A one-dimensional model of trail propagation by army ants

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Abstract. We develop and analyze a model for the swarming behaviour observed in army ants. The model assumes that the ants coordinate their movements by using chemical pheromones as trail markers. The markers continuously evaporate, and are reinforced by new markers laid down by the ants as they move. The motion of the swarm is modelled by a system of partial differential equations (PDEs). The equations are derived from the motions of the individuals, but represent the collective motion of the group, and the formation and decay of the trail network. The PDEs have travelling wave solutions which correspond to the propagation of the leading edge of the swarm. We describe these solutions qualitatively, and use them to determine how both the shape and the speed of the swarm depend on the parameters describing the motion of the individual ants.

Key words: Travelling waves – Qualitative analysis – Trail formation – Chemical communication – Self-organization

1 Introduction

A raiding column of a swarm of army ants maintains a regular structure and advances at a steady speed [20, 21, 22]. The purpose of this paper is to determine how the behaviour of the individuals in these swarms contributes to the 'shape' and speed of motion of the raiding column. Depending on the species, army ant swarms may consist of a few thousand, or several hundred thousand individuals. They have no fixed leaders, nor is there any apparent pattern or order at the level of the individual [23]. The movement of the swarm is coordinated through the use of trail pheromones [3, 4]. Each ant deposits these chemical trail markers as it moves. Those ants following previously laid trail markers will reinforce the existing trails. Any ant finding

itself on previously unexplored terrain will deposit a similar marker before returning to the swarm [22]. Schneirla [23] refers to these ants as the pioneers, and notes that their movements are faster, and more erratic than those of the ants following the trails. Since the pheromone is volatile [3, 4], the trails will decay if not continuously reinforced. Further, the ants have only a limited ability to follow these trails [4]. This leads to a continuous exchange between the followers and the pioneers. This feature of swarming has also been noted by Schneirla [23].

Laboratory experiments [2] suggest that the swarming patterns are self-organized. Self-organization is the hypothesis that the 'behaviour' of a group is not coordinated by a few 'privileged' individuals, but rather arises from interactions between many simple individuals [5, 7, 18]. Several previous studies [8, 13, 24] using cellular automata simulations show that swarming structures similar to those observed in nature can result from very simple models. These models are based on the differences in the behaviour of ants following trails and those exploring new ground, and on the known properties of the trail pheromones. Although these simulations are useful in examining the motions of the ants in two dimensions, they cannot provide a thorough analysis of the underlying models. A more rigorous analysis is provided by Edelstein-Keshet [10] who has developed a simpler model to predict the density of traffic on the trails. Her model is also based on the behaviours of the individual ants. She proposes a system of ordinary differential equations to model the densities of ants and the densities of trails. Her results indicate that small changes in the behaviours of the individuals can give rise to a switching between diffuse trail networks and concentrated trail columns. An alternate approach works from a point of view of statistical mechanics [15]. Here changes in the properties of the trails networks can be studied as phase transitions.

The model presented in this paper is intended to study the propagation of a raiding column. We develop a system of partial differential equations (PDEs) to describe the evolution of the density of the trail network, and the densities of the ants following the trails and those exploring new territory. The model is based on the movements and behaviours of the individual ants in the swarm. Our goal is to determine how the local behaviour of the individual ants in the swarm affects the global motions of the swarm.

To analyze the model, we first reduce the system of PDEs to a system of ordinary differential equations (ODEs) whose solutions represent travelling waves. This step is motivated by the observations that the swarm progresses at a steady rate and maintains a regular shape [21, 22]. We then analyze these equations qualitatively using the state space of the system. A travelling wave solution is represented in the state space by a heteroclinic orbit (a solution curve connecting two fixed points). The analysis leads to a simple numerical technique to test the existence of a structurally stable heteroclinic orbit for a given set of values for the parameters, and more importantly, provides us with a qualitative description of the travelling wave.

2 Development of the model

2.1 The basic model

For simplicity we will examine the motion of the ants along a single direction. We are ideally interested in swarm propagation in two, or even three spatial dimensions to account for movement over a complex environment such as a rain forest floor. At present, our investigations of two dimensional motions are limited to cellular automata simulations [24]. Scenarios where the motion of the ants is confined to a single dimension can be constructed and studied experimentally. For example Deneubourg et al. [6] restrict the movements of the ants to narrow bridges. Natural restrictions to motion also exist. Schneirla [22] has noted that the swarm often proceeds in the direction which offers the least resistance. When the ants first emerge from the nest, they will form trails in several directions. Over a period of approximately fifteen minutes a single direction will be chosen. The swarm then moves in this direction. In this preliminary analytical investigation we focus our attention on the movement of the developing swarm in this single direction.

In developing a model for the swarming behaviour of army ants, there are several known facts which must be incorporated.

F1. There are no fixed leaders [23].

F2. The ants communicate by using pheromones as trail markers. These chemical markers are deposited by the ants as they move, and are attractive to other ants [14].

F3. The pheromones used are volatile, and decay over time [3].

F4. The ants have a finite ability to detect the trails. Experiments show that they are able to follow a trail only a finite distance before turning off it [4]. This leads to a continuous exchange between followers and pioneers [23].

F5. The ants following the trails tend to make more directed motions than ants which are exploring new ground. The pioneer ants will move faster, and turn more frequently than the followers [23].

The limited ability of the ants to follow trails (F4) combined with the two distinct behaviours of ants following and not following trails (F5), prompts us to divide the ants into two groups: ants which are following trails (followers), and ants which are exploring and laying new trails (pioneers). The pioneer ants are observed to move faster and turn more frequently than the followers. Trails are laid by the pioneers, and reinforced by the followers.

Consider a domain with a fixed width which is small relative to its length (Fig. 1). Let x represent the distance along the length of this domain. The following state variables are defined as densities per unit length of this strip. We use the abbreviations d (distance), t (time), and # (number) for the

dimensions.

$T(x, t)$ = density of trails at (x, t),   [d/d]

$F(x, t)$ = density of trail followers at (x, t),   [#/d]

$L(x, t)$ = density of pioneers (lost ants) at (x, t).   [#/d]

The trail density $T(x, t)$ is defined so that $T(x, t)\, dx$ is the total length of all trails in the interval $(x, x + dx)$ (see Fig. 1). It is possible to approach this modelling problem in two distinct ways, namely by considering the physical length of the trails or the concentration of trail pheromone along the domain. The dichotomy between long, chemically weak trails, and short, but heavily marked trails has been explored by Edelstein-Keshet [10]. We do not explicitly consider this distinction here.

Since the ants may move in either direction along the trails, we must distinguish between those moving towards the nest, and those moving away from the nest.

$F^+(x, t)$ = density of followers moving away from the nest.

$F^-(x, t)$ = density of followers moving towards the nest.

$L^+(x, t)$ = density of pioneers moving away from the nest.

$L^-(x, t)$ = density of pioneers moving towards the nest.

A similar distinction was made by Pfistner [19] and Alt [1] in models for the motion of bacteria.

The above facts also suggest that the swarming structures arise from the collective behaviour of the individual ants. To incorporate this hypothesis into our model, we must base the derivations of the equations on the motions and behaviours of the individual ants. Further, the ants respond only to local signals. Thus we attempt to determine how the local interactions of the ants can give rise to a global swarm structure. This emergence of a global phenomenon from the simple local interactions of many individuals is a key feature of self-organizing systems. The following parameters are used to describe the behaviour of the individual ants, and the properties of the trail pheromone:

γ	rate of decay of the trails,	[1/t]
τ_f	rate of trail reinforcement by followers,	[d/t]
τ_l	rate of trail deposition by pioneers,	[d/t]
v	speed of the followers moving in either direction,	[d/t]
s	speed of the pioneers moving in either direction,	[d/t]
λ	reversal rate of pioneers,	[1/t]
ρ^+	rate of reversal for followers moving away from the nest,	[1/t]
ρ^-	rate of reversal for followers moving towards the nest,	[1/t]
ε	rate of trail loss for followers,	[1/t]
α	rate of recruitment of pioneers to trails.	[1/t]
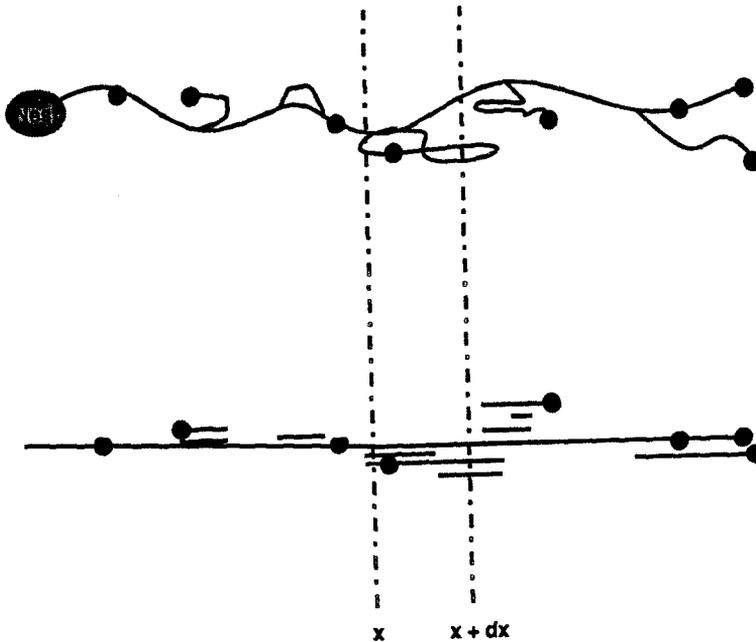
Fig. 1. The one-dimensional formulation of the trail network models trails as moving *towards or away from the nest*. Trail loops correspond to followers changing their direction of motion along parallel trails. The model sums the total concentration of parallel trails per unit distance from the nest. Thus, followers on looping trails are indistinguishable from followers reversing along the same trail (parameters $\rho^{\pm}$)

The parameters γ, τ_f, and τ_l govern the growth and decay of the trail network (F2, F3). The differences in the behaviour of followers and pioneers (F5) require us to define the two velocities v and s. The parameters λ, ρ^{+}, and ρ^{-} measure the average number of reversals per unit time. Since the motion of the pioneers is erratic (F5), λ will be large relative to ρ^{+} and ρ^{-}. The distinction between ρ^{+} and ρ^{-} is explained below. The exchanges between the followers and the pioneers (F1, F4) are described by the parameters ε and α.

We will approximate the decay of the trail pheromone by assuming that the total length of the trails in a given region decays exponentially at a rate γ. We further assume that the ants mark the trails using only a single pheromone which is secreted continuously and at a constant rate. However, we allow this rate to be different for followers and pioneers by introducing two rate constants τ_f for followers, and τ_l for pioneers. Edelstein-Keshet [10] and Watmough and Edelstein-Keshet [24] discuss these assumptions in more detail. These assumptions lead to the following equation for the evolution of the length density of the trail network:

$$\frac{\partial}{\partial t} T(x, t) = -\gamma T(x, t) + \tau_f F(x, t) + \tau_l L(x, t) . \tag{1}$$

There is, unfortunately, very little information on the values of γ, τ_f and τ_l. Edelstein-Keshet [11] tabulates several estimates of these parameters. For most species of trail following ants, $\tau_f, \tau_l \simeq$ 2–3 metres/minute, and $\gamma \simeq 10$ minutes^{-1}.

Equations for the rates of change of the densities of ants follow from considering the exchanges between pioneers and followers, and between ants moving to the left, and ants moving to the right. Pioneers will become followers at a rate αT as they encounter and begin following existing trails. Followers will lose the trail and become pioneers at a rate ε, and reverse their direction at rates ρ^+ and ρ^-. The looping motion of the pioneers corresponds to reversals at a rate λ (see Fig. 1). The rates of change of the densities of the ants at any given point (x, t) are modelled using the following equations:

$$\frac{\partial F^+}{\partial t} + v\frac{\partial F^+}{\partial x} = -\varepsilon F^+ + \alpha L^+ T - \rho^+ F^+ + \rho^- F^- , \tag{2}$$

$$\frac{\partial F^-}{\partial t} - v\frac{\partial F^-}{\partial x} = -\varepsilon F^- + \alpha L^- T + \rho^+ F^+ - \rho^- F^- , \tag{3}$$

for those ants which are following the trails, and

$$\frac{\partial L^+}{\partial t} + s\frac{\partial L^+}{\partial x} = \varepsilon F^+ - \alpha L^+ T - \lambda L^+ + \lambda L^- , \tag{4}$$

$$\frac{\partial L^-}{\partial t} - s\frac{\partial L^-}{\partial x} = \varepsilon F^- - \alpha L^- T + \lambda L^+ - \lambda L^- , \tag{5}$$

for those exploring new territory.

The parameter ε has been estimated by Calenbuhr [4] to be on the order of one per minute. Although there is little experimental evidence, we will assume that the parameter α is of the same order of magnitude. Schneirla [22] has measured the velocity of the followers, v, to be between 2 and 3 metres per minute. The speed of the pioneers, s, has not been measured, but is noted to be slightly faster. A realistic estimate is in the range of 3 to 5 metres per minute. The motion of the pioneer ants is erratic, consisting of rapid, short runs, punctuated by frequent turns. We therefore assume that λ, the rate the pioneers reverse their direction is on the order of 15 to 30 times per minute.

We assume that the distributions of the ants near the nest are homogeneous. This leads to the following boundary conditions:

$$
\begin{aligned}
F_x^+(0, t) &= 0 , & \lim_{x \to \infty} F_x^+(x, t) &= 0 , \\
F_x^-(0, t) &= 0 , & \lim_{x \to \infty} F_x^-(x, t) &= 0 , \\
L_x^+(0, t) &= 0 , & \lim_{x \to \infty} L_x^+(x, t) &= 0 , \\
L_x^-(0, t) &= 0 , & \lim_{x \to \infty} L_x^-(x, t) &= 0 .
\end{aligned}
\tag{6}
$$

Note that these are not zero flux boundary conditions since the densities F and L are the densities of ants moving with velocities v and s respectively. Thus there will be a steady flux of ants both into and out of the nest. For more realistic boundary conditions, the densities of pioneers and followers exiting the nest should depend on both the length of trails at the nest, and the number of ants inside the nest.

The above equations comprise a basic model based on the behaviours of the individual ants in the swarm. We will now proceed to make several simplifications based on the magnitudes of the parameters.

2.2 The simplified model

An equation for the evolution of the total density of followers at the point (x, t) is obtained by adding equations (2) and (3).

$$\frac{\partial F}{\partial t} + v\frac{\partial}{\partial x}(F^+ - F^-) = -\varepsilon F + \alpha LT . \tag{7}$$

There is some evidence that ants following a trail can determine the direction of the nest. Schneirla [22] speculates that the ants determine the direction to the nest by contacts with other ants on the trails. The trails themselves are not oriented. He also notes that during the initial stages of foraging, the majority of the ants are observed to be moving away from the nest. If we assume that ρ^-, the reversal rate for followers moving towards the nest, is much larger than the other parameters of equation (3), then changing the timescale of (3) and neglecting the smaller order terms implies that F^- decays rapidly to $\mathcal{O}(1/\rho^-)$. This assumes that the ants are more inclined to turn away from the nest than towards it. If F^- is small and can be neglected then equation (7) reduces to

$$\frac{\partial F}{\partial t} + v\frac{\partial F}{\partial x} = -\varepsilon F + \alpha LT . \tag{8}$$

The rate of change of the total number of pioneers is obtained by adding equations (4) and (5).

$$\frac{\partial}{\partial t}L + s\frac{\partial}{\partial x}(L^+ - L^-) = \varepsilon F - \alpha LT . \tag{9}$$

The rate of change of the total flux of pioneers is obtained by multiplying (4) and (5) by the speed s, and taking the difference of the two equations.

$$s\frac{\partial}{\partial t}(L^+ - L^-) + s^2\frac{\partial}{\partial x}L = s\varepsilon(F^+ - F^-)$$

$$- \alpha s(L^+ - L^-)\,T - 2\lambda s(L^+ - L^-) . \tag{10}$$

If we now differentiate (9) with respect to t, and differentiate (10) with respect to x, the resulting equations can be subtracted to yield

$$\frac{\partial^2 L}{\partial t^2} - s^2 \frac{\partial^2 L}{\partial x^2} = \frac{\partial}{\partial t}\left(\varepsilon F - \alpha L T\right) - 2\lambda s \frac{\partial}{\partial x}(L^+ - L^-)$$

$$+ s \frac{\partial}{\partial x}\left[\varepsilon(F^+ - F^-) - \alpha(L^+ - L^-)T\right]. \quad (11)$$

Dividing through by 2λ and using (9) to replace the second term on the r.h.s leads to

$$\frac{1}{2\lambda}\frac{\partial^2 L}{\partial t^2} + \frac{\partial L}{\partial t} = \frac{s^2}{2\lambda}\frac{\partial^2 L}{\partial x^2} - \varepsilon F + \alpha L T + \frac{1}{2\lambda}\frac{\partial}{\partial t}\left(\varepsilon F - \alpha L T\right)$$

$$+ \frac{s}{2\lambda}\frac{\partial}{\partial x}\left[\varepsilon(F^+ - F^-) - \alpha(L^+ - L^-)T\right]. \quad (12)$$

Note that if $s^2 \approx 16 \text{ m}^2 \text{ min}^2$, as noted above, and $\lambda \approx 15 \text{ min}^{-1}$, then the above equation can be approximated by the interaction-diffusion equation:

$$\frac{\partial L}{\partial t} = \frac{s^2}{2\lambda}\frac{\partial^2 L}{\partial x^2} - \varepsilon F + \alpha L T. \quad (13)$$

We have neglected the terms of $\mathcal{O}(1/\lambda)$ and $\mathcal{O}(s/\lambda)$. This is equivalent to observing the motion of the ants on a time scale which is larger than the rate of reversal of the pioneers, and on a spatial scale which is much smaller than the distance a pioneer ant would have travelled if it had moved at a constant speed s without reversing for a time t. This limit is discussed in greater detail in Othmer et al. [17]. As mentioned above, typical speeds are 3 metres per minute, and the reversal times are on the order of a few seconds or less. The swarm propagates at speeds of only 0.3 metres per minute, and so this approximation is expected to be valid for studying the variations in the swarm over periods of several minutes to a few hours.

Collectively, equations (1), (8), and (13) represent the evolution of the trail network in the case where the frequency of the random turns of the pioneers (λ), and the rate at which ants following trails towards the nest turn away from the nest (ρ^-) are large relative to the remaining parameters of the system. After deriving these equations from the considerations of the behaviours of the individual ants (microscopic), it is useful to discuss the physical and biological significance (macroscopic) of each term. For convenience we repeat the complete system below.

$$\frac{\partial T}{\partial t} = \underbrace{\tau_l L + \tau_f F}_{\text{(i)}} - \underbrace{\gamma T}_{\text{(ii)}}, \quad (14)$$

$$\frac{\partial F}{\partial t} = - \underbrace{\frac{\partial}{\partial x}(vF)}_{\text{(iii)}} \underbrace{- \varepsilon F + \alpha L T}_{\text{(iv)}}, \quad (15)$$

$$\frac{\partial L}{\partial t} = \underbrace{\mu \frac{\partial^2 L}{\partial x^2}}_{\text{(v)}} + \underbrace{\varepsilon F - \alpha L T}_{\text{(iv)}}. \quad (16)$$

The trail density T is the total length of trails per unit length of the strip $(0, \infty)$. F and L represent the total densities of followers and pioneers respectively. The parameter $\mu = s^2/2\lambda$ is known as a motility coefficient, and represents the scale of the random motion of the pioneers. Terms (i) depict the reinforcement of trails by each ant, and term (ii) the decay due to evaporation of the trails. Term (iii) represents the directed motion, or convection of followers along the trails at the velocity v. Terms (iv) represent the rate, ε, at which followers lose the trail, and the rate, α, per unit length of trail, at which the pioneers begin to follow an existing trail. The space independent version of this model is analyzed by Edelstein-Keshet [10].

3 Analysis

3.1 The dimensionless system

Upon introducing the rescalings:

$$t^* = \varepsilon t, \quad \begin{aligned} T^* &= \frac{\alpha}{\varepsilon} T, & \gamma^* &= \frac{\gamma}{\varepsilon}, \\ F^* &= \frac{\alpha\tau_l}{\gamma\varepsilon} F, & \mu^* &= \frac{\varepsilon\mu}{v^2}, \\ x^* = \frac{\varepsilon}{v} x, \quad L^* &= \frac{\alpha\tau_l}{\gamma\varepsilon} L, & \tau^* &= \frac{\tau_f}{\tau_l}, \end{aligned} \tag{17}$$

and dropping the $*$'s, we obtain the dimensionless equations:

$$T_t = \gamma(L + \tau F - T), \tag{18}$$

$$F_t = -F_x - (F - LT), \tag{19}$$

$$L_t = \mu L_{xx} + (F - LT). \tag{20}$$

We have rescaled space and time relative to the speed of the followers, and their ability to remain on the trails. The rescaled γ is the lifetime of the trails relative to the affinity of the followers to the trails. The dimensionless μ is a ratio of the motility of the pioneers to a measure of the motility of the followers. The values quoted in the previous section indicate that μ will be approximately 1/12.

3.2 Reduction to the travelling wave form

We are interested in examining solutions to this system which represent waves of a population propagating into an unexplored area. These solutions are characterized by a fixed profile moving at a constant speed c. Such solutions are known as travelling waves, and are studied by transforming the system to the moving coordinates $z = x - ct$, and $t' = t$ [9, 16]. The steady state

solutions of the PDEs in these new coordinates, found by setting the derivatives of T, F, and L with respect to the new time t' to zero, correspond to waves with a fixed profile, moving at a constant speed c in the original coordinate system. These steady state solutions will satisfy the following system of autonomous ODEs in the variable z:

$$-cT' = \gamma(L + \tau F - T) \, , \tag{21}$$

$$(1 - c)F' = -(F - LT) \, , \tag{22}$$

$$-cL' = \mu L'' + (F - LT) \, . \tag{23}$$

Note that the $'$ indicates differentiation with respect to the wave variable z.

These equations can be further simplified by the following operations. First, add equations (22) and (23) to produce the equation

$$(1 - c)F' - cL' = \mu L'' . \tag{24}$$

This equation can be integrated once from $-\infty$ to z to give

$$(1 - c)F - cL = \mu L' + k \, . \tag{25}$$

The constant of integration, k, is given by

$$k = cL_0 - (1 - c)F_0 + \mu(L')_0 \, , \tag{26}$$

where a zero subscript indicates evaluation at the point $z = -\infty$, the origin of the wave.

Replacing (23) with (25) leaves us with an autonomous system of first order ODEs. We can study the solutions to the original PDEs by examining the trajectories of the solution curves in the T-F-L state space. If these trajectories are to represent a wave profile travelling through a population, then they must satisfy the following criteria:

• Populations must remain bounded. Hence, the trajectories are restricted to homoclinic orbits (closed curves passing through a single fixed point), heteroclinic orbits (curves connecting two fixed points), or limit cycles (closed curves which do not pass through any fixed points).

• A population density must remain non-negative. Hence the trajectories must be contained in the positive octant of the state space.

• The waves represent a swarm propagating into an empty region of (physical) space. Hence the trajectory must end at the origin $(T, F, L) = (0, 0, 0)$. Further, the origin represents a homogeneous spatial distribution (no ants, and no trails) and must therefore be a fixed point. With regards to the variable z, the solution will asymptotically approach $(0, 0, 0)$ as $z \to \infty$. This fixed point will be referred to as the trivial steady state, and denoted by u_1.

• Finally, we expect that some fixed density is established behind the wave; hence the trajectory must originate at a fixed point in the state space. With regards to the variable z, the solution will asymptotically approach this fixed point as $z \to -\infty$. This fixed point will be referred to as the populated steady state, and denoted by u_0.

Taken together the above points imply that the travelling wave of interest is represented in the state space by a heteroclinic orbit connecting a fixed point in the first octant to the origin.

An inspection of (25) shows that the origin, u_1, is a fixed point if and only if $k = 0$. In addition, if u_0 is a fixed point then by definition $(L')_0 = 0$. With these simplifications (26) reduces to

$$cL_0 = (1 - c)F_0 . \tag{27}$$

Thus, given any initial steady state (T_0, F_0, L_0), there is a unique wave speed

$$c = \frac{F_0}{(L_0 + F_0)} , \tag{28}$$

for which the final state will be unexplored territory. Note that this is just the fraction of the ants which are following trails. Thus, the dimensionless wave speed c is restricted to the interval $(0, 1)$. In the original dimensions this restricts the speed to the interval $(0, v)$. That is the wave can travel no faster than the velocity of the followers. According to the observations of Schneirla [22], the speed of the swarm front is about 20 metres per hour, or 0.3 metres per minute. This is roughly one tenth the speed of the followers. Thus we expect that c is about 0.1, which indicates a ratio $L_0/F_0 = 9$. This is difficult to verify experimentally as the distributions of pioneers relative to followers are difficult to observe.

We have now reduced the original system of PDEs to the following system of first order ODEs:

$$T' = \frac{\gamma}{c}[T - L - \tau F] , \tag{29}$$

$$F' = \frac{1}{(1 - c)}[-F + LT] , \tag{30}$$

$$\mu L' = (1 - c)F - cL . \tag{31}$$

Setting the l.h.s. of these equations to zero we find that there are only two fixed points. The first of these is the origin, which we have already labeled u_1, and the second is the populated state u_0:

$$u_0 = \begin{pmatrix} \dfrac{c}{1-c} \\ \dfrac{c^2}{(1-c)(1-c+\tau c)} \\ \dfrac{c}{1-c+\tau c} \end{pmatrix} . \tag{32}$$

Since each of the quantities c, $1 - c$, and τ are positive, this fixed point is in the first octant of the state space.

3.3 Local analysis of the steady states

Linearizing equations (29–31) about a point $(\overline{T}, \overline{F}, \overline{L})$ yields the system:

$$\begin{pmatrix} T' \\ F' \\ L' \end{pmatrix} = \begin{pmatrix} \dfrac{\gamma}{c} & -\dfrac{\gamma\tau}{c} & -\dfrac{\gamma}{c} \\[2mm] \dfrac{\overline{L}}{(1-c)} & -\dfrac{1}{(1-c)} & \dfrac{\overline{T}}{(1-c)} \\[2mm] 0 & \dfrac{1-c}{\mu} & -\dfrac{c}{\mu} \end{pmatrix} \begin{pmatrix} T - \overline{T} \\ F - \overline{F} \\ L - \overline{L} \end{pmatrix}. \qquad (33)$$

Substituting $(\overline{T}, \overline{F}, \overline{L}) = (0, 0, 0)$, it follows that at the fixed point u_1, the linearized system has the eigenvalues:

$$\begin{aligned} \lambda_1 &= \gamma/c & &> 0 \ , \\ \lambda_2 &= -1/(1-c) & &< 0 \ , \\ \lambda_3 &= -c/\mu & &< 0 \ , \end{aligned} \qquad (34)$$

and eigenvectors:

$$\xi_1 = \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}, \quad \xi_2 = \begin{pmatrix} \dfrac{(1-c)^2 + \tau(c(1-c) - \mu)}{\mu(1 - c + c/\gamma)} \\[3mm] -\dfrac{1}{1-c} + \dfrac{c}{\mu} \\[3mm] \dfrac{1-c}{\mu} \end{pmatrix}, \quad \xi_3 = \begin{pmatrix} \dfrac{\gamma}{c} \\[2mm] 0 \\[2mm] \dfrac{\gamma}{c} + \dfrac{c}{\mu} \end{pmatrix}. \qquad (35)$$

Since $\gamma, \mu, c > 0$, we have that $\lambda_1 > 0$, and $\lambda_2, \lambda_3 < 0$ over the entire parameter space. This indicates that u_1 is the intersection of a two dimensional stable manifold W_1^S, and a one dimensional unstable manifold W_1^U.

At the populated steady state u_0 the eigenvalues of (33) are roots of the cubic equation

$$\lambda^3 + A\lambda^2 + B\lambda + C = 0 , \qquad (36)$$

where

$$A = \frac{c}{\mu} + \frac{1}{1-c} - \gamma/c , \qquad (37)$$

$$B = -\gamma\left(\frac{1}{\mu} + \frac{1}{c(1 - c + \tau c)}\right) , \qquad (38)$$

$$C = \frac{\gamma}{\mu(1 - c + \tau c)} . \qquad (39)$$

The fact that $B < 0$ and $C > 0$ for all values of the parameters implies that two of the eigenvalues have real parts greater than zero, and the third is real and negative. Thus, there are a two dimensional unstable manifold W_0^U and a one dimensional stable manifold W_0^S intersecting at u_0.
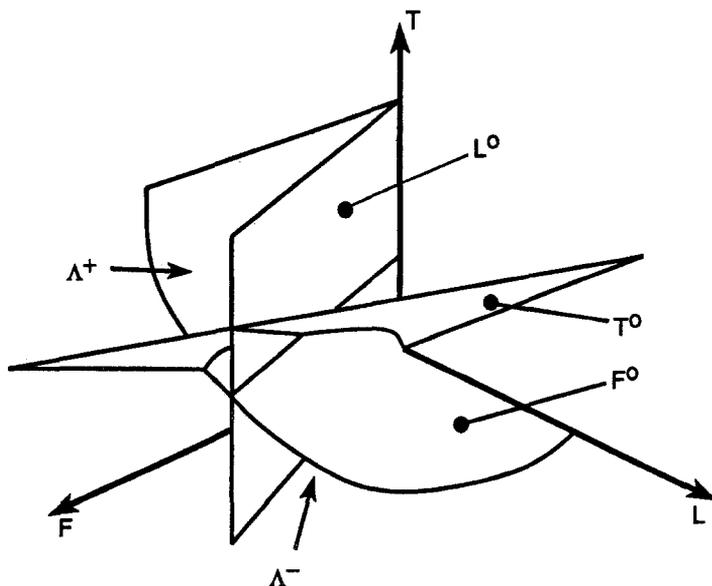
Fig. 2. The State Space (Octant I), showing the nullclines T^0, F^0, and L^0, and the regions Λ^+, and Λ^-. The monotonic travelling wave solution is contained in the region Λ^-

3.4 Global analysis

For systems of two ODEs, a qualitative, heuristic study of the global structure of the state space can often be performed quickly and easily. By contrast, our system consists of three ODEs, and such study proves more difficult. As with two dimensional systems, it is possible to examine the direction of the flow through the nullclines of the vector field, and also the direction of the flow through the different regions bounded by these surfaces. Simple geometric analysis can then be used to determine the possible locations of the stable and unstable manifolds W_1^S and W_0^U. The existence of the heteroclinic orbit requires the intersection of these two manifolds. Our analysis provides a simple numerical experiment to determine the existence of the heteroclinic orbit for a given set of parameter values. It also provides a qualitative description of the travelling wave.

The nullclines of the vector space can be used to determine the flow in the state space. At each point $u = (T, F, L)$ in the state space, we can define the vector $\omega = (T', F', L')$ by equations (29–31). This vector is tangent to the trajectory passing through each point. Let T^0, F^0, and L^0 denote the null-clines (see Fig. 2). These are the surfaces where the respective components of ω are zero, and are given by the following equations:

$$T^0 = \{(T, F, L)|T - L - \tau F = 0\} \, ,$$

$$F^0 = \{(T, F, L)|LT - F = 0\} \, ,$$

$$L^0 = \{(T, F, L)|(1 - c)F - cL = 0\} \, .$$
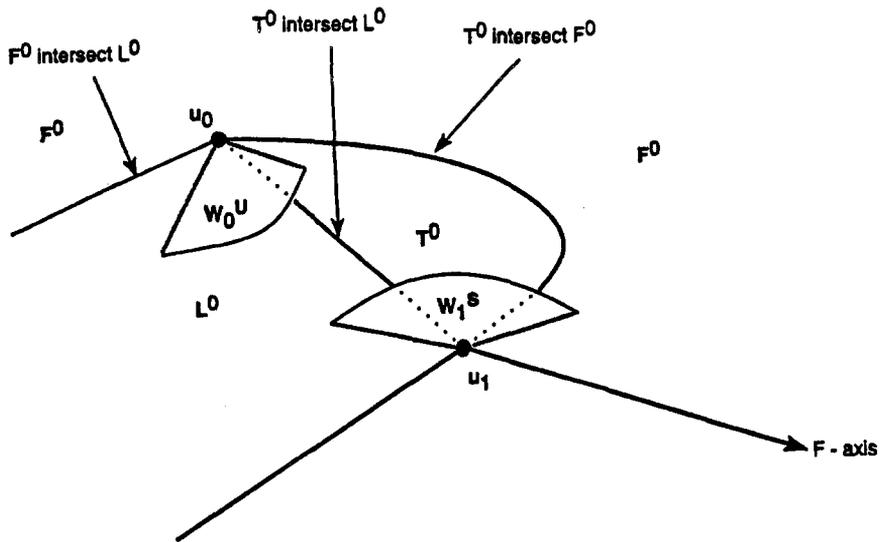
Fig. 3. A schematic showing the boundaries of Λ^- and their intersections with the manifolds W_0^U and W_1^S near the points u_0 and u_1 respectively. The F^0 surface has been distorted for clarity. For the existence of the travelling wave solution, the heteroclinic orbit must be contained in the intersection of the two manifolds

In addition, we define Λ^+ and Λ^- to be the portions of the positive octant in which each component of ω is positive and negative respectively. Computing the components of the vector field normal to the boundaries of the region Λ^- shows that: (1) any trajectory which passes through Λ^- must exit the region through either T^0, or the $T = 0$ plane; and (2) any trajectory which enters Λ^- must do so though either T^0 or F^0. Further, since the flow velocity (magnitude of ω) is everywhere decreasing and bounded away from zero, a trajectory cannot remain in Λ^-. This implies that there are no limit sets contained entirely in this region.

The unstable manifold W_0^U must pass through u_0 tangent to the unstable eigenspace of the linearized system near u_0. If we consider this eigenspace as a disc spanned by the unstable eigenvectors, then it follows that this disc must be imbedded in the state space near u_0, and that to do so, it must intersect both Λ^+ and Λ^-. For the case of real eigenvalues, a simple geometric argument is sufficient to show that the unstable eigenvectors of this system are directed into the sets Λ^- and Λ^+, and the above statement follows immediately. This argument consists of considering the vector associated with a point arbitrarily close to u_0. If this vector is to be oriented away from u_0 then it must lie in either Λ^- or Λ^+. For the case of complex eigenvalues, the proof of the statement uses the fact that intersection of the eigenspace and L^0 (a transverse intersection) must be a straight line. The only orientation of this line which is consistent with the vector field near u_0 implies that the unstable manifold intersects with Λ^+ and Λ^-. This intersection is shown in Fig. 3.

The intersection of the unstable eigenspace with T^0 must also be transverse, and lie below F^0 and to the right of L^0. Since the unstable manifold W_0^U must be tangent to the eigenspace at u_0 it must intersect with T^0 and L^0 as a continuous curve in these same regions. If this curve were to intersect u_1, then the intersection of W_0^U and W_1^S would follow immediately. Since a trajectory through Λ^- cannot leave through F^0, it follows that this curve cannot cross the line $T^0 \cap F^0$, nor can W_0^U intersect the portion of F^0 that makes up the boundary of Λ^-. For similar reasons, the curve cannot cross the line $T^0 \cap L^0$. However, the curve may be of finite length, and thus the intersection of W_0^U and W_1^S cannot be guaranteed based on the behaviour of W_0^U.

The stable manifold W_1^S intersects Λ^- for all parameter values, and passes though F^0, and L^0 near u_1. This follows since W_1^S is tangent to the eigenspace spanned by the vectors of (35). Since the stable manifold intersects with Λ^- near u_1 there must be a trajectory in the stable manifold which passes through Λ^-. As noted above, this trajectory must have either originated in Λ^-, or have entered Λ^- through either F^0 or L^0. The existence of a trajectory, other than one connecting u_0 to u_1, which is contained entirely in Λ^- is not possible. Such a trajectory would be decreasing in each of its components, and T would increase without bound as we integrated ω backwards along the trajectory. This contradicts the fact that Λ^- is bounded above at the height T_0.

The shape of the heteroclinic trajectory can be determined from the above arguments. For the case where the eigenvalues of the linearized system near u_0 are all real, the heteroclinic orbit would be contained entirely in Λ^- and therefore be monotonically decreasing in each component. For the case of complex eigenvalues, the orbit would oscillate about u_0 before reaching u_1; however, the orbit must remain in the positive octant, and can therefore represent a travelling wave of population expansion.

The only conditions under which the intersection of the two manifolds will fail is if the unstable manifold W_0^U is bounded. This would imply the existence of a limit cycle enclosing the point u_0. The system does not undergo a Hopf bifurcation for any values of the parameters. Therefore, such a limit cycle would necessarily arise from a global bifurcation of the system. Note that in this case it is still possible that there is an orbit connecting the limit cycle to the point u_1, and that this orbit is also a travelling wave solution of the PDE model.

Numerical experiments can be used to to determine the existence of the heteroclinic orbit at specific parameter values. The above analysis indicates that if the unstable manifold W_U^0 intersects the plane $T = 0$ then it must also intersect the stable manifold W_S^1. Further, this intersection will be transverse. The unstable eigenvectors of equation (33) about the point u_0 can be computed numerically, and used as initial values in equations (29–31). The solutions to these initial value problems will approximate the unstable manifold. If any of these solutions intersect the plane $T = 0$ then this is akin to showing the non-existence of a limit cycle separating u_0 from u_1.

(a)

(b)
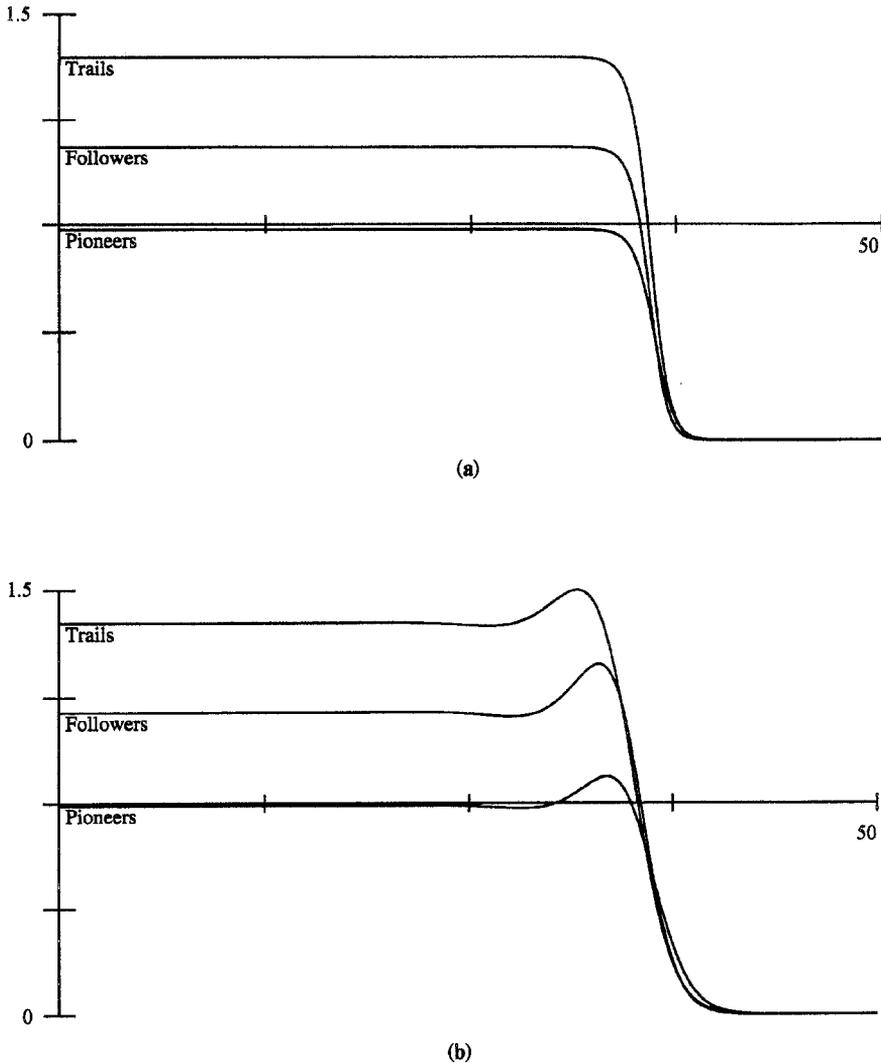
Fig. 4. Numerical solution of the PDEs (18–20) using Bard Ermentrout's xtc [12]. For (a) $\Delta x = 0.25$, $\Delta t = 0.05$, $\tau = 0.6$, $\mu = 0.2$, and $\gamma = 5$. For (b) $\Delta x = 0.0625$, $\Delta t = 0.005$, $\tau = 0.6$, $\mu = 0.2$, and $\gamma = 1$. The solutions were integrated from the initial conditions $T = F = L = e^{-x^2}$, until the solution appeared to stabilize to a travelling wave. In case (a), the solution is monotonic, corresponding to the case where the eigenvalues of u_0 are real. In case (b), an oscillating solution appears to be stable

3.5 Numerical analysis

We have used the program "xtc" written by Bard Ermentrout [12] to solve the full system of PDEs given by equations (14) through (16) and the boundary conditions (6). The equations were solved on the finite domain $0 < x < N$, with the initial conditions $T = F = L = e^{-x^2}$. In order to mimic the infinite

domain in the calculations, the domain width, N, was taken to be large enough that the evolving front did not propagate as far as the right boundary. The method of "Euler" was selected from the numerics menu of the program. This method proved faster than the other possible choices of "Gear" and "Backward Euler" despite the restrictions on the time step. The equations were solved for $\mu = 0.2$, $\tau = 0.6$ and $0.1 < \gamma < 5$. Two apparently stable travelling wave solutions are shown in Fig. 4. The solutions appeared to maintain their shape as the wave traversed the domain. Both monotonic and oscillating travelling waves were observed. The solution shown in Fig. 4(b) was recomputed over a refined grid, and did not appear to change. We therefore expect that the oscillating wave is a solution to the equations, and not an artifact of the discretization.

4 Discussion

Our initial analysis shows that if we are to achieve a travelling wave propagating at the observed velocities of roughly 10% that of the speed of the followers, then the ratio of pioneers to followers along developed portions of the trails should be on the order of 9:1. Unfortunately, there is little evidence at the present time to either support or refute this prediction.

One interesting prediction of the model is that travelling waves will develop with a monotonically decreasing density of pioneers. It seems more likely that the number of pioneers should attain a maximum near the fore of the wave, indicating a populated steady state u_0 with a small L component. Such a situation is not permitted by our model. Both steady states must lie on the L^0 nullcline. This nullcline is planar, and will be regardless of the mechanics of the exchange between followers and pioneers. It may be possible to achieve this effect by introducing dependence of the reversal rates ρ^+ and ρ^- on the state variables F and T.

We have also derived equations to model the motion of automata interacting with a trail network in two dimensions (Watmough, unpublished). Such a model would be better suited to examine the formation of a trail network in two dimensions. Although the full system in two dimensions is difficult to analyze, several simplifying assumptions can be made. For example, Edelstein-Keshet (unpublished) has developed a model with no spatial dependence to examine the orientational aspects of the pattern, and to determine the conditions necessary for a transition from a loose network of trails to a network with a strong directional order. A simulation of the full two dimensional model has also been studied [24]. Both of the above versions of the model indicate that introducing a dependence of the parameter ε on the trail density would promote the formation of stronger trails.

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