

FROM INDIVIDUAL TO COLLECTIVE RULES IN EMERGING TRAIL PATTERN FORMATION IN ARGENTINE ANTS (*LINEPITHEMA HUMILE*)

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Key words: Reinforced random walks, Ant foraging, Stochastic Processes

Abstract. We study the formation of trails by Argentine ants (*Linepithema humile*) when foraging in an empty arena. To do so, we first investigate the individual behavior by analyzing some experimental data. Based on these observations, we provide a distribution for the random change in direction that they approximately undergo while foraging as a mixture of a Gaussian and a Pareto distribution. As explained in previous work, two main ingredients are necessary in the model for the motion of ants in the plane: persistence and reinforcement. Numerical simulations based on this model lead to the formation of branched ant-trails similar to those observed in the experiments.

1 INTRODUCTION

In the recent years, many scientists have been studying the mechanisms by which a collection of individuals manage to communicate and organize themselves in order to produce a collective behavior or achieve some goal. This includes the pattern formation in slime molds and bacteria, fish schooling, bird flocking, trail formation in ants, etc. As a consequence, the study of these self-organization oriented to the achievement of a collective animal behavior is currently a very intense area of research in the frame of complex networks and a source of new and interesting mathematical problems (see, for instance, the books [1-3]).

There are many problems related to complex networks. Among the most interesting biological ones is the formation of large and intricate trail networks by multiple species of ants [4-8]. Their patterns that can extend up to a hundred meters from the nest result from the collective activity of thousands of individual workers laying and following pheromone trails as they explore and exploit their environment. Previous studies have shown that ant trail networks, formed by individuals with very limited cognitive capabilities, are nonetheless particularly efficient structures to facilitate the rapid exploitation of resources [9-11] and the

movement of ants across their territory [7]. This raises the following question: how can a group of cognitively limited individuals, with access to partial and local information only, build such efficient, large scale structures? From a mathematical point of view, the question can be reformulated as follows: what is the minimal set of ingredients that a model must incorporate to give rise to networks similar to those of ant colonies? This question can be extended to other self-organized network systems, such as the galleries of ant nests [12], but also trail systems created by humans [13, 14].

In order to answer this question, recent experimental and theoretical studies [11, 15, 16] have investigated the individual and collective behaviors of Argentine ants (*Linepithema humile*) when navigating graphs (i.e., networks of constrained paths). These studies suggest that a mechanism for the formation of ant trails should include an attractive, durable signal (pheromone) as well as motion persistence, that is, the tendency to move straight in the absence of external information. This kind of motion is known in the mathematical literature as *reinforced random walk* [17-19] and it is sufficient to reproduce the individual and collective movement patterns of ants on graphs [16].

In the present article, we propose to extend the previous findings by considering the motion of ants in the plane. In this situation, ants can significantly change direction at any point of their motion and not only at discrete points on a graph. Using experimental observations of ants exploring an empty circular arena, we will estimate the distribution of their direction changes and the degree of persistence of their motion. Based on this information, we will propose a model of the spontaneous motion of ants (i.e., in the absence of external information). We will also model the trail-following behavior of ants after the results of [20]. [20] shows that ants turn in response to the current, local pheromone distribution, while their speed is unaffected by the presence of pheromone. The response of ants to the local pheromone distribution follows Weber's Law: the difference between the quantities of pheromone on both sides of an ant divided by their sum determines the magnitude of the ant's turning angle. In our model however, we will not only consider the pheromone quantities on both sides of an ant, but we will instead integrate pheromone concentration over a circular sector that can be thought of as the region that can be reached by the ant's antennae. We will implement Monte-Carlo simulations of the complete model (motion persistence plus trail-following) and we will show that these simple rules are sufficient to create trail networks.

2 METHODS AND RESULTS

We perform two different types of experiments: in the first one we study the individual behavior of ants when foraging and in the second one we study the collective behavior and the formation of trails when foraging in an empty arena. To do so, we record the trajectories to collect data regarding the change in direction measured by the direction angles and perform a statistical analysis to find the best probability distribution that fit our data. Further details can

be found in [20, 21].

2.1 Individual trajectories

In the case of individual ants, in order to know the distribution of the difference in the direction angles when an ant moves, we consider 40 different ants and compute the variation in the direction between one step and the next one. We find that the best fit is a mixture of a Gaussian (for $|\alpha| < 2\sigma$) and Pareto (in the tails, for $|\alpha| > 2\sigma$) distributions (suitable normalized):

$$\begin{aligned}
 f(\alpha) &= \frac{1}{B} \frac{1}{\sqrt{2\pi}\sigma^2} e^{-\frac{(\alpha-\mu)^2}{2\sigma^2}}, \quad |\alpha - \mu| \leq 2\sigma \\
 f(\alpha) &= \frac{A}{B(\alpha - \mu)^2}, \quad |\alpha - \mu| > 2\sigma \\
 A &= \frac{4}{\sqrt{2\pi}} e^{-2} \sigma, \quad B = \frac{A}{\sigma} + \int_{-2}^2 \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}} dx.
 \end{aligned} \tag{1}$$

where α is the angle, μ is the mean and σ is the standard deviation of the Normal distribution.

There are 3 further observations to take into account when modeling ants as random walkers:

1. There exists a dependence between the length of each step of the random walk and the deviation angle: long steps are taken when the deviation is small while short steps are associated to a very large deviation.
2. When ants stop they take relatively long times before deciding in what direction to make the next move.
3. The average of the angle of deviation of the ant taken as a random walker is not zero in general.

Considering these observations, we perform Monte Carlo simulations for the ants and check that the simulations represent very well the experimental results (see figure 1 for an example).

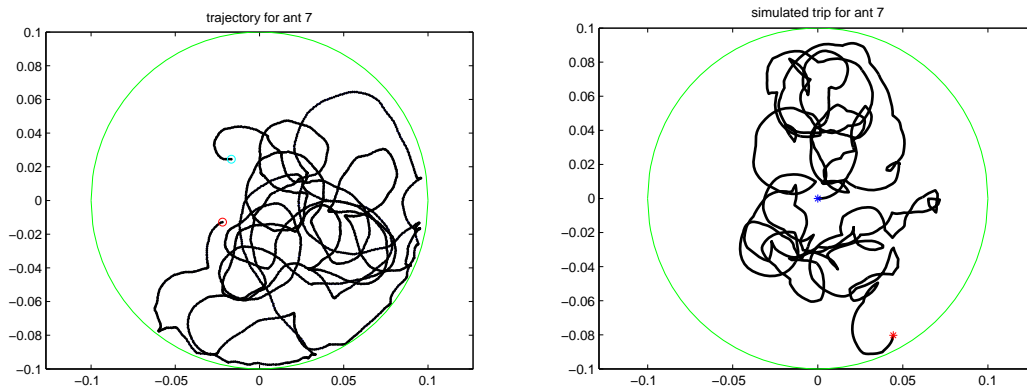


Figure 1: Comparison between the experimental path of ant 7 (left) and our random walk simulation (right).

2.2 Collective behavior: ants in a petri dish

In order to describe the collective behavior of ants when foraging in an empty arena, we perform Monte Carlo simulations to reproduce the experimental results reported in [20]. In each simulation we consider 500 ants that depart sequentially from the center of the circular arena. Ants start entering the arena soon after they are given access to it. In the simulations ants are treated as point-like objects and they deposit pheromone at every time step. We also consider evaporation effects as measured in real experiments so that, once the pheromone is deposited it evaporates according to an exponential law. Ants leave the center of the disc with a random initial direction. At every time step, the ant measures the amount of pheromone at the current position. In order to compute the new direction, we take into account a parameter that measures the importance of the pheromone-induced reinforcement. Before computing the new direction for the ant we introduce a noise term following the mixed Normal+Pareto distribution. We check if the ant is at the boundary and if so, we project the arrival direction over the tangent to the boundary and declare the new direction to be that of the tangent. The different values for the parameters are taken from the experiments (see [21] for a complete explanation).

We treat ants as pure random walkers when they detect an amount of pheromone that is below a certain threshold that represents the minimum amount of pheromone inducing the ant to respond to the chemical signals left by fellow ants. When the ant detects an amount of pheromone concentration beyond a certain threshold the motion is computed as the superposition of a random walk and reinforcement proportional to the gradient of the amount of pheromone. Next, we perform a suitable normalization of the new direction and introduce a restriction for the possible changes in direction (the change in direction cannot be larger than a certain angle $\alpha_0=\pi/3$, similarly as in [20]). Finally, when measuring the amount of pheromone in the neighborhood of the ant we only consider the points inside a sector with angle $\alpha_i=\pi/3$ around the direction of the ant (ants can only measure the amount of pheromone at certain angles that can be reached with the ant's sensors).

We have implemented the model described above with the parameters computed in the statistical analysis of real experiments. If we follow the evolution in time (see figure 2) the process of path ramification can be identified. In figure 2 we represent the evolution for $N=500$ ants at times 400, 800, 1200 and 1600 s. Notice that at early stages the behavior is diffusive, with the highest concentration of pheromone at the center of the disc, but an instability eventually develops and filamentary structures start to be created and progressively reinforced until a ramification network of paths between the disc center and the boundary is formed.

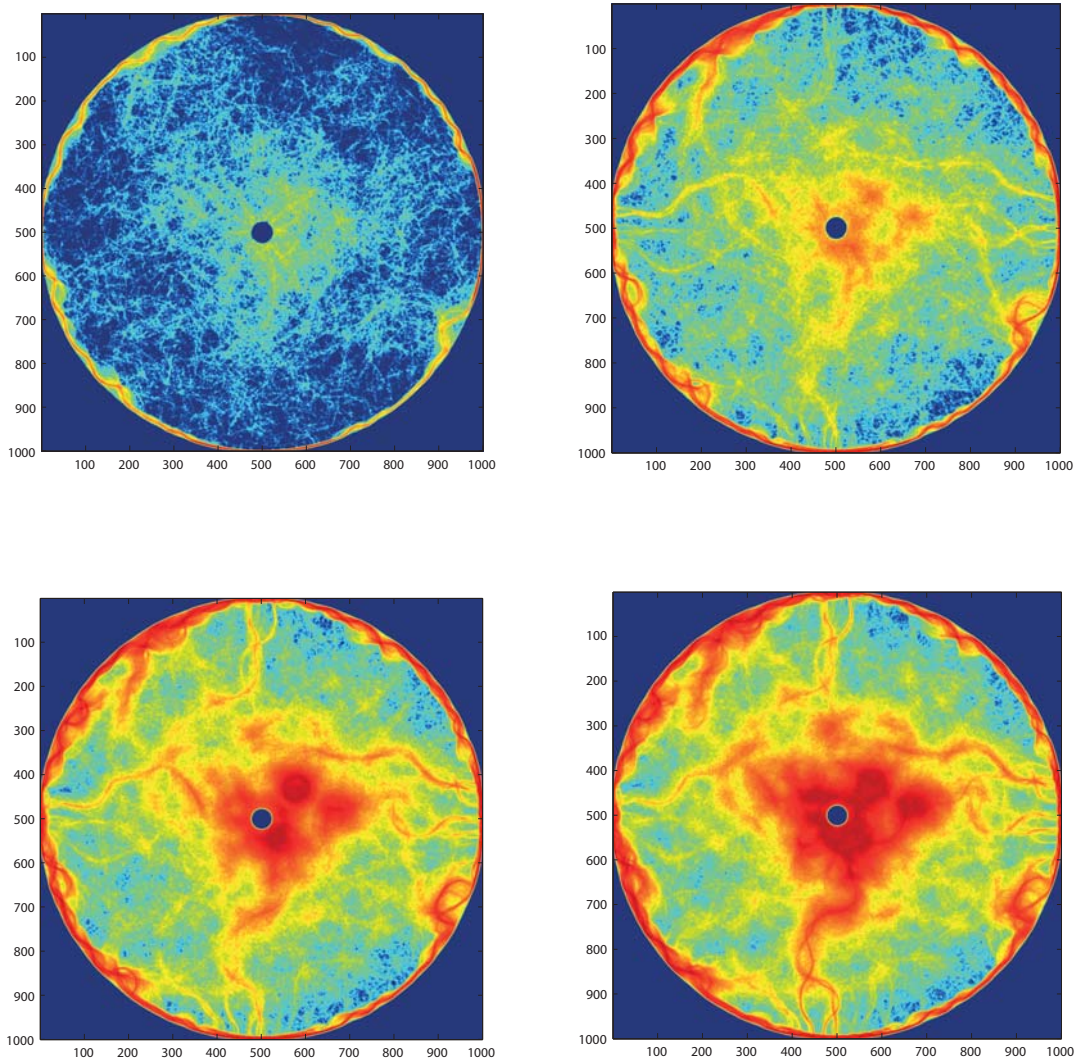


Figure 2: Concentration of pheromone after 6.67 min. (top left), 13.33 min. (top right), 20 min. (bottom left) and 26.67 min. (bottom right) with $N=500$. The red color means high concentration/visits, the blue color implies low concentration/visits.

4 CONCLUSIONS

We have described a model simulating the behavior of ants when foraging individually and a model that describes the formation of pheromone trails in the plane. Following the ideas presented in [16] we have considered the combination of reinforcement and persistence. That is, we consider ants as reinforced random walkers where the probability of moving in a specific direction is influenced by the concentration of pheromone near them, and we also consider persistence (tendency to keep the previous direction in the absence of any external effect).

We have also provided a distribution for the random change in direction that ants undergo while foraging, based on experimental observations. To do so, we have integrated pheromone concentration over a circular sector that can be thought of as the region that can be reached with the ant's antennae by turning its head. The Monte Carlo simulations show that after 20 minutes a branch-like pattern of trails has clearly developed. Later, ants reinforce both the trails and the boundary, as is the case for real experiments.

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