Behav Ecol Sociobiol (1995) 36:119–133

Leah Edelstein-Keshet · James Watmough
G. Bard Ermentrout

Trail following in ants: individual properties determine population behaviour

Received: 25 September 1993 / Accepted after revision: 3 October 1994

Abstract This paper deals with the purposeful marking of trails as a mechanism for coordinating movement. Patterns of motion are adapted to the environmental conditions, the functions to be carried out, and the condition of the organism; therefore, the networks of trails must change both quantitatively and qualitatively over time. The nature of such changes, and how they are controlled at the individual level are discussed. In particular, we show that slight modulations in individual traits, in the trail marker, or in the size of the group can account for major changes in movement patterns at the population level such as abrupt transitions from diffuse area-covering networks to focused trunk trails. Using a mathematical model and computer (cellular automata) simulation we show that trunk trails carrying a high density of traffic can form spontaneously under suitable conditions from an initially randomly distributed group. The key to this self-organizing property stems from interactions between individuals that lead to a "collective effect" in recruitment to trails: the influence of small groups of individuals increases rapidly with group size. The dichotomy between high traffic (strong) trunk trails versus diffuse (weak) networks is discussed.

Key words Ants · Model · Simulation · Trail patterns

Introduction

Unlike our roadways and highways, whose purpose is to endure, networks of trails in nature are not static. One of the main hypotheses of this paper is that patterns of motion of a population must continually change to keep up with the changing nature of tasks to be carried out for survival: finding food, escaping predation, seeking shelter, protecting young. Each of these tasks requires a distinct pattern of motion, and thus leaves a distinct record in the pattern of trails. Indeed, the form of the trail network is a precise record of the patterns of motion of the population, and contains valuable information about animal behaviour. This paper is an attempt to understand how to decipher this information by considering how behaviour at the level of the individual translates into the spatial pattern of trails.

It is known that societies of ants are not governed by leaders, or any type of central controllers. A limited intelligence exists at the level of the individual, and yet the functions performed by the colony are of amazing complexity. The idea of these societies as self-organizing systems has recently been noted (e.g. Deneubourg et al. 1989, 1990a). A hypothesis in this paper is that the changes in group behaviour must stem from changes in individuals, and/or their responses to one another. The colony must be able to control and adapt its pattern of motion and thus the form and function of the trail network must be plastic, and readily transformed through the cumulative effects of many individuals. We show that behaviour of the colony or population can be understood in terms of fairly subtle changes in individuals. A key assumption in the model is a *collective effect*: single ants have a very slight influence on recruitment to a trail, but the effect of a group increases with group size in a compounded (not simply additive) way. This effect is similar to autocatalysis, or positive feedback. Our premise is that a small number of parameters can be used to describe basic features of the motion and interaction of ants with a set of trails: these include the rate of deposition of chemical marker (pheromone, in the case of ants), the directional persistence of motion, the attraction to a new trail, the fidelity to a trail, and the effect of group size or of pheromone concentration on recruitment. Properties of the chemical such as rate of evaporation, and population size are also determining factors in group behaviour. The model is not meant to include all aspects of communication involved in re-

L. Edelstein-Keshet (✉) · James Watmough
Mathematics Department, University of British Columbia,
Vancouver, B.C. V6T 1Z2, Canada

G.B. Ermentrout
Department of Mathematics, University of Pittsburgh,
Pittsburgh, PA 15260, USA

cruitment. Other aspects such as tandem running (Wilson 1959), polyethic responses (Stuart 1975), and ortho- and klinokinetic responses to environmental stimuli (Fraenkel and Gunn 1961) play important roles that are not explicitly considered here.

Chemical trails

Trail-following is one of many mechanisms adapted by animals to orient and follow olfactory cues. Other mechanisms are discussed in the classic book by Fraenkel and Gunn (1961) and papers of J.S. Kennedy (e.g. Kennedy 1967, 1986). A survey of the literature reveals that trail marking has actually been adopted in many phyla throughout the animal kingdom. At the smallest size scale, unicellular organisms such as myxobacteria (Stanier 1942; Shapiro 1988) secrete slime trails. Cellular slime moulds also dump attractive chemicals (cyclic AMP) into their surrounding, but diffusion acts so quickly on these small sizes that no trails can be formed. In the insect world, gregarious caterpillars (Fabré 1979; Howard and Flinn 1990; Roessingh 1990; Deneubourg et al. 1990b) use silken web trails. Molluscs secrete and often follow slime trails (Focardi and Santini 1990; Focardi et al. 1985, Tankersley 1990; Wells and Buckley 1972; Chelazzi et al. 1990). Even mammals are known to secrete markers from special scent glands on hooves (Estes 1991; Wynne-Edwards 1972; Able 1980).

In ants and some of the other social insects, chemical communication via pheromones has been well known for some time (MacGregor 1947) but the actual identification of some of the trail-marker chemicals is recent (Evershed et al. 1982; Hölldobler and Wilson 1990 for a summary). The dimensions and longevity of an artificial pheromone trail on a non-absorbent surface were first described by Bossert and Wilson (1963) for the fire ant *Solenopsis saevissima*. (Later it was realised that the substrate affects trail longevity). The pheromone diffuses and is perceived by individuals within some "active space" surrounding the trail. To provoke a turning response, a threshold concentration difference between a pair of sensors is generally required, but it is conceivable that the required threshold depends on the condition of the individual, its history, or other factors. (Calenbuhr and Deneubourg 1990, 1992; Calenbuhr et al. 1992).

Not all ants form massive trail networks. In some species of ants, only individuals returning from a food source will lay a trail. In other cases (e.g. army ants and termites) or special situations (e.g. starvation, see Breed et al. 1987) trail marking can be continuous (reviews in Dumpert 1978; Wilson 1971 1975; Sudd 1967; Hölldobler and Wilson 1990). We are mostly interested in continuous trail-marking, because we are trying to understand how the structure of the trails can evolve under its own internal dynamics, rather than those imposed by a preexisting set of environmental cues such as food sources.

Trail networks: structure, function and formation

Sketches of ant trail networks can be found in Raignier and van Boven (1955), Rettenmeyer (1963), Schneirla (1971), Franks and Fletcher (1983), Burton and Franks (1985), Franks (1989). Some networks are initially diffuse and ill-coordinated, some develop into columns, or tree-like or fan-like structures. Recruitment trails for guiding workers to food finds tend to be direct and as short as possible, conveying food to the nest with least cost (Hölldobler and Lumsden 1980; Hölldobler and Wilson 1990). Trunk trails partition a region into smaller territories (Hölldobler 1976). Exploration trails aimed at finding new food tend to be fan-like, and highly reticulate, so as to efficiently cover an area. Long- range migration swarms, on the other hand, tend to form columns that have a well-defined directionality over some distance.

The simulations in this paper reproduce some of the morphologies of trail networks. The models attempt to explain how transitions from type to type can take place. We shall see that an initially disorganized mass of individuals can evolve over a short period of time into an organized pattern of traffic with a simple set of rules at the individual level. Our experiments are performed on the computer, where we can test simple sets of behavioural rules and determine their consequences. An ultimate goal is to relate computer experiments and analysis to experiments on the organisms themselves, as done recently by Camazine (1991) for patterns formed on the combs of honey-bees. As a first step, still short of this eventual goal, we have related our results to previous experimental work.

Materials and methods

Computer simulations

The computer simulations were written for the IBM PC, partly in assembly language, and partly in C with base-two calculations for speed. A rectangular lattice of size of 256 × 256 forms the spatial domain. Ants are released one by one from "the nest", with fixed speed and one of eight possible directions of motion. Ants can change direction with some persistence of current direction of motion, and deposit a trail-marker at each step. Ants leaving the region are replaced by a new ants at the nest. A preliminary version of this simulation has appeared in Ermentrout and Edelstein-Keshet (1993).

Analytical models

Differential equations describing the time rates of change of ant densities (followers and exploratory ants) and total trail length were analysed by linear stability methods (Edelstein-Keshet 1994a). Solutions were obtained using a PC software package, PhasePlane (Ermentrout 1990; Brooks/Cole Publ.).

Details of the simulation and models

Trail formation: behavioural rules and simulations

Individuals are represented by points moving over a rectangular region. The motion consists of straight runs interspersed with random turns. The trails gradually lose their chemical strength by "evaporation", that is, the level of pheromone at each point along a trail declines by one unit per time step. (The oldest section of the trails starts to disappear first.) The level of trail marking by a single ant is τ. Trail chemical marker is allowed to build up to a maximal level. The significance is that a trail behind a single ant is τ pixels long, whereas a trail that has been maximally marked and then abandoned for some reason will have decayed after t = MAX iteration units. For example, if $\tau = 8$ and MAX = 200, it takes 25 ants walking one after another to form a trail whose strength is MAX, and that trail will decay after 200 time units if it is not reinforced by other followers. The grey scale intensity of the path represents its pheromonal strength.

The following assumptions used in making the simulation models are based on behavioral patterns of individuals documented in the literature:

1. Each ant has a fixed probability (per unit time) of losing a path currently being followed (the probability can vary with pheromonal concentration; we discuss this issue further below).
2. Ants make occasional random turns.
3. Ants crossing the trail at an angle close to 90° may fail to turn to follow it. Those crossing at smaller angles turn with some finite probability.
4. Ants move at the same speed, whether they are following or laying a fresh trail.

A summary of systematic variation of the parameters in the simulation is described in detail by Watmough (1992). In this paper we restrict attention to a particular aspect of parameter variation which relates to the response of individuals to strength of the trail. A purely mathematical model of response to trail strength has been recently proposed by Edelstein-Keshet (1994), [which will be abbreviated EK (1994)]. In this paper we draw parallels between the results of the mathematical model and those of the simulation. As we shall see, while not all aspects of the model and the simulation are analogous, the main results are essentially in agreement: namely, that to be able to organize spontaneously into coherent trunk trails from any initial configuration, the collective effect must be strong enough: in this case we will assume that as trail pheromone accumulates due to repetitive use of the same trail, the fidelity of following on that trail increases.

Model assumptions

Aside from simulations, a simple mathematical model helps to understand that many competing effects must balance for order to be established: pheromone is secreted, but also disappears via evaporation; ants are recruited to trails but they also lose the trails. The model quantifies the precise relationships between parameters of individual behaviour which lead to a given type of collective behaviour. Note that this is in contrast to some of the more traditional models which do not stress parameter dependence (see Discussion). We define:

$T(t)$ = the total length of trails per unit area (cm per cm^2),
$F(t)$ = the total number of follower ants per unit area (number per cm^2),
$L(t)$ = the total number of non-follower (exploratory) ants per unit area (number per cm^2).

The variable T represents a sum of the lengths of all the trails in a given region divided by the size of the region. Followers are ants walking on (and adding pheromone to) trails that have already been made. Exploratory ants lay fresh trails. We are interested in the proportion of a given group that are exploratory (L) versus followers (F). We are also interested in the level of traffic on the trails. One way of characterizing *traffic density* is via the ratio of followers per unit trail length. We define traffic density as

$S(t) = F(t)/T(t)$ = average number of followers per unit length of trail

We will refer to $S(t)$ also as the *strength* of the trail. Thus a trail network is *strong* if there are many followers per unit length, and *weak* otherwise. Under certain conditions, this definition of strength is synonymous with the strength of pheromone along the trails, but this is not an essential assumption of the model. It is only necessary to assume that the stronger the trail, the more attractive it becomes to individuals. The mechanism for this recruitment response could be direct pheromonal sensing or any other chemical or physical signal associated with increased levels of traffic on trails.

The equations governing trail elongation and recruitment of individuals are:

rate of change of trail length
(i) = rate of elongation due to trail-marking by ants
(ii) − rate of decay due to pheromone evaporation (1)

(see Appendix I for the mathematical version). The numbered terms represent; (i) trails formed by ants depositing pheromone droplets; (ii) evaporation causing the trails to decay.

Further, we take the equation for the followers on trails:

rate of change of followers on trails
= recruitment of exploratory ants to trails
− loss of followers from trails (2)

Since we consider only two possible states for ants (followers and non-followers), the total population is

$$N = L + F$$

Ants exchange between these two classes, but none are added or removed, so that N = constant. The size of the population is a parameter of significance, and it will be clear later that collective behaviour depends on this parameter.

The assumptions below are used to derive a detailed set of equations which appear in the appendix to this paper:

1. Trails decay by simple linear kinetics, with fixed rate constant. This is the most convenient way of representing decay of a substance through dissipation or evaporation. The rate constant, Γ, has units of t^{-1}, and depends on the type of pheromone used, the temperature, and other conditions. The duration of a trail (TD in Table 1) and the half-life (HL) are proportional to $\ln(2)/\Gamma$.

2. There is some length of trail associated with a single exploratory ant. That is the length beyond which the trail has decayed to an imperceptible level. This will be called the length of a simple trail, and represented by d_s. Based on properties of pheromonal diffusion, Bossert and Wilson (1963) calculated that this distance is roughly 28 cm for *Solenopsis saevissima*.

3. Followers also contribute to maintaining the trails. If all the ants were following one another on a single trail and maintaining it at a constant length and pheromonal level, then, in the model, there would be some average distance of separation between the followers on a single trail, d_f. In the simulations, however, it is assumed that all ants secrete the same level of pheromone per unit time. In general it is true that the average follower spacing length is smaller than the simple trail length d_s, because otherwise there would be fade-out points between the followers, and they would not be truly following along a single trail.) One example of d_f is given by Wilson (1971) who describes *Camponotus paria* in which 10–20 workers follow single file behind one leader, with distance of separation 5–10 cm. (A single file is not essential, since the average spacing along a trail is simply the total number of followers divided by the length of the trail.)

4. The rate at which ants are recruited to a trail is proportional to the number of exploratory (nonfollower) ants present and the total length of trails available for recruitment, with constant of proportionality α (a standard mass-action kinetics, which means that ants have some probability of detecting a trail they encounter and deciding to follow it).

5. Followers on a trail have some probability per unit time, ε, of losing the trail. The average length of trail followed would be proportional to the speed of walking, v and to $1/\varepsilon$. The fidelity to a trail is also inversely proportional to ε (see Fig. 1).

The above five assumptions define individual terms in the equations above (see Appendix). If we stop here, the model so defined predicts that the population always attains some equilibrium proportion of followers and non-followers. This "null" model does not demonstrate any interesting range of behaviour. However, by including an additional reasonable assumption below, we obtain a much more interesting illustration of a *collective recruitment effect*:

6. *Stronger trails are more attractive*: as the strength, S, of the trails increases there is a greater attraction to follow the trails. Since S has been defined as the traffic density on a trail, this could be a result of response to increased pheromone levels on the trail, or other physical factors associated with increased traffic density (e.g. physical contact with other followers). It can be represented by either one (or both) of the effects below. As the strength of the trails, S, increases, either

a. The recruitment rate of lost ants to trails (α) increases, or

b. The drop-off rate (ε) of followers from trails decreases.

Either of these assumptions is reasonable, and both can be thought of as a recruitment response which either attracts new recruits, or increases the fidelity of followers. Pasteels et al. (1986) and Verhaeghe (1982) give evidence that rate of trail loss and recruitment to trail are concentration dependent. Van Vorhis Key and Baker (1986) found that one ant activates 5–20 additional workers. EK (1994a) discusses the fact that the dynamic behaviour of the model, the two assumptions are equivalent. Thus, attention can be focused on any one of these possibilities, e.g. 6b.

For example, EK (1994a) explored the assumption that

$$\varepsilon(S) = E\,e^{-bS}$$

This means that the probability of losing the trail declines exponentially with the strength of the trail. As shown on Fig. 1a, this function is a decaying exponential and at $S = 0$ it has slope $-bE$, and value E. In the simulations, fidelity is a decreasing linear function levelling off to a constant level (Fig. 1c), which results in the dependence shown in Fig. 1b for the trail loss probability. The exact functional form of this dependence is not important, but how rapidly the response changes with increasing trail strength, i.e. the parameter b, is critical. The full mathematical version of the equations is given in Appendix I and with more detail in EK (1994a). Here we only comment on aspects relevant for a biological interpretation of the model and its results.

Parameter dependence

The model contains five parameters for describing individual behaviour. They are:

d_s = length of a simple trail behind a single exploratory ant

d_f = length of links between followers (distance of separation along a trail)

α = rate of attraction to a trail per unit trail density per unit time

E = maximal rate of losing trail = ln 2/(half-life of typical follower on weak trail)

b = recruitment response distance, described below

The response distance b is an average distance between followers on a trail that is associated with a particular response to trail strength: when the distance between followers on a trail is $T/F = b$, (equivalently, the traffic density or the "strength" of the trail is $S = F/T = 1/b$) the probability that a given follower will lose the trail has fallen to $1/e$ = 37% of its maximal value ($e \approx 2.7$ is the base of the natural logarithm). Two other parameters associated with the pheromone and with the population size, are

Γ = decay rate of the trail per unit time = ln 2/(trail half-life)

N = population density

This makes for a total of seven possible parameters influencing behaviour. However, the type of behaviour found in the mathematical model actually depends only on certain groupings of these parameters (see EK 1994a), namely:

$A' = d_f/d_s$ = ratio of simple trail length to length of links between followers

$B' = b/d_s$ = ratio of recruitment response distance to links between followers

$E' = E/\Gamma$ = ratio of trail half life to half life of a follower on weak trail

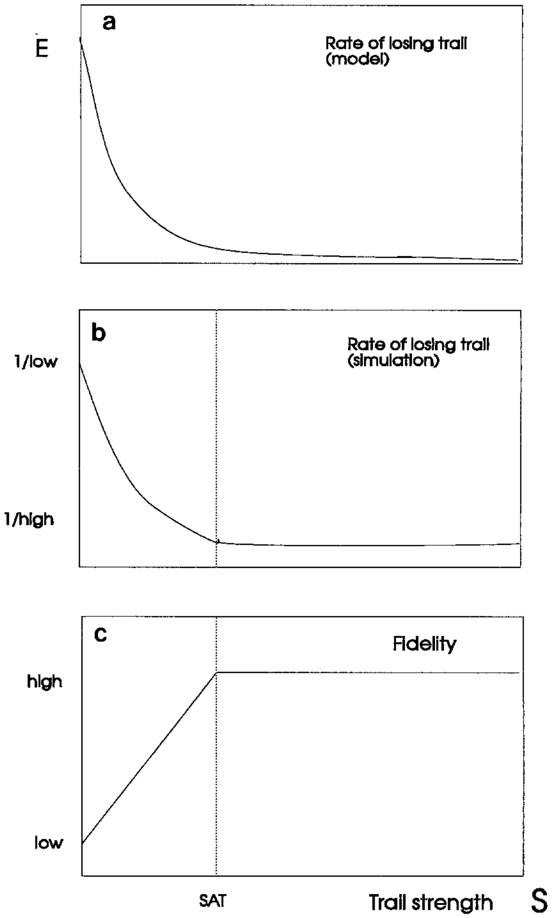


Fig. 1a–c In the model, trail followers have some probability of leaving a trail they are following. The probability of leaving a trail is assumed to decline as the strength of the trail increases. Two possible functional dependencies on trail strength are shown here. **a** Trail loss decreases exponentially with increasing trail strength (the version used in the mathematical model); **b** trail loss is a decreasing linear function of trail strength over some range of S (the version used in the simulations of ants); **c** Fidelity (tendency to stay on trail) used in simulation

$\alpha' = d_s\,\alpha\,N/\Gamma$ = probability that a single ant is recruited to any one of N simple trails during the trail half life

Dependence on group size thus appears only in the last parameter.

Results

Predictions of the model

It was shown by EK (1994a) that the model with varying response to trail strength is capable of producing a variety of possible behaviours, depending on the relative sizes of parameters. The most interesting type of transition occurs when the parameter b or B', associated with the recruitment response, is gradually varied. Several different natural situations might be associated with variations in such parameter values. Variations may occur on a timescale of hours, (due to changing colony conditions) days, months or seasons (due to changing

Table 1 Values of parameters given in literature. (N colony size, v individual velocity, *TD* trail duration, *HL* half-life, *artif* artificial trail, *PF* path length followed, *L* trail length, *RL* probability of losing trail per unit length walked, *F* percent of ants that turn and follow a trail they encounter)

Species	Parameter	Type of measurement	Source
Atta texana	TD > 6 days	artif	Moser and Silverstein (1967)[c]
	N = 10000000	field	Beckers et al. (1989)
Acromyrmex octospinosus	TD < 24 hr	field	Therrien et al. (1986)
	N = 50000	field	Beckers et al. (1989)
Eciton burchelli	v = 2–3 cm/s	circular mills	Franks et al. (1991)
	HL = 132 min	estimated[a]	ibid
	v = 4–11 cm/s	field	Franks (1985)
	N = 300000–650000	field	ibid
	v = 8 cm/s	field	Franks (1986)
	TD = 2.25–8.25 Days	field[b]	Torgersen and Akre (1970)
E. hamatum	TD = 2.5–7.5 Days	field[b]	ibid
	TD > 39 Days	field	Rettenmeyer (1963)[c]
	N = 300000	field	Beckers et al. (1989)
Eciton	TD > 31 Days	field	Schneirla and Brown (1950)[c]
Formica rufa	v = 0.6–1.5 cm/s	field	Holt (1955)
	N = 4000000	field	Beckers et al. (1989)
Iridomyrmex humilis	N = 150000	field	Beckers et al. (1989)
	TD = 30 min	estimate	J. L. Deneubourg et al. (1990a)
	v = 1.0 cm/s	artif	V. Calenbuhr[d]
	PF = 100–700 cm	artif	J. L. Deneubourg[d]
Lasius fulginosus	TD = 11 Days	artif	Hangartner (1967)[c]
	N = 2500000	field	Beckers et al. (1989)
Manica rubida	v = 1–3 cm/sec	artif	Jackson et al. (1990)
	TD < *Myrmica rubra*		ibid
Myrmica rubra	v = 1.3–1.5 cm/s	artif	Cammaerts et al. (1978)
	v = 1.2–1.9 cm/s	artif	Calenbuhr et al. (1992)
	F = 40–75	conc. dependent	ibid
	PF = 5–17 cm	conc. dependent	ibid
	PF = 5.–15. cm	artif	Pasteels et al. (1986)
	F = 65–78	artif	ibid
	RL = .15/cm	artif	ibid
	TD = 2–3 min	artif	Cammaerts-Tricot (1973) Cammaerts-Tricot et al. (1976)
	N = 1000	field	Beckers et al. (1989)
Pogonomyrmex badius	N = 4300	field	Beckers et al. (1989)
	TD = 35 s	artif	Wilson (1971)
	L = 20 cm	artif	ibid
Solenopsis saevissima	TD = 3.5–7 min	artif:glass	Wilson (1962)[c]
	TD = 20 min	artif: blotter paper	ibid
	TD = 104 s	artif:glass	Bossert and Wilson (1963)
	v = 0.4–0.8 cm/s	artif:glass	ibid
	L = 28 cm	calculated	ibid
	PF = 1.48 cm	artif	Wilson (1962a, b)
S. invicta	N = 100000	field	Beckers et al. (1989)
Tetramorium caespitum	N = 14000	field	Beckers et al. (1989)
	PF = 2–15 cm	conc. dependent	Pasteels et al. (1987a, b)
Veromessor pergandei	v = 0.6 cm/sec	field	Rissing (1982)

[a] From the assumption that velocity is proportional to pheromone strength

[b] Measurement varies from wet to dry seasons

[c] Cited in Torgersen and Akre (1970)

[d] Personal communication

Table 2 Values of parameters appearing in model

Species	Speed υ(cm/s)	Decay rate Γ(/s)	Rate lose trail, ε(/s)	Rate find path α(cm/s)
Eciton burchelli	3–10	4×10^{-7}	–	–
Formica rufa	v = 0.6–1.5	–	1.8×10^{-4}	0.7 v
Iridomyrmex humilis	v = 1.0	5×10^{-4}	0.003	0.7 v
Myrmica rubra	v = 1.3–1.5	0.005–0.008	0.1–0.26	0.85–1.2
Pogonomyrmex badius	v = 0.6	0.028	–	–
Solenopsis saevissima	v = 0.4–0.8	0.008–0.12	0.27–0.54	0.7 v
Tetramorium caespitum	v	–	0.06–0.5 v	0.7 v

environmental conditions). One would also expect different species to have different parameter values because of differences in habitat, life cycles, food type and/or availability, and other life-history factors (see Table 1 and 2 for examples).

In Figs. 2b,c and 3a the parameters A' and α', are fixed, and the recruitment response (either *E*' or *B*' or both) is changed. To show the predictions of the model (Eqs. 1 and 2) it is convenient to use a phase plane diagram which shows a simultaneous time evolution of the trail density, *T*, and the density of followers, *F*. The trail strength $S = F/\mathrm{T}$ can also be read-off these diagrams: see Fig. 2a). Several sample trajectories (labelled 1–4 on the *TF* plane in Fig. 3a) demonstrate dependence on initial conditions. The starting points 1 and 3 eventually approach *B* (labelled "weak"), whereas 2 and 4 approach *A* ("strong"). (Refer to Fig. 2a for trail strength at various positions in the *FT* plane).

The two heavy dots on Fig. 3a are stable steady states, but the open circle is unstable. Each of the trajectories 1–4 is also shown on graphs of *T* and *F* plotted against time, in Figs. 3b–e. Fig. 3 illustrates that the outcome can depend on the initial starting values. A population with trails that are initially strong enough will evolve towards a strong stable level of followers per unit trail length. The *TF* plane is separated into two basins of attraction by a separatrix, formed by the pair of trajectories approaching the unstable steady state.

Two other cases are shown in Figs. 2b,c, for different parameter settings. For low values of *B*', (large increase in trail strength causes small increase in trail fidelity), a system of weak trails always forms (Fig. 2b). For low values of *E*' (followers have a high fidelity to all trails, even weak ones), the population forms only strong trunk trails, as shown in Fig. 2c. For intermediate values (e.g. $A' = 0.1$, $\alpha' = 0.3$, $B' = 4.0$, $E' = 6.0$) the behaviour depends on the initial situation, as described in Fig. 3. Indeed, it is found that as *B*' varies continuously through a range of values, population behaviour undergoes abrupt transitions between the three cases shown in Figs. 2b,c and 3a. These bifurcations in behaviour carry implications that will be discussed later on.

Simulation results

Typical output from the simulation of ant trails is shown in Fig. 4. Ants moving freely tend to move along straight lines, but there is some probability at each time step that

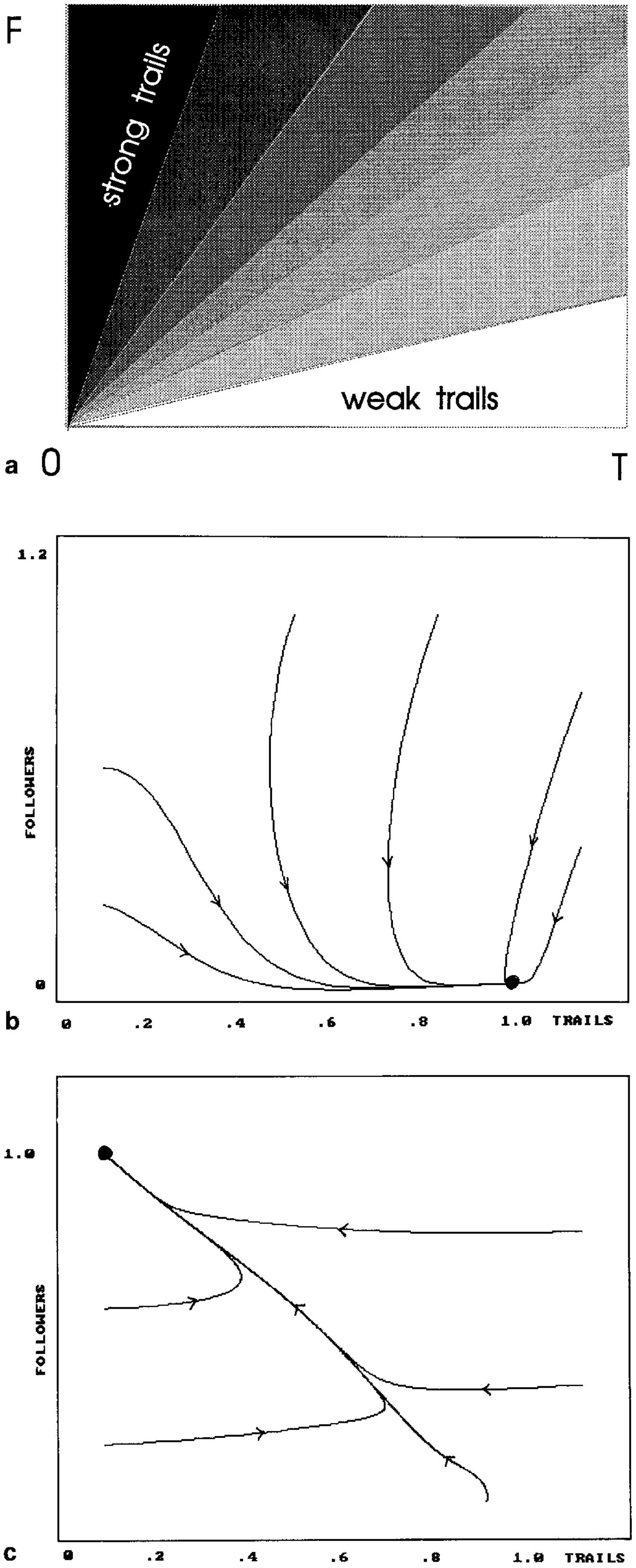
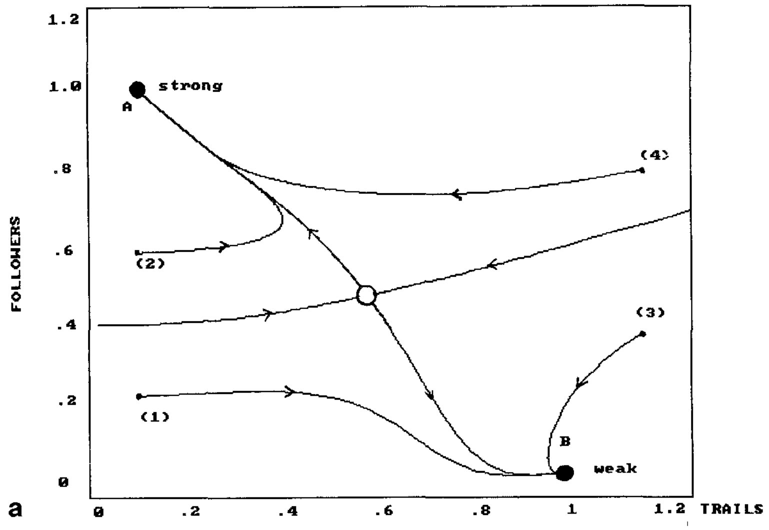
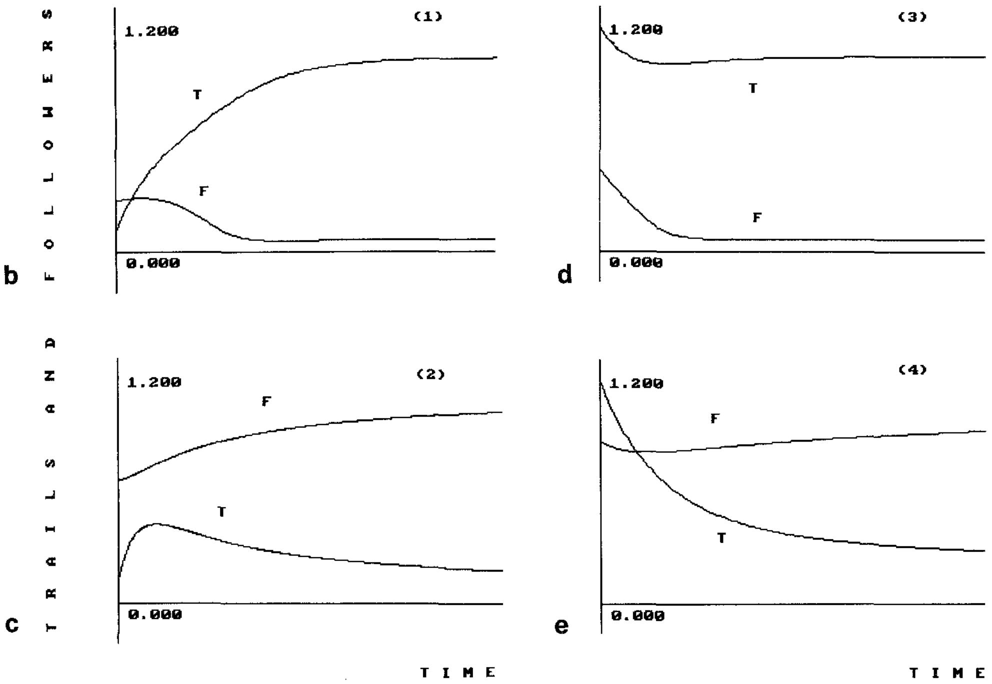


Fig. 2a A representation of the magnitude of the ratio $S = F/T$ (trail strength, or traffic density along the trails) is given here on a *TF* plane. *Points along lines close to the T axis* have low *F* values, so here *S* is small, and therefore represent weak trails. *Points on lines close to the F axis* represent strong trails. *b* Behaviour of the model is shown on a *TF* phase plane diagram. Values of the parameters were $A' = 0.1$, $\alpha' = 0.3$, $B' = 0.7$, $E' = 6.0$, and the differential equations were integrated using PhasePlane (B. Ermentrout). Regardless of the initial values of *T* and *F*, all points approach a single steady state (*heavy dot*) in the "weak" trails region of the *TF* plane. Thus, for this value of *B*' the trails will eventually become weak. **c** Values of the parameters were $A' = 0.1$, $\alpha' = 0.3$, $B' = 4.0$, $E' = 2.5$. Now all initial values evolve into strong trail networks (steady state represented by the *heavy dot* in the "strong network" portion of the *TF* plane)

Fig. 3a–e Behaviour of the model is shown **a** on a phase plane diagram, and **b–e** on conventional time graphs. Values of the parameters were $A' = 0.1$, $\alpha' = 0.3$, $B' = 4.0$, $E' = 6.0$). The four initial conditions *marked (1)–(4)* in **a** have values of (T,F) given by (0.1,0.25), (0.1,0.6), (1.1, 0.4), (1.1, 0.8) respectively. Both initial conditions (1) and (3) will eventually lead to a weak trail network, whereas (2) and (4) will eventually become strong trail networks. The *curves* pointing towards the unstable steady state (*open circle*) are exceptions, but these would rarely occur in a natural system. **b-e** (labelled 1–4) correspond to the trajectories shown in **a**





they will turn by angles 45°, 90°, 135° or 180° to the right or left. For example, the turning parameters used in the simulation shown in Fig. 5 (50, 20, 7, 4) are probabilities (out of a maximum of 256) of such turns. The meaning of the parameter 50 is that, with probability $50/256 \approx 0.2$ every iteration, an ant turns by 45° or more.

In the simulation, ants can only become followers if they either start out walking along a preexisting trail, or if they cross a trail. In the latter case, there is an angle-dependent probability that they will "detect" the trail and "decide" to follow it. As the length of trails in the region builds up, there are more opportunities for ants to cross the trails, so in this sense, the rate of conversion of lost ants to follower ants is similar to that assumed in the model.

Ants walking along trails have a variable level of "fidelity" to the trail. It is assumed in the simulation that the stronger the trail, the more likely is an ant to remain on that trail per iteration. The connection between fidelity in the simulation and trail drop off rates in the model is an inverse one (fidelity $\approx$ 1/trail drop-off rate) and the functional dependence on trail strength is semi-linear, as shown in Fig. 1c. The minimal and maximal levels of fidelity, and the trail strength (SAT) at which maximal fidelity occurs are selected in a given simulation. It is customary to let fidelity vary between a value close to (but not equal to) zero, and a level close to 256. The value of SAT therefore determines the slope of this linear dependence, which represents the extent to which the strength of the trail influences the decision to stay on it. This slope, and thus SAT, is therefore a crucial parameter in the simulation.

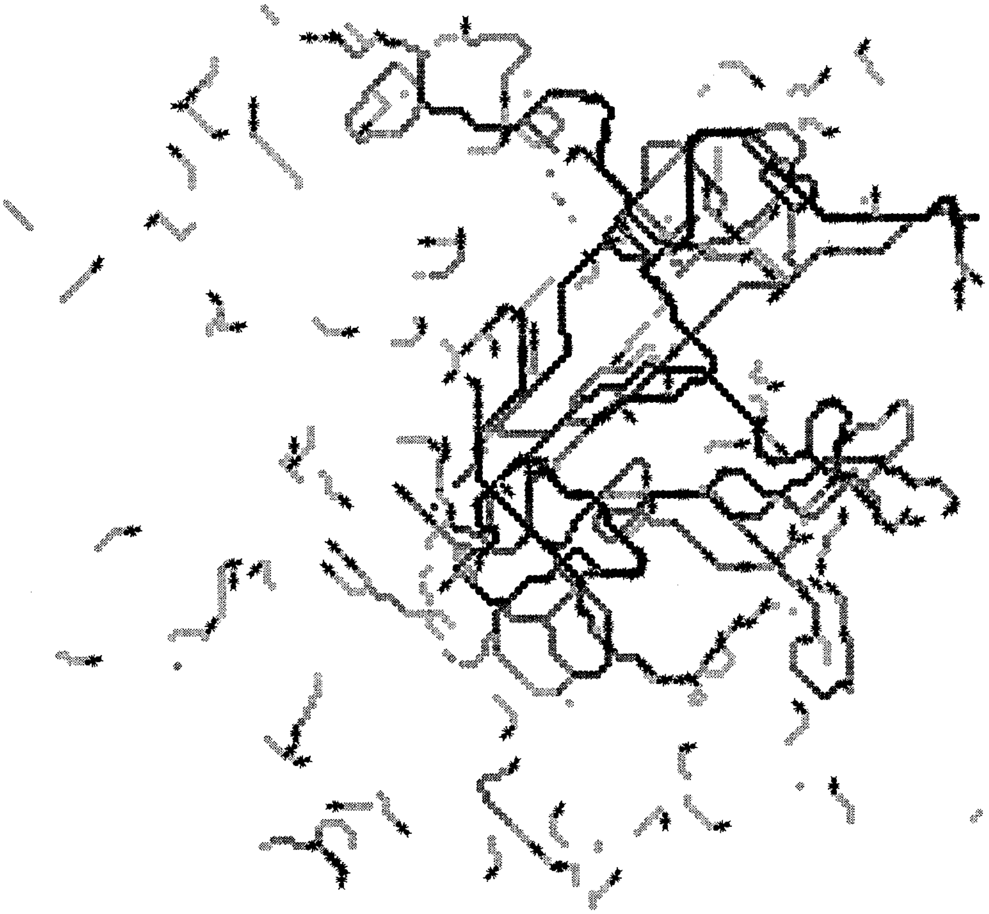


Fig. 4 Typical output from the simulation of ant trails. Shown are the positions of "ants" and trails that they have formed. The level of *grey* of the trails is indicative of trail strength

A *high turning rate* of ants is equivalent to a high degree of random motion. This results in more tortuous trails and interferes with ability to form strong trails: by turning rapidly, a given ant takes longer to get away from the nest area. Trails that span large distances from the nest are bound to lose more followers than attract new ones at their ends, and thus these trails cannot be maintained. One sees a cloud of ants milling about close to the nest, and gradually expanding outwards, but rarely able to form long-lived trails.

A combination of relatively *low individual trail marking* and *high maximal trail strength* tends to promote formation of strong trails. If individuals secrete too much pheromone, many weak trails of short duration will appear, forming a confusing network. It is thus important that the signal produced by any one individual should not last too long. Once a trail with many individuals on it has been formed, it is beneficial to stabilize it. This happens whenever the strength is allowed to build up to high values (MAX large). When MAX is high, strong trails that are by chance abandoned for a short period of time will persist until new ants find and follow them.

Figure 4 shows a typical simulation output showing positions of the ants and pheromonal strength of the trails. Figure 5 illustrates a typical sequence of events in the formation of a set of trails radiating outwards from a nest, when conditions favour strong trails(i.e. a low rate of random turning, a high maximal trail strength and a fairly low level of individual marking). Just before Fig. 5a, ants are randomly exiting from the nest (at the center of the region) as solitary individuals. Trail strength builds up close to the nest leading to formation of strong trails. These trails elongate (Fig. 5a–b) and absorb many exploratory ants, preventing other trails from forming nearby (see Beckers et al. 1990 for a similar conclusion). Ends of trails spill their followers into highly branched weak networks (barely visible in the figures). As waves of recruitment take place (due to the effect of replacement when ants leave the region), new trails are added. As seen in Fig. 5b–d the number of trails increases to eight.

When directional persistence is high, trails tend to be straight lines. Even if trails start convoluted, or with sharp bends they tend to straighten with time. (A straight line is the shortest path joining two points. Straight trails have the highest pheromone strength per unit length for a given number of followers, making them more attractive, and more long-lived than other trails. Random shortcuts that contribute to straightening a trail would thus persist.) By 7000 iterations, all eight trails emanating from the nest were straight, and six of them reached the boundary of the region.

As discussed in the modelling section of this paper, a key parameter is the steepness of response to increased trail strength. In the simulation, the parameter SAT

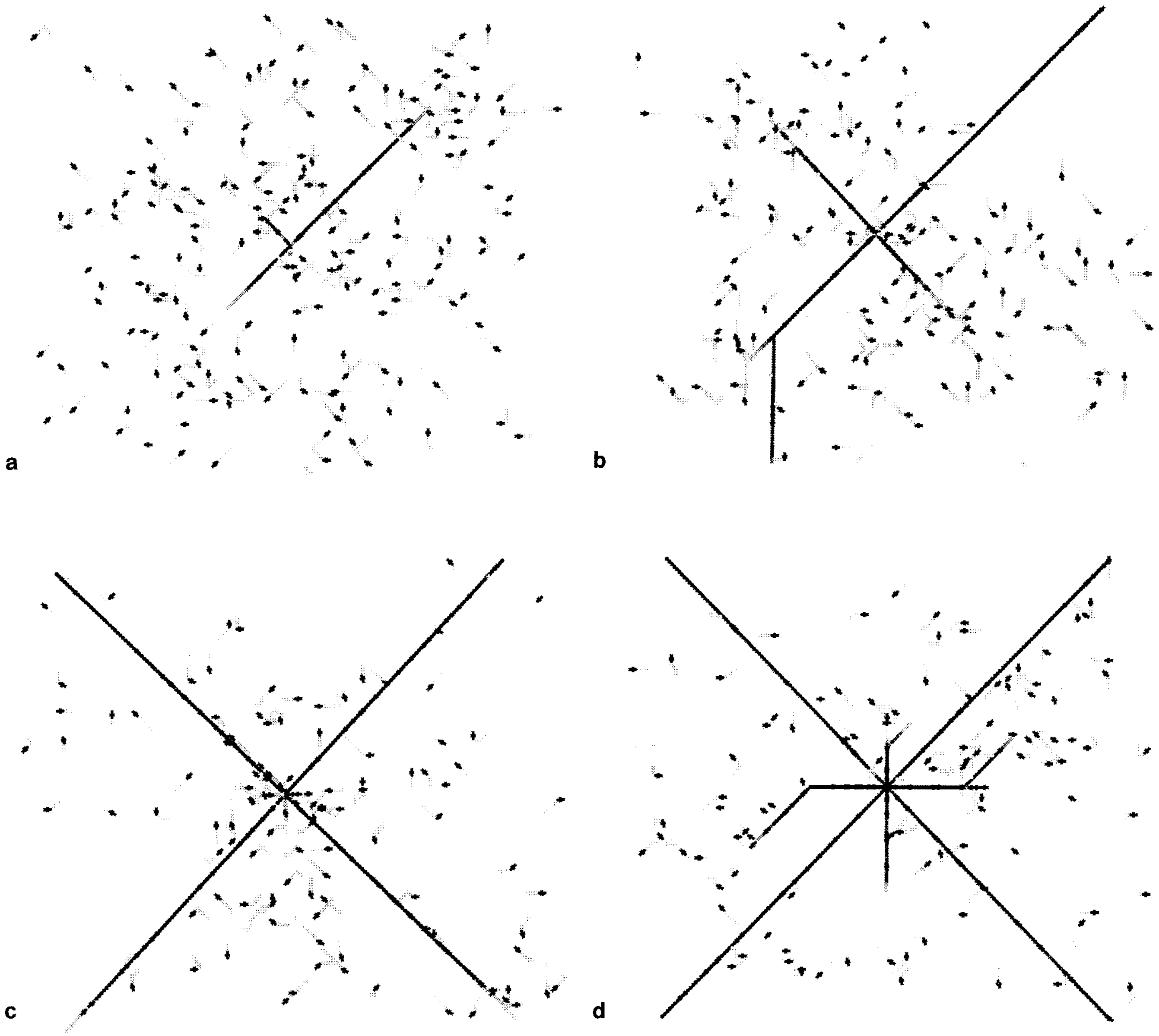


Fig. 5a,b A time sequence of trail formation produced by the simulation described in this paper. An initially randomly moving population evolves a set of trails of increasing complexity. The initial trail network has only one major axis of motion. Eventually, eight strong trails have been formed. The smaller trails will later lengthen, and their ends will straighten out. The times shown here are after **a** 1000, **b** 2000, **c** 3000 and **d** 4000 iterations. Parameters include: maximal trail strength (MAX) = 200, trail fidelity low value 20, high value 230, saturation at trail strength (SAT) = 50, trail length behind single ant $\tau = 8$. See text for details of the parameters

governs this slope. When SAT is small, the fidelity increases rapidly for a small difference in the strength of the trail. For example, if SAT = 40, and $\tau = 8$, it takes only 5 ants walking in a row to make a trail of maximal fidelity (a trail of strength 40 units (or more) is associated with a maximal level of fidelity.) If SAT = 200 and $\tau = 8$, it would take 25 ants walking one after another to create an equally attractive trail.

In the experiments conducted with the simulation, conditions were selected under which strong trails were generally favoured, and the effect of varying SAT was determined (see Fig. 6). Parameters were MAX = 200, $\tau = 8$, turning parameters (50,20,7,4), and low and high fidelity values (20, 230). For values of SAT = 100, 75, and 60 no strong trails could be detected, even after 3000 iteration steps. The ants continued to mill about randomly throughout the simulation. A typical result is shown in Fig. 6a. When SAT was set to 40, the steepness of the response to trail strength was just great enough that trails could be maintained (see Fig. 6b). As SAT was further decreased, the formation of trails became more rapid.

Comparison of model and simulations

The mathematical model and the computer simulation are two separate and distinct ways of representing trail

Fig. 6a,b The effect of steepness of response to trail strength on the ability to form strong trails is shown here. When the parameter SAT which governs the slope of the response curve, was set at SAT = 100, 75, or 60, the trail followers milled about randomly and did not succeed to form stable trails by 3300 iterations, as shown in **a**. (Only one output is shown, but all three were essentially the same). When SAT was given the value 40, trails formed by 1300 iterations, as shown in **b**. A yet lower value of SAT resulted in more rapid trail formation

following which share a number of common features. They differ in several important details listed below.

1. In the simulation, both the quantity (length), the quality (strength), and the positions of trails are shown. The model only describes trail length.

2. In the simulation, the total number of ants fluctuates as they are gradually introduced and randomly leave the region. In the model the total number of ants is assumed constant.

3. Trail decays linearly (by one unit of length per iteration) in the simulation, but at an exponential rate in the model.

4. In both model and simulation, there is a length of trail associated with one individual (the simulation parameter τ is identical with the model parameter d_s), but there seems to be no clear way of identifying a simulation parameter equivalent to the spacing between followers, d_f, of the model.

5. In the simulation, trail strength is represented by the chemical level associated with a given point along the trail. In the model, trail strength is an average network property based on the density of followers per unit length of trail.

6. In the model, the response of fidelity to trail strength is exponential, but in the simulation the response to S is semi-linear (needed to speed computation).

Despite these differences, we nevertheless observe a general agreement in the nature of predictions of the simulation and of the model. In both cases, there is clear evidence of the dichotomy in the kinds of trail networks that can form: very loose, weak networks that have a high proportion of lost ants, and never develop to full-blown stable trails, versus strong networks that have many followers per unit length, a high level of chemical marker, and long duration.

Further, both model and simulation illustrate how a collective effect can lead to spontaneous formation of strong "trunk" trails: The idea rests on the fact that one or two individuals cannot cause very significant changes in the population behaviour. However, groups of individuals have an influence that increases rapidly with group size: a group of ants walking together along one trail can increase the attractivity of the trail so as to recruit a large fraction of the population to it. The slope of the response to group pressure (governed by the parameter b in the model) or the response to the chemical strength of the trail (governed by SAT in the simulation) are the important in each case.

Discussion

Comparison with previous work

Models and observations of ant behaviour, of self-organization, and of recruitment responses have been studied by the Brussels group (Pasteels and Deneubourg 1967; Pasteels et al. 1987a,b; Goss et al. 1989; Aron et al. 1989, 1990a; Deneubourg et al. 1990a). Laboratory experiments are made under conditions in which the geometry of the arena, the locations of nests, food sites, and systems of bridges connecting them is externally imposed. Ants will select some subset of the routes to the food and abandon the other routes. Simulations of ant movements and/or trails appear in (Deneubourg et al. 1989; Aron et al. 1990b). The fact that there are many self-organizing aspects of ant societies has also been the main thesis of work by this group. The ideas of artificial life and tools of physics such as statistical mechanics have recently been applied to ant swarms by Millonas (1992, 1994). He stresses the network properties of the swarm which parallel other interconnected systems such as neural or immune networks.

Among the first theoretical treatments on the subject of trail-following were papers by Wilson (1962a,b). The rate of recruitment of ants to a food source and their accuracy of finding the targets were studied empirically, using an information-theoretic approach. Bossert and Wilson (1963), described the length, width, and longevity of a typical pheromonal trail laid by a single ant based on properties and solutions of simple diffusion equations. Their papers explore trail following from the perspective of an individual. A broader study of orientation of organisms at the individual level was given by Fraenkel and Gunn (1961).

Verhaeghe (1982) studied group leading as a method of recruitment to food sources in *Tetramorium impurum.* (The leaders, unlike our exploratory ants, know and lead the way to food.) In Verhaeghe and Deneubourg (1983) a model based on the logistic equation represents recruitment of *Tetramorium* from the nest to food. Deneubourg et al. (1983) concluded that some degree of random behaviour could optimize foraging in the presence of numerous food sources.

An interesting aspect of the work by Pasteels et al. (1986) are the measurements of the probability of reaching the end of a trail as a function of the pheromonal strength. (This is equivalent to determining ε as a function of S). The measurements were made by painting artificial circular trails with extracts of pheromone, and it was observed that beyond a threshold concentration the ants tended to be repelled from the trails. This may be because the higher concentrations were outside the normal biological ranges that ants can accommodate. Our model considers only an increasing probability of staying on trails as pheromone levels increase.

Patterns of exploratory trail-networks have been simulated in several sources. Deneubourg et al. (1989) and Franks and Bossert (1983) have simulated army ant raiding swarms. Deneubourg et al. (1990a) and Aron et al. (1990b) have simulated pheromone-based swarming of *Iridomyrmex.* (The individuals choose to go left or right depending on pheromonal concentration.) A recent paper by Reed and Cherrett (1990) describes a simulation of branching trails and foraging patterns of *Atta cephalotes* with extending, branching, and non-extending trails. Ganeshaiah and Veena (1991) give a branch analysis of the trails of the predatory ant *Leptogenys processionalis.*

Many papers cited above have the desirable feature of including both experimental and theoretical investigations and address the question of self-organization. However, several general drawbacks exist:

1. The importance of identifying and experimentally measuring a full set of parameters influencing trail formation has not been emphasized.
2. Models for recruitment tend to have fairly predictable results for *all* parameter choices: one route is always chosen out of many, or one food source is favoured.
3. Thus, the dependence of group behaviour on individual-based parameters has not been fully realized. [There is recognition, however, that population size is an important influence on self-organization; see in particular the excellent summary by Beckers et al. (1989), Verhaeghe (1982) and Pasteels et al. 1987a, Deneubourg and Goss 1990].
4. Simulations have been qualitative, without systematic understanding of the influence of parameter variations on the morphology of the trails.

The model presented here addresses some of these of these issues.

A number of outstanding issues remain to be addressed. These include (1) a detailed understanding of the spatial distribution of the organisms and trail networks, (2) some estimate of the speed of propagation over previously unexplored territory, and (3) some quantitative or qualitative prediction about directionality of the trails and the ability to form directed trails. Certain features of these problems have been treated in companion papers by Edelstein-Keshet (1994b), and Watmough and Edelstein-Keshet (1994), but many outstanding areas of investigation remain open.

Identification of parameter values

As discussed above, no full set of parameter values needed for the model can be found in any single paper or indeed in the literature for a single species of trail follower. This limits the current ability to test predictions of the model. However, to gain some insights about the types of parameters needed, and typical values in a variety of species, we list results obtained by combing through the literature in Table 1. Values vary over wide ranges in different species and conditions (e.g. artificial or natural trails). In particular, the duration of trails of various ants (TD in Table 1) and colony sizes (N) range over several orders of magnitude.

The raw values of various parameters from the literature can be combined (using suitable assumptions) to generate a set of values for the parameters discussed in the model. Representative examples are shown in Table 2. Since these are still incomplete, it is as yet premature to incorporate realistic values into the model or simulation. A goal of future work would be to determine or experimentally measure a complete set of values.

Implications

The model shows that the ability to self-organize from an initially random configuration to coherent motion on trunk trails is not universal: it depends on a balance between competing effects. In particular, the response of recruitment to increased trail strength (or equivalently to increased traffic on trails) is a key parameter. As this parameter varies gradually from a low to a high value, the population undergoes two abrupt transitions: at first it can form only weak, confused trails; then it can form strong trails but only when there are sufficiently many initial trail followers to recruit the rest; eventually, as this response is increased further, the population will always form strong trails exclusively.

These predictions have a number of implications about ant population behaviours. We first consider the timescale of hours or days. As noted in our introduction, over this timescale, the needs of the colony and potential threats from danger will change, requiring adaptation of the movement pattern. The predictions of this paper demonstrate that it is not necessary to conceive of an elaborate strategy for how such changes in the spatial organization of the colony might be controlled. Rather, we have shown that a fairly small change in a parameter associated with individual behaviour can produce a sharp transition in population behaviour. (We have dwelt on the acuity of response to recruitment, but actually, other parameters such as turning rates, rates of secretion, and/or attraction to trails also have similar effects.)

It is also worth considering the implications of these results on a longer timescale, that of evolution. Certain aspects of organism behaviour are "hard-wired", in the sense that they have been inherited from an ancestral organism. These aspects might include the chemical signals, the receptors that respond to these chemicals, and aspects of motor control in an individual. Natural selection and the environment in which the organism lives interact with these physiological attributes to fine tune the values of parameters associated with individual behaviour. (For example, mutations that change the affinities of receptors to signalling molecules might be selectively advantageous in certain environments.) Together, the forces of natural selection and environmental constraints gradually modify individual, and thereby also population behaviour. Consequently, the *emergent phenomenon* at the collective level, for example the ability to self-organize, is adaptive.

Further, we argue that models for animal behaviour such as the one presented here can give an indication of *optimal individual attributes.* Stated another way, not all (sets of) parameter ranges are equally efficacious. A careful investigation of parameter values of the model reveals that transitions in population behaviour occur close to particular values of the leading parameters. (Such points are called bifurcation values). Since a population that can respond rapidly to physical and environmental pressures has a selective advantage, it stands to reason that operating close to such bifurcation values will be rewarded by a process of natural selection. We have based the model on a number of biologically meaningful parameters (degree of random motion, fidelity to trails, pheromone deposition rate, attraction to trails, recruitment response, trail pheromone lifetime, and size of the population). We would speculate therefore, that over an evolutionary timescale, the biological ranges of such parameters should gradually shift closer to the values associated with the bifurcation points, at which the populations can most readily switch from one type of desirable behaviour to another.

Acknowledgements We are grateful to Scott Camazine for encouragement and for many insightful comments. V. Calenbuhr kindly supplied references for parameter values. We gratefully acknowledge support from the National Sciences and Engineering Research Council of Canada under grant number OGPIN 021. GBE was supported by a National Science Foundation grant DMS9002028.

References

Able K P (1980) Mechanisms of orientation, navigation, and homing. In: Gauthreaux SA (ed) Animal migration, orientation, and navigation. Academic Press, pp 283–373

Aron S, Pasteels JM, Deneubourg, J-L (1989) Trail-laying behaviour during exploratory recruitment in the Argentine ant, *Iridomyrmex humilis* (Mayr). Biol Behav 14:207–217

Aron S, Deneubourg J-L, Goss S, Pasteels JM (1990a) Functional self-organization illustrated by inter-nest traffic in ants: the case of the argentine ant. In: Alt W, Hoffmann G (eds) Biological motion (Lecture notes in biomathematics 89). Springer, Berlin Heidelberg New York, pp 533–547

Aron S, Pasteels JM, Goss S, Deneubourg J-L (1990b) Self-organizing spatial patterns in the Argentine ant *Iridomyrmex humilis* (Mayr). In: Vander Meer RK, Jaffe K, Cedeno A (eds) Applied myrmecology, a world perspective. Westview, Boulder, pp 438-451

Beckers R, Deneubourg J-L, Goss S, Pasteels JM (1990) Collective decision making through food recruitment. Insectes Soc 37:258–267

Beckers R, Goss S, Deneubourg J-L, Pasteels JM (1989) Colony size, communication and ant foraging strategy. Psyche 96:239–256

Bossert WH, Wilson EO (1963) The analysis of olfactory communication among animals, J Theor Biol 5:443–469

Breed MD, Fewell JH, Moore AJ, Williams KR (1987) Graded recruitment in a ponerine ant, Behav Ecol Sociobiol 20:407–411

Burton JL, Franks NR (1985) The foraging ecology of the army ant *Eciton rapax*: an ergonomic enigma?, Ecol Entomol 10:131–141

Calenbuhr V, Deneubourg J-L (1990) A model for trail following in ants: individual and collective behaviour. In: Alt W, Hoffmann G (eds) Biological motion (Lecture notes in biomathematics 89). Springer, Berlin Heidelberg New York, pp 453–469

Calenbuhr V, Deneubourg J-L (1992) A model for osmotropotactic orientation, I. J Theor Biol 158:359–393

Calenbuhr V, Chretien L, Deneubourg J-L, Detrain C (1992) A model for osmotropotactic orientation. II. J theor Biol 158:495–407

Cammaerts MC, Inwood MR, Morgan ED, Parry K, Tyler RC (1978) Comparative study of pheromones emitted by the workers of the ants *Myrmica rubra* and *Myrmica scabrinodis.* J Insect Physiol 24:207–214

Cammaerts-Tricot M-C (1973) Phéromone agrégeant les ouvrières de *Myrmica rubra.* J Insect Physiol 19:1299–1315

Cammaerts-Tricot M-C (1974) Piste et phéromone attractive chez la fourmi *Myrmica rubra.* J Comp Physiol 88:373–382

Cammaerts-Tricot M-C, Morgan ED, Tyler RC, Braekman JC (1976) Dufour's gland secretion of *Myrmica rubra*: chemical, electrophysiological and ethological studies. J Insect Physiol 22:927–932

Camazine S (1991) Self-organizing pattern formation on the combs of honey-bee colonies Behav Ecol Sociobiol 28:61–76

Chelazzi G, Della Santina P, Parpagnoli D (1990) The role of trail following in the homing of intertidal chitons: a comparison between three *Acanthopleura* spp. Mar Biol 105:445–450

Deneubourg J-L, Goss S (1990) Collective patterns and decision making, Ethol Ecol Evol 1:295–311

Deneubourg J-L, Pasteels JM, Verhaeghe JC (1983) Probabilistic behaviour in ants: a strategy of errors? J Theor Biol 105: 259–271

Deneubourg J-L, Goss S, Franks N, Pasteels JM (1989) The blind leading the blind: chemically mediated morphogenesis and army ant raid patterns, J Insect Behav 2:719–725

Deneubourg J-L, Aron S, Goss S, Pasteels JM (1990a) The self-organizing exploratory pattern of the Argentine ant. J Insect Behav 3:159–168

Deneubourg J-L, Grégoire JC, Le Fort E (1990b) Kinetics of larval gregarious behaviour in the bark beetle *Dendeoctonus micans* Coleoptera: Scolytidae. J Insect Behav 3:169–182

Dumpert K (1978) The social biology of ants (translated by C Johnson 1981). Pitman, Boston

Edelstein-Keshet L (1994a) Simple models for trail-following behaviour; trunk trails versus individual foragers. J Math Biol 32:303–328

Edelstein-Keshet L (1994b) Trail following as an adaptable mechanism for population behaviour. In: Parrish JK, Hamner WM, Prewitt CT (eds) Three dimensional animal aggregations. In press

Ermentrout GB (1990) Phase Plane, Brooks/Cole publishers

Ermentrout GB, Edelstein-Keshet L (1993) Cellular automata approaches to biological modelling. J Theor Biol 160:97–133

Estes RD (1991) The behaviour guide to African mammals: including hoofed mammals, carnivores, primates. University of California Press, Berkeley, CA

Evershed RP, Morgan ED, Cammaerts MC (1982) 3-ethyl-2,5-dimethyl pyrazine, the trail pheromone from the venom gland of eight species of *Myrmica ants*. Insect Biochem 12:383–391

Fabré JH (1979) Insectes. Felix Gluck, New York

Focardi S, Santini G (1990) A simulation model of foraging excursions in intertidal chitons. In: Alt W, Hoffmann G (eds) Biological motion (Lecture notes in biomathematics 89) Springer, Berlin Heidelberg New York, pp 319–330

Focardi S, Deneubourg J-L, Chelazz G (1985) How shore morphology and orientation mechanisms can affect the spatial organization of intertidal molluscs. J Theor Biol 112:771–782

Fraenkel GS, Gunn DL (1961) The orientation of animals; kineses, taxes, and compass reactions. Dover, New York

Franks NR (1985) Reproduction, foraging efficiency and worker polymorphism in army ants. In: Hölldobler B, Lindauer M (eds) Experimental behavioural ecology and sociobiology (Fortschritte der Zoologie 31). Fischer, Stuttgart, pp 91–107

Franks NR (1986) Teams in social insects: group retrieval of prey by army ants (*Eciton burchelli*, Hymenoptera, Formicidae). Behav Ecol Sociobiol 18:425–429

Franks NR (1989) Army ants: a collective intelligence. Am Sc 77:139–145

Franks NR, Bossert WH (1983) The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community. In: Sutton SL, Whitmore TC, Chadwick AC (eds) Tropical rainforest: ecology and management. Blackwell, Oxford, pp 151–163

Franks NR, Fletcher CR (1983) Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. Behav Ecol

Sociobiol 12:261–270

Franks NR, Gomez N, Goss S, Deneubourg J-L (1991) The blind leading the blind in army ant raid patterns: testing a model of self-organization (Hymenoptera: Formicidae). J Insect Behav 4:583–607

Ganeshaiah KN, Veena T (1991) Topology of the foraging trails of *Leptogenys processionalis* -- why are they branched? Behav Ecol Sociobiol 29:263–270

Goss S, Aron S, Deneubourg J-L, Pasteels J M,(1989) Self-organized shortcuts in the Argentine ant. Naturwissenschaften 76:579–581

Hangartner W (1967) Spezifität und Inaktivierung des Spurpheromons von *Lasium fulginosus* Latr. und Orientierung der Arbeiterinnen im Duftfeld. Z Vergl Physiol 57:103–136

Hölldobler B (1976) Recruitment behaviour, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. Behav Ecol Sociobiol 1:3–44

Hölldobler B, Lumsden CJ (1980) Territorial strategies in ants. Science 210:732–739

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge

Holt SJ (1955) On the foraging activity of the wood ant. J Anim Ecol 24:1–34

Howard RW, Flinn PW (1990) Larval trails of *Cryptolestes ferrugineus* (Coleoptera: Cucujidae) as kairomonal host-finding cues for the parasitoid *Cephalonomia waterstoni* (Hymenoptera: Bethylidae). Ann Entomol Soc Am 830:239–245

Jackson BD, Cammaerts M-C, Morgan ED, Attygalle AB (1990) Chemical and behavioral studies on Dufour gland contents of *Manica rubida* (Hymenoptera:Formicidae). J Chem Ecol 16:827–840

Kennedy JS (1967) Behaviour as physiology. In: Beament JWL, Treherene JE (eds) Insects and physiology. Oliver and Boyd, Edinburgh, pp 249–265

Kennedy JS (1986) Some current issues in orientation to odour sources. In: Payne TL, Birch MC, Kennedy CEJ (eds) Mechanisms in insect olfaction. Clarendon, Oxford, pp 11–25

MacGregor EG (1947) Odour as a basis for oriented movement in ants. Behaviour 1:267–296

Millonas MM (1992) A connectionist type model of self-organized foraging and emergent behaviour in ant swarms. J Theor Biol 159:529–552

Millonas MM (1994) Swarms, phase transitions, and collective intelligence. In: Langton C (ed) Artificial life III (SFI studies in the sciences of complexity Vol XVII). Addison-Wesley, Redwood City, CA, pp 417–445

Moser JC, Silverstein RM (1967) Volatility of trail marking substance in the town ant *Atta texana* Nature 215:206–207

Pasteels JM, Deneubourg J-L (eds) (1987) From individual to collective behaviour in social insects. Birkhauser, Basel

Pasteels JM, Deneubourg J-L, Verhaeghe JC, Boeve JL, Quinet Y (1986) Orientation along terrestrial trails by ants. In: Payne TL, Birch MC, Kennedy CEJ (eds) Mechanisms in insect olfaction. Clarendon, Oxford, pp 131–138

Pasteels JM, Deneubourg J-L, Goss S (1987a) Transmission and amplification of information in a changing environment: the case of insect societies. In: Prigogine I, Sanglier M (eds) Law of nature and human contact. Bruxelles, pp 129–156

Pasteels JM, Deneubourg J-L, Goss S (1987b) Self-organization mechanisms in ant societies. I. Trail recruitment to newly discovered food sources In: in: Pasteels JM, Deneubourg J-L (eds) From individual to collective behaviour in social insects. Birkhause, Basel, pp 155–175

Raignier A, Boven J van (1955) Étude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera:Formicidae). Ann Mus R Congo Belge NS 4 (Sciences Zoologiques) 2:1–359

Reed J, Cherrett JM (1990) Foraging strategy and vegetation exploitation in the leaf-cutting ant *Atta cephalotes* (L.) – a preliminary simulation model. In: Vander Meer RK, Jaffe K, Cedeno A (eds) Applied myrmecology, a world perspective. Westview, Boulder, pp 355–366

Rettenmeyer CW (1963) Behavioral studies of army ants. Univ Kansas Sci Bull 44:281–465

Rissing SW (1982) Foraging velocity of seed-harvester ants *Veromessor pergandei* (Hymenoptera:Formicidae). Environ Entomol 11:905–907

Roessingh P (1990) Chemical marker from silk of *Yponomeuta cagnagellus*. J Chem Ecol 16:2203–2216

Schneirla TC (1971) Army ants; a study in social organization. Freeman, San Francisco

Schneirla TC, Brown RZ (1950) Army ant life and behaviour under dry season conditions. IV. Further investigation of cyclic processes in behavioral and reproductive functions. Bull Am Mus Nat Hist 95:263–354

Shapiro JA (1988) Bacteria as multicellular organisms. Sci Am 258:82–89

Stanier RY (1942) A note on elasticotaxis in myxobacteria J Bacteriol 44:405–412

Stuart AM (1975) Chemoreception, behaviour, and polyethism in termites (Isoptera). In: Denton DA, Coghlan JP (eds) Olfaction and taste V. Academic Press, pp 343–348

Sudd JH (1967) An introduction to the behaviour of ants. Edward Arnold, London

Tankersley RA (1990) Trail following in *Littorina littorata*: The influence of visual stimuli and the possible role of tracking in orientation. Veliger 33:116–123

Therrien P, McNeil JN, Wellington WG, Febvay G (1986) Ecological studies of the leaf-cutting ant. *Acromyrmex octospinosus*, in Guadeloupe. In: Lofgren CS, Vander Meer RK (eds) Fire ants and leaf cutting ants, biology and management. Westview, Boulder, pp172–183

Torgerson RL, Akre RD (1970) The persistence of army ant chemical trails and their significance in the Ecitonine-Ecitophile association (Formicidae: Ecitonini). Melanderia 5:1–28

Van Vorhis Key SE, Baker TC (1986) Observations on the trail deposition and recruitment behaviors of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera:Formicidae). Ann Entomol Soc Am 79:283–288

Verhaeghe JC (1982) Food recruitment in *Tetramorium impurum* (Hymenoptera: Formicidae) Insectes Soc 29:67–85

Verhaeghe JC, Deneubourg J-L (1983) Experimental study and modelling of food recruitment in the ant *Tetramorium impurum* (Hym.Form). Insectes Soc 30:347–360

Watmough J (1992) Models for swarming behaviour in army ants. Msc Thesis, University of British Columbia, Vancouver

Watmough J, Edelstein-Keshet L (1994) A one dimensional model of trail propagation by army ants. J Math Biol, in press

Wells MJ, Buckley SKL(1972) Snails and trails. Anim Behav 20:345–355

Wilson EO (1959) Communication by tandem running in the ant genus *Cardiocondyla*. Psyche 66:29–34

Wilson EO (1962a) Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). 1. The organization of mass foraging. Anim Behav 10:134–147

Wilson EO (1962b) Chemical communication among workers of the fire ants *Solenopsis saevissima* (Fr. Smith). 2. An information analysis of the odour trail. Anim Behav 10:148–158

Wilson EO (1971) The insect societies. Belknap, Cambridge

Wilson EO (1975) Sociobiology, Belknap, Cambridge, MA

Wynne-Edwards VC (1972) Animal dispersion in relation to social behaviour. Hafner, New York

---

Appendix

Equations of the model

Aside from the variables, $T(t)$ (total length of trails per unit area), $F(t)$ (total number of followers per unit area), L(t) (total number of lost ants per unit area) defined in the text we also consider the additional parameters below:

N = total number of individuals per unit area = L + F [number A^{-1}],
ν = speed of motion of an individual [$d\, t^{-1}$],
Γ = rate of decay of trail pheromone [t^{-1}],
a = rate of trail reinforcement by a single follower [$d\, t^{-1}$],
ε = the rate of losing a trail [t^{-1}],
α = the rate of recruitment to a trail [$d\, t^{-1}$].

The equations of the model are derived below.

Trail behind a single individual

The trail behind a single individual is the distance between the point at which the fresh trail is being deposited, and its fade-out point. The length of trail secreted by a single ant is

$$\frac{dT}{dt} = \nu - \Gamma T. \qquad (1)$$

Eventually the rate of deposition just balances the rate of evaporation. This occurs when $T = \nu/\Gamma$. This length has been defined in the text as $d_s = \nu/\Gamma$ = the length of a simple trail.

Trails formed by N individuals

Suppose there are L(t) lost ants and $F(t)$ followers. These may secrete trail-marker at different rates. Then we modify the previous equation to include contributions of both:

$$\frac{dT}{dt} = \nu L + aF - \Gamma T. \qquad (2)$$

The ratio a/ν represents the relative contributions to trails by followers and leaders. Equation (2) is a phenomenological equation, and is one way of characterizing the trail formation. EK (1994a) discussed how this equation is related to detailed pheromone balance equations. A feature of this particular model is that when all individuals are followers, there is an average spacing between followers along a trail, $d_f = a/\Gamma$.

Exchange occurs between followers and lost ants, and this is modeled by mass action kinetics, representing "binding" and "unbinding" to trails. Thus the rates of change of followers and leaders are:

$$\frac{dF}{dt} = -\varepsilon F + \alpha L T, \qquad (3)$$

$$\frac{dL}{dt} = \varepsilon F - \alpha L T. \qquad (4)$$

The model has the property that the total number of individuals, $N = L + F$ is constant. By eliminating L from the equations we obtain

$$\frac{dT}{dt} = \nu(N - F) + aF - \Gamma T, \qquad (5a)$$

$$\frac{dL}{dt} = -\varepsilon F + \alpha(N - F)T. \qquad (5b)$$

Equations 5a and b can be studied with standard qualitative methods.

Strength of the trails

We have defined the idea of an aggregate trail strength in the model by
$S(t)$ = strength of the trail network = $F(t)/T(t)$ = density of followers per unit length of trail (traffic density).

The variable S varies between a minimum of $S = 0$ when all individuals are lost and $S = \Gamma/a$ when all are followers. We have assumed that in the model, the loss rate of followers from a trail, ε, is a decreasing function of trail strength,

$$\varepsilon(S) = E\exp(-bS) = E\exp(-bF/T) \tag{6}$$

where E is the rate of losing the trail by a follower in the absence of the group recruitment effect (i.e. when the trail is a weak one, $S = 0$) and b is a parameter that governs how rapidly this rate decreases as the strength of the trail increases.

Dimensionless version of the model

It is possible to reduce the number of parameters by using dimensionless ratios in the place of the original variables. We define these dimensionless variables as follows:
$T^* = T/(N\,d_s) = T\Gamma/(N\,\nu)$,
$L^* = L/N$,
$F^* = F/N$,
$t^* = t\,\Gamma$,
$S^* = F^*/T^* = F\,\nu/T\Gamma$.

The densities of followers and lost ants are scaled in units of the *total population*, N, and time is scaled in units of the *pheromonal half-life*, $1/\Gamma$. The trail length density is scaled by the total density of N simple trails. It can be shown that the dimensionless equations (written in terms of the * variables, but with the *s then dropped for notational convenience) are

$$\frac{dT}{dt} = (1-F) + A'F - T, \tag{7a}$$

$$\frac{dF}{dt} = -E'Fe^{-B'\frac{F}{T}} + \alpha'(1-F)T \tag{7b}$$

where the new dimensionless parameters are:

$$A' = \frac{a}{\nu},\; B' = \frac{b\Gamma}{\nu},\; E' = \frac{E}{\Gamma},\; \alpha' = \frac{\alpha\nu N}{\Gamma^2}. \tag{8}$$

The values of the dimensionless variables in these equations are restricted to the following ranges:$0 < T < 1$, $0 < L < 1$, $0 < F < 1$, $0 < S < \nu/a$.