Modeling ant foraging: A chemotaxis approach with pheromones and trail formation

Paulo Amorim

Instituto de Matemática, Universidade Federal do Rio de Janeiro, Av. Athos da Silveira Ramos 149, Centro de Tecnologia-Bloco C, Cidade Universitária - Ilha do Fundão, Caixa Postal 68530, 21941-909 Rio de Janeiro, RJ, Brazil

HIGHLIGHTS

- We model ant foraging behavior with partial differential equations of chemotaxis type.
- Numerical simulations show spontaneous formation of foraging trails.
- Trail formation is correlated with increased food removal efficiency.
- Simulation of the whole foraging cycle.
- Emergence of trail formation from simple modeling principles.

GRAPHICAL ABSTRACT
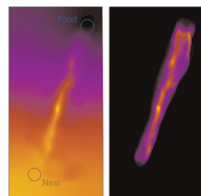
$$\begin{cases} \partial_t u - \Delta u + \nabla \cdot \left(u \chi_u \nabla v \right) = -uc + \lambda w N(x) + M(t) N(x) \\ \partial_t w - D_w \Delta w + \nabla \cdot \left(w \nabla a \right) = uc - \lambda w N(x) \\ \partial_t v = P(x) w - \varepsilon v + D_v \Delta v \\ \partial_t c = -uc. \end{cases}$$

Modeling ant foraging: a chemotaxis approach with pheromones and trail formation

→ Reaction-diffusion system to model ant foraging

→ Spontaneous formation of trails

→ Numerical simulations

ARTICLE INFO

ABSTRACT

We consider a continuous mathematical description of a population of ants and simulate numerically their foraging behavior using a system of partial differential equations of chemotaxis type. We show that this system accurately reproduces observed foraging behavior, especially spontaneous trail formation and efficient removal of food sources. We show through numerical experiments that trail formation is correlated with efficient food removal. Our results illustrate the emergence of trail formation from simple modeling principles.

1. Introduction

Ant foraging is among the most interesting emergent behaviors in the social insects. Perhaps the most striking aspect of ant foraging is how individuals following simple behavioral rules based on local information produce complex, organized and seemingly intelligent strategies at the population level. As such, ant foraging (along with most other activities of an ant colony) is a prime example of the so-called *emergent* behavior.

It has long been known that one of the main forms of communication among ants is the use of pheromones. These are chemical compounds which individual ants secrete and deposit on the substrate and which in effect are used as a means of communication between ants, transmitting a variety of messages such as alarm, presence of food, or providing colony-specific olfactory signatures used to identify nest-mates.

Among the many documented functions of ant pheromones, we are interested in their role as a chemical trail indicating the

E-mail address: paulo@im.ufrj.br
URL: http://www.im.ufrj.br/~paulo

direction to a food source. Many species of ants, especially trail-forming ones, are known to lay a pheromone as they travel from the food source back to nest. The main attribute of this pheromone is that it is attractive to other ants, who tend to follow the direction of increasing concentration of the chemical. These ants will then reach the food source and return to the nest while laying pheromone themselves, thus reinforcing the chemical trail in a positive feedback loop. This results in the formation of well defined trails leading from the nest to the food source, allowing for an efficient transport of the food to the nest. Thus, pheromones play a major role in food foraging, where they are widely used (among other strategies) to recruit nest mates to new food sources.

It is clear that the effective simulation and modeling of trail-laying and foraging behavior of ants is a crucial aspect in the understanding of ant ecology. Indeed, for invasive species such as the Fire Ant *Solenopsis invicta* (Tschinkel, 2006) foraging is, next to reproduction, the most important activity of the colony, and the sole means by which it can ensure its nourishment. A better understanding of foraging dynamics is bound to contribute to a more complete picture of ant ecology. Aside from the scientific value of such knowledge, a thorough understanding of ant behavior is essential in defining appropriate policies in those cases (as with *S. invicta*, Tschinkel, 2006, or the Pharaoh's ant, *Monomorium pharaonis* Jackson et al., 2004) where ant species are considered pests.

The entomological research body on ants, their behavior, and their olfactory means of communication is vast. Here, we content ourselves with citing some seminal works, as well as some more recent investigations with special relevance to our analysis. For a general reference on myrmecology (the branch of entomology that deals with ants), we refer to the encyclopedic book by Hölldobler and Wilson (1990). Therein may be found many relevant references up to 1990. The paper of Regnier and Law (1968) contains an overview of the chemical study of pheromones. Concerning the trail-laying behavior of ants, and foraging in general, we refer to Beckers et al. (1992), Bossert and Wilson (1963), Deneubourg and Aron (1990), Edelstein-Keshet (1994), Edelstein-Keshet et al. (1995), Ramsch et al. (2012), Rauch et al. (1995), Sumpter and Beekman (2003), Sumpter and Pratt (2003), Udiani et al. (2014), Vittori et al. (2004), Van Vorhis Key and Baker (1986), Vowles (1955), and Wilson (1962a,b,c), and the references therein, although of course many other papers could be cited.

Concerning the computational simulation of ant trail-laying, we refer to Boissard et al. (2012), Couzin and Franks (2002), Edelstein-Keshet et al. (1995), Johnson and Rossi (2006), Ryan (2015), Schweitzer et al. (1997), Sumpter and Beekman (2003), Watmough and Edelstein-Keshet (1995a,b), and Weyer (1985), although again this list is far from complete. See especially Boissard et al. (2012) for a recent approach involving directed pheromones, and an excellent, up-to-date review of available numerical and modeling strategies for ant foraging. We encourage the reader to consult that paper for an informative discussion and overview of the state of the art in ant trail-laying simulations.

Let us just point out that, as observed in Boissard et al. (2012), ant foraging simulations have in the past been mostly restricted to individual-based, or cellular automaton, models. That approach is certainly fruitful, but is generally limited to relatively small populations of ants, as well as somewhat restrictive modeling setups.

From what our bibliographical research could gather, only the work of Watmough and Edelstein-Keshet (1995a) presents a PDE model which (as our own) divides the ant population into two kinds, namely ants leaving the nest and ants returning to the nest (see also Johnson and Rossi, 2006, where the population is also divided in two different groups). However, the setting in Watmough and Edelstein-Keshet (1995a) is highly simplified, being one-dimensional, so no trail formation occurs, and the system proposed in that work is only explored numerically in a simplified ODE version.

Let us also refer to the work of Motta Jafelice et al. (2011), where a model for the dispersal of leaf-cutter ants is presented using PDEs. However, in that work trail-laying is not taken into account.

Thus, to the best of our knowledge, the present work is the first to consider the modeling and simulation of the whole cycle of food foraging by ants, comprising random foraging, discovery and transport of food, recruitment, formation of trails and fading of trails upon exhaustion of the food sources.[1]

An outline of the paper follows. In Section 2, we motivate the use of the mathematical framework of chemotaxis to model ant foraging. Next, in Section 3, we present our modeling assumptions derived from an analysis of the myrmecological literature, and deduce our model. In Section 4, we present and discuss various numerical simulations. In Section 5, we perform a parameter space exploration and discuss some consequences and possible experimental validations of the model. In Section 6 we draw some conclusions from our work, discuss some of its limitations, and suggest further lines of inquiry. Finally, the Appendixes deal with the nondimensionalization procedure and the details of the numerical scheme.

The main results of this paper were announced in Amorim (2015).

2. Modeling ant foraging

Many species of ants use recruitment of nest mates through chemical signals in order to efficiently exploit food sources. The goal is to concentrate the most individuals possible in a small region in space and time where the food source is located. This minimizes the risk of predation of the ants themselves and the removal of the food source by other foragers. To this end, eusocial insects have evolved several strategies, of which trail formation is one of the most well-known (Hölldobler and Wilson, 1990, Chapter 10).

Ants lay trails by depositing pheromones on the substrate, usually by pressing their sting against the substrate. Pheromones are chemical compounds that can diffuse through the substrate or through the air (Bossert and Wilson, 1963) and which the ants detect through their antennae. Importantly, ants can discern changes in concentration of the pheromone by measuring the difference in concentration between each antenna (see Boissard et al., 2012 and the references therein), thus allowing them to follow chemical gradients. A thorough description of foraging behavior for the fire ant *S. saevissima* can be found in Wilson (1962a,b).

Chemotaxis: In this work, we study ant foraging behavior from the mathematical point of view of *chemotaxis*. The term chemotaxis is used to describe phenomena in which the movement of an agent (usually a cell or bacteria) is affected by the presence of a chemical agent. Typically, individuals follow paths of increasing (or decreasing) concentration of the chemical agent, and often produce the agent themselves. This may originate a variety of phenomena, including finite time blow-up, segregation of species, and the formation of patterns, which are of interest to biologists and mathematicians alike.

The original chemotaxis model dates back to Patlak (1953) and Keller and Segel (1970, 1971), and was developed to model the evolution of a density $\rho(t, x)$ of bacteria and the concentration of a chemical $c(t, x)$, $t > 0$, $x \in \mathbb{R}^d$, according to the system (presented here in nondimensional form):

$$\partial_t \rho - \Delta \rho + \nabla \cdot (\rho \chi \nabla c) = 0,$$
$$\partial_t c - \Delta c + \tau c = \rho, \tag{2.1}$$

---

[1] As this work went to press, we learned of the paper of Bertozzi et al. (2014), which proposes a system sharing many similarities with our own.