

# Path efficiency of ant foraging trails in an artificial network

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## Abstract

In this paper we present an individual-based model describing the foraging behavior of ants moving in an artificial network of tunnels in which several interconnected paths can be used to reach a single food source. Ants lay a trail pheromone while moving in the network and this pheromone acts as a system of mass recruitment that attracts other ants in the network. The rules implemented in the model are based on measures of the decisions taken by ants at tunnel bifurcations during real experiments. The collective choice of the ants is estimated by measuring their probability to take a given path in the network. Overall, we found a good agreement between the results of the simulations and those of the experiments, showing that simple behavioral rules can lead ants to find the shortest paths in the network. The match between the experiments and the model, however, was better for nestbound than for outbound ants. A sensitivity study of the model suggests that the bias observed in the choice of the ants at asymmetrical bifurcations is a key behavior to reproduce the collective choice observed in the experiments.

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## 1. Introduction

In a lot of ant species foragers do not exploit food sources solitarily but use a recruitment process which allows the defense of the resources against competitors and a collective retrieval of the food to the nest (Hölldobler and Wilson, 1990). Among the different types of recruitment, chemical mass recruitment is certainly one of the most efficient because it allows a logistic build-up of the worker force at the food source. The dynamics of mass recruitment can be described as a self-organized process based on the interplay between a positive feedback (the reinforcement of the trail by recruited ants) and a negative feedback (the evaporation of the pheromone and the decrease in the frequency of trail-laying behavior due to the food exhaustion). This system allows ants to make adaptive choice, e.g. to select the most profitable (Beckers et al., 1993) or the most required type of food (Portha et al.,

2002) among several food sources or to use the shortest among several paths leading to the same food source (Aron et al., 1990; Goss et al., 1989).

When ants move in the dense network of the subterranean galleries of their nest (Cassill et al., 2002; Tschinkel, 2004) or in the network of above-ground foraging trails (*Formica rufa*: Gösswald, 1943; Skinner, 1980; *Lasius fuliginosus*: Quinet and Pasteels, 1991), they are faced with a succession of bifurcations. At each of these bifurcations they have to make a decision as to which gallery or trail they will take next. In absence of any other cues, this decision is based on the concentration of trail pheromone perceived on each branch (Goss et al., 1989). However, this system generates errors that accumulate over successive bifurcations and are bound to deeply influence the dynamics of collective path selection. The question arises therefore as to what extent in such situations ants are still able to collectively select the most efficient path to go from one point to the other.

In this paper we investigate the movement of ants in a relatively complex artificial network of galleries in which

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several possible interconnected paths can lead the insects from their nest to a food source. We first assess from experiments the probability for an ant moving either out- or nestbound to choose each possible path in the network and we compare these probabilities to those given by a null model in which ants orient randomly in the network. Based on the measures of several aspects of the ants' behavior in the experiments, we then build an individual-based model of the movement of the ants in the network and run a sensitivity analysis to assess the role of the different parameters of the model in the emergence of a collective choice. The model shows that the bias observed in the choice of the ants at asymmetrical bifurcations plays a key role for the emergence of a collective selection of a path, both in the out- and nestbound direction.

## 2. Material and methods

### 2.1. Species studied

We used the Argentine ant *Linepithema humile* (Newell, 1909), whose foragers lay a pheromone trail both in the out- and nestbound directions (Deneubourg et al., 1990). The ants were collected near Narbonne (South of France) while foraging outside the nest. They were distributed in 10 experimental queenless colonies, each containing around 2000 workers and no brood. Each colony was housed in a plastic container (20.0 × 20.0 × 7.0 cm), whose walls were coated with Fluon<sup>®</sup> to prevent ants from escaping. No interactions between colonies were possible. Inside each container ants nested in test tubes partially filled with water behind a cotton plug. Between experiments ants were fed with a solid food composed of carbohydrate and vitamin (Bhatkar and Whitcomb, 1970).

### 2.2. Experimental set-up and protocol

The experimental set-up consisted in a maze carved in a plastic slab (31.5 × 18.0 cm) covered by a glass plate. To prevent the use of any directional cues by the ants the whole set-up was surrounded by white sheets hanging from the ceiling and was lighted from above by four fluorescent lights placed at right angles. The maze galleries had a 0.5 cm square section. The network was composed of four identical lozenges assembled together (Fig. 1). The angles between the branches of the lozenges were equal to 60°. This angle corresponds to the standard value of branch bifurcation used in experiments with dual-choice bridges (Goss

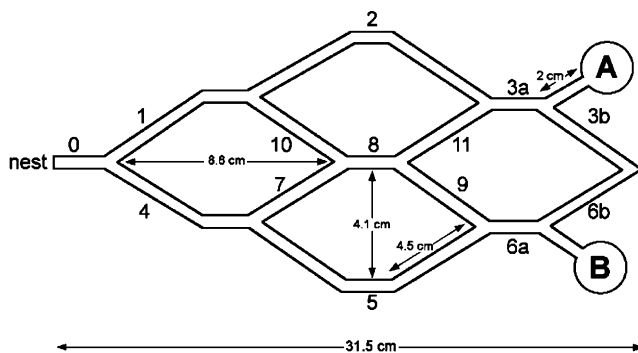


Fig. 1. Experimental set-up. The maze was carved in a plastic slab and the galleries had a 0.5 cm square section. During the experiments, the ants had access to a food source (a cotton plug soaked with 1 M sucrose solution) located either in chamber A or B.

et al., 1989; Beckers, 1992) and is closed to the mean bifurcation angle found in natural networks (Acosta et al., 1993; Jackson et al., 2004). An angle above this value induces many U-turns that slow down the progression of the ants in the network (Beckers et al., 1992). The maze also included two circular chambers ( $\phi = 2.0$  cm) in which food could be placed.

The colonies were starved for 4 days before the day of the experiments. At the beginning of each experiment, the container with the colony was connected by a plastic bridge to a small box placed in front of the entrance of the maze. One experiment was run with each experimental colony. For half of the colonies the food source (a cotton plug soaked with a 1 M sucrose solution) was located in one chamber and for the other half, in the other chamber (Fig. 1). After each experiment, the network was cleaned with alcohol to remove any residual chemical cues.

The duration of each experiment was set to 60 min and the ant behavior was recorded continuously with a high definition digital camera (Sony CDR-VX 2000 E) placed above the set-up.

### 2.3. Data analysis

#### 2.3.1. Individual behaviors

In order to assign realistic values to the parameters of the model, two characteristics of the behavior of individual ants were measured: (1) the ant speed, measured from the duration and length of the journey of a sample of 110 ants randomly chosen in the experiments and (2) the time spent in the chamber containing the food source, measured on a sample of 65 ants randomly chosen in the experiments.

#### 2.3.2. Collective choice

An experiment began when the first ant entered the network. The number of ants entering and leaving the network was sampled during 20 s every 3 min. During this same period of time, the choice of the ants at each bifurcation of the network was noted.<sup>1</sup> The number of ants coming from each branch of the bifurcation was counted and their choice noted. This number was cumulated over time to compute the probability  $p_{i,j}$  for an ant to select branch  $j$  when coming from branch  $i$ , where  $i$  is the label assigned to the branch of the network the ant is coming from and  $j$  is the label assigned to either branch found after the bifurcation (Fig. 1).

Coming from the maze entrance, ants can reach the food source without using twice the same branch by using 14 possible paths (Table 1). These paths can be classified in six categories according to their length: short, medium, long and very long (Table 1). The same 14 paths can also be considered for the journey back to the nest, from the food source to the maze entrance. The selection of any other path, e.g. looping paths, was considered as an absence of choice. The probability for an ant to select one of the 14 possible paths during an experiment was computed as the product of the probabilities, cumulated over the whole duration of the experiment, to select each branch of the path at the successive bifurcations encountered. For example, for an ant leaving the nest and moving towards the food source located in chamber A, the probability  $p_1$  of choosing path 1 of Table 1 was calculated as

$$p_1 = p_{0,1}p_{1,2}p_{2,3a} \quad (1)$$

Consequently, the probability for an ant to select a path different from those considered in Table 1 is given by

$$p_{\text{no choice}} = 1 - \sum_{i=1}^{14} p_i \quad (2)$$

<sup>1</sup>Note that, owing to the high density of ants at the first bifurcation of the network, it was impossible to observe the choice of nestbound ants (coming either from branch 1 or 4) at this bifurcation. Consequently, this bifurcation was not taken into account in the paths of returning ants.

and the probability to choose a path of a given category is given by

$$p_{\text{category}} = \sum_{i=1}^n p_i, \tag{3}$$

where  $n$  is the number of possible paths in the category.

Note that, in the absence of choice at each bifurcation, i.e. with an equal probability to choose one or the other branch, the probability to choose one of the path  $i$  of Table 1 is given by

$$p_i = 0.5^m, \tag{4}$$

where  $m$  is the number of bifurcations along the path.

Since the number of bifurcations differs from one path to the other the probabilities to select a path of a given category are not equal (Fig. 2). Note that the probabilities to select a path of a given category are different in the out- and nestbound direction owing to the fact that the first bifurcation of the network was not considered for returning ants (see footnote 1).

Table 1  
Possible paths that ants can use to go from the maze entrance to the food source without using twice the same branch

Number	Path (source in A)	Path (source in B)	Length
1	1-2-3a	4-5-6a	s—21.5 cm
2	1-10-8-11-3a	1-10-8-9-6a	
3	4-7-8-11-3a	4-7-8-9-6a	
4	4-5-9-11-3a	1-2-11-9-6a	m—30.5 cm
5	4-7-10-2-3a	1-10-7-5-6a	
6	4-5-6a-6b-3b	1-2-3a-3b-6b	
7	4-7-8-9-6a-6b-3b	1-10-8-11-3a-3b-6b	
8	1-10-8-9-6a-6b-3b	4-7-8-11-3a-3b-6b	
9	1-2-11-9-6a-6b-3b	4-5-9-11-3a-3b-6b	l—39.5 cm
10	1-10-7-5-6a-6b-3b	4-7-10-2-3a-3b-6b	
11	1-10-7-5-9-11-3a	4-7-10-2-11-9-6a	
12	4-5-9-8-10-2-3a	1-2-11-8-7-5-6a	vl—43.5 cm
13	4-7-10-2-11-9-6a-6b-3b	1-10-7-5-9-11-3a-3b-6b	vl—48.5 cm
14	1-2-11-8-7-5-6a-6b-3b	4-5-9-8-10-2-3a-3b-6b	vl—52.5 cm

s = short path, m = medium path, l = long path and vl = very long path.

### 3. Experimental results

#### 3.1. Behavior of individual ants

We found a mean value of  $1.06 (\pm \text{IC}_{0.95}) \pm 0.06 \text{ cm s}^{-1}$  for the speed of the ants. The average time spent by ants in the chamber containing the food source was equal to  $179.90 (\pm \text{IC}_{0.95}) \pm 39.04 \text{ s}$ . The logarithm of the proportion of ants still at the food source as a function of time is best described by a linear regression (Fig. 3), which means that ants leave the food source at a constant rate over time.

#### 3.2. Selection of a path

In most experiments the majority of ants selected the shortest paths, both in the out- (Fig. 2a) and nestbound (Fig. 2b) directions. For both directions, the probability of choosing the shortest path was much higher than that given by a random orientation of the ants in the network.

### 4. Model

#### 4.1. Model description

*L. humile* is a typical mass recruiting ant and the evolution of the flow of ants entering the network can thus be modeled by the logistic equation:

$$\frac{dF(t)}{dt} = rF(t) \left( 1 - \frac{F(t)}{K} \right), \tag{5}$$

where  $r$  stands for the recruitment rate and  $K$  represents the value of the flow at saturation, which is related to the number of foragers available for recruitment within the colony.

The flow of ants entering the network at each simulation step can be obtained by integrating Eq. (5) over

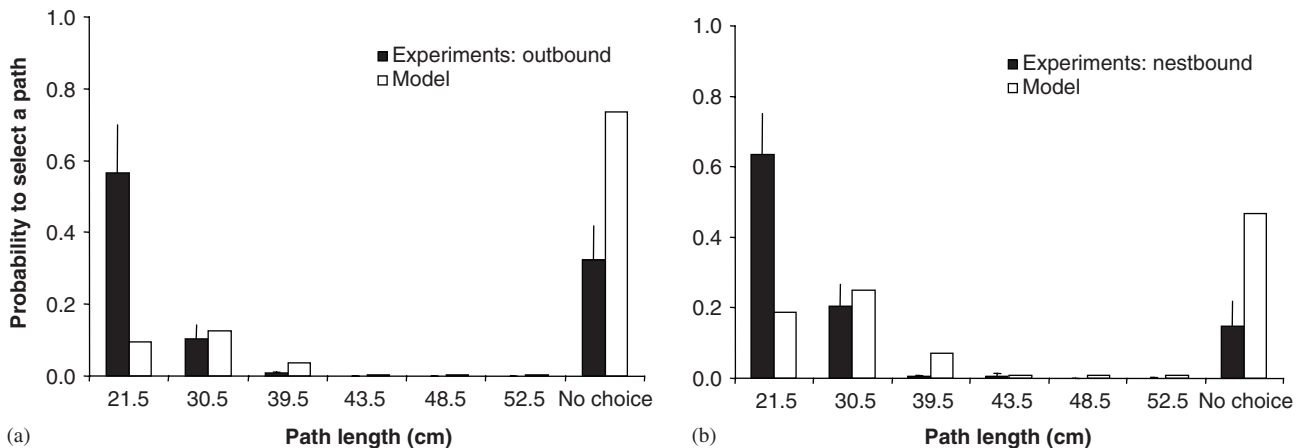


Fig. 2. Probabilities ( $\pm \text{IC}_{0.95}$ ) to select the different categories of paths of the network for ants in the experiments moving in (a) the outbound and (b) the nestbound direction, compared to the theoretical probabilities that would be obtained if ants were to choose equally between branches at each bifurcation of the network. The probabilities are computed as the average of  $N = 10$  experiments.

time, which gives

$$F(t) = \frac{F_{\max}}{1 + (F_{\max}/F_0 - 1)e^{-t/\tau}}, \quad (6)$$

where  $F_{\max}$  is the maximum value of the flow at saturation,  $F_0$  the initial value of the flow,  $\tau$  the time constant related to the rate of recruitment.

The values of the parameters  $F_{\max}$ ,  $F_0$  and  $\tau$  were estimated by taking the average value of the parameters of the logistic regression fitted to the curve describing the evolution of the flow of ants entering the network as a function of time for each experiment (Table 2).

When an ant moves in the network, it lays at each time step a quantity of pheromone  $q$  when moving towards the food source and a quantity  $Q$  when returning to the nest.

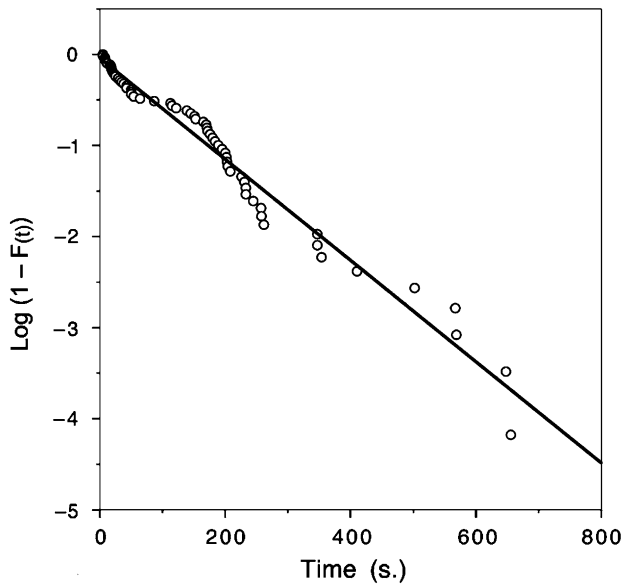


Fig. 3. Logarithm of the proportion of ants still at the food source as a function of the time elapsed since the arrival of the ant at the food source. The relationship is best described by the linear regression:  $y = -0.0056t$ ,  $R^2 = 0.97$ .

In the simulations, an ant reaching a bifurcation chooses one or the other branch depending on the trail concentration on each branch and its intrinsic degree of attraction. The probability to choose a branch is given by the choice function (Beckers et al., 1992; Deneubourg et al., 1990):

$$p_i = \frac{(k_i + C_i)^n}{(k_i + C_i)^n + (k_j + C_j)^n} = 1 - p_j, \quad (7)$$

where  $C_i$  ( $C_j$ ) is the concentration of the trail pheromone on branch  $i$  ( $j$ ) and  $k_i$  ( $k_j$ ) is its intrinsic degree of attraction in absence of pheromone. The parameter  $n$  determines the degree of nonlinearity of the choice.

Note that two types of bifurcations can be found in the network (Fig. 1): (i) symmetrical bifurcations, where the two branches form an angle of  $30^\circ$  with the direction of the branch the ant is coming from, e.g. the bifurcation between branch 1 and 4 for an ant that has just entered the network, and (ii) asymmetrical bifurcations, where a branch forms an angle of  $30^\circ$  and the other an angle of  $120^\circ$  with the direction of the branch the ant is coming from, e.g. the bifurcation between branches 1 and 2 for an ant coming from branch 10 and returning to the nest.

For a symmetrical bifurcation one can assume that the intrinsic degree of attraction of the branches is the same and thus we get  $k_i = k_j = k$ . When Eq. (7) was applied to the ant choice at symmetrical bifurcations in our experiments we found that the best fit was given by the values  $k = 20$  and  $n = 4$ .

For an asymmetrical bifurcation one can assume that the intrinsic degree of attraction of each branch differs because ants, as all organisms with a bilateral symmetry (Schöne, 1984), should have a natural tendency to proceed on the branch which deviates less from their initial direction. In order to check this we noted for a sample of 350 ants the choice they made at the asymmetrical bifurcations of the network in the quasi-absence of pheromone on the branches. This was done by measuring the choice of the first 10 ants reaching the bifurcation since the beginning of the experiment. Although one cannot exclude that a small quantity of

Table 2  
Values assigned to the parameters of the model in the simulations

Model parameters		Value	Origin
$F_{\max}$	Maximum flow of ants	$0.42 \text{ s}^{-1}$	Estimated from experiments
$F_0$	Initial flow of ants	$5 \times 10^{-4} \text{ s}^{-1}$	
$\tau$	Time constant related to the rate of recruitment	127.4 s	
$k$	Intrinsic degree of attraction of the branch	20	
$n$	Coefficient of non-linearity of the choice	4	Measured from experiments
$r_{\text{pref}}$	Preference ratio $k_{120^\circ}/k_{30^\circ}$	0.74	
$v_{\text{moy}}$	Average speed of the ants	$1.06 \text{ cm s}^{-1}$	
$v_{\text{SD}}$	Standard deviation of the ant speed	$0.34 \text{ cm s}^{-1}$	
$\varphi$	Average time spent at the food source	179.9 s	Arbitrary values
$q$	Quantity of trail pheromone deposited in the outbound trip	1	
$Q$	Quantity of trail pheromone deposited in the nestbound trip	1	

trail pheromone may be deposited at the passage of each ant and that the choice of one ant may be influenced by the choice of the ant that precedes her at the bifurcation, the concentration of the pheromone should be weak enough to be considered as negligible in the parameters determining the choice.

We found that 77% of the ants reaching an asymmetrical bifurcation proceeded on the branch that deviates less from their initial direction.

In the simulations the influence of the geometry of the bifurcation on the ant choice was taken into account by considering the ratio

$$r_{\text{pref}} = k_{120^\circ} / k_{30^\circ}. \quad (8)$$

Substituting  $k_i = k_{120^\circ}$  by  $r_{\text{pref}}k_{30^\circ}$  and  $k_j = k_{30^\circ}$  in Eq. (7) and taking the values  $k_{30^\circ} = k = 20$  and  $n = 4$  we get

$$r_{\text{pref}} = \sqrt[4]{\left(\frac{1}{p} - 1\right)}, \quad (9)$$

where  $p$  is the proportion of ants that choose the  $30^\circ$  branch. This yields the value of 0.74 for  $r_{\text{pref}}$ .

Taking into account the influence of the geometry of the bifurcation in the choice of the ants, Eq. (7) can be rewritten as

$$p_i = \frac{(k_i^* + C_i)^n}{(k_i^* + C_i)^n + (k_j + C_j)^n} = 1 - p_j \quad (10)$$

with  $k_i^*$  is  $k$  if branch  $i$  deviates by an angle of  $30^\circ$  from the ant's original direction and  $k_i^* = r_{\text{pref}}k$  if it deviates by an angle of  $120^\circ$ .

The model is implemented in the simulation as follows.

Each step of the simulation is equivalent to 1 s. At each simulation step an ant can enter in the network with a probability  $P_{\text{ent}}$  drawn from a uniform probability distribution  $U(0, F(t))$  where  $F(t)$  is given by Eq. (6). Whenever an ant enters a branch its speed is drawn from a normal distribution with a mean and standard deviation equal to the values measured from the experiments (Table 2). The time required to travel a branch is then computed and decremented at each time step. An ant going to the food source deposits a quantity  $q$  of pheromone on the branch it comes from, just before reaching the bifurcation, and a quantity  $q$  on the branch it chooses, just after the bifurcation, whereas an ant coming from the food source and going back to the nest deposits a quantity  $Q$  at each point. *L. humile* workers are known to deposit trail pheromone more frequently on their way back to the nest than when going to the food source (Deneubourg et al., 1990). In a first step, however, we considered that the same quantity was laid in both directions and ran the simulations with a ratio  $Q/q = 1$ . Moreover, as an approximation we considered that all ants in the simulations laid a trail whereas in experiments with *L. humile* the percentage of trail-laying ants is close to 90% (Deneubourg et al., 1990). Since the average lifetime of the trail pheromone in *L. humile* is long (20~30 min: Deneubourg et al., 1990) compared to the duration of the simulation (1 h),

we neglected the evaporation of the pheromone in our simulations. One can also assume that the air in the galleries is rapidly saturated by the trail pheromone during an experiment. For this reason, we also considered that the diffusion of the trail pheromone in the network was negligible and thus did not implement a diffusion function in our simulations. No crowding effect, either in the galleries (Dussutour et al., 2004) or at the food source (Halley and Burd, 2004), that could influence the dynamics of recruitment or path choice were considered in the simulations. Finally, the time spent by an ant at the food source was modeled by a negative exponential law with a characteristic time corresponding to the leaving rate of ants at the food source during the experiments (Fig. 3 and Table 2).

The simulations were run for 3600 time steps. Five hundred realizations of the simulations were run with the parameters given in Table 2. The simulation was implemented in Scilab (<http://scilabsoft.inria.fr>).

#### 4.2. Comparison of the model output with the experimental results

The choice of the different categories of paths in the simulations is computed in the same manner as in the experiments, i.e. by computing the probability for an ant, over the whole duration of the simulation, to choose a given branch at each bifurcation of the network. Note that, because of the 50-fold difference in sample size between the number of simulations and the number of experiments, we did not perform any statistical tests to compare the results of the simulations to those of the experiments for the different categories of paths. The statistical power of such a test will indeed be so low that it will be nonsensical. The indication of the 95% confidence interval on Figs. 2 and 4 gives an idea of the fit between the model and the empirical data.

We first checked the computer implementation of our model by running the simulations with the parameter values given in Table 2 but with no pheromone deposit and without introducing any bias in the choice of the ants at asymmetrical bifurcations. In that case the probabilities to choose the different categories of paths in the network were exactly the same as those given by the theoretical probabilities computed for a random choice at all bifurcations (Fig. 2).

When the simulations were run with ants depositing pheromone and with the geometrical bias taken into account, the agreement between the model and the experimental results was different for out- and nestbound ants. For ants returning to the nest the probabilities we obtained were close to that found in the experiments (Fig. 4b). In the outbound direction, however, the probability to choose none of the 14 possible paths was much higher in the experiments than in the simulations (Fig. 4a). This was due to the fact that a number of ants followed looping paths in the network.

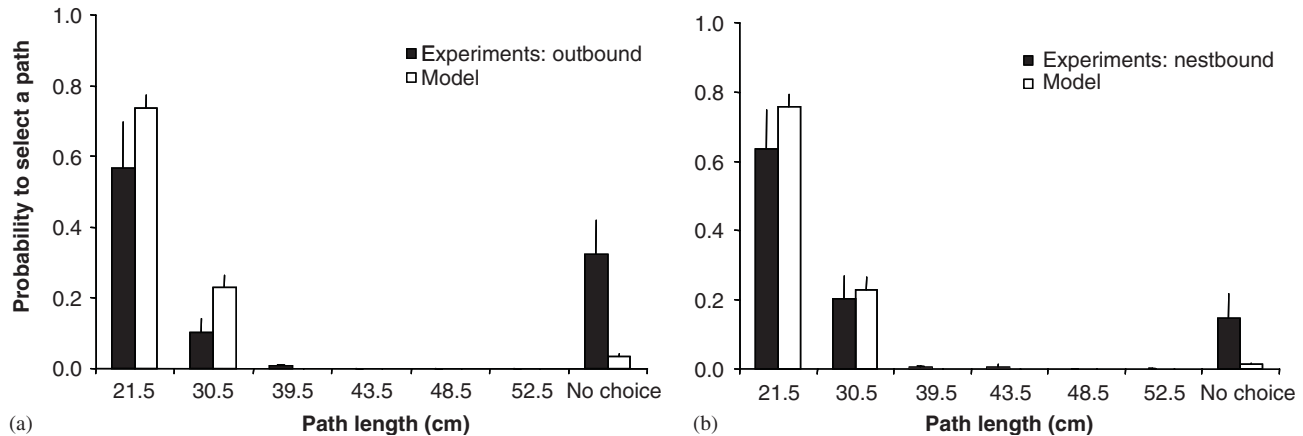


Fig. 4. Probabilities ( $\pm IC_{0.95}$ ) to select the different categories of paths of the network in the simulations and in the experiments for ants moving in (a) the outbound and (b) the nestbound direction. The probabilities are computed as the average of  $N = 10$  experiments and  $N = 500$  simulations.

#### 4.3. Sensitivity analysis

The sensitivity of the model to its different parameters was assessed by varying the value of one parameter while keeping the others constant. Five hundred realizations of the simulation were run for each parameter tested. The results are displayed in Fig. 5.

The probability to select a short path increases with the value of the maximum flow (Fig. 5a). The time constant related to the rate of recruitment does not influence the choice of the ants, except when it took an extreme value, in which case most simulations ended with an absence of choice (Fig. 5b).

The probability to select a short path slightly decreases when ants spend more time at the food source (Fig. 5c). It also decreases dramatically when the geometrical bias in the choice of the ants at network bifurcation was reduced (Fig. 5f). In the absence of bias most simulations ended with an absence of choice.

We found an optimum value for the choice of a short path when the speed of the ants or the ratio of the quantity of pheromone dropped in the out- and nestbound direction were changed. The choice was maximum when the speed took a value close to that found in the experiments (Fig. 5d) and when the quantity of pheromone dropped in the nestbound direction was twice as high to that dropped in the outbound direction (Fig. 5e).

## 5. Discussion

The results of the experiments show that ants did not move randomly in the network: the probability to select one of the shortest paths to go from the nest to the food source or from the food source to the nest was much higher to that given by a random orientation of the workers in the network. Ants were slightly more efficient on their way back to the nest than when going to the food source. In order to better understand this result we measured the choice frequency of the ants at each bifurcation in the

network and developed an individual-based model in which the rules we hypothesized for the movement of the ants in the network were implemented. The simulations were run with the values assigned to the parameters of the model measured from the experiments.

Overall, the agreement between the simulations and the experimental results was best only when the concentration of the trail pheromone over the branches and the bias due to the geometry of the bifurcations were considered in the ant decision. The sensitivity analysis underlines the importance of the geometrical bias for reproducing the experimental results: in the absence of bias, a decision based merely on the pheromone concentration on the branches was unable to generate a significant choice of the ants in the network (Fig. 5f). The decision of the ants as to which branch to choose when reaching a bifurcation in the network thus depends on two parameters: the concentration of the trail pheromone they perceive on the branch and its deviation from their initial direction.

How could one explain this geometrical bias? The first mechanism one could think of is path integration (see review by Wehner and Srinivasan, 2003). Ants could be able to integrate their outbound path while moving in the network and thus to come back to their nest by following the shortest possible path. In that case one would expect nestbound ants to choose one of the shortest paths in the network with a higher probability than outbound ants, which is what we actually observed. Nestbound ants could navigate in the network by choosing at bifurcations the branch that deviates less from the direction indicated by their path integration vector. In fact, Bisch-Knaden and Wehner (2001) have shown that foragers of the species *Cataglyphis fortis* returning to their nest are able to find the shortest way around an obstacle by using their path integration system. The pheromone deposited by nestbound ants will then guide the outbound ants on their way to the food source. It is, however, unlikely that path integration was at work in our experiments. In fact, ants are unable to proceed path integration on the basis of

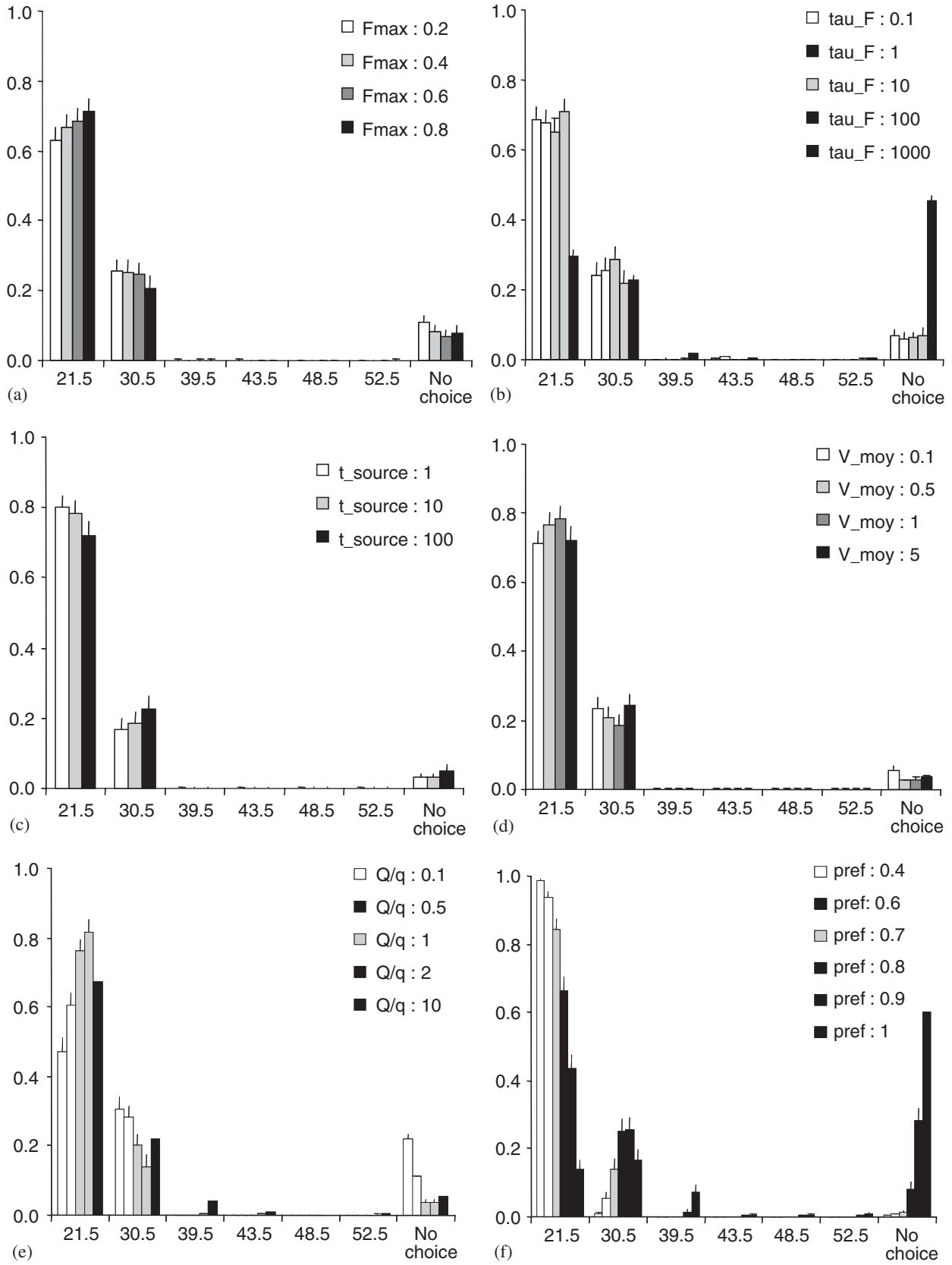


Fig. 5. Probabilities ( $\pm IC_{0,95}$ ) to select the different categories of paths of the network for ants moving from the nest to the food source for different values of (a) the maximum flow of ants in the network,  $F_{max}$  (b) the time constant related to the rate of recruitment,  $\tau$  (c) the average time spent at the food source (d) the average speed of movements of the ants (e) the ratio  $Q/q$ , i.e. the amount of pheromone dropped in the nestbound on the amount of pheromone dropped in the outbound direction (f) the geometrical bias in the choice of the ants at network bifurcation,  $r_{pref}$ .  $N = 500$  simulations for each set of parameters.

proprioceptive stimuli only; they need to have a compass at their disposal, for example in the form of a directional light (Shen et al., 1998). This was not the case in our experiments since we took care of getting rid of any orientational cues by surrounding the maze with white curtains and lighting it homogeneously from above.

The second mechanism that could account for the geometrical bias at the bifurcation could be based on a sensitivity of the ants to the bifurcation angles. It has indeed been recently shown in the Pharaoh's ants *Monomorium pharaonis* that the branching geometry of natural trail networks provides foragers with directional information that they can use to determine the way to the nest or out to the foraging area (Jackson et al., 2004). By using information given by the trail bifurcation angles within the network, foragers joining a trail can adaptively reorient themselves if they initially walk in the wrong direction (e.g. fed foragers walking in the outbound direction, or unfed foragers walking in the nestbound direction). Our results show that a similar mechanism could be at work in the Argentine ants when they are constrained to travel in an artificial network of tunnels. In addition to provide directional information, our results show that the bifurcation angles in the artificial network could play a key role in the optimization of the length of the paths selected by ants. Measures on the mean angle of the trails' bifurcations in the natural foraging networks constructed by Argentine ants should confirm this result. Moreover, one prediction of the model is that when the bifurcation angle in the network equals  $120^\circ$ , i.e. when no geometrical information is present, ants should not be able to find the shortest path to the nest. We are currently testing his prediction in another set of experiments.

Another interesting result of the simulations is that the probability of choosing none of the defined categories of paths in the set-up was much higher in the experiments than in the simulations (Fig. 4). The choice of out- and nestbound ants in the simulations were practically identical and resulted mostly in the selection of the categories of short and medium paths. This means that the model is perhaps too deterministic and does not capture the stochastic element in the ant behavior. Many ants were indeed observed to follow looping paths in the network, especially when going to the food source (Fig. 4a). These looping ants could be patrollers exploring the network (Gordon, 1987), rather than foragers going to or coming from the food source, and this category of ants may be less sensitive to the pheromone concentration or the bifurcation geometry. Another explanation may be linked to the fact that the air in the maze was confined and that saturation effect of the trail pheromone on some branches may occur as the experiment proceeds. Finally, the results of the simulations exploring the sensitivity of the model to the geometrical bias (Fig. 5f) suggest that the higher probability to choose none of the 14 possible paths for outbound ants compared to nestbound ants (Fig. 4) could also be explained by the fact that ants may be less sensitive

to the geometry of the bifurcations when going to the food source than when returning to the nest. Jackson et al. (2004) found indeed that in *M. pharaonis* the percentage of foragers that reoriented themselves on a natural foraging trail when placed facing the wrong direction at a bifurcation (i.e. towards the nest for unfed ants, or away from the nest for fed ants) was higher for fed than for unfed ants (75% vs. 65%).

It is important to note that our study focuses on the behavior of ants in a static condition, i.e. in a situation in which the traffic in the network is not submitted to any perturbations along the time. A next step would be to study the behavior of the ants, and the flexibility of their collective choice, when abrupt changes occur in the network, for example when an established path is suddenly interrupted by an obstacle, or when ants are forced to make long detours to reach a food source before being allowed to take a shorter path again (Vittori et al., 2004).

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