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Research article

Decay rates of attractive and repellent pheromones in an ant foraging trail network

E.J.H. Robinson[1,2], K.E. Green[1], E.A. Jenner[1], M. Holcombe[3] and F.L.W. Ratnieks[1]

[1] *Laboratory of Apiculture and Social Insects, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK, e-mail: Elva.Robinson@bristol.ac.uk*
[2] *present address: School of Biological Sciences, Bristol University, Woodland Road, Bristol, BS8 1UG, UK*
[3] *Department of Computer Science, University of Sheffield, Sheffield, S1 4DP, UK*

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Abstract. Pharaoh's ants (*Monomorium pharaonis*) use at least three types of foraging trail pheromone: a long-lasting attractive pheromone and two short-lived pheromones, one attractive and one repellent. We measured the decay rates of the behavioural response of ant workers at a trail bifurcation to trail substrate marked with either repellent or attractive short-lived pheromones. Our results show that the repellent pheromone effect lasts more than twice as long as the attractive pheromone effect (78 min versus 33 min). Although the effects of these two pheromones decay at approximately the same rate, the initial effect of the repellent pheromone on branch choice is almost twice that of the attractive pheromone (48 % versus 25 % above control). We hypothesise that the two pheromones have complementary but distinct roles, with the repellent pheromone specifically directing ants at bifurcations, while the attractive pheromone guides ants along the entire trail.

Keywords: Pheromones, foraging, decay rate, ants, *Monomorium.*

Introduction

Pheromonal communication is used for many different purposes, from signalling sexual attraction (Li et al., 2002) to raising the alarm (Hughes et al., 2001). Among social insects, communication between members of the same colony allows more effective foraging (Wilson, 1971). In ants, the most common way of doing this is by laying pheromone trails (Beckers et al., 1992; Hangartner, 1969; Wilson, 1962). The trails form a dynamic communication system, acting as an external repository of information for the colony and helping to guide workers from the nest to sources of food. How long these trails last is a key mechanistic factor in their function. For example some ants employ pheromones with decay rates of several days (Simon et al., 1991) if they are foraging on stable long-term food sources such as aphid populations (Quinet et al., 1991), or the foliage of particular trees (Howard, 2001). In contrast, opportunistic scavenging ants such as the fire ant, *Solenopsis invicta* exploit ephemeral food sources and use rapid-response recruitment pheromones which decay within minutes (Wilson, 1962).

The Pharaoh's ant, *Monomorium pharaonis* is an opportunistic scavenger. It uses three types of foraging pheromone. Two are attractive pheromones: one of these pheromones forms a stable trail network and is sufficiently long-lasting to allow trails to be re-located and reused even after several days of non-use (Jackson et al., 2006); the other guides workers to current food sources, and decays in minutes if not reinforced (Jeanson et al., 2003). The third pheromone is different. It is repellent, acting as a "No Entry" signal causing avoidance behaviour in ants (Robinson et al., 2005).

Many biological systems are regulated by multiple signals, from wound healing (Smith et al., 2006) to lymphocyte development (Reth et al., 2004). The fact that Pharaoh's ants use three trail pheromones raises the questions of why they have multiple pheromones and how these different pheromones interact. As an important step towards answering these questions, we measured the decay rates of the effects of both the repellent and short-term attractive pheromones on ant workers at a trail bifurcation. To understand how the different pheromones used by the Pharaoh's ant work together, we need to understand the effects on ant behaviour that each pheromone has independently. This will enable us to build up a more complete picture of the highly successful Pharaoh's ant foraging system.

Methods

Study species: The ten study colonies of *Monomorium pharaonis* (L.) each had approximately 1500 workers, 15–30 queens and brood of all stages. *M. pharaonis* is unicolonial and no nestmate discrimination (Hölldobler et al., 1990) was evident among our colonies, which all originated from the same unicolonial population. Colonies lived in wooden nest boxes (120 × 80 × 22 mm) within plastic foraging arenas (560 × 360 × 180 mm). The experimental room was maintained at 24±2°C, LD 12:12 h. Colonies were given water *ad libitum*, mealworms (*Tenebrio molitor*) daily and dried liver monthly. Sugar syrup was withheld for a week prior to experiments. Colonies received 1M sucrose during trials which took place on alternate days.

Attractive pheromone: Trials were performed using a Y-bifurcation apparatus, similar to the experimental apparatus used by Jeanson et al. (2003). Prior to a trial, the bifurcation apparatus was left in the foraging arena for 24 hours, with Eucalyptus Chlorine-Free (ECF) paper covering the top surface of the Y to allow familiarisation and marking with territorial chemicals (Fourcassié et al., 1992). Trail substrate affects the decay rate of ant pheromones (Jeanson et al., 2003) so we used this inert type of paper which has been used in several other Pharaoh's ant studies (Jackson et al., 2006; Robinson et al., 2005), to maintain comparability. Each trial commenced with a 10 minute exploration phase, during which one branch of the bifurcation was masked at the decision point (Fig. 1a). A syrup feeder containing 1M sucrose solution was then placed at the end of the branch without the masking, and the ants foraged for 20 minutes (exploitation phase). The apparatus was then rotated by 180° or 90° to prevent use of visual cues and the feeder and masking were removed for the test phase. During the test phase ants were brushed off the apparatus after making a decision (crossing a decision line on Fig. 1a), so no further trail pheromones could be laid. Brushing ants away does not affect the pheromone trail (Jeanson et al. 2003). The branch to be masked was alternated between trials. Trials were video recorded and video data was analysed by recording the decision each ant made during 2 minute periods commencing at minute 0, 10, 20, 40 and 60 of the test phase. Ten trials were carried out.

Repellent pheromone: To isolate the effect of the repellent pheromone (as opposed to lack of attractive pheromone), substrate marked with the repellent pheromone could not be studied *in situ*, because the attractive trail on the stem of the apparatus might lead the ants towards the branch leading to food. Even with the attractive pheromone after the bifurcation masked, the decay of this attractive trail on the stem would be confounded with the decay of the negative pheromone. For this reason, two colonies were used per trial: one a trail-laying colony (A), the other a test colony (B) (Robinson et al., 2005) (Fig. 1b). We placed a Y-bifurcation apparatus into the foraging arena of each colony 24 hours prior to the trial with ECF paper as before. A control piece of ECF paper was placed in the foraging arena of colony A, away from foraging trails to water and food but where the ants could still mark it with territorial pheromones (Fourcassié et al., 1994). We used Colony A to mark two pieces of ECF paper for use in Colony B; one with trail marks which we predicted would include repellent pheromone, and the other to control for the effect of territorial marks.

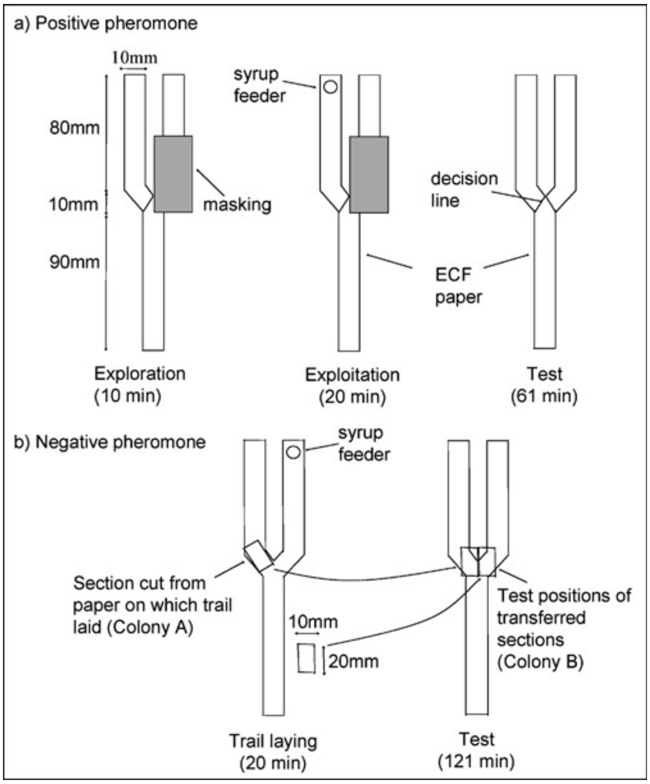

Figure 1. ECF paper overlaid onto foraging apparatus. 1a. Attractive pheromone: ECF paper overlay which was placed onto bifurcation apparatus prior to trials. Ants crossing the decision lines were considered to have chosen a branch. The largest natural Pharaoh's ant trails are 5 mm wide (Sudd 1960), so the apparatus stem and branch width of 10 mm eliminates congestion which could otherwise affect bifurcation decisions (Dussutour et al. 2004). 1b. Repellent pheromone: Trail was formed on an ECF paper overlay in colony A. Sections were transferred to a colony B for testing the effect of the pheromone (Robinson et al., 2005).

We began each trial by placing 1M sucrose feeders (Jackson et al., 2004) at the end of one branch (alternated between trials) in colony A and both branches in colony B. Foraging took place for 20 minutes. The feeders were removed and a 10mm × 10 mm section of paper was cut from the unrewarding side, 3 mm after the bifurcation, from the apparatus in colony A. This section and the control section were transferred to the bifurcation region of the trail apparatus in colony B. Ants choosing one branch had to walk over a 10 mm piece of paper substrate from the unrewarding branch of the foraging trail system. To choose the other branch, ants had to walk over a 10 mm piece of colony A control paper. The control was marked with the colony's territorial pheromones, but not trail pheromones attracting to a current food source (Robinson et al., 2005). We did not use fresh paper as a neutral control because Pharaoh's ants actively recruit to new territory (Fourcassié et al., 1994). Each ant was brushed from the apparatus after it passed the bifurcation to prevent further pheromone deposition (Jeanson et al., 2003). After two minutes of trail choice, the paper sections were removed and the feeders replaced to allow foraging to continue. Without some foraging success, foragers would not have continued visiting the apparatus for the full 2 hours of the trial. Foraging was allowed during the intervals in between data collection periods. Trail choice data were collected for two-minute periods commencing at 0, 10, 20, 40 and 60 minutes after the deposition of the repellent pheromone ceased for 12 trials and 0, 40, 80, 100 and 120 minutes after deposition for 12 trials. The data for 0 and 40 minutes were compared between the two sets of trials, and no significant difference was found (GLMM, df=35, t=1.25, p=0.2), so both sets of data were pooled for further analysis. The distribution of Pharaoh's ants at two feeders is rarely even (Sumpter et al., 2003), so the numbers of ants choosing left and right at the bifurcation in colony B was counted for 2 minutes immediately prior to each test phase as a measure of the "background" traffic against which the test traffic could be compared. Four colonies were used for each set of 12 trials, each three times as colony A and three times as colony B. Initial data analysis was carried out using a Generalized Linear Mixed Model in R 2.1.1-A, Language and Environment © 2005, the R Development Core Team (Venables et al., 2002).

In addition, a further four colonies were used for a control experiment to test the hypothesis that paper from the bifurcation region of a Y-apparatus is always more repellent than paper from the arena, due to different densities of territorial markings. The experimental bioassay for the negative pheromone described above was repeated, but comparing the control paper from the arena with a paper section taken from the bifurcation region of the apparatus (Fig. 1b) without a feeder ever having been present. Ant branch choice was recorded for 2 minutes.

Results

Decay of attractive pheromone

There was a significant decrease in the proportion of ants choosing the side which had led to food over time (GLMM t=4.9, df=1376, $p<0.0001$) showing that, as expected, its attractive effect decayed. For analysis of the decay rate, the data are expressed as the ratio:

(percentage of ants choosing branch with attractive pheromone : 50 percent of ants)

so a ratio of 1 indicates that there is no longer a significant effect of the attractive pheromone. The 95 % confidence interval of the decay curve fitted to the response to the attractive pheromone reaches this no-effect ratio (1) at 33 minutes (Fig. 2).

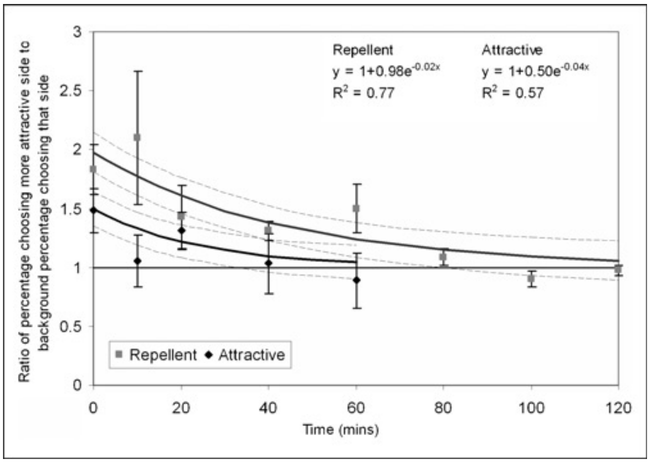

Figure 2. Decay of the effect of the attractive and repellent pheromones. For the attractive pheromone the response term is expressed in terms of the ratio of the percentage responding to the attractive pheromone by choosing the attractive branch to the random expectation. For the repellent pheromone the response term is expressed in terms of the ratio of the percentage responding to the repellent pheromone by choosing the branch without repellent pheromone to the percentage choosing that branch during the previous foraging period (background). The parameter 1 in the fitted models gives the repellent exponential an asymptote of 1, the no-effect ratio. Points are the mean ratio ± SE. Solid line at ratio of 1 indicates random choice of branch; dotted lines indicate 95 % confidence interval of fitted line.

Decay of repellent pheromone

There was a significant increase in the proportion of ants choosing the repellent side over time (GLMM, df=109, t=5.8, $p<0.0001$) showing that, as expected, the repellent effect decayed. The background flow rate also had a significant effect (GLMM, df=109, t=4.58, $p<0.001$) on the choices made. This is likely to be because in the cases of background flow rates which were biased to one side, more ants were likely to approach on that side of the trail so the absolute number of ants on that side during the test would be high, even if significantly lower than the background number. To take this into account in the analysis of the decay rate, the responses to the repellent pheromone were expressed as a ratio in comparison to the background effect at each time interval:

(percentage choosing branch avoiding repellent pheromone: background percentage choosing that branch)

Background flow ranged from 12–117 ants/minute, but did not change significantly over time (regression of background flow on time, $R^2=0.012$, p=0.42).

Although there was a significant effect of the repellent pheromone with all trials included in the GLMM, some individual trials showed no initial repellent effect. Pharaoh's ants lay sinuous trails and the repellent pheromone is localized near the trail bifurcation (Robinson et al., 2005). It is possible that for some trials, the trail bifurcated on the stem of the apparatus, before the apparatus bifurcated, and in this case paper cut from the non-feeder side of the bifurcation apparatus may miss the location of the repellent pheromone. To avoid trials where the repellent pheromone was missed in the cutting of the paper biasing the decay rate calculation, for the further analysis the data for the initial period (commencing at 0 min) for each trial was compared to the binomial expectation using the background flow rate. Only those eleven trials where the initial choice showed a response to the repellent pheromone significant at $p<0.05$ were included in the further analysis. When the ratio of ants choosing a branch to the background percentage choosing that branch decayed to 1, the repellent pheromone was assumed to be no longer having any effect. The 95 % confidence interval of the fitted curve reaches the no-effect ratio (1:1) at 78 minutes (Fig. 2).

Comparison of the two pheromones

The gradients of the decay rates of the responses to the short-term attractive and the repellent pheromones are highly similar (t-test t=0.17, df=9, p=0.87), so the longer lasting effect of the repellent pheromone is not due to a slower decay, but due to its significantly higher initial effect (t-test t=2.87, df=9, $p<0.05$). The attractive pheromone had an initial ratio of 1.50, equivalent to a response +25 % when compared to the random expectation of 50:50. In contrast, the repellent pheromone had an initial ratio of 1.98 which would be equivalent to an effect of -49%. The repellent pheromone has almost twice the effect of the attractive pheromone in influencing trail choice (–49% versus +25%). It also continues to have a significant affect on trail choice for more than twice as long (33 minutes versus 78 minutes).

Control for territorial effects

Our control tested whether the repellent effect seen above could be explained by different concentrations of territorial markings. If the density of territorial markings on a narrow bridge is causing the repellent behaviour, ants should avoid this paper. Our results clearly show that the ants do not avoid the paper from the bifurcation compared to paper from the foraging arena (Table 1). In three trials there was no significant difference between the numbers choosing each branch, and in one trial significantly more of the ants actually chose the branch with the paper from the bifurcation region. The hypothesis that the paper from the bifurcation region is intrinsically more repellent than paper from the arena, can therefore be rejected.

Table 1. Data for control experiment: Numbers of ants choosing each of two branches when presented with paper from the bifurcation region of the apparatus on which no food had been present compared to a piece of paper taken from the foraging arena.

Colony	Paper from bifurcation	Paper from foraging arena	Total ants	χ^2	*p*
1	28	20	48	1.33	NS
2	17	18	35	0.03	NS
3	29	19	48	2.08	NS
4	32	16	48	5.33	$p<0.05$

Discussion

Two short-term pheromones

The data clearly show that the repellent pheromone has a much greater initial effect on branch choice than the attractive pheromone. This suggests that the repellent pheromone is important in providing information to aid trail choice at a bifurcation where one trail branch is rewarding, and one unrewarding – acting like a ”No Entry” sign at a junction. This role is also consistent with data showing that it is laid most strongly just after a bifurcation on the unrewarding side of a trail bifurcation (Robinson et al., 2005). Our control experiment shows that this is not an artefact of a high density of territorial markings in the bifurcation region. In contrast, the role of the attractive pheromone is concerned more with marking a trail to follow all the way from the nest to food. During foraging, passing ants will reinforce both sets of signals, but more ants will pass the attractively marked areas. The repellent pheromone continues to have an effect on behaviour for longer than the short-term pheromone, but both effects decay in minutes, while the long-term exploration pheromone can be detected after several days (Jackson et al., 2006). The volatility of a pheromone has two important effects on its function. Volatile pheromones form a vapour cloud which can be detected from a distance and without the ants touching their antennae to the substrate. On the other hand volatile pheromones will also last for a shorter length of time than non-volatiles. The repellent pheromone is sufficiently volatile for ants to detect it up to 30 mm in advance and causes them to increase zigzagging behaviour, which may help them to find the correct trail at a bifurcation (Robinson et al., 2005), but the effect of the pheromone is all gone in less than two hours – very rapidly compared to the non-volatile long-term attractive pheromone which has an effect lasting for days. The short-term attractive pheromone is also volatile which may aid easy detection, but it cannot act as a warning of a bifurcation, as it is present throughout the foraging trail. The repellent pheromone, however, is found most strongly at bifurcations (Robinson et al., 2005) so can be used to alert ants to a nearby branch in the trail. The mechanism by which the ants focus the repellent pheromone at the bifurcation is a matter for future investigation.

Hypothesis of roles

Our understanding of the decay patterns of responses to the Pharaoh’s ant foraging pheromones allows us to hypothesize about their roles within the foraging system as a whole. This is discussed in figure 3. In summary, the trail network is marked with the long-term non-volatile “memory” pheromone. The two short-term pheromones are laid on to parts of this network, depending on where foraging is occurring at that moment. The short-term attractive pheromone is laid on trails leading to food, and at trail bifurcations the non-rewarding branches are marked with the volatile no-entry pheromone. The repellent pheromone aids in trail choice during active foraging by closing off unrewarding trails at the bifurcations. When a previously exploited source of food is exhausted, the responses to both short-term pheromones decay rapidly, but of these, the repellent pheromone persists longer. The short-term attractive pheromone is involved in branch choice, but also in guiding along the trail and in recruitment of new workers. This loses its effect first, and the prolonged effect of the repellent pheromone may cause a bias towards previously productive trails, without actively recruiting new workers.

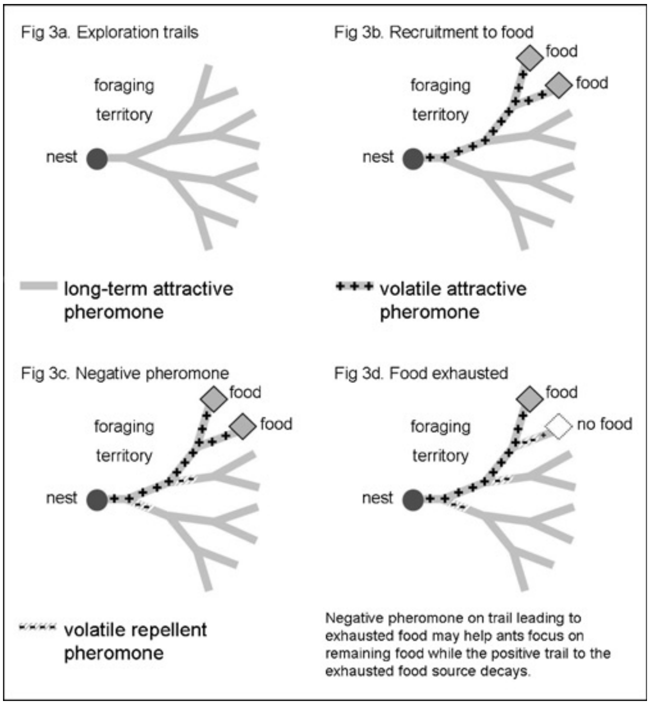

Figure 3a. The colony's stable trail network is marked out with attractive non-volatile pheromone. This acts as a long term memory of where the colony has been foraging and walking. It branches throughout the colony's territory, including to all locations where food has been collected in the past few days and where food may perhaps be found again. The two short-term pheromones are laid on to parts of this broad network, conveying up-to-date information about the presence or absence of food.

3b. If food is found at a particular location the path is marked with the volatile attractive pheromone, which both guides ants along the correct path and also helps them chose the correct branch to take at trail bifurcations.

3c. At trail bifurcations the non-rewarding branch is marked with the volatile no-entry pheromone. This helps close off unrewarding branches.

3d. When a food source is exhausted previously attractive branches become non-attractive by the decay of the volatile attractive pheromone and the laying of the no entry pheromone. Both volatile pheromones decay within two hours, allowing the area to be re-explored to detect renewed food sources.

Multiple signals in foraging

We now have information about the decay patterns of responses to three pheromones used in the foraging networks of *M. pharaonis.* Multiple signals are a feature of several foraging systems. Honeybees use many signals to regulate the numbers of foragers and nectar receiving bees; so far four physical signals and a pheromone (Anderson et al., 1999; Leoncini et al., 2004) have been described, and honeybees also use a form of repellent signal during foraging, in that they are able to detect and avoid recently visited flowers due to scent marks left by previous foragers (Giurfa et al., 1992). As combinations of signals can have different meanings to a signal alone, increasing the number of signals dramatically increases the flexibility of a communication system. However in the honeybee system, the information is concentrated at key points: the hive is the main focus of information transfer, with some information available at the food source. During the foraging trips, up to 14 km from the hive (Beekman et al., 2000), no communication or regulation can take place. In contrast, pheromone trail systems allow communication and feedback throughout the foraging network. Multiple signals are seen in ant trail systems too, for example *Leptogenys distinguenda* army ants, which use at least three separate signals to co-ordinate group raiding (Witte et al., 2002). However, the roles these signals cover (orientation, attraction and recruitment), are all fulfilled in the Pharaoh's ant by the long- and short-term attractive pheromones. The Pharaoh's ant repellent pheromone provides a further level of fine control, so their system can recruit foragers, guide them to food, and also close off unrewarding regions. Understanding how these signals complement each other allows us to better understand this highly sophisticated and successful foraging system.

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