

Modulation of Trail Laying in the Ant *Lasius niger* (Hymenoptera: Formicidae) and Its Role in the Collective Selection of a Food Source

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Foragers of the ant Lasius niger exploiting a 1 M sugar source were found to lay 43% more trail marks than those exploiting a 0.05 or a 0.1 M source. The trail laying per forager decreased during the course of individual recruitment episodes, and the mean lifetime of the trail pheromone was estimated to be 47 min. A mathematical function describing the probability that a forager chooses one of two paths in relation to the amount of trail pheromone on them closely fitted experimental data. These results were incorporated into a model describing the recruitment dynamics of L. niger. Simulations of this model showed that the observed modulation of trail laying with respect to food source quality is sufficient in itself to account for the systematic selection of the richer source seen in the experiments.

KEY WORDS: *Lasius niger*; trail following; trail laying; pheromone evaporation; mathematical model.

INTRODUCTION

In two earlier articles, we made a number of hypotheses to explain how colonies of trail-laying species, such as *Tetramorium caespitum* and *Lasius niger* (Pasteels *et al.*, 1987; Beckers *et al.*, 1990), select the richer of two sugar sources. The essential mechanism was assumed to be that mass-recruiting ants modulate their trail-laying behavior as a function of the sugar concentration. Hangartner (1970), for example, showed that *Acanthomyops interjectus* foragers increase

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their trail-laying activity when recruiting to richer sugar solutions, although the differences were not always very great. [See also *Myrmica rubra* (Cammaerts, 1977), *Formica oreas* (Crawford and Rissing, 1983); and *Paraponera clavata* (Breed *et al.*, 1987).]

This paper aims to show that such modulation actually occurs and we hypothesize that it is sufficient to explain the collective choice of the richer source. We measure this modulation for *Lasius niger*, together with the mean lifetime of the trail pheromone and the probability that a forager will choose one of two paths as a function of the amount of trail pheromone on them. To test this hypothesis, we use a model which incorporates these data and earlier measurements of the recruitment process to a single food source (Beckers *et al.*, 1992a).

METHODS

Choice of Food Source. In each trial, one of 10 laboratory colonies of *L. niger* (2000–3000 workers) was starved for 4 days and given access to a Y-shaped cardboard bridge. The two branches of the Y were separated by an angle of 60° and each led to a platform. The ants were allowed to explore the bridge for 2 h before placing a 2-cm-diameter drop of sucrose solution on each platform. The changes in the number of ants at each source over time were followed.

Modulation of Trail-Laying Behavior. In a number of these trials the trail-laying behavior on the last 20-cm section of each branch was quantified for 30–45 min (depending on the strength of the recruitment episode) using video recording. A forager was judged to be laying trail pheromone if its gaster curved to touch the bridge and was backed up for a fraction of a second (Beckers *et al.*, 1992a). This technique was used to measure the number of marking actions (or marks) each ant made on its way to and from the source, rather than the actual quantity of pheromone laid, although we assume the two to be closely related. Thus when we refer to the quantity of pheromone on a trail, we mean more exactly the amount of previous trail-laying behavior, taking evaporation into account.

Four choice situations were presented:

- (a) 1 vs 1 *M* ($n = 15$; with 2718 ant passages from three experiments analyzed in detail);
- (b) 0.5 vs 1 *M* ($n = 12$; no ant passages were analyzed);
- (c) 0.1 vs 1 *M* ($n = 14$; with, respectively, 1134 and 331 ant passages from two experiments analyzed in detail); and
- (d) 0.05 vs 1 *M* ($n = 17$; with, respectively, 1426 and 3731 ant passages from five experiments analyzed in detail).

Choice of Path as a Function of Pheromone Quantity. The above experiments provided data on the proportion of ants choosing one of two branches as

a function of the amount of previous trail laying on each branch. These data were used to fit a mathematical function describing this choice.

Estimation of the Mean Lifetime of the Trail Pheromone. In each experiment ($n = 6$), one of the colonies was starved for 4 days and given access to a linear cardboard bridge connected to a box containing a drop of 1 M sucrose solution. After a variable time period, of less than 15 min, the bridge was removed. The trail-laying behavior on the 10-cm horizontal section of the bridge was quantified using video recording.

This marked section was then joined with an equivalent unmarked section to form a Y-shaped bridge connecting a different colony to an empty box. The number of ants selecting each branch was counted for a period of 10 min. Once an ant chose a branch, it was immediately removed. The original marked branch was then joined to a new unmarked branch to form a Y-shaped bridge as before, but with the position of the marked branch inversed (to limit external bias). The bridge was then used to link a different colony to an empty box and the same procedure repeated.

The amount of pheromone on the original marked branch decreased with time due to evaporation. No trail pheromone was added by the ants to the marked branch during the choice phase of these experiments, as we know that *L. niger* foragers do not lay trail until they have been in contact with a food source (Beckers *et al.*, 1992a). Furthermore, the unmarked branch was replaced each time in case there had been any other chemical marking. In this way the choices made by the foragers were quantified between 0 and 10, 15 and 25, 30 and 40, 45 and 55, and 60 and 70 min after the branch was originally marked.

RESULTS

Choice of Food Source. Table I summarizes the preference shown by the colonies for the 1 M source in the trials described above. It is clear that the greater the difference in concentration between the two sources introduced simul-

Table I. The Percentage of Experiments and Corresponding Simulations (See Text) in Which the 1 M Source Was Chosen in Preference to a Second Source of Varying Concentration^a

Concentration of 2nd source (M)	% preference for the 1 M source			
	Experiments		Simulations	
	<i>n</i>	%	<i>n</i>	%
0.5	12	50	—	—
0.1	14	86	1000	89
0.05	17	100	1000	96

^a A source was considered chosen if more than 60% of the ants went there.

taneously, the greater the proportion of trials in which the majority of the foragers exploited the 1 *M* source (confirming earlier results of Pasteels *et al.*, 1987; Beckers *et al.*, 1990). The values 86 and 100% for the 0.1 and 0.05 *M* concentrations are both significantly different from 50% (binomial test, $P = 0.007$ and $P < 0.001$, respectively) but not from each other (Fisher's exact test, $P = 0.196$).

Modulation of Trail-Laying Behavior. Table IIa shows the average number of marks per passage for the first 10 min of the trials. These results indicate that overall trail laying per passage was 43% greater for the 1 *M* sources than for the 0.05 and 0.1 *M* sources $[(2.0-1.4)/1.4 = 0.43]$.

While there is no difference between the overall number of marks per passage for the 0.05 and 0.1 *M* solutions, the difference between the pooled data for these two concentrations and the 1 *M* solution is statistically significant (Mann-Whitney *U* test, $z_{\text{corr}} = 1.785$, $P < 0.05$). For those ants returning to the nest, and that had therefore visited the source at least once, the number of marks per passage increased progressively with the trail (Jonckheere test, $J^* = 5.136$, $P < 0.001$). These values were used in the simulations presented below. The results were less consistent for those ants going to the source, as many were making their first trip and thus did not lay trail pheromone (Beckers *et al.*, 1992a).

Table II. The Average Number of Marks per Passage (\pm SE) for 2420 Passages Analyzed During the First 10 min of the Experiments, for Ants Going Both to and from the Nest (a). This Measurement Is Divided into Its Two Components, Namely, the Intensity of Trail Laying (Number of Marks per Trailing Passage, i.e., per Passage in Which the Forager Made at Least One Mark) (b) and the Frequency of Trail Laying (Percentage of Trailing Passages) (c)

	Nest source	Source nest	Total
(a) Marks/passage			
0.05 <i>M</i>	1.4 \pm 0.12	1.3 \pm 0.13	1.4 \pm 0.09
0.1 <i>M</i>	1.1 \pm 0.18	1.7 \pm 0.26	1.4 \pm 0.16
1 <i>M</i>	1.5 \pm 0.11	2.5 \pm 0.14	2.0 \pm 0.09
(b) Intensity			
0.05 <i>M</i>	3.1 \pm 0.18	3.2 \pm 0.22	3.2 \pm 0.14
0.1 <i>M</i>	3.6 \pm 0.36	3.6 \pm 0.43	3.5 \pm 0.30
1 <i>M</i>	4.5 \pm 0.23	4.8 \pm 0.20	4.7 \pm 0.15
(c) Frequency (%)			
0.05 <i>M</i>	46	42	44
0.1 <i>M</i>	30	48	39
1 <i>M</i>	33	51	42

If we separate trail laying into its two components, frequency (percentage of trailing passages, i.e., passages in which the forager makes at least one mark; Table IIc) and intensity (number of marks per trailing passage; Table IIb), the same tendencies were found, especially for the intensity. Thus when confronted with a richer source, more foragers lay trail, and each lays more marks per passage. Hangartner (1970) found similar results in similar proportions for the ant *A. interjectus*.

If we examine the changes over time of the number of marks laid per passage, there is a strong general tendency for both the frequency and intensity of marking per individual to decrease (Fig. 1). Figure 1 also confirms the consistently greater trail laying for the 1 M source compared to the 0.1 or the 0.05 M sources, as presented in Table IIa.

Choice of Path as a Function of Pheromone Quantity. The following function represents the probability that an individual ant chooses between two possible paths, left and right, as a function of the pheromone on them, L and R (or more precisely the number of trail laying ants that have previously taken that branch):

$$P = \text{prob. choose left} = \frac{(k + L)^n}{(k + L)^n + (k + R)^n}$$

(1)

Thus

$$\ln \left(\frac{1}{p - 1} \right) = n \ln \frac{(k + R)}{(k + L)}$$

(2)

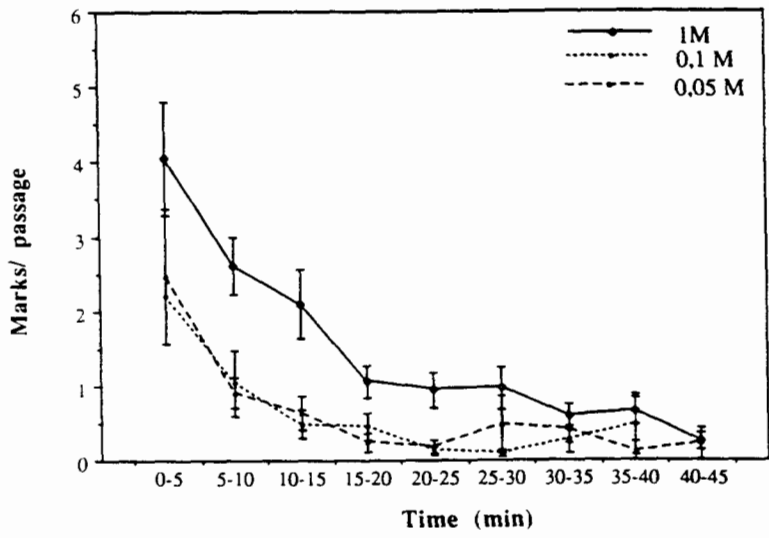


Fig. 1. The change over time of the mean number of marks per passage for 1, 0.1, and 0.05 M sugar sources (for a total of 8603, 1134, and 1426 analyzed passages from 7, 2, and 5 trials, respectively, with SE). The number of marks is systematically greater for the 1 M source.

The parameters n and k control the steepness of the choice function. With a high value for n , for example, a small difference between L and R is sufficient to induce a large majority of foragers to choose the more strongly marked branch. This function was used previously to quantify path choice in the ant *Iridomyrmex humilis*, and an experimental fitting gave $n = 2$ and $k = 20$ (Deneubourg *et al.*, 1990). Here we fit these parameters for *Lasius niger*.

The trials analyzed in detail in the series above gave us the cumulative number of marks on each branch (L and R) at time t (in minutes) and the proportion of ants during the period $t + 1$ that chose the left branch (p). The best linear regression of Eq. (2) using these data (118 points) gave $n \approx 2$ and $k = 6$ ($y = 0.38 - 2.07x$; $r = 0.81$).

Note that the data were based on the first 10 min of the recruitment episodes, limiting any potential effects of the evaporation of the trail pheromone or memory of the location of the food source previously visited (most ants leaving the nest during this period are doing so for the first time). These results can be compared with those of Hangartner (1969), who showed for *L. fuliginosus* that the proportion of ants following one of two trails was roughly proportional to the ratio of the amount of trail pheromone (gland extracts) on the two branches, within a certain range.

Estimation of the Mean Lifetime of the Trail Pheromone. In the context of these experiments, and applying Eq. (2) as fitted above, one obtains

$$h = \frac{(k + L_0 e^{-\alpha t})^2}{k^2} \quad (3)$$

$$\sqrt{h} = 1 + \frac{L_0 e^{-\alpha t}}{k} \quad (4)$$

and thus

$$\ln(\sqrt{h} - 1) = \ln\left(\frac{L_0}{k}\right) - \alpha t \quad (5)$$

where h is the ratio of the number of ants taking the marked branch to the number choosing the unmarked branch at time t . L_0 is the number of marks on the marked branch at the moment when this branch was joined with the unmarked branch to form the Y-shaped bridge, and a is the inverse of the mean lifetime of the trail pheromone (assuming an exponential decay).

The linear regressions of Eq. (4) for the six trials gave an average value for the mean lifetime ($1/a$) of the trail pheromone of ≈ 47 min (SE = 9.5 min), with the corresponding correlation coefficient (r) ranging from 0.62 to 0.99.

MODEL OF TRAIL LAYING AND CHOICE OF SOURCE

We use a model that reproduces the recruitment dynamics of *L. niger*, incorporating data from Beckers *et al.* (1992a) and from the experiments described above, to test how far the individual trail-laying and trail-following behavior can generate the overall choice of food source by a colony. This model embodies a more precise description of individual forager behavior than that originally used by Beckers *et al.* (1990).

The model describes the following behavior. Of the 100 ants constituting an average forager force, 20% are scouts and can leave the nest spontaneously as well as being recruited. This fraction is based on an estimation of the proportion of workers that regularly leave the nest outside recruitment episodes, although of course at any one moment the fraction outside the nest is much lower. When a recruitment trail is present, the remaining 80% (the recruits) can also leave the nest. The probability per second that an ant of either category leaves the nest for the first time is given by the following formula, fitted as closely as possible to typical experimental recruitment curves:

$$p \text{ scout leaves nest} = \frac{0.01(50 + Q)^2}{(50 + Q)^2 + 1200} \quad (6)$$

$$p \text{ recruit leaves nest} = \frac{0.01Q^2}{Q^2 + 1200} \quad (7)$$

where Q is the trail pheromone concentration [$Q = L + R$ as defined for Eq. (1)]. All the ants that leave the nest choose which source to go to according to Eq. (1), arriving there after 10 s, feed for 50 s, return to the nest in 10 s, and stay in the nest for 250 s before returning to the food source [rounded average times from Beckers *et al.* (1992a)]. Once they have left the nest, they continue this cycle until the end of the simulation. The model keeps track of the number of ants in the nest at any one moment that are ready to start foraging.

The ants do or do not lay trail according to the food source concentration and the number of trips they have made. Scouts and recruits obey the same rules but with different probabilities. In detail, for a 1 *M* sugar source, the probabilities that a scout or a recruit start to lay trail for the first time, and also continue to lay trail on each subsequent trip, are 0.5 and 0.25, respectively, as measured by Beckers *et al.* (1992a). If they did not start to lay trail on the first trip or subsequently stopped laying trail, then the probabilities that they start to lay trail (for the first time or again) are 0.1 and 0.05, respectively (Beckers *et al.*, 1992a). For poorer sugar sources, all these constants are multiplied by a factor $e < 1$, derived from Table II ($e = 1, 0.7$, and 0.5 for 1, 0.1, and 0.05 *M*, respectively). If an ant has previously visited the poor source and subsequently arrives at a rich source without laying trail, it is considered to act as if discovering a source

for the first time. Finally, the trail pheromone has a mean lifetime of 0.75 h (as measured above).

The results of the simulations are closely comparable to the experimental results (Table I), confirming that the differences in Table II are sufficient to determine the systematic choice of the richer source observed experimentally. The values of 89 and 96% are both significantly different from 50% (binomial test, $P < 0.001$ each), and significantly different from each other ($\chi^2 = 53.0$, $P < 0.001$).

Although the trail laying was not quantified for 0.5 M sources (and the simulations not therefore carried out), the fact that the 1 M source was selected in only approximately 50% of the 1 vs 0.5 M experiments suggests that there is not much difference in the trail laying for 1 and 0.5 M sources. The simulations further suggest that if such a difference does exist, it must be very small indeed, as with $e = 0.95$, as many as 68% of the colonies select the 1 M source.

DISCUSSION

Our simulations show that the modulation observed, while appearing relatively slight, is sufficient to account for the strong and systematic selection of a richer source. The basic mechanism is extremely simple, even though the model takes into account a number of secondary complexities quantified in an earlier paper (Beckers *et al.*, 1992a), such as how the trail-laying activity of a *Lasius niger* forager can vary depending on whether it is a scout or a recruit or on how many trips it has already made [see Nelson *et al.* (1991) for similar measurements on *Paraponera clavata*].

An equivalent process can be seen in the collective selection of the shorter of two paths, in which *L. niger* foragers modulate their behavior as a function of their deviation from the nest-food axis (Beckers *et al.*, 1992b).

Honeybee colonies also use a similar process to select richer food sources. In a recruitment context and in relation to the richness of the food source, the foragers modulate the strength of their waggle dancing, the tempo of their visits to the food source, their likelihood of returning there (Seeley *et al.*, 1991; Camazine and Sneyd, 1991), and the receptivity of the workers in the nest.

Apparently simplistic, these mechanisms developed by social insects are in fact extremely powerful. The interplay between competition and amplification inherent in the recruitment process enables the colony to focus its activity on what is usually the most rewarding food source by exploiting small differences in the reactions of its individual foragers.

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