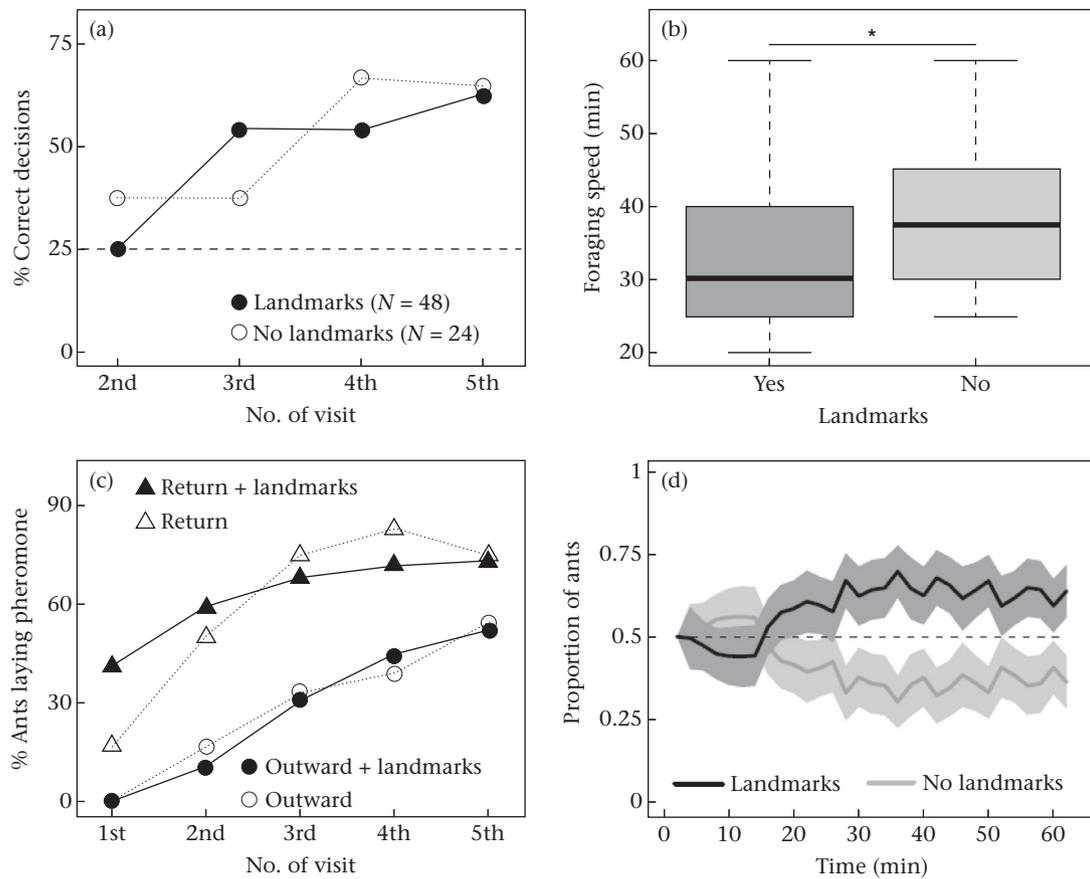
Figure 3. Experiment 2. (a) Proportion of ants choosing the correct route to the feeder for each visit. The dashed line shows the expected percentage (25%) if ants chose routes randomly. (b) The time it took ants to visit the feeder five times depending on whether routes were marked with landmarks. Box plots show medians, quartiles and fifth and 95th percentiles. *$P < 0.05$. (c) Effects of landmark presence, visit number and walking direction on the probability of depositing pheromone. (d) The proportion of ants visiting the two feeders during the collective foraging experiment. $N = 10$ colonies.

First, ants that initially visited the more difficult to learn feeder were more likely to make navigational mistakes that led them to the alternative feeder than ants that initially visited the easier to learn feeder (65.3% versus 10.4% error probability on the second visit; Fig. 2c). This confirms the findings of a recent study on route learning in a similar maze (Czaczkes, Grüter, Ellis, et al., 2013). Some routes might be intrinsically more difficult to learn because of how ants use visual information for image matching during navigation (Collett et al., 2013; Czaczkes, Grüter, Ellis, et al., 2013). Second, naïve ants had a preference for the repeating route on an unmarked trail (also called 'outline tracing'; Jander, 1990). Natural selection might have favoured innate preferences for route patterns that are easier to learn if this leads to quicker and more efficient exploitation of food sources, ultimately because fewer foragers get lost. A similar argument has been used to explain the benefits of handedness in *Temnothorax albipennis* during nest site selection (Hunt et al., 2014). It is not currently known whether individual *L. niger* foragers have a preference for either leftward or rightward 'outline tracing' and we found no overall preference for one side. Third, a tendency of ants to follow walls or edges (e.g. Dussutour et al., 2005) might have led more ants to the repeating feeders. We did not measure edge following in our study, but we observed that naïve ants did not consistently follow one edge when exploring the maze, but frequently switched from one side of the trail to the other. However, more research is needed to explore the effects of edge following in T-mazes with multiple bifurcations.

In experiment 2, we found that colonies preferentially exploited feeders marked by prominent visual landmarks. Since both feeders were placed at alternating locations (LR and RL), neither 'outline tracing' nor edge following could contribute to the preference for the landmark feeders. Visual landmarks play an important role in route learning in ants and other insects (Collett et al., 2013, 2003; in *L. niger*: Aron et al., 1993; Evison et al., 2008; Sakiyama & Gunji, 2013) and in our study landmarks helped test ants make their series of five trips in 20% less time (Fig. 3b). The observation that ants made a similar number of mistakes on routes with landmarks demonstrates that the landmark effect is not due to an innate attraction to the landmarks used in our study. Instead, we repeatedly observed that ants were quicker to correct mistakes on the route with landmarks. Furthermore, ants might also have increased their walking speed (Czaczkes et al., 2011). At first sight, it might seem puzzling that colonies developed a preference for the landmark feeder (Fig. 3d), despite the finding that landmark presence did not reduce the number of mistakes at bifurcations during the individual learning trials (Fig. 3a). However, animals often face a trade-off between speed and accuracy (Chittka, Skorupski, & Raine, 2009) and whether ants use route learning to reduce the number of mistakes or to increase walking speed might depend on the costs of navigational errors (Chittka et al., 2009). Further evidence that landmarks aid in route learning rather than simply being attractive comes from our collective foraging data: the preference for landmark feeders only became apparent after 15–20 min (Fig. 3d). This

is expected if the two routes differed in learnability but not if there were differences in attractiveness.

Landmark presence did not affect the pheromone deposition rate of foragers. However, pheromone depositions might still have contributed to the preference for the landmark feeders if the faster foraging tempo (more visits per unit time) caused a faster build-up of pheromone on the landmark route. Future research could explore whether and how learning effects combine with pheromones to cause a preference for easier to learn foraging locations. The interplay and synergy between route learning and trail pheromones is a potentially important but poorly understood area of research (Czaczkes et al., 2011, 2015).

While it might be beneficial for a colony to focus its foraging on easy to learn foraging sites in an environment with food sources of similar quality, this might not be the case when food sources vary greatly in profitability. In the latter case, learning constraints are likely to limit a colony's ability to exploit the best food sources available if these are located at more difficult to learn sites. *Lasius niger* foragers are able to counter this effect to some degree by depositing more pheromone on a trail after they have made navigational mistakes, and trail pheromone appears to assist in route learning (Czaczkes, Grüter, Ellis, et al., 2013). Our results provide further support for the view that individual and collective decision making in ants is a complex and nuanced process with many interacting factors (Czaczkes et al., 2015).

Acknowledgments

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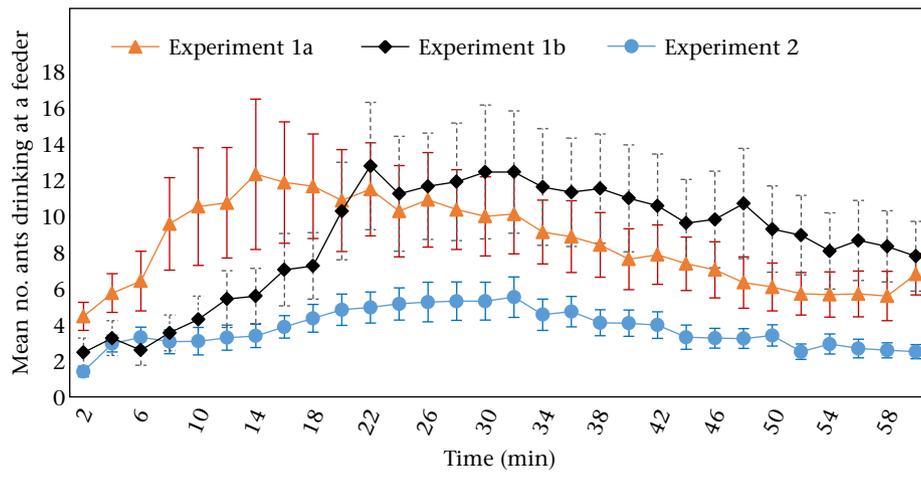
Appendix

Fig. A1. Number of foragers simultaneously drinking at 1 M sucrose feeders during the course of a trial. Mean and SEs are shown.