



## Perception of collective path use affects path selection in ants



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Social animals rely heavily on social cues to make foraging decisions. In social insects such as ants, perceived use of paths by nestmates is an important cue which allows ants to adjust foraging behaviours. Ants that encounter other ants on a trail reduce trail pheromone deposition. This has been predicted to allow ants to preferentially select underused paths, and thus avoid overcrowding. Here we tested this hypothesis by providing ants with two identical paths to a feeder. On the treatment path we placed 10 'dummy ants', i.e. glass beads coated in nestmate cuticular hydrocarbons, and on the control path 10 untreated beads. Contrary to expectations, ant colonies preferentially chose the treatment path. This preference was unrelated to pheromone deposition, as it arose before any pheromone was deposited. Ants performed more U-turns on the control path, and thus were more likely to switch paths if they entered the control path. Path preference disappeared when three of the untreated beads on the control path were replaced by dummy ants, demonstrating that it is the perceived absence of nestmates on a path, not the relative path use, that drives colony-level preference. By preferentially using paths containing nestmates, ants may benefit from increased information transfer and recruitment potential. The presence of nestmates on a path coupled with a lack of alarm pheromones may be a 'reassurance' that the path is safe and productive. Although ants have various mechanisms for coping with trail crowding, they in fact prefer paths that are already in use.

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Animals use a variety of information sources when foraging. For social animals signals and additional social cues are particularly important, and can provide group members with useful information such as food quality, safety and patch productivity (Galef & Giraldeau, 2001). Often, several sources of social information will be available. The situation can be complicated if one source of social information affects the perception, sharing or impact of other sources of information. For example, mate choice is often informed not only by direct signalling but also by other, often inadvertent, public cues, such as the decisions of other conspecifics (Mery et al., 2009; Vakirtzis, 2011). Many animals, both vertebrate and invertebrate, take public information as well as private information into account when deciding how to respond to risky situations (Coolen, Dangles, & Casas, 2005; Phelps, Rand, & Ryan, 2007). Different sources of information, both public and private, may be used hierarchically or may interact additively or synergistically. Understanding how different sources of information affect group decisions poses a major challenge to biologists and ecologists (Schmidt, Dall, & Van Gils, 2010).

Social insects, such as mass-recruiting ants and honeybees, rely heavily on signalling for recruitment and the organization of foraging (Detrain, Deneubourg, & Pasteels, 1999; Hölldobler & Wilson, 1990). In a classic ant foraging bout, scouts that find rewarding food sources return to the nest depositing pheromone trails along the substrate. These trails act as a signal to other ants that food has been found, and provide an orientation cue that can be followed to the food. These ants in turn return while depositing more pheromone, which forms a feedback loop of ever-increasing recruitment strength, until counteracted by overcrowding, satiation or food depletion (Wilson, 1962). When there are two paths to a food source, amplification of pheromone concentration on the paths by positive feedback usually results in one of the paths being used almost exclusively (Dussutour, Fourcassie, Helbing, & Deneubourg, 2004; Goss, Aron, Deneubourg, & Pasteels, 1989; Sumpter & Beekman, 2003). If the trails are identical, small initial differences in pheromone concentration seed this choice. However, if, for example, one of the paths is longer, positive feedback will work more slowly on it, resulting in an ant colony 'selecting' the shorter path (Goss et al., 1989). Likewise, if one of the paths is narrower and can only support a limited number of ants, the wider path will be selected (Dussutour et al., 2004). *Lasius niger* ants could avoid choosing the narrower trail because a higher ant density, and thus more crowding, forces other ants onto the wider one.

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However, such a mechanism may not function if the bottleneck is distant from the choice point.

However, ants, like most animals, use multiple sources of information. Ants do not follow trail pheromones blindly. For example, they can extract information from the geometry of their trail network or the scent of their surroundings (Dupuy, Sandoz, Giurfa, & Josens, 2006; Forster et al., 2014; Jackson, Holcombe, & Ratnieks, 2004). They can also access many types of social information, such as the scent of food returned by foragers (Czaczkes, Schlosser, Heinze, & Witte, 2014) or the presence of home range markings deposited by nestmates (Devigne & Detrain, 2006; Devigne, Renon, & Detrain, 2004). The presence and behaviour of other individuals is an important source of information for many animals (Coolen et al., 2005; Phelps et al., 2007), and ants also make use of this information: interactions with nestmates can affect which tasks workers perform (Gordon & Mehdiabadi, 1999; Greene & Gordon, 2007) or the preference of workers for different food sources (F. Roces, personal communication).

Collective decisions during trail foraging are not mediated solely by initial trail choice. U-turns can play a large role in collective decision making. For example, when presented with a long and a short path to a single food source, *L. niger* ants performed more U-turns on the longer path, which deviated more strongly from the straight nest–food line (Beckers, Deneubourg, & Goss, 1992a). This may strongly contribute to the ability of these ants to select the shorter of two routes. Similarly, Argentine ants, *Linepithema humile*, and Pharaoh's ants, *Monomorium pharaonis*, also perform more U-turns as they deviate more from their original path, a behaviour also implicated in their ability to choose the shortest path to a food source (Garnier, Guérécheau, Combe, Fourcassié, & Theraulaz, 2009; Helanterä, Walsh, & Ratnieks, 2011). In the Argentine ant, U-turns can also act to strengthen a pheromone trail, by allowing an individual ant to repeatedly mark the trail in one journey (Reid, Latty, & Beekman, 2012). As mentioned above, collisions on a highly crowded trail may force ants to turn around and select a different path (Dussutour, Nicolis, Deneubourg, & Fourcassié, 2006). Ants will perform U-turns when stepping off a pheromone-marked path, presumably in order to relocate the path (Czaczkes, Grüter, Jones, & Ratnieks, 2011).

Gaining information from one source can affect how information in another modality is deployed. For example, encounters with nestmates on a trail affect pheromone deposition rates. In two recent studies, Czaczkes, Grüter, and Ratnieks (2013a, 2014) described a negative feedback effect in the foraging system of *L. niger*. Ants that encountered other ants on a trail, or that encountered dummy ants composed of black beads coated in nestmate cuticular hydrocarbons, reduced the amount of trail pheromone they deposited. Ants that encountered just 10 such dummy ants were 45% less likely to deposit trail pheromone. This effect was postulated to have several roles, including preventing unnecessary use of trail pheromone and maintaining foraging flexibility. Another possible role for this mechanism could be to allow ant colonies to avoid recruiting to crowded trails or trails with a bottleneck somewhere along their length. It was postulated that on more crowded trails ants will experience more head-on encounters, and thus reduce their pheromone deposition. This would then seed a difference in pheromone levels between more and less crowded paths, resulting in more ants choosing the less restricted path. On the other hand, this effect would also predict that on nonlimited path systems with identical paths, such as perhaps those used in previous dual-path experiments (Dussutour et al., 2004; Goss et al., 1989), a uniform use of both paths would be observed, as the negative feedback effect first favours one and then the other path in a homeostatic manner. Such a pattern, however, is not observed. Rather, a single path is usually chosen.

In this series of experiments we explored how ants use information derived from encounter rates on a trail to make collective decisions. We also attempted to reconcile this discrepancy between theory and observation mentioned above. We experimentally manipulated perceived path use on path selection by ant colonies. By using a dual-path design with dummy ants on one path and unmarked beads on the other, we could test whether ant colonies preferentially used underused paths as predicted by the results of Czaczkes et al. (2013a), while keeping all other aspects of the paths identical. We used ant-mimicking beads to simulate a path in use, the precursor to a crowded trail, as opposed to simulating highly crowded paths.

## METHODS

### *Study Species*

We studied six *L. niger* colonies collected on the Ludwig-Maximilian University Planegg campus, in Munich, Germany. Colonies were housed in plastic foraging boxes (40 × 30 cm and 20 cm high). The bottom of each box was covered with a layer of plaster of Paris. Each foraging box contained a circular plaster nestbox (14 cm diameter, 2 cm high). The colonies were queenless with 1000–2000 workers and small amounts of brood. Queenless colonies forage, make pheromone trails and care for brood, and are frequently used in foraging experiments (Czaczkes et al., 2013a; Devigne & Detrain, 2002; Dussutour et al., 2004; Evison, Petchey, Beckerman, & Ratnieks, 2008; Portha, Deneubourg, & Detrain, 2002). While being from a queenless colony may slightly affect the behaviour of the ants, this is unlikely to affect the result of this experiment, especially as brood was present in the nest (Herbers & Choiniere, 1996; Portha, Deneubourg, & Detrain, 2004). Colonies were fed three times per week with Bhatkar diet, a mixture of egg, agar, honey and vitamins (Bhatkar & Whitcomb, 1970). Colonies were deprived of food for 4 days prior to a trial in order to achieve uniform and high motivation for foraging. Water was provided ad libitum.

### *Dummy Ant Preparation*

Dummy ants made by coating glass beads in cuticular hydrocarbons have been used in many studies of ant behaviour, to simulate both nestmates and non-nestmates (Akino, Yamamura, Wakamura, & Yamaoka, 2004; Czaczkes et al., 2013a; Michael J. Greene & Gordon, 2003; Ozaki et al., 2005). Thirty workers were removed from the colony to be tested, and chilled at –20 °C for about 10 min. They were then placed in a 2 ml glass extraction vial (Sigma Aldrich) and covered in pentane to a level at least 1 mm above the ants. The vial was agitated for 5 min at 30 °C so as to dissolve the cuticular hydrocarbons from the ants' cuticle. The ants were then removed from the pentane–CHC solution, and 12 black glass beads (diameter 2.5 mm, height 1 mm; KnorrPrandell GmbH, Lichtenfels, Germany) were placed in the solution. The solution and beads were then agitated at 30 °C until all the pentane had evaporated, thus coating the beads in CHCs. By then extracting the CHCs from the beads and comparing them to those of nestmates, we confirmed that the beads were indeed coated with nestmate CHCs, and that these CHCs were similar to those extracted directly from ants (see Appendix for details).

### *Ethical Note*

The animals in this study are not subject to ethical standard laws in the country in which these experiments were performed. Moreover, there is little research into the humane treatment and

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