

Modeling Ant Behavior Under a Variable Environment

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Abstract. This paper studies the behavior of ants when moving in an artificial network composed of several interconnected paths linking their nest to a food source. The ant responses when temporarily blocking the access to some branches of the maze were observed in order to study which factors influenced their local decisions about the paths to follow. We present a mathematical model based on experimental observations that simulates the motion of ants through the network. In this model, ants communicate through the deposition of a trail pheromone that attracts other ants. In addition to the trail laying/following process, several other aspects of ant behavior were modeled. The paths selected by ants in the simulations were compared to those selected by ants in the experiments. The results of the model were encouraging, indicating that the same behavioral rules can lead ants to find the shortest paths under different environmental conditions.

1 Introduction

Ant colonies are very interesting entities because of their capacities to collectively achieve complex decisions and patterns through self-organization processes based on simple behavioral rules and the use of local information and indirect communication [6,7]. The decisions of the ants are controlled by the laying/following of trails of a chemical substance, called pheromone [22]. When given the choice among several alternative paths, ants choose a path in a probabilistic way, based on the pheromone concentration over the possible paths. This mechanism allows the selection of the shortest path among several ones [1,10,11]. Shorter paths are completed earlier than longer ones. Hence, the pheromone concentration on those paths increase more rapidly and they attract more ants. This process of indirect communication relies on a positive feedback mechanism [12,15] and depends on the environment characteristics, e.g. colony size [13], food type [18,19],

number of food sources [16,17], and the nature of the substrate on which the ants are moving [9].

In this paper, we investigate the ant foraging behavior in a relatively complex environment, composed of an artificial network of paths where several interconnected routes can lead the insects to a food source. Our aim was to study the responses of ants when sudden changes occur in the structure of the network. The ant decisions were analyzed at two different levels: (1) at the collective level, we analyzed the paths chosen by ants to reach the food source and return to the nest; (2) at the individual level, we quantified several behavioral parameters of the ants' actions. Finally, we show through a mathematical model that the same behavioral rules can lead the ants to find the shortest paths under the different network conditions studied.

This paper is organized as follows. In Section 2 we describe the experiments and the results we obtained. In Section 3 we present the model we developed and compare its output with the responses of the ant colonies. Finally, in Section 4 we discuss the performance of the model and comment on future research.

2 Methods and Results

In this section, we describe the experimental set-up, the insects used, the experiments performed and the results obtained, both at the collective as at the individual level.

2.1 Experimental Set-Up and Procedures

The experimental set-up consisted in a maze carved in a plastic slab (31.5 x 18.0cm) covered by a glass plate. The maze was composed of four identical lozenges assembled together (fig. 1). The branches of each lozenge formed an angle of 60 [3] and the maze galleries had a 0.5 x 0.5 cm section. Five circular chambers (ϕ 2.0 cm) were built at the extremity of some of the branches of the maze.

We used the Argentine ant, *Linepithema humile* [14], to perform our experiments. Foragers of this species lay a pheromone trail both in their outbound and nestbound movements [2,3,8]. The ants were collected near Narbonne (France) and were distributed in ten experimental colonies, each containing around 2,000 individuals. All individuals were collected outside the nest and could thus be considered as foragers. The ants were fed with a solid food composed of carbohydrate and vitamin [5]. Each colony was housed in a plastic container (20.0 x 20.0 x 7.0 cm), with the walls coated with Fluon® to prevent escape. Ants nested in test tubes, partially filled with water behind a cotton plug, placed into each container. No interactions between nests were possible.

The colonies were starved for four days before the day of the experiments. At the beginning of each experiment, the nest was connected to a glass box (35.0cm²) by a plastic bridge (40.0cm²). Ants had then access from this box to the maze and to the food source (1 M sucrose solution, the food was spread on

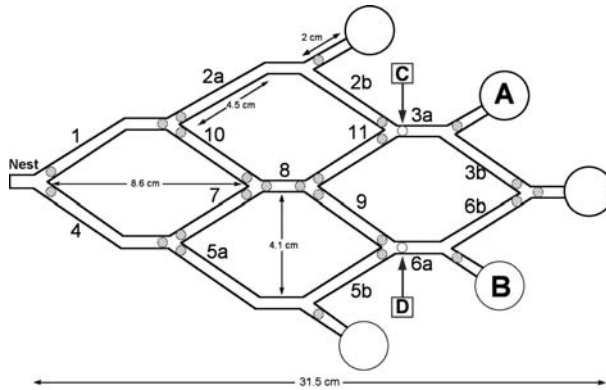


Fig. 1. Experimental set-up. The maze was carved in a plastic slab and the galleries had a 0.5 x 0.5 cm section. During the experiments, the ants had access to a food source (1M sucrose solution) located either in chamber A or B. The access to branch 3a and 6a can be blocked in C and D respectively

a surface large enough to avoid crowding effects). In half of the experiments, the food source was located in chamber A and in the other half, in chamber B (fig. 1). The access to the other chambers of the maze was denied during the experiments. After each experiment, the network was cleaned with alcohol to remove any residual chemical cues.

An experiment began when the first ant entered the network and the duration of each experiment was set to 60 min. The ant behavior was continuously recorded with a high definition camera (Sony CDR-VX 2000 E) placed above the set-up. The traffic of ants in the network was sampled during 20s every 3 min. The network offers twelve possible paths to connect the nest to the food source. These paths can be classified in four categories, according to their length: short, medium, long and very long (Table 1). The ten experimental colonies were tested under three conditions:

1. Control situation: the ants had access to the food source and no change was made on the network.
2. Block-after situation: in the first 30 minutes ants had access to all parts of the network, as in the control situation. After 30 minutes, the access to a branch next to the food source was denied (the branch 3a when the food was in chamber A, and the branch 6a when the food was in chamber B).
3. Block-before situation: the access to some branches was denied during the first phase of the experiments (0-30min.), forcing ants to use a long path. When the food was in chamber A, the ants could use only the route 1-10-7-5-9-11, and when the source was in chamber B, they could use the route 4-7-10-2-11-9-6a. After 30 min., the access to all the branches was allowed.

Whether a branch was selected or not at a bifurcation was tested by applying a binomial test [21] on the cumulated flow of ants on each branch. This allowed

Table 1. Possible paths to the food source and their lengths. s = short path, m = medium path, l = long path and vl = very long path.

Paths(source in A)	Paths(source in B)	Length
1-2a-2b-3a	4-5a-5b-6a	s - 21,5 cm
1-10-8-11-3a	1-10-8-9-6a	
4-7-8-11-3a	4-7-8-9-6a	
4-5a-5b-9-11-3a	1-2a-2b-11-9-6a	m - 30,5 cm
4-7-10-2a-2b-3a	1-10-7-5a-5b-6a	
4-5-6a-6b-3b	1-2-3a-3b-6b	
4-7-8-9-6a-6b-3b	1-10-8-11-3a-3b-6b	
1-10-8-9-6a-6b-3b	4-7-8-11-3a-3b-6b	
1-2-11-9-6a-6b-3b	4-5-9-11-3a-3b-6b	l - 39,5 cm
1-10-7-5-6a-6b-3b	4-7-10-2-3a-3b-6b	
1-10-7-5-9-11-3a	4-7-10-2-11-9-6a	
4-7-10-2-11-9-6a-6b-3b	1-10-7-5-9-11-3a-3b-6b	
		vl - 48,5 cm

us to determine the overall path selected by the ants through the network. Note that several paths could be selected in the same experiment when no significant choice was made at one or several bifurcations.

2.2 Experimental Results

In the control situation, ants selected one of the shortest paths of the network, in most experiments when going to the food source, and in all experiments when returning to the nest (fig. 2a).

In the first phase of the block-after situation, when ants had access to all parts of the network, the results were comparable to those obtained in the control situation: in the majority of experiments one of the shortest paths was selected (fig. 2b). In the second phase of the block-after situation, when the most direct access to the food was blocked, some colonies appeared to be unable to find a path, and instead performed loops in the network (fig. 2c). However, in most experiments ants chose a medium path, which was the shortest one towards the source in this situation. Some long paths were also selected. When returning to the nest on the other hand, all colonies selected one or two of the shortest paths.

In the second phase of the block-before situation, when the access to all the branches of the network was allowed again, the majority of the colonies found one of the shortest paths towards the food source (fig. 2d).

However, some colonies continued to use the long path they had selected in the first phase of the experiment, and one colony used both a short and a long path to reach the food. In the opposite direction, towards the nest, most of the colonies selected a short path. Only one colony chose a medium path.

We conclude that in most experiments ants found one of the shortest path in the network, both to reach the food source and to return to their nest.

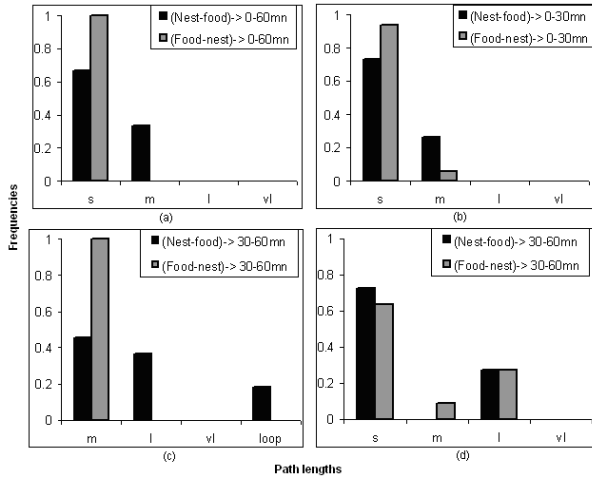


Fig. 2. Distribution of the outcome of the experiments.(a) in the control situation, when ants had access to all branches, (b)-(c) in the block-after situation, when one branch was blocked after 30 min.(d) in the block-before situation when several branches were blocked during the first 30 min of the experiment. s = short path, m = medium path, l = long path and vl = very long path. $N=10$ experiments for each situation

2.3 Individual Behaviors

We measured three behavioral characteristics at the individual level in the control situation: (1) the ant speed (2) the probability to make a U-turn and (3) the time spent at the food source.

The speed of the ants was computed from the measure of the time spent by individuals to travel long and short paths towards the food source. We found a mean value of 1.10 cm/s (\pm SD 0.48, $N = 123$).

We measured the frequency of U-turns made by ants both in the outbound and nestbound direction over a long path. A total of 521 ants were considered. We found a frequency of U-turn per ant of 0.15 ($N = 521$ ants) and 0.10 ($N = 458$ ants) for the outbound and nestbound direction respectively.

The average time spent by ants at the food source was 185.30 s (\pm SD 167.62, $N = 43$). The maximum number of ants in the network was equal to 100 individuals on average.

3 Model Description

In this section, we describe the parameters of our model and compare its output to the experimental results we obtained in the three experimental situations we tested.

3.1 Structure of the Model

Each step of the model was equivalent to 1 s. As the maximum number of ants moving through the network at any moment in the experiments was assessed to 100 individuals on average, we decided to use this limit in our model.

In addition to the parameters measured at the individual level, we estimated other parameters from previous studies, and introduced them in the model. The values of all the parameters we used in our model are given at the end of this section.

As it is known that the ant flux is related to the size of the colony, we estimated the probability for an ant i to enter in the environment at each simulation step t as:

$$P_{ent_i}(t) \approx U(\phi) \tag{1}$$

where: ϕ = ant flux; $\phi = 1/\text{maximum number of ants}$, and U represents a uniform probability distribution.

The distance traveled by an ant i at each step t was estimated as the ants speed V_i incremented by a random error ε :

$$D_i(t) = (V_i + \varepsilon) \tag{2}$$

where $\varepsilon \approx N(0, V_i/10)$, N represents a Normal distribution and

$$V_i = \eta + \zeta \tag{3}$$

η = constant measured in the experiments; $\zeta \approx U[0; \iota]$.

When an ant i moves through the network, it lays a quantity f_l in each branch l it travels. The model considered that ants deposit trail pheromone more frequently on their way back to the nest than when going to the food source [8]. The quantity of pheromone Q_l gradually decreases over time in a proportion fixed by a parameter δ :

$$Q_l(t) = \delta Q_l(t - 1) \tag{4}$$

where δ is a constant empirically obtained.

When reaching a bifurcation, the choice of a specific branch l depends on two characteristics: the pheromone concentration on the branches and their orientation relative to the ant direction of movement. As the ants have the capacity to locate the direction of the nest and the direction of the food source once they have found it [3], we considered that the orientation of a branch can be important in determining the course of an ant through the network.

The probability $P_c(j, k, t)$ for an ant of choosing branch j when it is at the bifurcation j - k at step t was thus estimated by using two probabilities: (i) $P_{pher}(j, k, t)$, the probability of choosing branch j as a function of the pheromone concentration on the branches j and k at the bifurcation j - k and (ii) $P_{dir}(j, k, t)$, the probability of choosing branch j as a function of its orientation.

$$P_c(j, k, t) \approx U \left(\frac{\rho(P_{pher}(j, k, t) + \tau P_{dir}(j, k, t))}{\rho + \tau} \right) \tag{5}$$

where:

$$P_{pher}(j, k, t) = \frac{(\sigma + Q_j)^\beta}{(\sigma + Q_j)^\beta + (\sigma + Q_k)^\beta} \tag{6}$$

$$P_{dir}(j, k, t) = \frac{(\cos\theta)^\alpha}{(\cos\theta)^\alpha + (\cos\omega)^\alpha} \tag{7}$$

θ and ω are the angles formed respectively by the branch j and the branch k with the longitudinal axis of the set-up; $\rho, \tau, \sigma, \alpha, \beta =$ constants empirically obtained. Equation (6) was proposed in earlier experiments with Argentine ants [4].

An ant i can change its direction of movement when traveling along a branch l by performing a U-turn. The estimation of the probability $P_{u_i}(t)$ for an ant i to make a U-turn at each step t over a short branch l , (labeled 3a, 6a and 8 in fig. 1), was based on previous results [4]:

$$P_{u_i}(t) \approx U \left(\frac{\varphi}{1.0 + \Pi Q_l(t)} \right) \tag{8}$$

where φ represents the maximum number of U-turns that can be performed on a short branch and Π is a constant empirically obtained.

Ants can also make a U-turn when the selected branch is not available, represented by Ω . Based on previous evidences [4], we estimated that the probability for an ant i to make a U-turn over a long branch l at each time t follows a sigmoidal law:

$$P_{u_i}(t) \approx U \left(\frac{v}{1.0 + \exp(-\psi Q_l(t))} \right) \tag{9}$$

where v represents the maximum number of U-turns that can be performed on a long branch and ψ is a constant empirically obtained.

Finally, ants can also make a U-turn when the selected branch is blocked. In this case the probability to make a U-turn is fixed:

$$P_{u_i}(t) \approx U(\Omega) \tag{10}$$

The time $T_{s_i}(t)$ spent by an ant i at the food source from instant t was also considered:

$$T_{s_i}(t) = (\kappa + \chi) \tag{11}$$

where: $\chi \approx N(0, \kappa/\mu)$ is a random error and κ, μ are two constants empirically obtained.

The values set to the parameters were: $\phi=0.01, \eta=1.0, \zeta=0.3, f_l=1.0$ in the outbound direction, $f_l=5.0$ in the nestbound direction, $\delta=0.99, \rho=1.0, \tau=0.4, \sigma=5.0, \beta=3.5, \alpha=3.0, \varphi=0.01, \Pi=1.0, v=0.07, \psi=0.003, \kappa=60.0s, \mu=5.0$ and $\Omega=0.005$. The simulations were run for 36,000 time steps and we performed 200 simulations for each situation.

When the parameter values could not be estimated from the experiments they were empirically adjusted in order to increase the fit between the results of the model and that of the experiments.

3.2 Comparison of the Model Output with the Experimental Results

In the control situation, ants found 252 paths to reach the food source. Most of them corresponded to the shortest paths (237 out of 252)(fig. 3). There was a good agreement between the solutions found by ants in the model and in the experiments. In the nestbound direction, the ants found 204 paths, all of them corresponding to the shortest paths. Only in four simulations did ants use simultaneously two short paths to reach the nest.

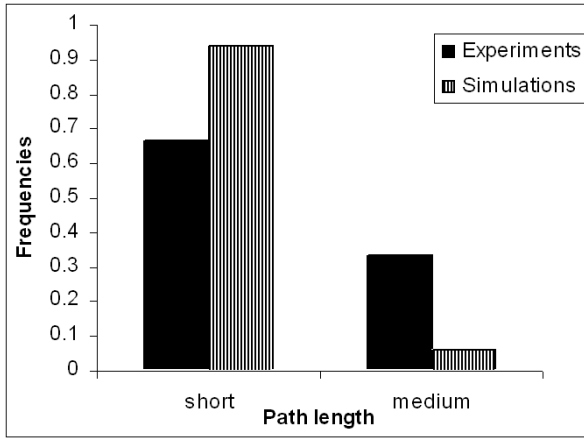


Fig. 3. Frequency distributions of the lengths of the paths chosen by the ants in the model and in the experiments for the outbound direction in the control situation (0-60 min.). s = short path and m = medium path

In the first phase of the block-after situation, ants selected 464 paths to reach the food source. Most of them corresponded to the shortest paths (248 out of 464), followed by medium paths (182 out of 464)(fig. 4a), in the same order as in the experiments. The model also generated some simulations where the long and very long paths were selected (7.33%). As this outcome was relatively rare, we considered that there was generally a good fit between the model and the experiments. In the nestbound direction, ants selected 539 paths in the simulations. Most of them corresponded to the short paths (275 out of 539) and medium paths (209 out of 539) (fig. 4b). Once again, the model generated some simulations where long and very long paths were selected (10.20%). However, the low level of occurrence of this outcome suggested a good agreement between the simulations and the experiments.

In the second phase of the block-after situation, the ants in the simulations selected 247 paths to reach the food source. The shortest paths (medium paths in this case) were selected in the majority of the simulations (164 out of 247) (fig. 5a). As in the experiments, the occurrence of loops was also observed (76

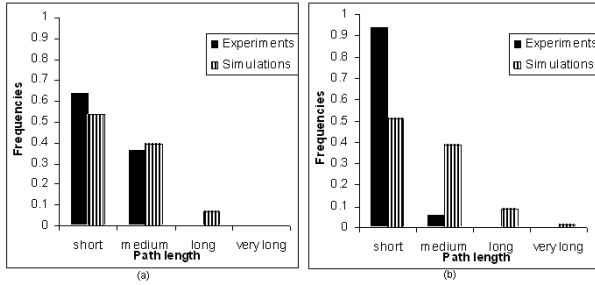


Fig. 4. Frequency distributions of the lengths of the paths chosen by ants in the model and in the experiments in the (a) outbound direction and (b) nestbound direction in the first phase of the block-after situation, when the access to all branches was allowed(0-30 min.)

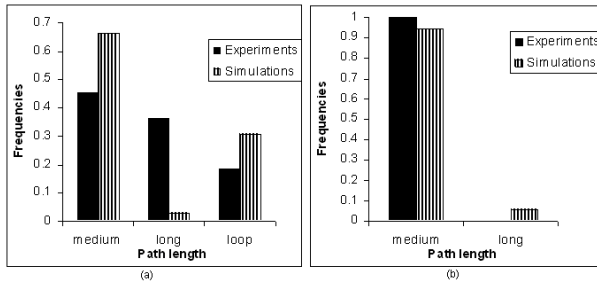


Fig. 5. Frequency distributions of the lengths of the paths chosen by ants in the model and in the experiments in the (a) outbound direction and (b) nestbound direction in the second phase of the block-after situation, when the access to some branches was denied(30-60 min.)

out of 247 paths). The long paths were also selected, representing a minor part of the paths selected (7 out of 247). In the nestbound direction, ants selected 227 paths; almost all of them corresponded to medium paths (214 out of 227)(fig.5b). This performance was similar to that observed in the experiments.

In the second phase of the block-before experiments, when all branches could be used, the ants selected 331 paths to reach the food (fig. 6a). These paths were distributed as followed: short paths (269 out of 331), medium paths (26 out of 331), long paths (35 out of 331) and loop (1 out of 331). As the occurrence of loops was reduced in this direction, we considered that the model performed satisfactorily. We noted nonetheless that the model performed rather badly in this situation. This was explained by the fact that, in the experiments, the high concentration of pheromone deposited on the branches used during the first 30 minutes attracted a lot of ants. These ants persisted therefore to use long paths.

When returning to the nest, ants selected 212 paths in the simulations (fig. 6b), most of them corresponding to the short paths (206 out of 212). Some

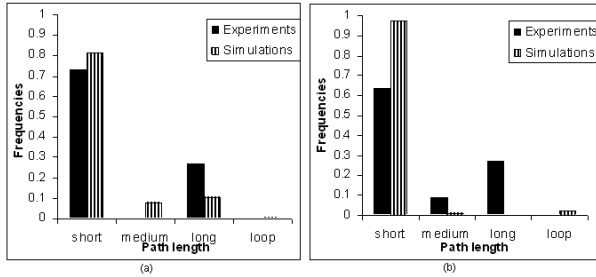


Fig. 6. Frequency distributions of the lengths of the paths chosen by ants in the model and experiments in the (a) outbound direction and (b) nestbound direction in the second phase of the block-before experiments, when the access to all branches was allowed again.(30-60 min.)

paths corresponded to loops (4 out of 212) and medium paths (2 out of 212). Otherwise, the ants in the simulations can be considered as more efficient than those in the experiments because they selected only short paths.

4 Conclusion

The aim of this work was to study how ants adapt their foraging behavior when environmental conditions are suddenly changed, e.g. when a path towards a food source is obstructed or when new and shorter routes are offered to the ants to reach a food source. Such changes are likely to arise in the natural environment and it is important to understand how ants react to them behaviorally and on which time-scale they are able to adapt.

In this study we introduced Argentine ants in a complex network, in which several paths of different lengths can lead to a food source. We changed the organization of the network, allowing or denying the access to some branches. The ant behavior was analyzed both at the collective and individual levels, and several aspects of their behavior and movement through the network were quantified. The paths selected by the ants, both when moving towards the food and the nest, were noted when the access to all branches was allowed and when one or several branches were blocked. The results show that ants were able to find the shortest paths in all situations, specially when returning to their nest. This result has been observed in previous studies [2,20], indicating the ability of the ants to locate the nest and return straight to it.

After the experimental study we developed an individual-based model whose parameters were based on the different decisions made by real ants when moving in the network when the access to all branches was allowed. The model was applied to the same situations tested in the laboratory with real ants, and the output of the model was compared to the results of the experiments. There was in general a good agreement between the results of the simulations and those of the experiments. In most simulations generated by the model the ants selected

one of the shortest path, both in the outbound and nestbound direction. The model proved to be flexible enough to adapt to the various situations tested. It can also be considered as robust since the same set of parameter values was used in all situations. The next step will be to apply the model to other situations we tested in the laboratory with Argentine ants, and most importantly, to use the model to make prediction about the ant behavior in different environmental conditions not yet tested.

Acknowledgments

This work was supported by a doctoral grant from FAPESP to Karla Vittori.

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