326

Trail Following as an Adaptable Mechanism for Population Behaviour

Leah Edelstein Keshet
Mathematics Department
University of British Columbia
Vancouver, B.C. V6T 1Z2

September, 1992

604-822-5889 (office)
604-873-0957 (home)
604-822-6074 (fax)
USERKESH@UBCMTSG

Swarm of the Army Ants, Eciton hamatum.
From W F Kirby (1898) Marvels of Ant Life, SW Partridge

Abstract

Social organisms have evolved a variety of mechanisms for maintaining group cohesion, including marking and following trails. Trail following can be used to coordinate foraging, to explore a new area, or to guide mass migrations. Individuals following fairly simple algorithms, and relying on a limited number of sensory inputs without necessarily having a sense of the whole can form a variety of aggregations. Different movement patterns necessitate different spatial aggregations. The types of trail-networks created are plastic, and easily adapted to changing conditions. In some social organisms, including insects, there are no leaders to coordinate activity, and hence the behaviour of the population stems directly from the collective behaviours of many individuals. We show, using a mathematical model for trail-following, that it is possible to understand the behaviour of the group in terms of a few experimentally measurable parameters associated with the individual. Specific attention is paid to the following features of trail-following: (a) swarm migration along trails (b) selection of a direction of motion (c) adaptability of the trails to different tasks.

Introduction

Trail-following can serve one of several functions: exploration, migration, foraging, predation, or defense. Since these functions dictate different social groupings, and different movement patterns, the nature of the trails varies from one situation to another, within and between different species,and for different environmental conditions. A typical case of trail-following behaviour occurs in the ants, where volatile substances called pheromones are used as markers. But trail following has evolved independently in several unrelated species, and it is reasonable to suggest that this behaviour could have been attained through natural selection only if it is adaptable, and easily modified to respond to the environment.

In this review we discuss a type of aggregation in populations in which individuals do not have a sense of the whole, and frequently change places. By following elementary algorithms the population can become coordinated, in the sense that a direction is selected, the density of traffic is regulated, and migration occurs in a cohesive way. Further, we note that relatively small changes in the behaviour of individuals marking and/or following trails can lead to significant modifications in the way that the aggregates are organized.

In order to understand the population consequences of individual trail marking and following we must be able to bridge the gap between properties and behaviours of the individual, and those of the population that stem as a direct consequence of numerous individuals behaving in essentially similar ways. To do so, it proves profitable to examine mathematical models, since the interactions are not easily analyzed by simple verbal arguments. The goal of this paper is to discuss how mathematical models can be used for understanding trail-following behaviour.

The paper is organized as follows: In section 1 we describe biological systems in which the marking and following of trails is known to occur, and give a brief description of pertinent properties of the organisms, as well as phenomena observed at the collective level. In section 2 we outline the specific phenomena which are to be explored, and the types of models dealing with such phenomena. In section 3 we display the actual models and give a brief description of their results and references. In section 4 we discuss implications and compare with previous work.

1 Trail following in social and cellular systems

In social insects, trail networks are used for communication, foraging, and migration. (Able, 1980, Wynne-Edwards, 1972; Hölldobler and Wilson, 1990). The pheromones used by ants and termites are volatile. Individuals that cross or approach the trail will turn and follow it. One of the first papers to describe the shape and longevity of a typical chemical trail is due to Bossert and Wilson (1962). A recent mathematical model that describes the turning response of ants appears in Calenbuhr and Deneubourg, 1990.

Trail-following occurs in many other biological systems. One example is the family of Myxobacteria, unicells that secrete slime trails on which aggregation and collective gliding motility occur. Mathematical models and computer simulations for their movement was proposed by Pfistner and Stevens in a recent volume on Biological Motion edited by Alt and Hoffmann (1990). Slime molds also secrete chemical attractants, namely Cyclic AMP (CAMP), but it is likely that the rapid rate of diffusion of these small molecules prevent well-defined or long-lived trails from forming. Chemical trail-following can be viewed as a special example of chemotaxis in which lateral diffusion of attractant is limited relative to the forward motion of the individual.

The development of multicellular organisms involves cell motion and directed migration over long distances. This is particularly true in the formation of the nervous system, where path-finding neurons interact with glia, and with a variety of adhesive molecules in homing in on their targets. Here path-marking and path-following are only one part of a rather complicated process, which includes recognition of targets, and interactions with a complex and changing cellular milieu.

Many types of larvae and caterpillars are gregarious, and move along silk-like threads in long columns (Deneubourg et al, 1990). Anecdotes of caterpillars marching endlessly on a circular tether are common (e.g. Fabré 1979). Molluscs also secrete slime trails used for homing (Focardi and Santini, 1990; Focardi et al 1985, Tankersley, 1990, Wells and Buckley, 1972, Chelazzi et al, 1990).

Trail-following and marking also occurs in numerous mammals. Ungulates and other herding mammals have scent glands on their lower legs and feet. Photographs of elk, caribou, wildebeest, and many other migratory or territorial mammals will often reveal a distinct set of trails along which migration takes place. (Wynne-Edwards, 1972; Able, 1980; Estes 1991).

2. Phenomena stemming from trail-following

In ants and other social insects the behaviour of the population is an outcome of the individual behaviours of hundreds or thousands of individuals. (In most species of ants, there are no leaders, and individuals frequently change places and reverse direction.) Yet these populations function efficiently and meet the challenges of an uncertain environment. Their behaviour includes foraging, migration, or defence along a network of trails that changes with time, with the season, or with the conditions. This type of population behaviour has been called " collective decision making" and "self-organization" (See, for example Camazine (1991), Deneubourg et al, 1989, 1990).

In this paper we ask how alterations in individual responses can lead to population changes. Indeed, one goal of modelling this problem is to bridge between experimentally measurable properties at the level of the individual, and observable population behaviour. Typical examples of parameters at the level of the individual would include, for example, the rates of secretion and chemical strength of the pheromone or other marker, the probability of tracking the path per unit time or distance, the degree of random motion of individuals, and their ability to sense and respond to trail-markers. The size of the population and the diffusivity of the pheromone also prove to be important in the interactions.

A number of questions common to many papers in this volume are of interest. How should we distinguish between order and disorder? What are the rules obeyed by individuals that lead to order, and what types of spatial patterns can thereby be explained? Why should certain patterns exist, and how can they be changed to suit the needs of the population? We discuss these in the context of mathematical models which are first motivated in the next section. The section is subdivided into units that deal with (a) the spatial distribution of trails and followers, (b) the choice of directions of motion, and (c) the distribution of traffic and the adaptability of the trails to diffuse exploration or concentrated migration columns. Each of these problems can be addressed, but separate approaches are suitable.

2a) Spatial Patterns and density distributions within a swarm

Evolution of spatio-temporal patterns such as swarming is described in the biological literature. Figure 1 , adapted from Rettenmyer (1963) shows the branching swarm raid patterns of two species of army ants, *Eciton hamatum*, and *E. burchelli.* Other examples are given by Schneirla, 1971. (See also Franks and Fletcher, 1983, Burton and Franks, 1985; Franks, 1989.) It is evident that the spatial pattern can differ from one species to another, as well as from one physical location to another. Figure 2, after Raignier and van Boven, (1955) shows a time sequence in the swarming of a colony of Dorylus. An initial mass of ants is shown to emerge from the nest in a rather disorganized, milling fashion. Gradually a direction of motion is selected and the traffic pattern crystallizes to form a single column. The population migrates outwards in a nearly one-dimensional route before fanning out in an exploratory pattern at the front of the swarm, where food is collected.

The spatial behaviour of a swarm can be approximated by a discrete or a continuous spatio-temporal model which accounts for the depositions of trails, the individuals following the trails, and those milling about randomly off trails. (See Watmough 1992). If one considers individuals moving in 1 dimension (along the length of the swarms in Figures 1 or 2) it is possible to make explicit predictions about the density profile of the population and the speed of migration of the swarm. A typical set of equations for swarming is given in section 3b.

A second approach is to treat the problem by simulating actual motion of a collection of "individuals" and then watching the time-course of a "population" under a variety of conditions and parameter values. This type of simulation, called a cellular-automaton simulation, and has been used previously (e.g. by Edelstein-Keshet and Ermentrout (1990) to study collective behaviour in a population of cells. Simulations of trail following have been written by Ermentrout (1990, unpublished) and by Watmough (1992). See *Figure 3* for a typical example. These simulations are ideal for experimenting with a variety of rules and parameter regimes, but are best used in conjunction with other modelling efforts.

2b) Selecting a preferred direction

As seen in Figure 2, a transition from random milling and exploration ("disorder") to directed motion ("order") occurs in the early stages of directed migration. This transition takes spontaneously, through the collective motions, trail marking and following by individuals. Clearly, in a natural setting there would be some directional biases, including food distribution, light, or other cues that give a directional preference. But do ants or other trail followers also have an innate ability to collectively decide on a preferred direction, or to amplify minute environmental biases in finding the right direction?

Consider the angular distribution of the trails and individuals creating them. It is possible to formulate a set of equations (See section 3c) that describe how this angular distribution changes with time. Suppose individuals are initially uniformly distributed and moving in random directions over some small region (e.g. in the early formation of a swarm). Suppose that by random fluctuation, the number of individuals moving in some particular direction is slightly higher than in other directions. The model predicts that this may cause the entire traffic pattern to shift so that this direction becomes dominant. However, the model also predicts that this effect occurs only when the right balance exists between effects that tend to promote order (affinity to the trails, likelihood of finding and staying on trails) versus those that tend to introduce noise and disorder (tendency to fall off trails, degree of random motion of individuals, rate of decay of pheromone). The implication is that the mechanism of trail-following can amplify and enhance even minute gradients or signals, and so serve to help select a preferred direction. A similar model was discussed by Edelstein-Keshet and Ermentrout (1990).

2c) Diffuse exploration versus cohesive migration

Figures 1a and 1b illustrate differences between major routes along which steady traffic streams, and diffuse exploratory networks (the fan-shaped region) in which the trails are much longer but contain fewer followers per unit length. How does a transition from a coherent to a diffuse motion take place? Different conditions may favour distinct traffic patterns: In cases of mass migration from one bivouac to another, or in cases of purposeful motion, the population benefits from strict cohesion and motion in a tight formation, along a well-travelled migration column. In other cases, such as exploration of a new territory in search for food, it is beneficial to cover as large an area as possible. It is reasonable to expect that controls of the morphology and density of trails should exist within the population. But since societies of ants have no decision makers or traffic controllers, such controls must issue from the collective behaviours of the individuals themselves.

In a recent paper, Edelstein-Keshet (1992) shows that this behavioral transition from high to low traffic densities is a simple consequence of sensitivity to the strength of the trail-marker. The argument is based on the idea that the density of individuals along the length of a trail will influence the level of marker and hence the affinity to the trail. The higher the affinity, the greater the density on the trails. A discussion of this idea, and of the model that deals with it appears in section 3d.

3 Minimal models for trail-following behaviour

The mathematical models are based on the variables and parameters below:

$T(t)$ = total length of trails per unit area at time t,
$F(t)$ = total number of followers (on trails) per unit area at time t,
$L(t)$ = total number "lost" (not on trails) per unit area at time t,
v = speed of an individual,
a = rate trail reinforcement by follower,
Γ = rate of decay of trail marker,
ε = the rate of losing a trail being followed,
α = the rate of attraction to the trails.

Individuals are assumed to walk at a fixed speed, v, and are either Lost or Following a trail. Both types of individuals secrete trail markers, at possibly different rates.In models in which the spatial or directional distribution of the population is of interest, the variables above are assumed to depend also on position, x, or on direction angle Θ. We initially assume that the parameters v, Γ,ε, α are constants, but later indicate how such assumptions can be relaxed, and what are possible consequences.

3a) Basic Model Equations

A basic framework for a model for trail following based on these variables is:

$$\frac{dT}{dt} = \nu L + a F - \Gamma T$$

$$\frac{dF}{dt} = -\epsilon F + \alpha L T$$

$$\frac{dL}{dt} = \epsilon F - \alpha L T.$$

Observe that the total number of individuals, $N = L + F$ = constant. It is thus possible to eliminate the third equation and to rewrite the equations in terms of F and T alone. In these equations, single individuals secrete continuously and lengthen the trails . The decay of the trail-marker (e.g. by evaporation of pheromone) will cause the trail length to decrease at the back. It is assumed that the rate of decay is a linear process with rate constant Γ.

The second and third equations of the model describe exchange that takes place between the number of individuals on and off the trails. (This can be viewed as "binding" and "unbinding" to the trails.) This ordinary differential equation model has a single equilibrium. The percentage of followers and of lost individuals at the equilibrium depends on the size of the population and on the other parameters. In the sections below we discuss how these basic equations are modified to deal with spatial, angular, and density variations.

3b) 1D Swarm migration Model

By redefining variables as functions of position x and time t, and incorporating random motion of lost individuals and directed motion of followers, we obtain a spatio-temporal version of the above model:

$$\frac{\partial T(x,t)}{\partial t} = \nu L(x,t) + a F(X,t) - \Gamma T(x,t)$$

$$\frac{\partial F(x,t)}{\partial t} = -\frac{\partial [\nu F]}{\partial x} - \epsilon F + \alpha L T$$

$$\frac{\partial L(x,t)}{\partial t} = \mu \frac{\partial^2 L}{\partial x^2} + \epsilon F - \alpha L T$$

Watmough (1992) discusses the behaviour of solutions to these equations that represent the advance of a swarm., i.e. a constant swarm density profile moving at a fixed speed without changing shape. He shows that the above equations admit so called **travelling wave solutions** and describes them analytically and numerically. The basic result is that the interior of the swarm consists of a high level of follower and lost ants, whereas the front of the swarm gradually declines in density. The speed of this collective motion depends on the size of the swarm and the rate of "binding" and "unbinding" to trails. However, swarms are shown to move forward at a rate that is slower than v, the walking speed of the individual.

3c) Orientation of individuals and selection of swarming direction

To study the directions of motion of individuals and ask how individual turning probabilities affect the angular distribution of the population and its trail networks, we define

$F(\Theta,t)$, $L(\Theta,t)$ = F or L individuals currently moving in direction Θ,
$T(\Theta,t)$ = density of trails made by individuals moving in direction Θ.
$K(\Theta,\Theta')$ = probability that individual moving in direction Θ will turn and follow a trail in direction Θ'.
$R(\Theta,\Theta')$ = probability that individual moving in direction Θ will randomly turn in direction Θ'.

Then a set of equations for these variables would be

$$\frac{\partial T(\theta,t)}{\partial t} = vL(\theta,t) + aF(\theta,t) - \Gamma T(\theta,t)$$

$$\frac{\partial F(\theta,t)}{\partial t} = -\epsilon F + \alpha T(\theta,t) K * L,$$

$$\frac{\partial L(\theta,t)}{\partial t} = \epsilon R * (F+L) - \alpha L K * T.$$

In these equations the terms $K*T$, $K*L$ $R*(F+L)$, etc are **convolutions**, integrals that sum up all the possible transitions from one direction to another. For example,

$$K*L = \int K(\theta-\theta') \; L(\theta',t) \; d\theta$$

is the net rate that individuals initially moving in any direction would turn and follow a unit length of trail whose direction is Θ. If there are many trails in this direction, i.e. $T(\Theta,t)$ is large, clearly this would increase the likelihood of such turns, hence the term $\alpha T(\Theta,t)K*L$ appears in the equation for the rate at which followers (at angle Θ) are accumulating. A similar interpretation for other terms in the equations can be made. Information about turning probabilities of individuals can be ascertained by experimental manipulation.

Equations such as these can be analyzed to address the selection of a preferred direction. Using linear stability theory, and assuming small initial bias in one or several directions, one seeks conditions under which such small biases can get amplified. Typically one finds that only a limited range of individual parameters lead to the ability to select a dominant direction. If individuals have a high tendency for directional persistence, the formation of a directed migration column is favoured. Figure 4 shows a typical numerical simulation of the equations given above. An initially uniform angular distribution of followers, lost individuals and trails develops peaks, and eventually two antiparallel directions are formed. The method of analysis and simulations for this model are analogous to that treated in Edelstein-Keshet and Ermentrout (1990).

3d) Adaptable trails: light and heavy traffic patterns

The variables in the models are defined as densities (of individuals, of trails, etc) per unit area. However, the traffic volume along the trails is given by the number of followers per unit length of the trail. Define

$S(t) = F(t)/T(t)$ = number of followers per unit length of trails.

Since by assumption, each individual on a trail secretes trail marker (or has the probability of secreting trail marker), the variable S can also represent the chemical strength of the accumulated marker. Thus we could describe the dichotomy between "strong" (cohesive) and "weak" (exploratory) trails, or between high traffic and low traffic trails by high or low values of this quotient. The fan-shaped migration front of army ants, which consists of a highly reticulate meshwork would be an example of a network of weak exploratory trails, whereas the trunk-trail formed from the nest along which steady traffic flows would be a strong cohesive trail.

Since ants respond to pheromone signals in a graded way, the rate of finding trails, the rate of reinforcing a trail, and the fidelity to the trail (or conversely, the rate at which followers lose the trails they are following) is likely dependent on the strength of the trail. This can easily be incorporated into the model by modifying the parameters defined in section 3a), previously taken as constants.

Edelstein-Keshet (1992) argues that one reasonable assumption is that the rate of getting lost diminishes as the strength of the trail increases, for example that it drops off exponentially as a function of S, i.e., that

$$\varepsilon = \varepsilon(S) = E \exp(-b S) = E \exp(-b F/T).$$

By analysis of the system of equations with this functional form replacing the previously constant value of ε, it can be shown that a variety of behavioral outcomes result. Figure 5 a), b), and c) illustrate three possibilities obtained by varying the parameters E and b. In Figure 5a) the equilibria include one representing weak trails (close to the horizontal axis) and one representing strong trails (close to the vertical axis). Different initial conditions, (e.g. different initial ratios of follower ants and lost ants) lead to different eventual outcomes. In Figures 5b) and 5c), the trails are eventually exclusively weak (5b) or strong (5c). A transition from one case to the other can occur as slight variations are made in the parameters of the individual motion. For example, by increasing E, which is associated with the tendency to make random turns (and promoting a tendency to lose trails being followed), a transition to loose exploratory-type low-traffic trails is made. By increasing b, the sensitivity to trail strength, a transition to strong, high-traffic trails can occur. The implication of this result is that the parameters associated with the individual behaviour and with acuity of the trail-detection mechanism can control the global population behaviour. More details about this model and its predictions are given by Edelstein-Keshet (1992).

4 Discussion

We briefly outline previous theoretical and experimental work on trail-following and self-organization, and draw a comparison. Wilson (1962 a,b) and Bossert and Wilson (1963) laid the foundations for an analysis of olfactory communication, by analyzing the implications of pheromone diffusion on the length and width of a trail, and by considering trail-following from an information theory perspective. These early works were not, unfortunately extended.

More recently extensive work at the level of group phenomena has been carried out by the Brussels group (See references under Pasteels et al; Deneubourg et al, Goss, et al, Aron et al). They have carried out experiments in which groups of ants traverse bridges connecting nests and/or food sites, showing that some routes will be selected at the expense of others. Models and simulations of the phenomena exhibit the same behaviour.

A few papers address issues both at the individual and population levels, one notable case being Calenbuhr and Deneubourg (1990). Simulations of spatial patterns and swarming behaviour appear in Deneubourg, Goss, Franks and Pasteels (1989), Franks and Bossert (1989) (Army Ant raiding swarms) and Deneubourg, Aron, Goss and Pasteels (1990) and Aron, Pasteels, Goss, and Deneubourg (1990) (other species of ants). In these simulations, pheromone influences the local direction and speed of motion of the ants. A clear distinction between individual trails, or individual ant positions is not made, since a large number of individuals are included. A rough qualitative agreement with patterns seen in nature has been obtained by these studies. To our knowledge, there is not yet a full simulation model in which a full set of biologically correct values of parameters are used.

In models and simulations described in this paper we have addressed similar topics but from a slightly different perspective. An emphasis has been placed on parameters associated with the individual, its motion, its ability to detect and to follow a trail. Models which share a common framework, but which differ in the level of complexity (e.g.spatially independent, angle dependent, space and time dependent, as well as detailed simulations) have been developed. These models give qualitative as well as quantitative predictions for how changes in individual behaviour affect the population as a whole.

We have considered a limited number of algorithms based on the individual's ability to detect and follow trails with fidelity that is sensitive to the strength of the trails. It is clear that even this limited set of rules can already account for some of the groups properties. Individuals need not necessarily have a sense of the whole, nor do they need leaders to direct their movement. The models predict that the population is capable of a repertoire of possible responses, and that transitions between one regime and another may occur quite suddenly, as minor changes in individual properties are made. The precise pattern of environmental effects has not been explicitly included in any of our models. But we would argue that environmental effects (e.g. homogeneous v patchy food distributions) impinge on the population by changing the behaviour of individuals. i.e., by causing slight shifts in the parameters of individual movement described in this paper.

Acknowledgements. This work has been carried out under support from the National Sciences and Engineering Research Council of Canada, grant number OGPIN 021. I would like to thank James Watmough and G.B. Ermentrout for discussions during various stages of this project.

References

Able K P (1980) Mechanisms of Orientation, Navigation, and Homing.In: Gauthreaux S A (ed) Animal Migration, Orientation, and Navigation. Academic Press, NY pp 283-373

Alt W, Hoffmann G (eds) (1990) Biological Motion (Proceedings: Königswinter, 1989) Lecture Notes in Biomathematics 89. Springer Verlag, Berlin

Aron S, Deneubourg J L, Goss S, Pasteels J M (1990) Functional Self-organization illustrated by inter-nest traffic in ants: the case of the argentine ant. In: Alt W, Hoffmann G (eds) see above.

Aron S, Pasteels J M, Deneubourg, J L (1989) Trail-laying behaviour during exploratory recruitment in the Argentine ant, Iridomyrmex humilis (Mayr). Biology of Behaviour 14(3): 207-217

Aron S, Pasteels J M, Goss S, Deneubourg J L (1990) Self-organizing spatial patterns in the Argentine Ant Iridomyrmex humilis (Mayr). In: Vander Meer R K, Jaffe K, Cedeno A (eds) Applied Myrmecology, A World Perspective. Westview Press, Boulder CO, pp 438-451

Bossert W H, Wilson E O (1963) The analysis of olfactory communication among animals. J theor Biol 5: 443-469

Burton J L, Franks N R (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) see above. pp 453-469

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. Marine Biology (Berlin) 105(3): 445-450

Deneubourg J L, Aron S, Goss S, Pasteels J M (1990) The self-organizing exploratory pattern of the Argentine ant. J Insect Behav 3(2): 159-168

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

Deneubourg J L and Goss S (1990) Collective patterns and decisi[illegible] making, Ethology, Ecology and Evolution 1: 295-311

Deneubourg J L, Grégoire J C, Le Fort E (1990) Kinetics of la[illegible] gregarious behaviour in the bark beetle <u>Dendeoctonus micans</u> (Coleoptera: [illegible]lytidae}). J Insect Behav 3(2): 169-182

Deneubourg J L, Pasteels J M, Verhaeghe J C (1983) Probabilistic behaviour in ants: a strategy of errors? J theor Biol 105: 259-271

Edelstein-Keshet L (1988) Mathematical Models in Biology. Random House, NY

Edelstein-Keshet L (1992) Simple models for trail-following behaviour; Adaptability to low and high traffic patterns, Submitted for publication.

Edelstein-Keshet L, Ermentrout G B (1990) Models for contact-mediated pattern formation: cells that form parallel arrays, J Math Biol 29:33-58.

Fabré, J H (1979) Insects, Felix Gluck Press, C. Scribners, NY

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

Focardi S, Santini G (1990) A simulation model of foraging excursions in intertidal chitons In : Alt W , Hoffmann G (eds) see above, pp 319-330

Franks N R (1989) Army ants: a collective intelligence. American Scientist 77: 139-145

Franks N R, Bossert W H (1983) The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community. In: Sutton S L, Whitmore T C, Chadwick A C (eds) Tropical Rainforest: Ecology and Management, Blackwell, Oxford. pp 151-163

Franks N R, Fletcher C R (1983) Spatial patterns in Army Ant foraging and migration: <u>Eciton burchelli</u> on Barro Colorado Island, Panama, Behav Ecol Sociobiol 12:261-270

Franks N R, Gomez N, Goss S, Deneubourg J L (1991) The blind leading the blind in Army Ant raid patterns: testing a model of self-organization. J Insect Behav (in press)

Gauthreaux S A, ed (1980) Animal Migration, Orientation, and Navigation, Academic Press. NY

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

Hölldobler B, Wilson E O (1990) The Ants. The Belknap Press of Harvard University Press, Cambridge, MA

Moffett M W (1986) Maurauders of the jungle floor, National Geographic 170(2) (Feb): 273-286

Pasteels J M, Deneubourg J L, Verhaeghe J C, Boevé J L, Quinet Y (1986) Orientation along terrestrial trails by ants. In: Payne T L, Birch M C, Kennedy C E J (eds) Mechanisms in Insect Olfaction. Clarendon Press, Oxford, pp 131-138

Pasteels J M, Deneubourg J L, eds, (1987a) From Individual to Collective Behaviour in Social Insects, Birkhauser, Basel

Pasteels J M, Deneubourg J L, and Goss S (1987b) 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 Conduct. G.O.R.D.E.S., Bruxelles, pp 129-156

Pasteels J M, Deneubourg J L, Goss S (1987c) Self-organization mechanisms in ant societies (I) Trail recruitment to newly discovered food sources. In: Pasteels J M, Deneubourg J L eds, (see above) pp 155-175

Pfistner, B (1990) A one-dimensional model for the swarming behavior of myxobacteria. In: Alt W, Hoffmann G eds, (see above) pp 557-563

Raignier A, van Boven J (1955) Étude taxonomique, biologique et biométrique des Dorylus du sous-genre Anomma (Hymenoptera: Formicidae). Annals du Musée Royal du Congo Belge n.s. 4 (sciences zoologiques) 2:1-359

Rettenmeyer C W (1963) Behavioral studies of army ants. Univ Kansas Sci Bull 44(9): 281-465

Schneirla T C (1971) Army Ants; A Study in Social Organization. W H Freeman, San Francisco.

Stevens A (1990) Simulations of the gliding behaviour and aggregation of myxobacteria. In: Alt W, Hoffmann G eds., see above pp 548-555.

Tankersley R A (1990) Trail following in Littorina littorata: The influence of visual stimuli and the possible role of tracking in orientation. Veliger 33(1): 116-123

Watmough, J (1992) Modelling the swarming behaviour of Army ants, Msc Thesis, University of British Columbia.

Wells M J, Buckley S K L (1972) Snails and Trails. Anim Behav 20: 345-355

Wilson E O (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 E O (1962b) Chemical Communication among workers of the fire ant Solenopsis saevissia (Fr. Smith) 2. An information analysis of the odour trail. Anim Behav 10: 148-158

Wilson, E.O. (1971) The Insect Societies, Belknap/Harvard, Cambridge, MA.

Wilson, E.O. (1975,1980) Sociobiology, Belknap, Cambridge, MA

Wynne-Edwards V C (1972) Animal Dispersion in Relation to Social Behaviour, Hafner, NY.

Figure Captions

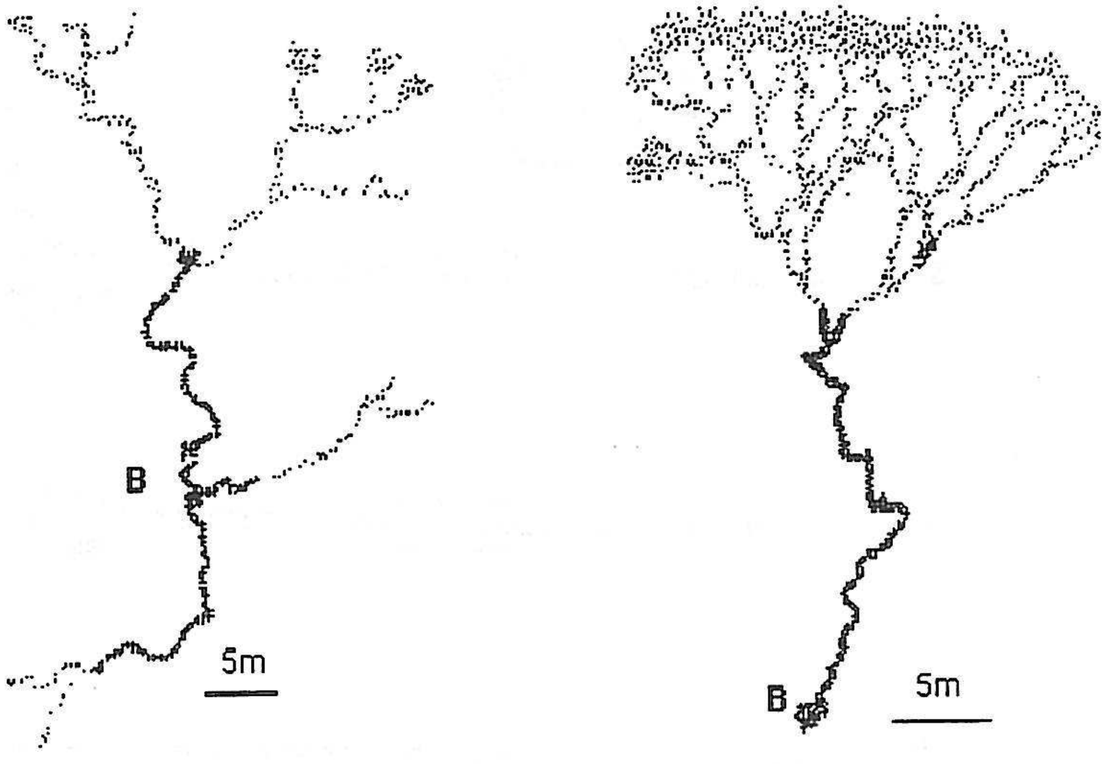
Figure 1: Trail networks formed by swarms of the Army ants *Eciton hamatum* and *Eciton burchelli*. B = bivouac. Note the major trunk trails, the bifurcations, and the diffuse exploratory fan at the swarm front. Based on Rettenmeyer, 1963.

Figure 2: Temporal sequence in the formation and eventual retreat of a swarm raid produced by a colony of *Dorylus* ants. The initially confused random milling eventually establishes a direction along which the swarm propagates. Sketch based on Raignier and van Boven (1955).

Figure 3: A computer simulation of ant-like automata following trails and obeying simple turning rules. Such simulations allow us to explore the consequences of changing rules, parameters or turn angle distributions on the formation of pattern and type of aggregation. Simulations were written by James Watmough.

Figure 4: Models for angular distributions of the directions of motion in a population (see section 3c) can describe how a set of preferred directions could arise spontaneously. Shown here are numerical simulation of the angle distribution equations for the trails and the followers starting from a nearly uniform initial distribution. With time, a direction (and it's antiparallel direction) become dominant.

Figure 5: The model in section 3d) predicts that slight changes in the parameters governing tendency for random turns (*E*) and sensitivity to trail pheromone (*b*) can lead to these transitions in population behaviour. (a) Both weak and strong trails can occur, but their formation depends on the initial numbers of followers and trails. (b) only weak trails occur (c) only strong trails occur.



Eciton hamatum

Eciton burchelli

Figure 1

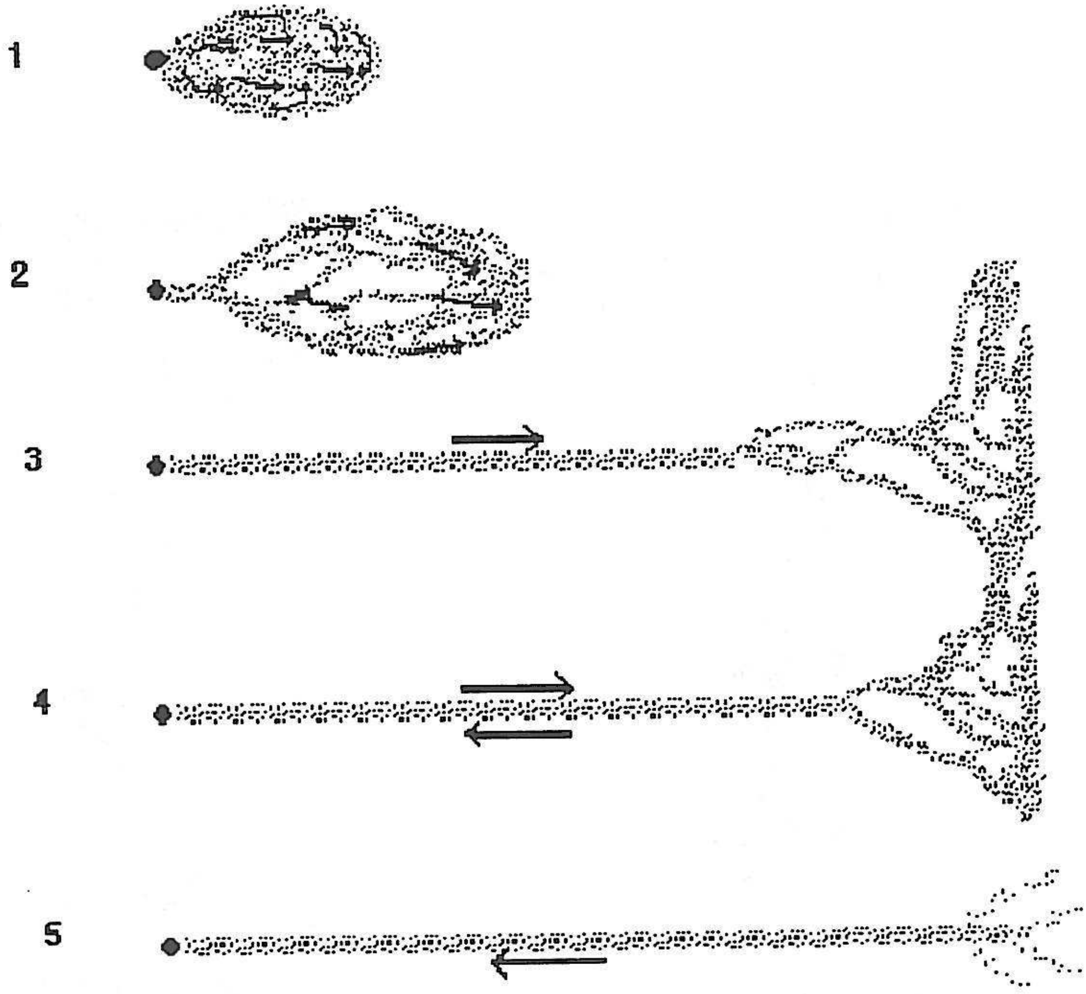


Figure 2

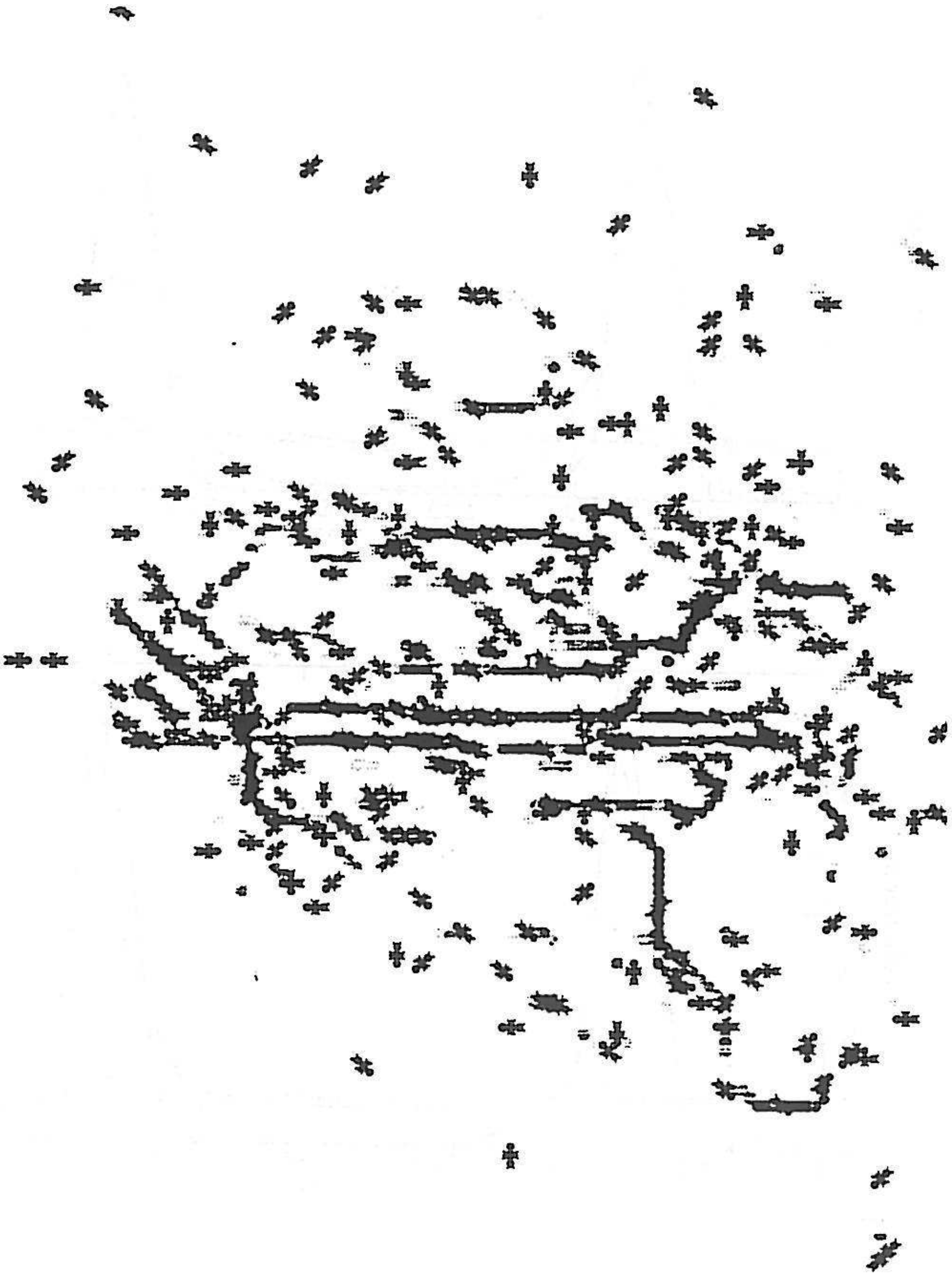


Figure 3

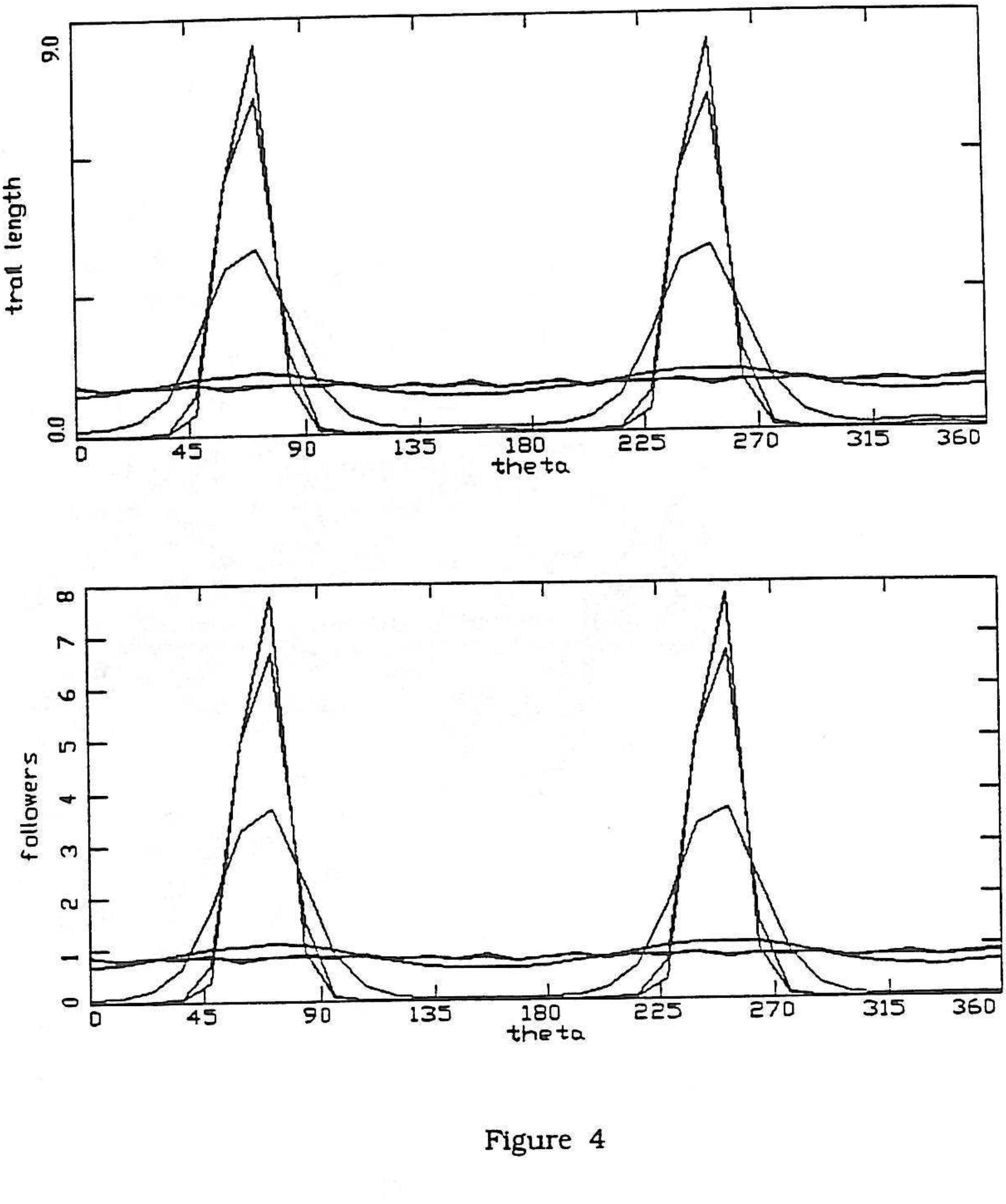
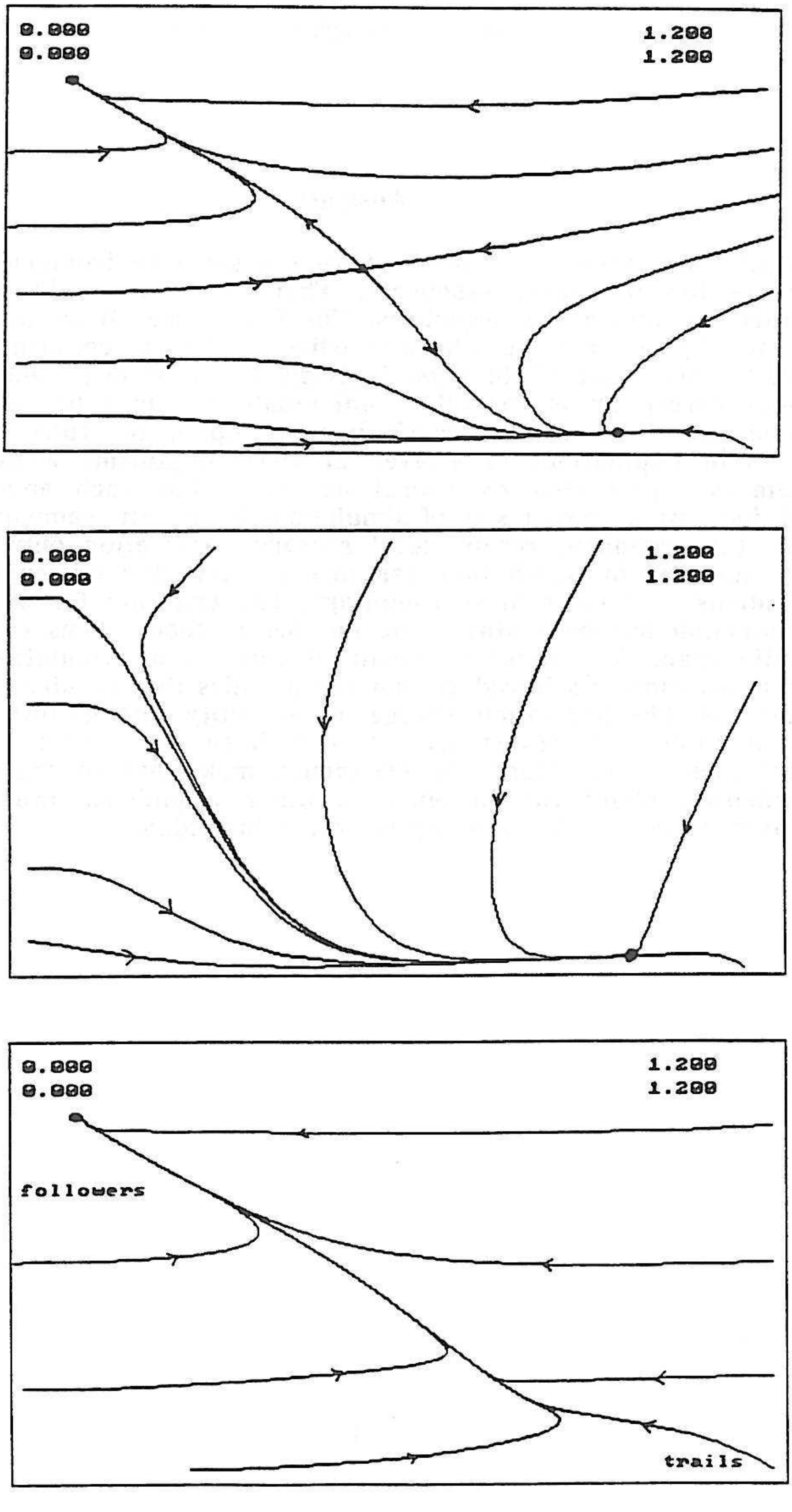

9.0
trail length
0.0
0
45
90
135
180
225
270
315
360
theta
8
7
6
5
4
3
2
1
0
followers
0
45
90
135
180
225
270
315
360
theta

Figure 4

Figure 5


0.000
0.000
1.200
1.200
0.000
0.000
1.200
1.200
0.000
0.000
1.200
1.200
followers
trails