Models of Ant Foraging Lines.

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**Abstract**

The objective of this problem is to study ant foraging lines in one and two dimensions in order to understand their dynamics and examine the fitness of ant colonies. A simple model to describe ant traffic is formulated using conservation laws and a behavioral model. In this work, the behavioral model assumes that the concentration of pheromones is simply proportional to the density of ants. This leads to a hyperbolic system for the density and velocity of ants. The system is reduced to a system of second order PDEs which is analyzed using Fourier series. The Fourier analysis predicts the existence of phase speeds in the ants’ motion which can be verified experimentally.

The group divided into two teams in order to study the one-dimensional and the two-dimensional cases separately. The two-dimensional analysis was done numerically using a stochastic model and simulated using cellular automata. This simulation provided qualitative information to study the formation of foraging lines. In particular, this model shows the importance of large populations. Also, additional constraints on the model were considered in order to make it more realistic. For the one-dimensional analysis, the first goal was to find representative Froude numbers for the ants’ movement from the experimental data. The full hyperbolic system was analyzed and its characteristic speeds identified. Numerical solutions of the problem were obtained using both a Lax-Friedrichs and a Lax-Wendroff scheme.
1 Problem Description.

The objective of this problem is to study ant foraging lines in one and two dimensions in order to understand their dynamics and examine the fitness of ant colonies.

Individual ants are considered “expendable resources”. Their lifespan is 1 to 2 years, they are nearly blind and therefore their censorial abilities rely in the detection and creation of chemical trails of pheromones. They are fast movers and carriers and, in addition to consuming food, they can regurgitate it through antennation. These characteristics make them individually inept; their functions consist of very simple tasks, such as searching for food (foraging), carrying food, recruiting others, etc. On the other hand, ant colonies form very robust systems. Their lifespan is of the order of tens of years and are resistant to environmental changes. They perform sophisticated tasks, such as finding the minimum path between the hive and food sources with multiple barriers and obstacles without the necessity of central control. Ants account for 15–20% of the total animal biomass of the Earth, making them one of the most successful animal on the planet, and thus they have become the inspiration for swarm algorithms.

The most basic description of the formation of foraging lines is the following. Individual ants leave the hive searching for food. When one or more ants find a food source, they release pheromones, leaving a trail on their way back to the hive. This trail is detected by other ants and can be followed by ants in the vicinity of the trail and by ants leaving the hive. The first path created by the ants carrying food from the food source to the hive is not necessarily the optimal one, but as more ants follow the trail, it eventually gets optimized according to the minimum distance, considering barriers and obstacles. Schematically, this description can be represented as in Figure 1.

Several questions can be addressed from this basic heuristic algorithm. From observation and measurements, we can ask whether or not ants have memory, how they communicate with each other, how they select a trail from many choices. In trying to understand foraging lines algorithms, we can ask if these algorithms can be used for solving harder problems such as the TSP. In complex system analysis, we can study how simple rules can generate complex systems. For traffic analysis, we can investigate how ant densities impact foraging dynamics.

1.1 Traffic Modeling Essentials.

A simple model to describe ant traffic can be formulated using conservation laws. Consider ants moving along a trail with density $\rho(x,t)$ and speed $v(x,t)$. Given that the number of ants must be conserved in time and space, we can write

$$\frac{\partial}{\partial t} \rho(x,t) + \frac{\partial}{\partial x} (\rho(x,t)v(x,t)) = 0.$$  

Assuming $v = v(\rho)$, we get the conservation law

$$\frac{\partial}{\partial t} \rho + \frac{\partial}{\partial x} q(\rho) = 0;$$
Figure 1: (a) Ants leaving the hive looking for food, (b) pheromones path created by ants returning to the hive, (c) and (d) path selection according to the minimum distance, (e) and (f) path optimization.

where \( q(\rho) = \rho v(\rho) \) is the flux of ants. This partial differential equation can lead to rarefaction waves and shocks. The simplest model of \( v \) as a function of \( \rho \) is linear dependence (see Figure 2), often cited in simple models of traffic flow on crowded highways. A more realistic behavior is shown in Figure 3 based on experimental observations. These observations led us to the conclusion that simple traffic models for ants are not good enough and that more careful experiments are needed.

\[
v = v_{\text{max}} \left( 1 - \frac{\rho}{\rho_{\text{max}}} \right).
\]

Figure 2: A simple relationship between \( v \) and \( \rho \) given by \( v = v_{\text{max}} \left( 1 - \frac{\rho}{\rho_{\text{max}}} \right) \).

In order to improve the model, a conservation law is needed together with a behavioral model. Consider two ant populations. Let type A be the ants going to get food and type B be the ants returning to the hive. Moreover, the ants can accelerate or decelerate to minimize
stress caused by pheromone gradients or other factors. We then get two conservation laws

\[
\frac{\partial}{\partial t} \rho_A + \frac{\partial}{\partial x} (\rho_A v_A) = 0,
\]

\[
\frac{\partial}{\partial t} \rho_B + \frac{\partial}{\partial x} (\rho_B v_B) = 0,
\]

and two behavioral models,

\[
\frac{d}{dt} (v_A(x,t)) = \frac{\partial}{\partial x} \sigma_F(x,t),
\]

\[
\frac{d}{dt} (v_B(x,t)) = \frac{\partial}{\partial x} \sigma_H(x,t),
\]

where \(\sigma_F\) and \(\sigma_H\) are the stresses of the foraging ants and the ants returning to the hive, respectively. The simplest stress would be \(\sigma_F = K_A \rho_B\) and \(\sigma_H = K_B \rho_A\), with \(K_A\) and \(K_B\) constants. This model combines many effects including pheromone chemotaxis, antennation
and collision exchange. Also, it assumes that ants are mainly attracted to pheromones and that the pheromones diffuse and decay at a slow rate. Therefore, the concentration of pheromones is simply proportional to the density of ants. Taking derivatives explicitly we obtain:

\[
\begin{align*}
\frac{\partial}{\partial t} v_A + v_A \frac{\partial}{\partial x} v_A &= K_A \frac{\partial}{\partial x} \rho_B, \\
\frac{\partial}{\partial t} v_B + v_B \frac{\partial}{\partial x} v_B &= K_B \frac{\partial}{\partial x} \rho_A.
\end{align*}
\]

To linearize the system we write

\[
\rho_A(x, t) = \rho_A^{(0)} + \epsilon \rho_A^{(1)}(x, t),
\]

\[
v_A(x, t) = v_A^{(0)} + \epsilon v_A^{(1)}(x, t),
\]

and similarly for \(\rho_B\) and \(v_B\). It is reasonable to consider \(V = -v_A^{(0)} = v_B^{(0)}\), then the system of four coupled first order partial differential equations can be reduced to a system of two coupled second order partial differential equations. Thus, after making a rescaling of variables the system can be written as

\[
\begin{align*}
\frac{\partial^2}{\partial t^2} \rho_A^{(1)} - 2i k \frac{\partial}{\partial x} \rho_A^{(1)} + \frac{\partial^2}{\partial x^2} \rho_A^{(1)} + \kappa_A \frac{\partial^2}{\partial x^2} \rho_B^{(1)} &= 0, \\
\frac{\partial^2}{\partial t^2} \rho_B^{(1)} + 2i k \frac{\partial}{\partial x} \rho_B^{(1)} + \frac{\partial^2}{\partial x^2} \rho_B^{(1)} + \kappa_B \frac{\partial^2}{\partial x^2} \rho_A^{(1)} &= 0,
\end{align*}
\]

where

\[
\kappa_A = \frac{K_A \rho_A^{(0)}}{V^2}, \quad \kappa_B = \frac{K_B \rho_B^{(0)}}{V^2}.
\]

It is important to point out that if there was no interaction, the uncoupled equations describe two waves moving to the left and to the right. If we look for solutions to these equations in the form of Fourier series and assuming periodicity in the foraging line,

\[
\rho_A^{(1)} = \sum_{n=-\infty}^{\infty} D_n(t) \exp\left(\frac{in\pi x}{\lambda}\right),
\]

\[
\rho_B^{(1)} = \sum_{n=-\infty}^{\infty} E_n(t) \exp\left(\frac{in\pi x}{\lambda}\right),
\]

we arrive at a coupled system of ordinary differential equations for each mode \(n\),

\[
\begin{align*}
D'' - 2i k D' - k^2 D - k^2 \kappa_A E &= 0, \\
E'' + 2i k E' - k^2 E - k^2 \kappa_B D &= 0,
\end{align*}
\]

with \(k = n\pi/\lambda\). This system can be written as \(x' = Mx\), and the solution depends on the eigenvalues and eigenvectors of the matrix \(M\), given by

\[
c = \pm ik \sqrt{1 \pm \sqrt{\kappa_A \kappa_B}}.
\]
Therefore, the solution describes a linear combination of traveling waves with two possible phase speeds $c_1 = \sqrt{1+\sqrt{\kappa_A\kappa_B}}$ and $c_3 = \sqrt{1-\sqrt{\kappa_A\kappa_B}}$ moving to the left and to the right, respectively. Experimental data shows evidence of these traveling waves as shown in Figure 5.

Based on these observations, one can conclude that acceleration/deceleration play a significant role in ant traffic dynamics. Also, the simplest behavioral model yields a set of equations similar to a two-fluid flow model but with a strange stress term with only two unknown parameters related to the coupling. One can ask if this is enough to capture the essential dynamics of a foraging line. Linear analysis predicts waves with two phase speeds, which is a result supported by experimental data.

The remaining objectives of this research group are to further analyze this model incorporating history effects in the ant stress, to do a full nonlinear computation in one dimension or more, to use different boundary conditions (periodic boundary conditions were assumed before), to further study the linear theory including modulations and to do an analysis of the two-dimensional behavior.
2 Analysis.

The group divided into two teams to work on the two different approaches to the problem, the one-dimensional and the two-dimensional case.

2.1 Two-Dimensional Analysis.

The two-dimensional model provides a qualitative analysis of the formation of foraging lines using a stochastic model and solved numerically with a cellular automata. Initially, a certain number of ants leave the hive searching for food. To model the trajectories of these ants a Brownian motion with momentum is used. This means that the ants take the next step following a Brownian motion weighted in the direction that they have been following. At this stage there are no pheromones in the environment. The ants have a radius of perception where they are able to detect pheromones or other ants. When an ant finds the food, it has to return to the hive. This is modeled again with a stochastic motion weighted in the direction of the greatest density of ants (this gives the ant the direction towards the hive). As the ant returns to the hive, it leaves a trail of pheromones. If this trail is in the radius of perception of other ants, their movement will be weighted by the direction of the pheromone trail. Then, they will be able to find the food and return to the hive following a locally determined trail given by the pheromones. This model demonstrates the importance of large populations. When a small initial number of ants is used, the food is never found, whereas a large initial number of ants leads to a successful foraging line. This simulation also provides a qualitative description of how the foraging line is created, the usefulness of pheromones and the complexity of ants’ movements. This is a very basic model that does not consider boundary conditions (in the previous model, if an ant reaches the boundary of the matrix it is considered as a dead ant), ant-ant communication and more than one pheromone trail. Its strengths rely on the stochastic motion incorporating momentum, the pheromone attraction, the qualitative description of the formation of foraging lines and the estimate of the fitness of the nest. Using this model, only one third of the initial number of ants return to the nest with food. Further considerations may include additional pheromones trails and their optimization, ant-ant communication, more robust boundary conditions and alteration of parameters.
2.2 One-Dimensional Model.

2.2.1 Froude Number Analysis.

The first goal in the one-dimensional model is to obtain an estimate of the product of the Froude numbers $\kappa_A\kappa_B$. Recall that

$$\kappa_A = \frac{K_A\rho_A^{(0)}}{V^2},$$

$$\kappa_B = \frac{K_B\rho_B^{(0)}}{V^2},$$

Estimates may be obtained from the work of Johnson and Rossi "Mathematical and Experimental Study of Ant Foraging Line Dynamics." These numbers are obtained from the fast and slow phase velocities

$$c_1 = \sqrt{1 + \sqrt{\kappa_A\kappa_B}},$$

$$c_3 = \sqrt{1 - \sqrt{\kappa_A\kappa_B}},$$

respectively (see Figure 6). It is then found that

$$c_1 = 1.36 \text{ cm/sec},$$

$$c_2 = 0.55 \text{ cm/sec}$$

and therefore $V \approx 1.04 \text{ cm/sec}$ and $\kappa_A\kappa_B = 0.5$. The strengths of this analysis are that the data was sampled over a large number of 100 second intervals and multiple speeds were taken from each to come up with a reasonable maximum and minimum speed. Also, $V$ is close to 1 cm/sec, which was expected. The weaknesses of this analysis are the places for human error in the speed approximations and that the nature of the data prevents a detailed analysis for movement of individual ants, leading to poor analysis of the traveling waves (speed, density).

2.2.2 Full Model Redux.

Returning to the full model, we have an hyperbolic system of the form $u_t + Au_x = 0$ where

$$A = \begin{bmatrix}
  v_A & 0 & \rho_A & 0 \\
  0 & v_B & 0 & \rho_B \\
  0 & -k_A & \frac{1}{2}v_A & 0 \\
  -k_B & 0 & 0 & \frac{1}{2}v_B
\end{bmatrix}.$$

The eigenvalues of this matrix are

$$\frac{1}{2} \left( v_B + v_A \pm \sqrt{(v_a - v_B)^2 + 4\sqrt{k_Ak_B\rho_A\rho_B}} \right).$$

If this system is hyperbolic, then the eigenvalues must be real, which implies that small values of $k_A$ and $k_B$ are needed, which, in turn, implies “lightly programmed” ants. The
boundary condition to the system of equations can be chosen from many options. One can think of radiation conditions, where ants are entering or leaving the boundary, or a “revolving door” condition, where all the ants arriving to the boundary are reflected into the domain of work. For this model, periodic boundary conditions are chosen, given its simplicity to implementation and the experimental evidence. Numerical solutions of the model were obtained using two schemes, both standard for hyperbolic problems. In the second-order Lax-Wendroff scheme, dispersion error was introduced. This error grew in time as it interacted with the ants’ densities. The first-order Lax-Friedrichs scheme did not presented this problem, but the numerical diffusion killed small signals, making it difficult to check the linear case. Also, diffusion muted the sharp interactions one might expect from a hyperbolic system.

The simple model has some weaknesses that must be improved in order to get a more accurate description, especially concerning the physical world limitations. At the nest, one must consider limited storage space for food, the time needed to deposit and store the food, external agents such as predator and competing ants leading to possible raids on food stores and warfare, and the inevitable loss of ants due to predators and unsuccessful foragers who get lost. At the food source, one must consider issues to improve the model such as feeding time which can produce traffic jams if the density is high, food source can be sporadic or periodic in time, or simply the existence of alternating feeding sites, which results in another “sink” for otherwise unsuccessful foragers.
3 Conclusions.

The two-dimensional analysis was done using a stochastic model and solved numerically using cellular automata. This approach did not provide quantitative data but it was helpful to understand qualitatively the formation of foraging lines. In particular, it emphasized the importance of large populations. It was observed in the simulations how a small ant population tends to die quickly whereas a bigger population survives for longer periods of time. On the other hand, the stochastic model, which uses Brownian motion for the ants’ movement, showed qualitatively how the foraging line is created. This model appears to be a good approximation to the problem. Several further constraints to the model were discussed in order to make it more realistic such as additional pheromone trails and more robust boundary conditions. For the one-dimensional model, the first goal was to obtain representative Froude numbers using the data from the work done by Johnson and Rossi. The full hyperbolic system was analyzed examining the eigenvalues of the matrix that results from the linear approach. Periodic boundary conditions were chosen in order to solve the problem numerically. The numerical approaches were the Lax-Friedrichs scheme and the Lax-Wendroff scheme. The Lax-Wendroff scheme introduced dispersion error that grew in time. The Lax-Friedrichs scheme seemed to be a better approach to the problem, but it killed small signals and muted the sharp interactions one might expect from a hyperbolic system. Finally, further analysis of how to make the model more realistic was discussed. Predators and the loss of unsuccessful foragers, for instance, must be considered in order to improve the model.