# A mathematical and experimental study of ant foraging line dynamics

Katie Johnson<sup>a</sup> Louis F. Rossi<sup>a</sup>

<sup>a</sup>Department of Mathematical Sciences University of Delaware Newark, DE 19716 USA

# Abstract

In this article, we present a mathematical model coupled to an experimental study of ant foraging lines. Our laboratory experiments do not support the common traffic modeling assumption that ant densities and velocities are directly correlated. Rather, we find that higher order effects play a major role in observed behavior, and our model reflects this by including inertial terms in the evolution equation. A linearization of the resulting system yields left- and right-moving waves, in agreement with laboratory measurements. The linearized system depends upon two Froude numbers reflecting a ratio of the energy stored in the foraging line to the kinetic energy of the ants. Furthermore, the model predicts and the measurements support the existence of two distinct phase velocities.

Key words: Mathematical modeling, ant colony, self-organization, foraging lines.

# 1 Introduction

Ants form one of several insect societies that organize themselves into a robust collective organism, and as such, provide rich theoretical ground for the exploration and understanding of complex collective behavior through the self-organization of simple organisms. One distinct advantage to studying ants is that careful experiments are inexpensive to implement and relatively easy to perform. Another is that there is a wealth of observational data on many ant species providing considerable insight on individual behavior and the various modes of local communication that facilitate colony behavior [HW94,Wil62]. Ants communicate locally through chemicals which can alert the ants of enemies or guide them to the food source and

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back to the hive. More specifically, and are able to communicate with one another through secretions, passing excitement or odors [PL65]. Ants do not smell food, rather they follow the scent left by other ants who come across food. If the food source is moved from its original location after a pheromone trail is developed, ants will continue to follow the trail even though it no longer leads to food. However, a trail laid by an ant has a short lifetime of roughly six minutes and therefore must be sustained by a regular flow of foraging ants [Goe57]. By "regular flow," we do not imply that the flux of ants is constant. To the contrary, our measurements and model predictions indicate that this is not the case generically. Rather, a regular flow means that many ants traverse any given position on the trail during any six minute interval. In addition, it has been observed through experimentation that ants return to the hive following their own scent trail [Ska61]. What fascinates most investigators is that there has been no observation or measurement of global control or coordination. Rather, the global behavior of the colony is a product of simple, local interactions. Therefore, parameters governing simple individual behavior impact the growth and development of the entire ant colony complex. Our ability to identify and understand the parameters driving these behaviors will help resolve fundamental questions of the duration, fate and long term evolution of insect societies [BTD<sup>+</sup>97,Sch00]. Thus, we turn our attention to a detailed study of ant foraging line behavior, so that we can deduce fundamental local parameters that govern global outcomes.

Generally, the ants are nearly blind and possess little or no memory of past activity. Cognition appears to be limited to the operation of different states, as if individuals switch from one basic algorithm to another from a limited selection of available algorithms. Examples include searching for food, transporting food or material to or from the hive or being alarmed. One of the simplest units of collective behavior is the foraging line, a bi-directional flow of ants between a food source and the hive. The ant colony we study, *Formicidae Pheidole*, exhibits the foraging behavior commonly seen on kitchen counters and picnic tables. The original aim of this project was to find parallels between ant traffic patterns and human vehicular traffic, similar in spirit to the study by Burd et. at. and John et. al. [BAAS02, JSCN04]. In particular, we were interested in whether ants would resolve traffic paradoxes where humans behavior fails to achieve optimal configurations (see [AS94] for some sample configurations). These traffic studies have at their core the assumption that there is a functional relationship between density and flow rate. A large number of observations and measurements led us to the conclusion that such a functional relationship does not exist for our ant colony, even in well-established foraging lines (for example, look ahead to Fig. (3)). Instead, we observe a rich spatio-temporal pattern of waves moving back and forth through the foraging line. Since the foraging line is the fundamental unit of organized behavior in ant colonies, it is crucial that it be studied systematically. This paper is an attempt to model ant foraging lines systematically and match model predictions with laboratory observations and measurements.

Leaving aside the spatio-temporal dynamics of the foraging line, a large number of notable investigations have been dedicated to modeling ant colony behavior as a whole, or using general properties of ant foraging to develop useful algorithms. For instance, Dorigo et al. have developed an array of algorithms for solving the Traveling Salesman Problem, quadratic assignment and the job-shop scheduling problem [BDT00,DMC96] with considerable success. Others have proposed using ant inspired algorithms for diverse applications such as robotic control [Zit05], managing peer to peer networks [SA03,SJ05] and self-assembly using swarm robotics [WMSFS04].

Another line of investigation is to attempt to create artificial systems inspired by ant colonies and then understand its complexity [CGNS02,KPRT98]. Indeed, there is no disputing that very simple computational algorithms or physical mechanisms can produce very complex observable behavior, a theme at the core of Braitenberg's classic *Vehicles, experiments in synthetic psychology* [Bra84]. Thus, observing complex behavior from simple organisms in ants, one can develop artificially simple structures and observe whether or not they produce complex behavior as a group, and if so, what sort of complex behaviors correspond to what features in the simple structures.

In this paper, we develop a simple model of an ant foraging line in the hopes that the analysis of the resulting system can inform us about real ant behavior and vice versa. Thus, the interplay between experimental observation and theoretical modeling play a central role in this paper. This investigation into spatio-temporal evolution of ant foraging lines was driven by experimental observations such as those shown in Fig. (1). Our goal is to develop a simple model with a small number of parameters that is capable of reproducing observed ant behavior. We find that this model predicts ant density waves along single foraging lines. Finally, we will present experimental measurements of simple ant foraging lines which clearly exhibit traveling waves in agreement with the model.

This paper is organized as follows. In §1, we review the literature upon which this work is based and describe how this project relates to other investigations. In §2, we outline our fundamental assumptions and then derive a set of evolution equations for the densities of ants in an established foraging line. In §3, we study the properties of the linearized evolution equations and determine and compare these results to measured quantities. In §4, we provide the details of the ant colony experiments and measurements which inspired our modeling efforts and support the conclusions of our mathematical analysis. In §5, we summarize our findings and lay out a plan for future investigations.

# 2 Modeling a foraging line

# 2.1 Assumptions

Models of individual foraging lines vary considerably from one investigation to the next, and highlight important modeling issues. Discretization of time and space rapidly becomes an



Fig. 1. Observations of ant foraging behavior. The ant density is measured in numbers of ants per centimeter along an ant foraging line. The ant hive is to the right of the domain over which measurements are made. The food is to the left of the measurement domain. More details on the experimental procedures are contained in §4. The foraging line was observed for over an hour. Ant densities are observed to fluctuate in both space and time as waves traveling left and right. At left, three high density waves are observed, two move to the left and one to the right. At right, many left- and right-moving waves are present. The ant foraging line can be a very complex environment with many waves interacting with one another. Notice that the phase velocities are the same in both segments.

issue in all investigations, whether one is modeling the hive, a colony or a network of foraging lines. For instance, if one develops a cellular model for ant behavior, the cell size and time step become model parameters. To connect the model to actual ant behavior, one must refine the study to a point where the effect of the time step and the cell size are negligible in the process. Before we develop our model, we advance two facts.

- (1) Ant pheromone trails evolve as a continuum process. That is, the mean free path of the pheromones is orders of magnitude smaller than the size of the ant that detects it.
- (2) Ants are discrete objects. While ants have finite size and so occupy a finite area in a domain, one can describe a point in space as being either occupied by an ant or not.



Fig. 2. Physical domain and configuration for the ant model. Population A ants leave the hive and seek food. Population B ants leave the food and seek the hive.

This model proposed in this paper treats both the pheromone trail and the ants themselves as a continuum, and so we depart from fact #2. Thus, any results apply in a regime where ant densities are large, which is not always the case in our experiments. A number of behavioral assumptions lie at the heart of our modeling activities.

- (1) We assume there are two modes of operation in the foraging line, ants that are seeking food and ants that are transporting food to the hive. There is ample evidence that these two modes exist, along with many others in ant species (see [HW94] for a survey). For instance, Kluegl, Puppe, Raub and Tautz have developed a discrete space-time cellular automata model that includes the effects of foraging, recruiting, energy storage, breeding and recruitment among others [KPRT98].
- (2) We assume that the ants possess no internal memory of past activities. Studies by Beckers, Deneubourg and Goss support this hypothesis in *Lasius niger* [BDG92b].
- (3) We assume that ants communicate with other nearby ants through physical or chemical encounters. There are a number of modes of communication including transporting hive pheromone, laying trails via the ants' Dufour's gland, regurgitation and antennation [BDG92a,BDGP90,BA03,Wil62]. A common theme in most of these forms of communication is that ants moving in one direction along the foraging line are passing information to ants moving in the opposing direction. This will be reflected in our ant behavior model.
- (4) We assume no U-turning behavior on the foraging line. Thus, ants seeking food continue until they find it, and ants transporting food continue until they reach the hive. Uturning behavior, studied in detail by Beckers, Deneubourg and Goss [BDG92b], may play an important role in recruitment and initial trail laying and development. We limited our study to well-established foraging lines, and we did not detect any U-turning behavior in our foraging line measurements.

With these relatively minor assumptions, we have a durable framework for modeling a single foraging line.

# 2.2 Quantification of foraging ants

To begin, we model two populations of ants, ants that are moving from the hive toward the food and ants that are moving from the food toward the hive. The first group of ants shall be referred to as population A. They shall have density  $\rho_A(x,t)$  and travel with velocity  $v_A(x,t)$ . Similarly, the second group shall be referred to as population B with density and velocity  $\rho_B(x,t)$  and  $v_B(x,t)$ , respectively. Each population has a density and speed governed by physical requirements and behavioral parameters. With four unknown functions, we seek a model for the foraging process that will involve four equations. While ant path integration is a fascinating topic all by itself [CF03,MW88], our experimental and mathematical domain is the simplest possible. The domain shall consist of a single one dimensional interval as shown in Fig. (2), and we assume that ants have no difficulty passing by one another another as they travel back and forth.

To find a set of evolution equations for  $\rho_A$ ,  $v_A$ ,  $\rho_B$  and  $v_B$ , we first apply the basic conservation principle that ants are conserved. That is, ants are neither created nor destroyed. The flux of A and B ants from left to right is  $\rho_A v_A$  and  $\rho_B v_B$ , respectively. Considering any interval [a, b] of the domain, we can see that a difference in flux entering or leaving the interval must be balanced by a change in the total occupancy in that interval. The Fundamental Theorem of Calculus transforms this into a simple conservation principle for ants.

$$\frac{d}{dt} \int_{a}^{b} \rho_{A}(x,t) dx = \rho_{A}(b,t) v_{A}(b,t) - \rho_{A}(a,t) v_{A}(a,t).$$
$$\frac{d}{dt} \int_{a}^{b} \rho_{A}(x,t) dx = \int_{a}^{b} \frac{\partial}{\partial x} (\rho_{A}(x,t) v_{A}(x,t)) dx$$
$$\int_{a}^{b} \frac{\partial}{\partial t} \rho_{A}(x,t) dx = \int_{a}^{b} \frac{\partial}{\partial x} (\rho_{A}(x,t) v_{A}(x,t)) dx$$
$$\int_{a}^{b} \left[ \frac{\partial}{\partial t} \rho_{A}(x,t) + \frac{\partial}{\partial x} (\rho_{A}(x,t) v_{A}(x,t)) \right] dx = 0$$

Since this is true for any interval [a, b], under reasonable assumptions about the continuity of  $\rho$  and v, the integrand must be zero, and so we obtain at the following system of conservation equations.

$$\frac{\partial}{\partial t}\rho_A + \frac{\partial}{\partial x}(\rho_A v_A) = 0 \tag{1a}$$

$$\frac{\partial}{\partial t}\rho_B + \frac{\partial}{\partial x}(\rho_B v_B) = 0 \tag{1b}$$

This is analogous to continuity equations arising in the study of fluid dynamics, and this would be the natural limit of any cellular model as the number of cells grows infinite.

To close the system, we model the behavior of the ants. Our simple model is based on momentum conservation. The momentum of a group of ants will be changed by a biochemical

#### Ant traffic observations



Fig. 3. Measurements of ant flow rate versus ant density. Six 3 cm subregions along the foraging line were marked for measurements. The ant densities were measure manually at 30 second intervals along a fully developed foraging line. The flow rates were calculated by manually counting numbers of ants passing crossing the midplane of each region every 30 seconds.

gradient or stress causing them to accelerate or decelerate. This in contrast to the anttraffic study by Burd, Archer, Aranwela and Stradling where one assumes that there is a functional relationship between the ant flow rate and the density:  $q \equiv q(\rho)$ . There are two reasons why we looked beyond this assumption. First, their data does not support such a functional relationship (see [BAAS02]), nor do we see any clear functional relationship in our experiments as shown Fig. (3). Similar results to those shown in Fig. (3) were obtained in careful experiments were the width of the foraging line was systematically constrained using petroleum jelly in an attempt to artificially raise the ant density. We succeeded in raising the density, but we did not succeed in controlling the ants' speed variations. Our second reason for avoiding a direct flow-density relationship is that solutions to such a formulation may lead non-physical solutions such as rarefactions and shocks in  $\rho$ . Higher order vehicular and pedestrian traffic models remedy these deficiencies by including acceleration terms (for example, see [Whi74] for discussion and analysis). We offer a similar remedy here though our traffic is bi-directional, and the system of equations arising from our simple assumptions about ant communication is somewhat unique.

With this reasoning, we aggregate a number of different physical processes that ants use to communicate. Ants transporting food communicate with foraging ants through pheromone secretion, regurgitation and sometimes auditory cues [HW94]. Similar studies with leaf-cutting ants (*atta cephalotes*) have found that ants exchange information and leaf-fragment exchange between individual ants moving in opposite directions [BA03]. We consolidate all of the short-range information exchanged between food-bound and hive-bound ants into distinct ant stresses. The ant stress can be interpreted as a simple chemical concentration, but it could include other effects as well. If we denote the ant stress for the hive-bound ants as  $\sigma_H(x, t)$  and for the food-bound ants  $\sigma_F(x, t)$ , then changes in  $\sigma_F$  will cause population

A ants to accelerate or decelerate.

$$\frac{d}{dt}(v_A) = \frac{\partial}{\partial x}\sigma_F(x,t) \tag{2a}$$

$$\frac{d}{dt}(v_B) = \frac{\partial}{\partial x}\sigma_H(x,t) \tag{2b}$$

The left hand terms can be expanded further.

$$\frac{d}{dt}v_A(x,t) = \frac{\partial}{\partial t}v_A(x,t) + \frac{dx}{dt}\frac{\partial}{\partial x}v_A(x,t) = \frac{\partial}{\partial t}v_A(x,t) + v_A(x,t)\frac{\partial}{\partial x}v_A(x,t),$$

and similarly for the  $v_B$  acceleration term. In the fluids literature, this is often referred to as a material or convective derivative since one is calculating a time derivative while following the material trajectory of an ant. The stress terms  $\sigma$  would correspond to the negative of a fluid pressure. Finally, we need to model  $\sigma_F$  and  $\sigma_H$ . For simplicity, we do not include pheromone history effects and assume that the ant stress is proportional to the ant density. Since the A ants carry the hive pheromone and have also been observed to exhibit distinct trail marking behaviors from the B ants, we assume  $\sigma_H = k_B \rho_A$ , and similarly  $\sigma_F = k_A \rho_B$  where  $k_A$  and  $k_B$  are constants. This model can also be interpreted to capture regurgitation as a means of communication because the frequency of antennation with the returning ant population would be proportional to its density  $\rho_B$ , or the exchange of other foreign materials such as leaf fragments for similar reasons. The colloquial analogy would be to consider a hungry graduate student wandering through the halls of a building. If this student sees others with donuts, the hungry student will quicken his pace toward those with food, correctly or incorrectly inferring that they have acquired what he desires. If number of students with donuts diminishes, he slows thinking he is on the wrong track. Using the same technique as before, we conserve momentum noting that the only process that will change the momentum of a group of ants. Our simple behavioral model is

$$\frac{\partial}{\partial t}v_A(x,t) + v_A(x,t)\frac{\partial}{\partial x}v_A(x,t) = k_A\frac{\partial}{\partial x}\rho_B(x,t),$$
(3a)

$$\frac{\partial}{\partial t}v_B(x,t) + v_B(x,t)\frac{\partial}{\partial x}v_B(x,t) = k_B\frac{\partial}{\partial x}\rho_A(x,t).$$
(3b)

Thus, we hope to model an ant foraging line with (1) and (3) along with suitable initial data and boundary conditions.

## 3 Linear analysis of the ant foraging line model

The ant foraging line model (1,3) from the previous section is a coupled system of nonlinear partial differential equations, and so finding large, useful families of exact solutions proves difficult. Certainly simulations are possible, but in this section, we seek to gain some physical

insight in the roles of the model parameters, by studying a linearization of this system. Thus, we will assume that ant densities and velocities are constant, signified with a "0", with small spatial and temporal disturbances, denoted by "1":

$$\rho_A(x,t) = \rho_A^{(0)} + \epsilon \rho_A^{(1)}(x,t), \tag{4a}$$

$$v_A(x,t) = v_A^{(0)} + \epsilon v_A^{(1)}(x,t),$$
 (4b)

$$\rho_B(x,t) = \rho_B^{(0)} + \epsilon \rho_B^{(1)}(x,t), \tag{4c}$$

$$v_B(x,t) = v_B^{(0)} + \epsilon v_B^{(1)}(x,t),$$
(4d)

where  $\epsilon$  is a small parameter, and we could interpret the constant quantities as a mean density or velocity. If we substitute (4) into (1) and (3), collect all the terms at order  $\epsilon$  and neglect higher order terms of order  $\epsilon^2$  as being so small as to be discarded, we arrive at the following coupled, linearized system:

$$\frac{\partial}{\partial t}\rho_A^{(1)} + \rho_A^{(0)}\frac{\partial}{\partial x}v_A^{(1)} + \left(\frac{\partial}{\partial x}\rho_A^{(1)}\right)v_A^{(0)} = 0$$
(5a)

$$\frac{\partial}{\partial t}\rho_B^{(1)} + \rho_B^{(0)}\frac{\partial}{\partial x}v_B^{(1)} + \left(\frac{\partial}{\partial x}\rho_B^{(1)}\right)v_B^{(0)} = 0$$
(5b)

$$\frac{\partial}{\partial t}v_A^{(1)} + v_A^{(0)}\frac{\partial}{\partial x}v_A^{(1)} = k_A\frac{\partial}{\partial x}\rho_B^{(1)}$$
(5c)

$$\frac{\partial}{\partial t}v_B^{(1)} + v_B^{(0)}\frac{\partial}{\partial x}v_B^{(1)} = k_B\frac{\partial}{\partial x}\rho_A^{(1)}$$
(5d)

For the duration of this paper, we will assume that hive-bound and food-bound ants move at the same speed [Ska61], so  $V = -v_A^{(0)} = v_B^{(0)}$ .

With (5a) and (5b), we can solve for  $\frac{\partial}{\partial x}v_A^{(1)}$  and  $\frac{\partial}{\partial x}v_B^{(1)}$  in terms of the densities alone. If we differentiate (5c) and (5d) with respect to time, and replace terms involving  $\frac{\partial}{\partial x}v_A^{(1)}$  and  $\frac{\partial}{\partial x}v_B^{(1)}$ , we can reduce (5) to a second-order coupled system in density only.

$$\frac{\partial^2}{\partial t^2}\rho_A^{(1)} - 2V\frac{\partial^2}{\partial x\partial t}\rho_A^{(1)} + V^2\frac{\partial^2}{\partial x^2}\rho_A^{(1)} + k_A\rho_A^{(0)}\frac{\partial^2}{\partial x^2}\rho_B^{(1)} = 0$$
(6a)

$$\frac{\partial^2}{\partial t^2}\rho_B^{(1)} + 2V\frac{\partial^2}{\partial x\partial t}\rho_B^{(1)} + V^2\frac{\partial^2}{\partial x^2}\rho_B^{(1)} + k_B\rho_B^{(0)}\frac{\partial^2}{\partial x^2}\rho_A^{(1)} = 0$$
(6b)

Now we examine the units of model quantities and the role they play in the dynamics of this system. Aside from the dependent space and time quantities, and the densities and velocities, we see that the k's have units of *energy per unit density*. Also, if we designate a timescale  $\tau$ , we determine a natural length scale  $\tau V$ . If we rescale space and time with a simple change of variables from x to  $\tilde{x}$  and t to  $\tilde{t}$  where

$$\tilde{x} = x/\tau V, \quad \tilde{t} = t/\tau,$$

and then dropping the tildes, we see that the system depends upon only two dimensionless parameters:

$$\frac{\partial^2}{\partial t^2}\rho_A^{(1)} - 2\frac{\partial^2}{\partial x \partial t}\rho_A^{(1)} + \frac{\partial^2}{\partial x^2}\rho_A^{(1)} + \kappa_A \frac{\partial^2}{\partial x^2}\rho_B^{(1)} = 0$$
(7a)

$$\frac{\partial^2}{\partial t^2}\rho_B^{(1)} + 2\frac{\partial^2}{\partial x\partial t}\rho_B^{(1)} + \frac{\partial^2}{\partial x^2}\rho_B^{(1)} + \kappa_B \frac{\partial^2}{\partial x^2}\rho_A^{(1)} = 0$$
(7b)

where

$$\kappa_A = \frac{k_A \rho_A^{(0)}}{V^2},\tag{8a}$$

$$\kappa_B = \frac{k_B \rho_B^{(0)}}{V^2}.$$
(8b)

The dimensionless quantity  $\kappa_A(\kappa_B)$  is a *Froude number* for the ant system, representing the ratio of potential energy stored in the B (A) ants to kinetic energy of the A (B) ants.

We can glean some information from this linear system. First, we can study this problem on an unbounded domain if the system is decoupled ( $\kappa_A = \kappa_B = 0$ ). Then, we arrive at two parabolic partial differential equations (PDEs). Parabolic PDEs have only one real characteristic, meaning that given some state  $\rho(x, 0)$ , information will only follow one path through space-time. In the case of (7a), for example, information travels to the left at speed 1. The full decoupled version of (7) would take the form:

$$\rho_A^{(1)}(x,t) = f_1(x+t) + t f_2(x+t), \tag{9a}$$

$$\rho_B^{(1)}(x,t) = f_3(x-t) + tf_4(x-t).$$
(9b)

Thus, we see that disturbances from equilibrium in the food-bound ants will travel to the left and disturbances from equilibrium in the hive-bound ants will travel to the right in the uncoupled or weakly coupled system.

Second, we can study the coupled system on a periodic domain, with period  $\lambda$ , as one might expect to observe in a very long foraging line. In this case, we can express the ant densities as complex Fourier series.

$$\rho_A^{(1)} = \sum_{n=-\infty}^{\infty} D_n(t) e^{\frac{i n \pi x}{\lambda}},$$
(10a)

$$\rho_B^{(1)} = \sum_{n=-\infty}^{\infty} E_n(t) e^{\frac{in\pi x}{\lambda}}.$$
(10b)

Since densities are real, we know that  $D_n(t) = \overline{D_{-n}(t)}$  and  $E_n(t) = \overline{E_{-n}(t)}$  where the overbar denotes complex conjugation (CC). The problem is linear, so it is enough to solve for  $D_n$  and

 $E_n$  for a single mode  $k = \frac{n\pi}{\lambda}$ . A full solution would then be a superposition of such solutions as represented in (10). If we make the substitution,

$$\rho_A^{(1)} = D(t)e^{ikx} + CC, \tag{11a}$$

$$\rho_B^{(1)} = E(t)e^{ikx} + \text{CC.}$$
(11b)

in (7), we can reduce our coupled system of PDEs into a system of coupled ODEs.

$$D'' - 2ikD' - k^2D - k^2\kappa_A E = 0, (12a)$$

$$E'' + 2ikE' - k^2E - k^2\kappa_B D = 0,$$
 (12b)

If we define

$$\vec{x} = \begin{bmatrix} D \\ E \\ D' \\ E' \end{bmatrix}, \quad M = \begin{bmatrix} 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ k^2 & k^2 \kappa_A & 2ik & 0 \\ k^2 \kappa_B & k^2 & 0 & -2ik \end{bmatrix},$$
(13)

then we can solve (12) by solving

$$\frac{d\vec{x}}{dt} = M\vec{x}.$$
(14)

The dynamics of this system are determined by the eigenvalues of M which are  $\pm ik\sqrt{1 \pm \sqrt{\kappa_A \kappa_B}}$ . Thus, for small coupling coefficients,  $\kappa_A \kappa_B < 1$ , we see that solutions are periodic. If we define the following,

$$c_1 = \sqrt{1 + \sqrt{\kappa_A \kappa_B}},\tag{15a}$$

$$c_3 = \sqrt{1 - \sqrt{\kappa_A \kappa_B}},\tag{15b}$$

we can write the full solution to (12) in terms of (13) as

$$\vec{x}(t) = a_1 \vec{v}_1 e^{ik(x-c_1t)} + a_2 \vec{v}_2 e^{ik(x+c_1t)} + a_3 \vec{v}_3 e^{ik(x-c_3t)} + a_4 \vec{v}_4 e^{ik(x+c_3t)} + \text{CC},$$
(16)

where the *a*'s are constants determined by the initial conditions and the  $\vec{v}$ 's are eigenvectors corresponding to the individual eigenvalues of M. Thus, we can see that the solution to the linearized problem is composed of two distinct sets of left- and right-moving waves, one set moving with phase speed  $c_1$  and the other with the lesser speed  $c_3$ . When many of these waves are superposed such as in Fig. (1) (right), modulations are likely to obscure direct observation of phase velocities. In cases like Fig. (4), one can see that measurements support the model predictions that there are two distinct phase velocities. Furthermore, the two wavetrains shown appear to be synchronized with one another.



Fig. 4. Isolated waves traveling at different speeds. This observation shows two distinct phase velocities as predicted in §3. As further evidence of the two populations of ants driving one another, we note that the A and B ants are moving at different phase velocities, but the two wave trains in this series are sychronized in the sense that the temporal separation between to the two left-moving waves (40 seconds) is the same as the temporal separation between right-moving waves.

# 4 Experimental procedures and data collection

In the experiments we conducted, the ants were fed about a tablespoon of ant food inspired by the Bhatkar Diet, after being starved for a couple days [HW94]. The food was placed on the experimental side of the ant table allowing the foraging line from the ant hive to be twenty nine centimeters long. After the ants had found the food and a foraging line had formed (approximately one hour after the food was placed on the ant table), the foraging line was videotaped for one hour using the Canon Fluorite 100x 3CCD video camera.

The video was then loaded into the computer and saved capturing five frames per second. The original size of the images were 320 by 240 pixels. We collected 18,000 frames in the series used for this paper. We apply a binary threshold to each bitmapped frame so that pixels are either black or white, and ants would appear as a certain number of black pixels. Thus, we can "count" the number of ants in an image or any region within an image by counting

#### Pixel density vs ant occupancy



Fig. 5. To certify that the computed pixel densities were an accurate representation of the number density of ants along the foraging line, we compared ant occupancy levels manually with computed pixel densities over a random sample of frames. We obtained a linear correspondence as we hoped. The foraging line is divided into six segments for consideration. No systematic aberrations indicative of spatial bias were observed, so we see that pixel densities in foraging line segments is an accurate representation of the number ants present in a segment of a foraging line.

the number of black pixels. The digitalized frame was cropped to include only the foraging line at 120 by 280 pixels. As shown in Fig. (5), the fraction of pixels occupied by ants is directly proportional to the number of ants in the image. Ants densities were calculated over subintervals of the full foraging line. The measurements presented in this paper were made over seven subintervals, each having a length of 2.89 centimeters. Since ants only occupy a small number of pixels owing to the resolution of our camera, slight movements from one frame to another creates slight density variations from frame to frame. In order to smooth out these variations, we used a moving average when the images were processed to calculate the density. Another interpretation of this procedure is that our  $\rho$  can be interpreted as the probability that ants are occupying that space rather than being the exact density of ants in that specific time and space. If  $d_i^k$  is the pixel density of subinterval *i* at frame *k*,  $\bar{d}_i^k$  is the average pixel density in subinterval *i* over *m* frames.

$$\bar{d}_i^k = \frac{1}{m} \sum_{n=0}^{m-1} d_i^{m+k} \tag{17}$$

In our case, we average over m = 3 frames. Ants in the foraging line travel at about 1 cm per second, thus it takes an ant roughly 2.9 seconds to traverse one subinterval. Our averaging period is 0.6 seconds, so we are eliminating noise while still accurately tracking the ant density evolution.

In this paper, we have presented controlled experiments of single ant foraging lines, we observe complex patterns of traveling waves consisting of food-bound and hive-bound ants. These measurements support the work of others that there is little direct correlation between speed and density in the ant foraging lines, as is often assumed in low order traffic models. Based on these observations and the work of others, we have systematically derived a continuum model for the evolution of ant densities under reasonable assumptions. Using a simple expression for ant stress, we find that the entire system can be reduced to two Froude numbers quantifying the coupling between hive-bound and food-bound ants. We have found that the linearized model exhibits two periodic modes, corresponding to fast and slow moving waves, and the data supports this conclusion.

There are a variety of directions to follow from this point, and we hope to continue along these lines of investigation. The ant stresses do not include history effects, but chemical markers and other information can last for minutes along a foraging line. One could and should include history effects in the ant stress terms. Appropriate boundary conditions are far from clear for ant foraging lines. Non-reflecting conditions are appropriate for population B ants returning to the hive, and specifying an outward flux of A ants from the hive is reasonable. However, ants swarm around the food, and modeling the interplay between arriving A ants and departing B ants will prove challenging. Also, there are many directions in which one could proceed to refine the ant stress model. One could adjust  $\sigma_F$  by adding a small term proportional to  $\rho_A$  to include recruitment effects. Searching behavior, a transient rather than periodic effect, could be included by adding a small stochastic term. While the linearization of the problem is beneficial for gaining physical insight into the essential mechanisms in the problem, full nonlinear calculations would also prove interesting. For instance, the linear theory predicts exponential growth if the coupling between population A and B ants is strong. However, in the nonlinear regime, this growth may saturate. Converged numerical simulations in one spatial dimension are easily within reach, and two space dimensions plus time are certainly possible.

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