

Pheromone trail decay rates on different substrates in the Pharaoh's ant, *Monomorium pharaonis*

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Abstract. Many ants use pheromone trails to organize collective foraging. This study investigated the rate at which a well-established Pharaoh's ant, *Monomorium pharaonis* (L.), trail breaks down on two substrates (polycarbonate plastic, newspaper). Workers were allowed to feed on sucrose solution from a feeder 30 cm from the nest. Between the nest and the feeder, the trail had a Y-shaped bifurcation. Initially, while recruiting to and exploiting the feeder, workers could only deposit pheromone on the branch leading to the feeder. Once the trail was established (by approximately 60 ants per min for 20 min), the ants were not allowed to reinforce the trail and were given a choice between the marked and unmarked branches. The numbers of ants choosing each branch were counted for 30 min. Initially, most went to the side on which pheromone had been deposited (80% and 70% on the plastic and paper substrates, respectively). However, this decayed to 50% within 25 min for plastic and 8 min for paper. From these data, the half-life times of the pheromone are estimated as approximately 9 min and 3 min on plastic and paper, respectively. The results show that, for *M. pharaonis*, trail decay is rapid and is affected strongly by trail substrate.

Key words. foraging, *Monomorium pharaonis*, pheromonal decay, pheromone trail.

Introduction

The organization of animal societies requires information transfer to coordinate the activities of individuals (Hölldobler & Wilson, 1990; Seeley, 1995; Detrain *et al.*, 1999; Camazine *et al.*, 2001). One common type of signalling is the use of marked trails, which occurs in several contexts (e.g. foraging, nest relocation), and in different taxa such as caterpillars (Fitzgerald, 1976, 1995), social spiders (Lubin & Robinson, 1982; Vollrath, 1982; Saffre *et al.*, 1999), wasps (Jeanne, 1981) and mammals (Galef & Buckley, 1996; Judd & Sherman, 1996).

Marked trails probably reach their greatest sophistication and ecological importance in ants. Ant trails are used in a wide range of collective behaviours, including colony migration (e.g. *Eciton* army ants) (Wilson, 1971; Franks, 1989; Franks *et al.*, 1991) and foraging (Hölldobler & Wilson, 1990; Camazine *et al.*, 2001). When marked trails are used in foraging, many factors that affect the properties of the trail, or the ability of individuals to deposit or detect pheromones, could also affect the colony's foraging pattern. For example, *Eciton* army ants have to walk over various substrates (roots, logs or rocks) which could result in different trail decay rates (Togerson & Akre, 1970). In *Solenopsis saevissima*, an artificial trail formed by using the gland contents of a single worker decayed more slowly on blotting paper (up to 20 min) than on glass (3.5–7 min) (Wilson, 1962). Detrain *et al.* (2001) showed that, in *Lasius niger*, the selection of one of two alternative paths leading to food depends on the physico-chemical properties of the foraging substrates that influence pheromone trail longevity.

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Although it is qualitatively well known that different surfaces might affect the persistence of trails, few quantitative studies have investigated this in detail.

The aim of this study was to quantify the decay rates of natural foraging trails of the Pharaoh's ant, *Monomorium pharaonis* (L.), on two different substrates, plastic and newspaper, using trail following as a behavioural assay. The Pharaoh's ant, *M. pharaonis*, is a 'tramp' species that has been introduced worldwide and is often a pest inside buildings (Passera, 1994). *Monomorium pharaonis* uses chemical communication during exploration of novel areas (Fourcassie & Deneubourg, 1992, 1994) and foraging (Sudd, 1957). The active compound of the trail, faranil (Ritter *et al.*, 1977), is produced by the Dufour's gland (Billen & Morgan, 1998). The results show that the substrate greatly influences the decay rate of a well-established trail to a syrup feeder. Within 8 min on newspaper and 25 min on polycarbonate plastic, foragers walking towards the feeder display random choice at a trail bifurcation for which only one branch had been previously marked by foragers.

Materials and methods

Study organisms

The study was carried out with two colonies of *M. pharaonis*, each with approximately 2000 workers, 25 queens and brood of all stages. Sheffield colonies originated in 1995 from a culture that had been maintained in the laboratory for many years previously by the Central Science Laboratory, York, U.K. Colonies were housed in a climate room (temperature $28 \pm 1^\circ\text{C}$, relative humidity approximately 30%, LD 12:12 h). Each colony was housed in a wooden nest box ($13 \times 8 \times 1$ cm) within a large plastic box ($45 \times 30 \times 18$ cm) that was used as a foraging area. Colonies were given water *ad libitum*, and fed segments of fresh mealworms three times per week. Colonies were normally fed sugar syrup or honey, but were deprived of this for 10 days before and during the experiment to ensure that they would readily form foraging trails to the syrup feeder. During the experimental period, colonies had 60 min per trial day to feed on 1 M sucrose (342 g L^{-1}).

Experimental set-up

A Y-shaped platform with two parallel branches was fixed at the top of an L-shaped stand (Fig. 1a). The day before trials began, this experimental set-up was placed in each colony's foraging box where it remained throughout the experimental period (Fig. 1a). To quantify the influence of the substrate on trail decay, two contrasting substrates were chosen for their different absorbing properties and surface texture: plastic (commercially available polycarbonate: a smooth clear plastic as sold in hardware shops and used as an alternative to window glass) and paper (news-

print: chosen for its rough surface and absorbent properties). Although these are man-made materials, Pharaoh's ants are likely to come into contact with them when foraging in the buildings that they frequently infest. During a trial, a syrup feeder filled with 1 M sucrose solution was placed at the end of one branch. To encourage the ants to walk only on the upper surface of the platform, its edges were coated with Fluon[®] (Whitford France, France), a slippery material that ants cannot climb.

Experimental procedure

In the bioassay, an objective means was required to determine which branch ants took at the trail bifurcation. Consequently, a 'line of decision' was established at the bifurcation (Fig. 1b).

Each trial lasted 60 min and was recorded using a digital video camera directly above the platform. Each trial had three phases (Fig. 1b).

Exploration phase (10 min). A piece of masking plastic coated with Fluon[®] was placed on half of the decision line of the Y-shaped platform to prevent the ants from depositing any pheromone on this branch.

Exploitation phase (20 min). The feeder was placed at the end of the nonmasked branch of the platform. The masking remained in place on the other side.

Test phase (30 min). The feeder was removed and the platform was turned by 90° to eliminate any information from visual or other cues which might affect branch choice. The ants on the branch with the feeder were then gently removed using a fine paintbrush, and the plastic masking was removed. This took approximately 1 min. For the next 30 min, ants walking towards the feeder were gently removed with a paintbrush as they crossed the decision line to prevent reinforcement of either branch. During the test phase, ants had a binary choice between a branch with decaying trail pheromone and an unmarked branch.

For each colony, three trials per day were conducted. Each colony was used in turn, and the order of the first colony used was alternated on successive days. Between each trial on the same colony, the position of the plastic box containing the colony and trail system was turned by 90° or 180° , but with the platform in the same place in the plastic box. The branch with the feeder was alternated between successive trials.

Once all trials with plastic had been conducted, the platform was removed from the foraging box. The whole platform was then covered with newsprint, replaced in the foraging box and a second series of trials was made using the same protocol as for the plastic substrate. In total, 22 trials were made with plastic and 18 with paper substrates.

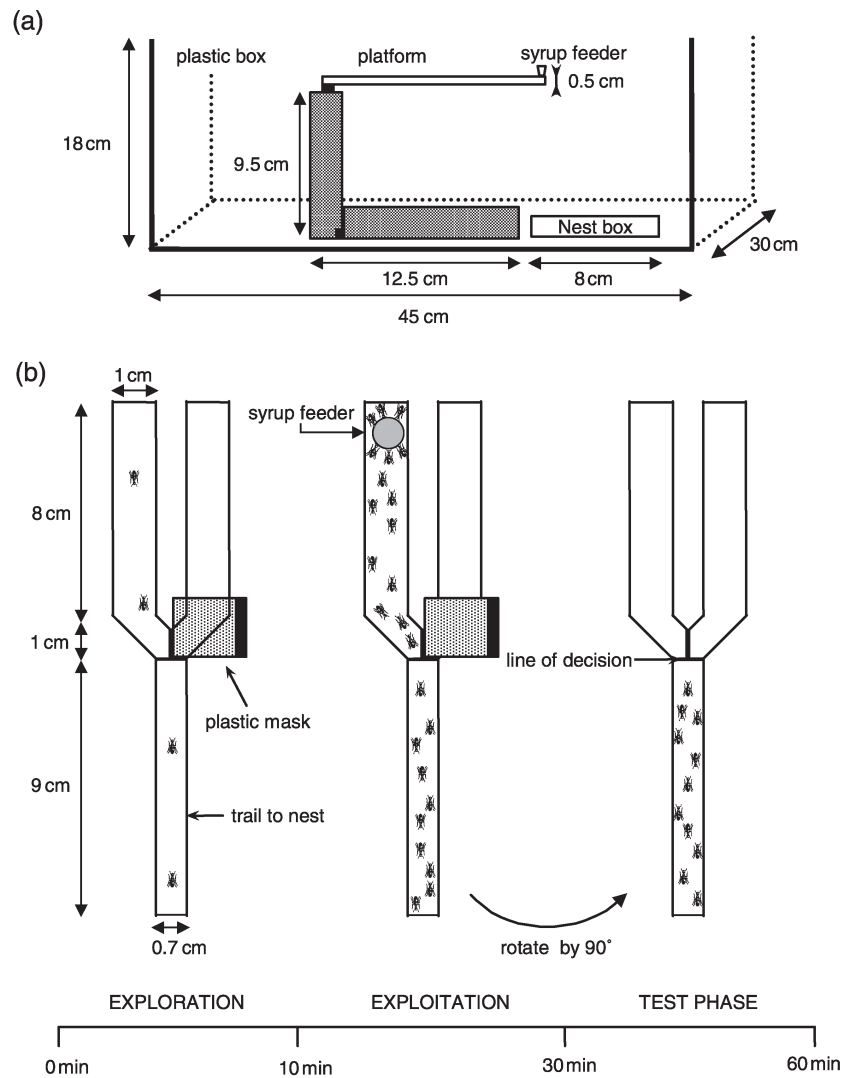


Fig. 1. (a) Side view of the plastic box which formed the foraging environment, the nest-box and the platform with the syrup feeder. (b) Top view of the platform and syrup feeder for the three different phases of a trial: exploration, exploitation and test phase. Between the exploitation and test phase, the platform was rotated by 90° (ants not shown to scale; a Pharaoh's ant is approximately 2 mm long).

Control experiment

This experiment was designed to ensure that the observed decay of the trail was due to natural decay, not to pheromone removed by the paintbrush during the test phase. Methods were as described above except that, at the beginning of the test phase, the ants were not allowed to reach the decision line but were blocked on the common trail leading to the bifurcation with a piece of plastic coated with Fluon[®]. After 8 min for paper and 17, 25 and 29 min for plastic (six replications for each condition), the blocking piece of plastic was removed and, for 1 min, the ants could freely access the decision line and choose one of the two branches. The ants were removed 5 cm from the decision line, in the middle of the lateral branches.

It was predicted that, if the use of the paintbrush at the decision line had no effect on the trail, then trail choice during a normal trial, in which the paintbrush was used, and a control trial, in which the paintbrush was not used, would be equal.

Videotape analysis and data collection

From the video recordings of the last 5 min of the exploitation phase, the total number of ants was counted going to and coming from the syrup feeder to ensure that the foraging activity was equal on both substrates. The video recordings were also analysed to assess the number of ants choosing each branch every 1 min during the test phase. If

an ant crossed into the area to the left of the decision line it was considered to have chosen the left branch and vice versa. In this way, the protocol allowed the measurement of the proportion of ants that turned towards the trail side, using only the information provided by the dissipating trail.

Statistical analysis

For each substrate and for each colony, data were pooled across all trials for the number of ants for the last 5 min of the exploitation phase (foraging activity) and Wilcoxon paired-sample test and *t*-tests, respectively, were used to determine the influence of substrate or colony on foraging activity.

Data were pooled for every 1 min of the test phase, across all trials, on the number of ants choosing the trail and nontrail branches for each substrate (paper or plastic) and the proportion choosing the trail side calculated, per min and per substrate. Random selection of either branch occurred when 50% (equal choice) was included within the 95% confidence intervals of the observed proportion.

Results

Foraging activity at the end of the exploitation phase

For each colony, the number of foraging ants in the final 5 min (plastic: mean = 345.4 ants, SE = 13.58 ants, *n* = 22; paper: mean = 383.8 ants, SE = 15.9 ants, *n* = 18) of the exploitation phase was not significantly different between trials conducted on paper and plastic (Wilcoxon paired-sample tests: Colony I: *Z* = 2.09, *P* > 0.05; Colony II, *Z* = 0.42, *P* > 0.05). This indicates that there was no difference in the foraging behaviour of the ant colonies during the periods in which the two trail substrates were studied. In

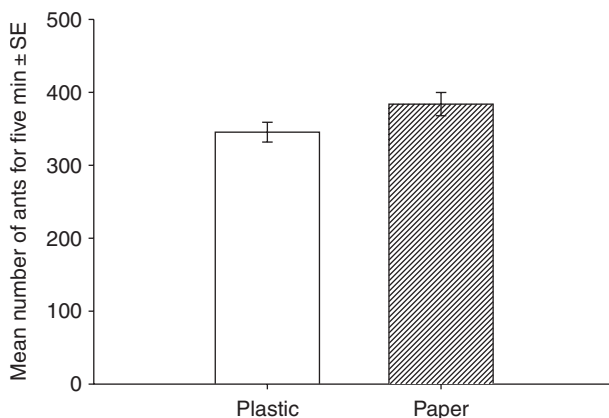


Fig. 2. Mean number of ants (\pm SE) going to and coming from the sugar feeder for the last 5 min of the exploitation phase on paper and plastic.

addition, there was no difference in the number of foraging ants between the two study colonies (*t*-test: $t_{38} = -1.09$, *P* > 0.05) (Fig. 2) for data pooled across both substrates per colony.

Control experiment investigating possible effect of paintbrush on trail decay

In these control experiments the proportions of ants choosing the trail side were determined at 17, 25 and 29 min for plastic and 8 min for paper. The choices of at least 110 ants were recorded per substrate. There was no difference between the proportion of ants choosing the trail side during the test phase in normal and control trials for the same elapsed time on either paper ($\chi^2 = 0.35$, d.f. = 1, *P* < 0.05) or plastic (for 17, 25, 29 min, respectively, $\chi^2 = 0.14$, $\chi^2 = 1.5$, $\chi^2 = 0.28$, d.f. = 1, *P* > 0.05). These data clearly indicate that removal of the ants with the paintbrush did not interfere with the natural decay of the pheromone trail.

Trail decay: behavioural response

The initial proportion of ants turning toward the side with the trail was significantly higher for plastic (0.78) than for paper (0.70) ($\chi^2 = 5.42$, d.f. = 1, *P* < 0.05) (Fig. 3). The first random choice occurred at 7 min on paper and 17 min on plastic.

Assessment of pheromone life time on the two substrates

In this analysis, it was assumed that the response of the workers to pheromone titre was the same for both substrates. Previous experimental and theoretical studies have used the following function to model the probability that an individual ant chooses one of two possible branches, left and right, as a function of their pheromone titres (C_i and C_j) (Deneubourg *et al.*, 1990; Beckers *et al.*, 1993):

$$P_i = \frac{F(C_i)}{F(C_i) + F(C_j)}$$

$F(C)$ is a non linear function, such as a power [$= (k + C)^\eta$] or exponential function $e^{\eta C}$, as used here for simplicity:

$$P_1 = \frac{e^{\eta C_1}}{e^{\eta C_1} + e^{\eta C_2}} = \frac{1}{1 + e^{-\eta(C_1 - C_2)}} \quad (1)$$

and

$$P_2 = 1 - P_1$$

Equation 1 is a choice function which depends on the ratio of pheromone concentrations of the two branches. The probability, *P*, of choosing one of the branches varies

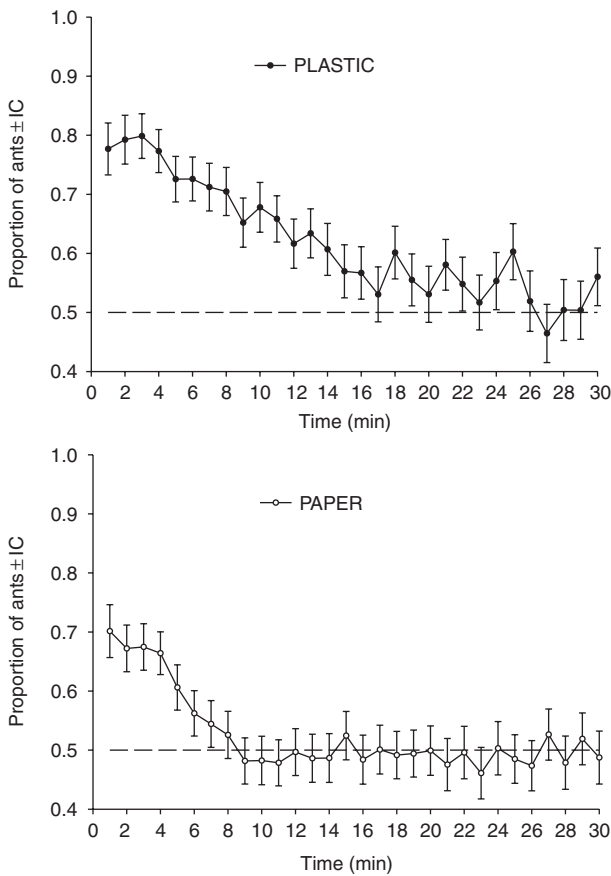


Fig. 3. Mean proportion of ants ($\pm 95\%$ confidence interval) turning to the trail side for paper (18 trials) and plastic substrates (22 trials) as a function of the time elapsed from the start of the test phase (trail no longer being reinforced). The dotted line corresponds to equal (random) branch choice.

between 0 and 1. If the concentrations are equal on both branches, $P = 0.5$. The parameter η controls the degree of nonlinearity of the choice. The probability of choosing one branch increases as η increases. Even if there is only a slight difference in pheromone concentrations, large η can lead to a substantial preference. If it is assumed that individual behaviour is not affected by substrate then η is equal for both substrates (i.e. $\eta_{\text{plastic}} = \eta_{\text{paper}}$).

In the present experiments, ants could only lay pheromone on one branch, so that $C_1 = C_R$ (R, reinforced branch) and $C_2 = 0$:

$$P_R = \frac{1}{1 + e^{-\eta C_R}} \quad (2)$$

From Eq. 2:

$$\eta C_{R\text{plastic}} = -\ln\left(\frac{1}{P_{R\text{plastic}}} - 1\right) \quad (3a)$$

$$\eta C_{R\text{paper}} = -\ln\left(\frac{1}{P_{R\text{paper}}} - 1\right) \quad (3b)$$

At the beginning of the test phase, the proportions of ants choosing the trail sides are:

$$P_{R\text{plastic}} = 0.78 \text{ and } P_{R\text{paper}} = 0.70$$

Substituting these values into Eqs 3a and 3b gives the following values:

$$\eta C_{0,R\text{plastic}} = 1.26 \text{ and } \eta C_{0,R\text{paper}} = 0.85$$

It is assumed that the rate of pheromone decay at any time is proportional to the pheromone quantity at this time and to a constant v (exponential decay), specific for each substrate, which is the inverse of the mean life time of the pheromone.

$$C_{R\text{plastic}} = C_{0,R\text{plastic}} e^{-v_{\text{plastic}} t} \quad (4a)$$

$$C_{R\text{paper}} = C_{0,R\text{paper}} e^{-v_{\text{paper}} t} \quad (4b)$$

thus:

$$\eta C_{0,R\text{plastic}} e^{-v_{\text{plastic}} t} = -\ln\left(\frac{1}{P_{R\text{plastic}}} - 1\right) \quad (5a)$$

$$\eta C_{0,R\text{paper}} e^{-v_{\text{paper}} t} = -\ln\left(\frac{1}{P_{R\text{paper}}} - 1\right) \quad (5b)$$

The rate of decay for both substrates, v_{plastic} and v_{paper} , is estimated from the data by determining the value of v that minimizes the residual sum of squares between the left and right side of Eqs 5a and 5b. Equation 5 was linearized through a log-transformation:

$$\ln\left(-\ln\left(\frac{1}{P_R} - 1\right)\right) = -vt + \ln(\eta C_0)$$

For each substrate, the value of v was assessed from the slope of the linear regression. It was found that $v_{\text{plastic}} = 0.08 \text{ min}^{-1}$ ($r = 0.94$) and $v_{\text{paper}} = 0.23 \text{ min}^{-1}$ ($r = 0.96$) with corresponding life times of approximately 12.50 min and 4.33 min and a half-life time of pheromone on both substrates:

$$T_{1/2} = \frac{\ln(2)}{v}$$

$$T_{1/2\text{plastic}} = 8.66 \text{ min and } T_{1/2\text{paper}} = 3.01 \text{ min}$$

Discussion

The data clearly show that, in the behavioural assay of branch choice, trail pheromones of *M. pharaonis* decay rapidly and that the rate of decay depends upon the substrate. At the beginning of the test phase, the proportion of ants choosing the trail side is lower for paper (0.70) than for plastic (0.78), declining to equality in 7–10 min and 20–25 min, respectively. From these data, the half-life times of the pheromone are calculated as approximately 3 min and 9 min, respectively, on paper and plastic. The method of calculating the half-life assumes that responses of workers to pheromone are identical for both substrates but is

independent of the trail laying level (proportion of ants laying pheromone or the intensity of trail laying, e.g. numbers of marks per ant). The number of foraging ants on the two substrates is equal. Because the rate of decay is higher on paper, the concentration of pheromone should be lower on paper, even at the beginning of the test phase, and thus explains why a lower proportion of ants chose the marked branch at the beginning of the test phase on paper than plastic.

Trail persistence depends on pheromone longevity and other factors, such as the number of trail laying ants, the intensity of trail laying by individuals and environmental conditions (Blum, 1974). For example, trail persistence in *Eciton* is greater during colony emigration than during foraging exploration because more ants are laying trail in the former situation (Togerson & Akre, 1970). In this case, the trail longevity may depend upon the traffic or the individual trail laying intensity modulated by the food source characteristics.

Food resource distribution is an important ecological factor that influences the foraging strategy, including trail behaviour, in ants (Traniello, 1989). For species only using chemical communication in foraging, the longevity of the trail could be linked to the feeding ecology. In species commonly feeding on long-lived food sources, permanent trails are adaptive because they facilitate repeated exploitation of the same resources. In *Tapinoma simrothi*, workers use long-lived trails to forage on predictable honeydew sources from aphid colonies (Simon & Hefetz, 1991). Such persistent trails allow colonies to expand their foraging networks. Short-lived pheromone trails are adaptive for species exploiting ephemeral food sources as this facilitates the rapid abandonment of depleted sources. The pheromone duration of *M. pharaonis* is similar to that of another tramp species, the Argentine ant *Linepithema humile*, which is close to 30 min (Deneubourg *et al.*, 1990). Both species have opportunistic feeding and nesting and therefore probably benefit from their short-lived pheromone, which may also be a factor suiting them to the tramp lifestyle. *Monomorium pharaonis* and *L. humile*, similar to many other species with large colonies (e.g. in *Pheidole pallidula*) (Detrain *et al.*, 1991), lay trail pheromones during exploration, even before the discovery of food (Deneubourg *et al.*, 1990; Fourcassié & Deneubourg, 1992, 1994). The adaptive value of this behaviour may depend on the life-time of the pheromone, with a long-lived pheromone reducing the plasticity of these exploratory-foraging networks. However, the potential existence of long-lasting components in the trail of Pharaoh's ants cannot be ruled out (Blum, 1966), as it has been already described in other ants species such as *Solenopsis richteri* (Blum, 1974) or in *Lasius fuliginosus* (Quinet *et al.*, 1997) that combined permanent and short-lasting trails.

Although short-lived pheromones allow rapid abandonment of depleted food sources, they require a continual flow of workers to replace any pheromone that decays, and trails to new food sources can only be established with a relatively large number of foragers (Beekman *et al.*, 2001).

Consequently, large colonies could extend their exploitation network and exploit food sources discovered further from the nest, in contrast to smaller colonies that are restrained by the longevity of the trail and their number of available foragers.

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