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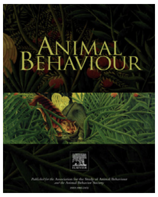

Collective decision making in a heterogeneous environment: *Lasius niger* colonies preferentially forage at easy to learn locations

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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 landmarks 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