



Ants (*Lasius niger*) deposit more pheromone close to food sources and further from the nest but do not attempt to update erroneous pheromone trails

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Abstract

Many social insects use pheromone trails to recruit workers to resources. Pheromone trails have some limitations, however. Two major limitations are that they evaporate over time, meaning that more distant locations may be more difficult to recruit precisely to, and that they cannot be removed if laid erroneously, or if they become outdated. Here, we ask whether *Lasius niger* ants can adaptively modulate pheromone deposition to overcome these limitations. Specifically, we first ask whether ants which have followed a pheromone trail to a wrong (unrewarded) location upregulate pheromone deposition to the correct food location to compete with the erroneous trail. They do not. Then, we examine how food distance and proximity to food influence pheromone deposition. We find that ants deposit up to 22 times more pheromone within 10 cm of a food source compared to when they are about to reach the nest. Moreover, they deposit up to four times more pheromone next to a food source placed 100 cm away from the nest as compared to one placed 20 cm away from the nest. *Lasius niger* ants thus do not display a mechanism for overcoming outdated or erroneously-laid trails by strengthening correct alternatives in our experiment, but do strongly upregulate recruitment to more distant food sources, which are more difficult to locate and recruit to.

Keywords Recruitment · Pheromone trails · Strategic information provision · Error correction

Introduction

Pheromone trails are commonly used by social insects to recruit nestmates to resources, such as nesting sites and food sources (Cronin 2012; Reichle et al. 2013; Czaczkes et al. 2013c), or to places where labour is needed, such as battlegrounds or lost brood (Lubbock 1884; Hölldobler and Wilson 1978; Fourcassié et al. 2012). By modulating their response to, and deposition of, recruitment pheromone trails, social insects can coordinate collective behaviours at large scales. This can result in emergent behaviour patterns at the colony level, such as collective choice of the best of multiple food sources, or the shortest of multiple paths to a resource

(Reviewed in Detrain et al. 1999; Czaczkes et al. 2015). This is especially true for mass-recruiting species, such as many ant species, in which the presence of a pheromone trail alone can result in recruitment and trail-following of tens, hundreds, or thousands of workers (Wilson 1962). The rules by which mass-recruiting social insects modulate their pheromone trail deposition behaviour determine the foraging behaviour of the colony as a whole, and are thus expected to be under strong adaptive selection pressure. Modulation of pheromone trail recruitment to food resources is driven by a very broad range of factors, related to the state and experience of the individual, the state of the colony, and the environment and state of the recruitment trail.

Modulation of pheromone trail recruitment and following is affected by several colony-level parameters, most notably food deprivation: individuals from starved nests may recruit more strongly (Hangartner 1969) or may not (Mailleux et al. 2010). Ants must consume a critical minimum volume to trigger recruitment (Mailleux et al. 2000), and this critical volume is larger in starved colonies (Mailleux 2006). Ants from starved colonies also respond more strongly to recruitment pheromones, requiring a lower threshold of

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recruitment pheromone to be emitted by successful scouts to trigger inactive workers to exit the nest and begin foraging (Mailleux 2006; Mailleux et al. 2011). Sensing of starvation level in the nest is likely via individuals measuring how full their own crop is (Greenwald et al. 2018). Colonies with brood may recruit somewhat more strongly than colonies without (Portha et al. 2004). All effects of colony-level states must, ultimately, be responses of individuals to what they are sensing.

Many aspects of individual worker experience and internal state influence recruitment modulations—whether pheromone is deposited or not (recruitment propensity), and if yes, how much pheromone is deposited (recruitment intensity). These are often co-modulated but can also be separately modulated (e.g., Portha et al. 2004). Perhaps the most important influence on recruitment modulation is the individual estimate of resource quality the worker makes: ants recruit more strongly to higher quality food sources (Hangartner 1970; Jaffe and Howse 1979; Verhaeghe 1982; Jackson and Châline 2007; Frizzi et al. 2018; Wendt et al. 2019), or to larger food sources which ants thus find difficult to move alone (Schatz et al. 1997; Robson and Traniello 1998; Czaczkes and Ratnieks 2012). However, assessment of food quality is relative to expectations: ants expecting high-quality food reduce recruitment to a moderate-quality food source relative to ants which expected a moderate-quality food source (Wendt et al. 2019). Recruitment is increased for resources which are assessed as more valuable even due to cognitive illusions, such as the food source requiring more effort to reach (Czaczkes et al. 2018), being an expected flavour (Oberhauser and Czaczkes 2018), or being presented all together, as opposed to in multiple smaller resource units (De Agrò et al. 2022) but see also (Mailleux et al. 2003). Scouts—those which discover food independently—recruit more strongly than recruited ants (Beckers et al. 1992; Frizzi et al. 2018). Ants tend to reduce recruitment over subsequent visits to a food source (Beckers et al. 1992; Czaczkes and Heinze 2015). Task state also may influence response to pheromone trails: Recruiters (also called scouts—ants which are naïve to food presence, and find the food independently) have been reported by Detrain et al. (2019) to follow pheromone trails more accurately than recruits (ants which find a food source after being recruited to it). However, Czaczkes et al. (2017) found no differences in pheromone following between ants in various task states. Recruiters tend to recruit more strongly than recruits (Beckers et al. 1992).

Finally, the environment and state of the recruitment trail and resource also strongly influences recruitment modulation. Several negative feedback effects are built into ant recruitment behaviour: Ants recruit less strongly to food sources where other workers are feeding (Wendt et al. 2020), or after encountering multiple returning ants on their way to the food source (Czaczkes et al. 2013a). If a food source

is overcrowded and cannot be fed from, recruitment stops (Wilson 1962). Ants recruit less strongly on paths already marked with trail pheromone (Beckers et al. 1992; Czaczkes et al. 2013b, 2016b; Frizzi et al. 2018). However, pheromone recruitment is stronger on paths marked with home-range markings (cuticular hydrocarbons passively deposited as ants walk over a surface)—this is achieved by an increased likelihood of recruitment resumption after a U-turn (Devigne et al. 2004).

An important strategic consideration when deploying pheromone is how important the information will be to recruits. When visual navigation is difficult due to low-light levels, ants deposit more pheromone, and are more likely to follow pheromone trails (Jones et al. 2019). If a route is difficult to learn, recruitment should be upregulated. Indeed, ants which make mistakes when searching for food, or which discover food in an unexpected location, deposit more pheromone when returning to the nest than ants which found food where they expected it (Czaczkes and Heinze 2015). This may be important, because pheromone trails cannot be removed if they are found to be outdated or erroneous—the only response may be to strengthen the alternative, correct, trails.

A further strategic consideration when modulating pheromone deposition is the distance from the nest, and distance from the food source. Since pheromone evaporates over time, it may be adaptive to deposit more pheromone when further from the nest. Additionally, depositing more pheromone closer to the food source may help recruits locate the food source precisely. Indeed, pheromone is not deposited evenly along foraging trails (Beckers et al. 1992; Frizzi et al. 2018). Beckers et al. (1992) report that *Lasius niger* ants returning from a food source increase pheromone depositions closer to the food source. However, it is unclear whether this is due to returning ants depositing more pheromone when further away from the nest, or when closer to the food source, or both. In an important study for the current work, Devigne and Detrain (2006) disentangled food distance from food proximity by measuring pheromone deposition of ants returning from 1 M sucrose found on a foraging platform, connected to the colony by 30, 60, or 120 cm-long paths, quantifying pheromone deposition on every 10 cm section. Importantly, they include treatments in which home-range markings (cuticular hydrocarbons laid passively by ants as they walk) are removed, remain on the path, or remain on the path but are scrambled so as not to provide distance information (Devigne et al. 2004). They report that ants deposited very high amounts of pheromone on a the 13 × 13 cm foraging platform at the end of the path, but no effect of path length on recruitment at the foraging platform. Then, on the path leading to and from the foraging platform to the nest, they tend to show decreasing

recruitment strength along the whole path, and overall higher pheromone deposition for food sources closer to the nest. This was in line with the other observations on this species, where more pheromone was deposited closer to the food sources (De Agrò et al. 2022). Devigne and Detrain (2006) also report that the presence of home-range markings tended to boost pheromone deposition by causing ants to continue depositing pheromone for longer, and potentially, as the home-range marking strength becomes stronger nearer the nest, causing ants to begin pheromone deposition again. On paths without home-range markings, however, ants tended to deposit more pheromone for closer food sources. Recruitment dynamics can thus vary strongly depending on whether the food source has been previously well explored, and thus the path marked with home-range markings, or newly discovered. On paths unmarked by home-range markings, ants decrease recruitment as they get further from the food source at the same rate regardless of the distance of the food from the nest, implying that they do not have a higher motivation to recruit to closer food sources. Indeed, overall recruitment was stronger for closer food sources, as a result of a constant rate of recruiters stopping their recruitment, meaning that a higher proportion of workers recruited throughout the path on shorter paths.

Here, we set out to examine strategic information provision in the ant *Lasius niger*. We asked two major questions:

- (1) Do ants deposit more pheromone when the pheromone trail they followed leads to a location with no food, possibly in an effort to rectify earlier recruitment mistakes? We predicted that they would, as ants seem to respond to making navigational errors when returning to a food source (Czaczkes and Heinze 2015).
- (2) Do ants returning from a food source deposit more pheromone for more distant food sources, and do they deposit more pheromone closer to the food source? We predicted higher recruitment closer to the food source, in line with previous findings (Beckers et al. 1992; Devigne and Detrain 2006), and when the food source was further from the nest, since the further a food source is from the nest, the harder it will be to find by chance.

Methods

Ant maintenance

Lasius niger workers were collected from 8 wild colonies on the University of Regensburg campus, and housed in flouon-lined plastic boxes with a plaster of Paris base. Such queenless colony fragments (henceforth colonies) produce male brood, and forage and deposit pheromone in a very similar way to queenright colonies (Portha et al. 2004; Evison et al. 2008; von Thienen et al. 2014). Colonies contained 500–2000 workers and small amounts of worker-derived male brood. Colonies were offered water, 0.5 M sucrose, and freeze-killed cockroaches ad libitum, and deprived of food 4 days prior to experimentation, to produce a high and consistent level of foraging motivation.

Experiment 1: do ants deposit more pheromone when a trail leads in the wrong way?

The aim of this experiment was to test whether ants deposit more pheromone towards a food source when a competing pre-existing trail leads away from it. In addition, we explored whether initially choosing a path leading to a food source, or a path ending with an unrewarded dead end, affected pheromone deposition. By varying whether there was a pheromone trail present and whether the ant initially chose the rewarded or unrewarded Y-maze arm, we produced four treatment groups: (1) no pheromone correct, (2) no pheromone incorrect, (3) pheromone correct, and (4) pheromone incorrect (see Table 1 for an overview).

A 3D-printed Y-maze base was covered with disposable paper overlays to form a Y-maze with arms 10 cm long and 1 cm wide, tapering to 2 mm at the bifurcation (see Fig. 1). The stem of the Y-maze was unmarked. The arms of the Y-maze were either both marked with 6 µl of dichloromethane (DCM, solvent control) or one arm with 6 µl DCM and one with 6 µl a pheromone solution. The pheromone solution consisted of 6 ruptured hindgut glands per 3 ml DCM, to produce a strong but realistic pheromone trail [following (von Thienen et al. 2014)]. DCM or solution was applied by sucking up 2 µl of the solution using a 5 µl capillary tube, drawing the solution over the paper

Table 1 Treatment overview for experiment 1

Treatment	Pheromone trail presence	Initial Y-maze arm choice
(1) No pheromone correct	No pheromone trail on Y-maze	Arm with food
(2) No pheromone incorrect	No pheromone trail on Y-maze	Arm with no food
(3) Pheromone correct	Pheromone trail on the Y-maze arm leading to a food source	Arm with food
(4) Pheromone incorrect	Pheromone trail on the Y-maze arm which does not lead to a food source	Arm with no food

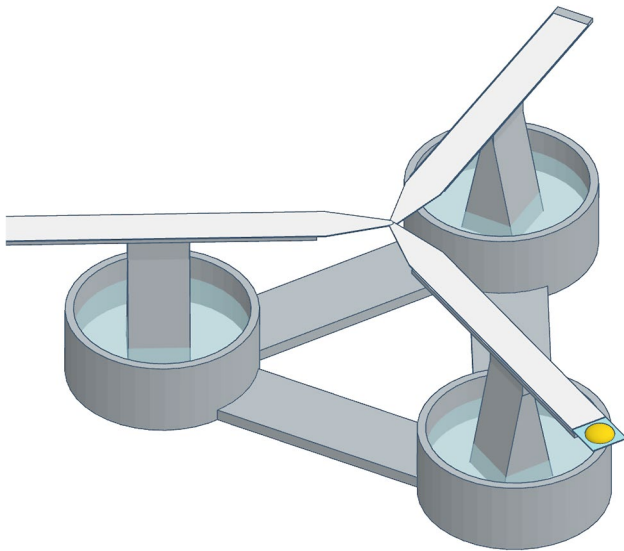


Fig. 1 Y-maze schematic. A 3D-printed base (Grey) with water moats (blue) supports three paper overlays (white), which meet centrally to form a bifurcating path. At the end of one arm, an acetate sheet offers a drop of 0.8 M sucrose (yellow). Overlays are 10 cm long, 1 cm wide, tapering to 2 mm at the bifurcation

overlay, repeating three times. A drop of 0.8 M sucrose was placed on a small acetate platform attached to the end of one arm of the Y-maze.

A colony was connected to the Y-maze via a drawbridge, and a single ant was allowed to walk up the drawbridge, and onto the Y-maze. It then chose one of the arms, and proceeded to the end. In treatments with a pheromone-marked arm, we discarded any ants which did not follow the pheromone trail to the end of the Y-maze arm. Eventually, the ant discovered the drop of sucrose and began drinking. While the ant drank, the paper overlays were replaced with identical but fresh overlays (to remove any pheromone or footprint markings the ant may have left). After drinking to satiation, the ant began returning to the nest. We counted all pheromone deposition events the ant produced on the arms and the stem of the Y-maze, until the ant exited the Y-maze. Pheromone deposition in *Lasius niger* is a highly stereotyped behaviour, involving a c. 0.2 s pause in which the ant presses the gaster tip against the substrate (Beckers et al. 1993). This behaviour is easily and reliably quantified by eye (see results). The ant was then permanently excluded from the colony, and the Y-maze cleaned with ethanol before the next ant was tested. Using naïve ants in pheromone deposition experiments is important, since firstly ants deposit progressively less pheromone on repeat returns from a known food source (Beckers et al. 1992; Czaczkes and Heinze 2015), and secondly ants which find food in an unexpected location upregulate pheromone deposition (Czaczkes and Heinze 2015).

The entire experiment was filmed from above using a Raspberry Pi Noir camera. 47 videos were randomly selected and analysed frame-by-frame, counting pheromone depositions. This was done to ascertain whether real-time counting of pheromone by eye is a reliable method, as it was assumed that frame-by-frame analysis will be highly accurate. 487 ants were tested in total.

Experiment 2: do ants deposit more pheromone closer to the food and for more distant food?

An individual ant was allowed to walk onto a piece of paper in the nest, and then gently lifted out and allowed to walk off the paper onto the start of a 20 or 100 cm-long, 1 cm-wide runway, covered in a disposable paper overlay, with a drop of 0.8 M sucrose solution at the end. The runways were split into ten sections, with the section nearest the food numbered one, the subsequent section 2, and so on. Thus, the short runway consisted of two sections (1, 2), and the long runway consisted of ten sections (1–10). As in experiment 1, an individual ant was allowed onto the apparatus, eventually located the sucrose, drunk to satiation, and was allowed to return to the nest. Pheromone deposition events were counted separately for each runway section. Once the ant left the runway, it was permanently removed from the colony, the paper overlay was disposed of, and the runway cleaned with ethanol. 102 ants were tested on the short runway, and 103 ants on the long runway.

Statistical analysis

All analyses were carried out in R (4.0.3) (R Core Team 2023) via Rstudio (RStudio Team 2015). We used generalised linear mixed models via the package glmmTMB (Magnusson et al. 2020). Post-hoc pairwise comparisons were performed using the emmeans package (Lenth et al. 2020). Model fit checks were performed using the DHARMA package (Hartig 2020).

To test the effect of pheromone presence and navigation errors on pheromone deposition (experiment 1), we conducted a GLMM analysis to predict pheromone deposition by an interaction of pheromone presence and whether the ant made an initially correct choice or not, with the correct side (left or right) as an additional predictive variable and colony as a random effect, varying both by intercept and slope. As the data are count data, a Poisson error family was used, with the addition of a zero-inflation term to account for zero-inflation (90 out of 486 measurements were zeros).

To test the effect of food distance and distance from the food on pheromone deposition (experiment 2), we conducted a GLMM analysis to predict pheromone deposition by the segment number and the runway length (long or short), with colonyID as a random effect, varying in intercept. A Poisson

error family was used, with the addition of a zero-inflation term to account for zero-inflation (113 out of 206 ants deposited no pheromone).

Correlation between real-time collected pheromone deposition data and pheromone deposition data collected via video analysis was performed with a Pearson's test. Figure creation was via GGplot2 (Wickham et al. 2020).

The entire statistical analysis code, and analysis output, is provided in supplement S1.

Results

The complete raw data from both experiments are provided in supplement S2 (experiment 1) and S3 (experiment 2).

Correlation between real-time pheromone deposition analysis and video analysis

We found a correlation of 0.93 between the real-time and video analysis data sets from experiment 1 (Pearson's product-moment correlation, $t = 15.41$, $DF = 35$, $P < 0.0001$, 95% CI for the correlation 0.87–0.97). We therefore consider it reasonable to rely solely on real-time collected data for all future analyses.

Experiment 1: do ants deposit more pheromone when a trail leads the wrong way?

We found no significant interaction between pheromone presence and first arm choice ($X^2 = 1.13$, $P = 0.289$, see Fig. 2). Ants did not deposit significantly more pheromone if they had initially chosen the unrewarded arm ($X^2 = 3.20$, $P = 0.074$). However, ants deposited slightly less pheromone when pheromone was present on the Y maze (mean depositions 6.90) compared to when pheromone was absent (mean depositions 7.44) ($X^2 = 4.03$, $P = 0.045$). There was no significant difference in pheromone deposition when the correct arm was on the left (mean depositions 7.31) or right (mean depositions 7.03) ($X^2 = 2.74$, $P = 0.098$).

Experiment 2: do ants deposit more pheromone closer to the food and further away from the nest

We found a significant effect of distance ($X^2 = 224.79$, $P < 0.0001$), runway length ($X^2 = 22.55$, $P < 0.0001$), and the interaction between the two ($X^2 = 17.38$, $P < 0.0001$) on pheromone deposition. Ants deposit more pheromone on long runways and more pheromone closer to the food (see Fig. 3). Note that pheromone deposition at 0–10 cm from the food on the short runway is significantly higher than at 80–90 cm from the food on the long runway ($Z = 2.7$,

$P = 0.0064$), even though both segments are the same distance from the end of the runway.

Discussion

Ants deposited less pheromone on trails which were already marked with pheromone, confirming several previous results (Beckers et al. 1992; Czaczkes et al. 2013b, 2016b). However, contrary to our hypothesis, we found no effect of a trail leading to an unrewarded location on pheromone depositions. In other words, ants do not seem to react to an erroneous trail by upregulating recruitment on the correct path. While ants upregulate recruitment when they themselves have made a navigational error (or appear to have, due to experimenters changing the environment) (Czaczkes and Heinze 2015), in the current study, all the ants were naïve, and had encountered the food source for the first time. The lack of a correctional mechanism in pheromone deposition suggests that *Lasius niger* ant colonies may be slow to respond to rapidly changing food distributions, and indeed ant colonies are known to be easily 'trapped' in feeding patterns, and can struggle under laboratory conditions to shift foraging efforts from low-quality food to high-quality food discovered later (Beckers et al. 1990; Nicolis and Deneubourg 1999; Camazine et al. 2003; Grüter et al. 2012; Latty and Beekman 2013; Czaczkes et al. 2016a). To our knowledge, the ability of ant colonies to collectively refocus foraging after a food source has completely vanished has not been tested, but our results suggest that they may struggle. While one species of ant, *Monomorium pharaonis*, has been reported to deploy a 'no entry' pheromone when a food source disappears (Robinson et al. 2005, 2008), to our knowledge, this finding has never been replicated in other species.

By contrast, we found a very clear effect of both path length and proximity to the food on recruitment: ants returning from a food source deposit a lot more pheromone when the food is more distant from the nest, and deposit more pheromone closer to the food source. This confirms and refines the previous finding that ants deposit more pheromone closer to the food (Beckers et al. 1992; Devigne and Detrain 2006): it is now clear that both food proximity and path length modulate recruitment. The effect of path length is especially dramatic: within the first 10 cm of the food source, ants deposit more than twice as much pheromone when recruiting to a food source 100 cm from the nest than when recruiting to one 20 cm from the nest. *L. niger* regularly forage at locations several meters from the nest (Devigne and Detrain 2005), or in trees which are several meters high (TJC, Pers. Obs.), and it is unclear whether recruitment to food sources even more distant than 1 m from the nest is even higher, or whether the effect plateaus.

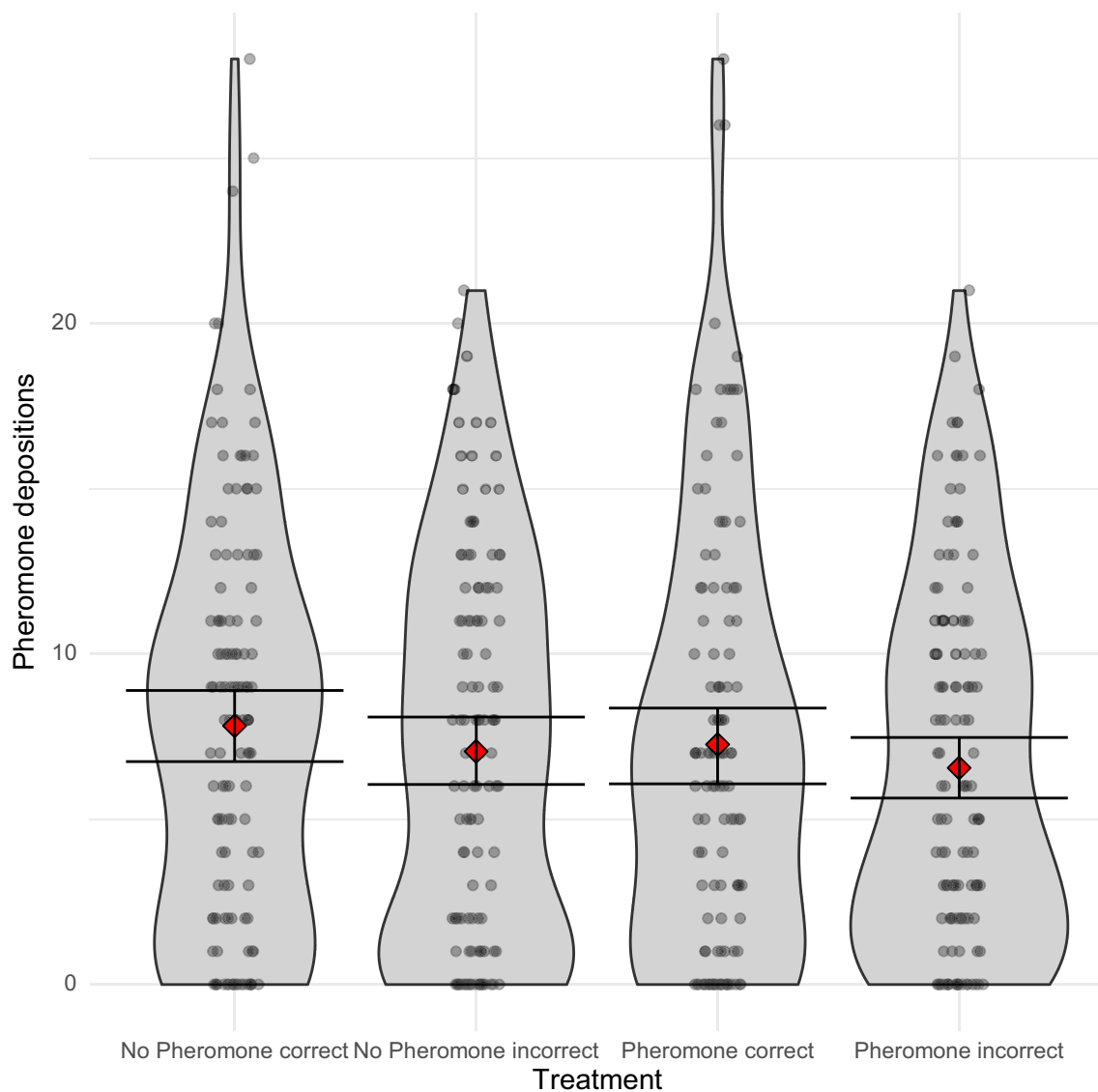


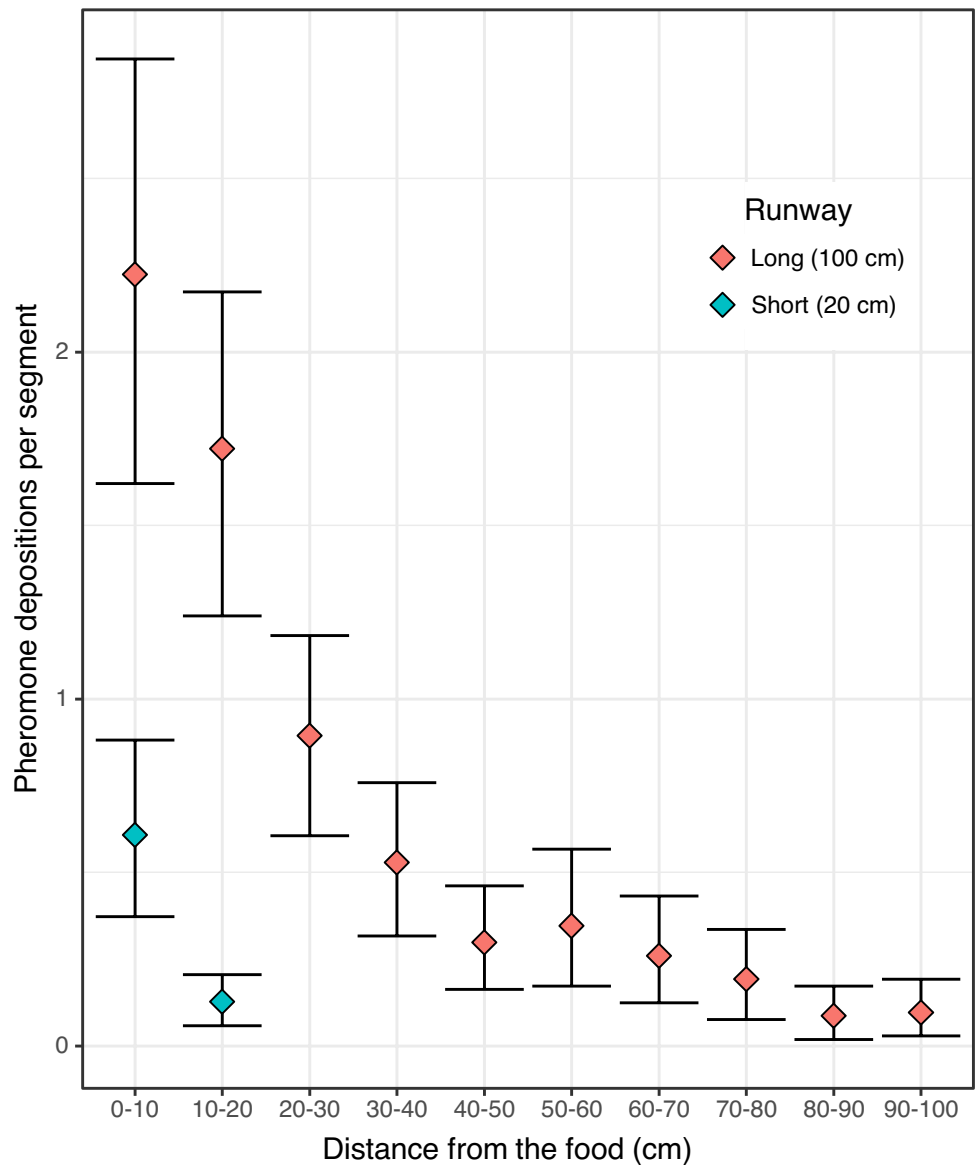
Fig. 2 The effect of initially choosing the wrong path and pheromone presence on one arm of the Y maze on pheromone deposition (experiment 1). Ants deposit slightly less pheromone when pheromone is already present on the apparatus. There is no effect of choosing the initially unrewarded path on pheromone deposition. Ants do not

deposit more pheromone if the pheromone trail led along an unrewarded arm. Red diamonds are means, whiskers are bootstrapped 95% confidence intervals, points are individual datapoints, and ribbons represent the data distribution pattern

Strangely, our findings corroborate some of the results of Devigne and Detrain (2006), but contrast sharply with others. Specifically, both studies found that recruitment drops with distance from the food source. However, Devigne and Detrain (2006) report no difference in recruitment for 30, 60 or 120 cm-long runways leading to a 13×13 cm foraging platform. We note that in both experiments, ants were starved for 4 days before testing. While we used 0.8 M sucrose during testing, and Devigne and Detrain (2006) used 1 M, recruitment intensities to these two molarities are indistinguishable (Wendt et al. 2019). One possibility is that the use of the foraging platform

by Devigne and Detrain confused the ants. Ants seem to monitor their own navigational certainty, and reduce pheromone deposition when uncertain (Czaczkes and Heinze 2015). Ants which stop pheromone deposition almost never resume recruitment on the current foraging bout, as long as home-range markings are not present (Beckers et al. 1992; Devigne et al. 2004). The ants may have struggled to find the exit of the platform, became confused, and reduced recruitment. This seems to be reflected in the overall pheromone depositions in the Devigne & Detrain study, but not in the percentage of active recruiters (see Fig. 1 in Devigne and Detrain 2006), implying that the ants

Fig. 3 The effect of proximity of the ant to the food, and the food to the nest, on pheromone deposition. Ants deposit more pheromone closer to the food, and deposit more pheromone for more distant food sources. Diamonds are means, and whiskers are 95% bootstrapped confidence intervals



may have downregulated recruitment without stopping it altogether.

Another possibility is that the ants in the Devigne and Detrain experiment had less-reliable distance cues, as the entire apparatus was surrounded by a 50 cm-high wall to obscure landmarks. This is in contrast to the current study, where no walls surrounded the experiment, so the lab space and concomitant visual cues were available. While desert ants can measure distance travelled using a step-counting odometer (Wittlinger et al. 2006), ants in general tend to use multiple information sources when making navigational decisions (Wystrach et al. 2015). This seems to us a likely explanation for the discrepancy in results.

Why would ant colonies benefit from depositing more pheromone to more distant food sources, when they are less valuable, all else being equal? The energetic cost of walking in

ants is minimal (Lipp et al. 2005; Schilman and Roces 2006; Holt and Askew 2012). Moreover, food return rate may be limited by the productivity of the food source (often nectaries or a honeydew-producing insect colony), rather than the travelling time as can be seen by frequent queuing at such food sources, although to our knowledge, this has not been systematically explored. However, the benefits of locating a new, productive food source, and monopolising it, may be great. More distant food sources will be more difficult to locate by chance, as the area to be searched increases with distance from the nest. Moreover, due to the gradual decay of pheromone, a stronger pheromone trail will have to be laid for more distant food sources, for it to be detectable by the time recruits can be mobilised to it and follow the trail to its source. This would explain both the tendency to deposit more pheromone for more distant food, and to deposit more pheromone closer

to the food source. We do not expect this tendency to deposit more pheromone to more distant food to interfere with collective choice of the closest food source: first, positive feedback for closer food sources will very likely overpower any difference in recruitment, and second, the choice point between two alternative paths will be near the nest, where pheromone deposition is similar for more and less distant food. Note that an increase in pheromone deposition does not imply that ants prefer more distant food sources: indeed, ants strongly prefer following cues associated with close food sources over distant ones (De Agrò et al. 2022). While pheromone deposition often correlates with preference, this is not always the case (De Agrò et al. 2022).

Importantly, we note that we only examined the pheromone deposition on the first return to the nest by otherwise naïve ants. Outgoing ants may well deposit more pheromone closer to the nest (Beckers et al. 1992), and it is unknown how path length will influence their recruitment behaviour.

A major open question in ant pheromone recruitment is why pheromone deposition variability is so high, even under identical conditions (see Fig. 1). The variability reported here is typical of such datasets, with large proportions of ants (14–70%) not depositing any pheromone (Aron et al. 1989; Beckers et al. 1992; Maillieux et al. 2005). Even within ants which do choose to deposit pheromone, we see massive variability, over an order of magnitude, in recruitment strength, with some inter-individual persistence in recruitment strength (Maillieux et al. 2005). The modulation pattern we report is driven both by ants choosing to deposit pheromone or not, and differential deposition by those which do choose to deposit pheromone (see supplement S1)—as is often the case in such situations [e.g., (Beckers et al. 1992; Devigne et al. 2004a; Czaczkes et al. 2013a; Czaczkes and Heinze 2015)]. What drives the variability we see in recruitment, and what the evolutionary advantage of this variability is, is unclear.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00040-024-00995-y>.

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Data availability The complete raw data from both experiments are provided in supplement S2 (experiment 1) and S3 (experiment 2). The complete analysis code and output is provided in supplement S1.

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