Geodesic trail formation in a two-dimensional model of foraging ants with directed pheromones

Nils Caillerie

Geodesic trail formation in a two-dimensional model of foraging ants with directed pheromones

Nils Caillerie *

April 4, 2018

Abstract

We introduce a model of interacting particles imitating a colony of ants looking for a food source in a continuous plane. The mechanism describing communication between ants *via* pheromone deposition is inspired by a model of directed interacting particles previously introduced in [Boissard Degond Motsch, *Trail formation based on directed pheromone deposition*]. Here, we add a food source and introduce two types of pheromones: one pointing to the food source and one pointing to the nest. The particularity of our model is that we let the ants disperse in a two-dimensional space without a pre-existing lattice and we do not assume that the ants know their way back to the nest. We present simulations of our model and we investigate the ability of the colony to select the shortest path from the nest to the food source in various situations: with one or several food sources, with a food source whose location changes, with a food source behind an obstacle. Finally, we discuss the biological relevancy of our assumptions.

Key-words: velocity-jump process, foraging ants, Self-propelled particles, pheromone deposition, pattern formation, alignment interactions.
AMS Class. No: 92D50, 92B05, 60G50, 60J75, 60J25

Acknowledgment

The idea of this paper was born after a friendly conversation with Pierre Degond and thanks to Sébastien Motsch's patient answers to the author's emails. The author would like to thank them both for discussing about their model with him.

Research of the author was partially supported by the National Science Foundation grant 1615126 to Judith R. Miller.

1 Introduction

Social interaction is a key element for the survival of a colony of ants. Ants are known to have low cognitive capacities but are able to survive as a group using work division, invasive and defensive strategies, communication, food stocks and sometimes harvests. Very simple interactions between individuals with low cognitive capacities can achieve very complex tasks, such as building a nest for the colony [Khuong et al., 2016], developing war strategies to protect the nest [Whitehouse

*Department of Mathematics and Statistics, Geogetown University, Saint Mary's Hall, 3700 Reservoir Rd NW, Washington, DC 20007, USA. E-mail: nc691@georgetown.edu

and Jaffe, 1996], following routes and regulate the traffic to reduce congestion [Couzin and Franks, 2003, Dussutour et al., 2004] or find food and bring it back to the nest using an optimal route in the process [Garnier et al., 2009, Goss et al., 1989]. Is has indeed been observed that some ants, *e.g.* the Argentine ants *Iridomyrmex humilis*, can walk their way into a maze, find a food source and bring it back to their nest using a short path [Goss et al., 1989]. In this paper, we are interested in the issue of food localization and optimization of the transport by a colony of ants.

The formation of trails in ant colonies has been understood a while ago. There is already a wide biological literature on the subject [Beckers et al., 1992a, Couzin and Franks, 2003, Detrain et al., 2001, Edelstein-Keshet, 1994, Edelstein-Keshet et al., 1995, Watmough and Edelstein-Keshet, 1995b, Watmough and Edelstein-Keshet, 1995a]. The general observation is that the formation of trails is a result of simple local interactions, such as brief antennas contacts [Gordon et al., 1993, Mailleux et al., 2010] or distant communication, *via* deposition of chemical markers called pheromones. We will focus only on pheromones deposition in this paper.

The principle of pheromone communication is simple. An ant can leave a pheromone drop using the sting on its abdomen [Beckers et al., 1992a, Hangartner, 1969, Jackson and Châline, 2007, Jeanson et al., 2004, Wilson, 1962, Witte and Maschwitz, 2002]. The ant then keeps walking but the pheromone drop remains where the ant left it. When a new ant arrives on site, it obtains the information that an ant was formerly here, but not only. Biologists argue that the pheromone drop carries more information. Depending on the studied species, pheromones drops can give different types of information. An ant can for instance obtain information on the orientation of the ants which laid the pheromone through a mechanism called osmotropotaxis [Calenbuhr and Deneubourg, 1992, Calenbuhr et al., 1992, Couzin and Franks, 2003] or about the chemical composition of the pheromone [Wyatt, 2003]. For example *Myrmica sabuleti* specimens can leave different pheromones depending on the food they found [Cammaerts and Cammaerts, 1980], the Pharaoh's ant *Monomorium pharaonis* is also able to depose attractive or repellent pheromones [Robinson et al., 2008]. Other species such as the Argentine ant *Iridomyrmex humilis* [Deneubourg et al., 1990, Garnier et al., 2009, Vittori et al., 2006], the black garden ant *Lasius niger* [Beckers et al., 1992b, Beckers et al., 1993, Dussutour et al., 2004, Nicolis and Deneubourg, 1999] and the Army ant *Eciton burchelli* [Brady, 2003, Couzin and Franks, 2003, Franks et al., 1991], on the other hand, are known to lay only one type of pheromone. An ant which lays a pheromone signal can also modulate the importance of the information by leaving long or short-lasting pheromones. This was observed, among other species, for the Pharaoh's ant [Beekman et al., 2001, Fourcassié and Deneubourg, 1994, Jackson et al., 2007, Jackson and Châline, 2007, Jeanson et al., 2003, Sumpter and Beekman, 2003] or for the big headed ant *Pheidole megacephala* [Dussutour et al., 2009]. These signals carry simple informations (location and orientation of the ant, chemical concentration, chemical composition...) but through multiplication of a large number of signals, the colony as a whole is able to develop complex social structures, in particular, to form patterns such as trails.

When a colony of ant carries food from a location to the nest, one can observe the formation of a trail (that is, a path with a high concentration of ants and pheromones) between the food source and the nest. One remarkable observation about those pheromone trails is that they optimize the time of food transport. Simply put, the ant colony is able to find the shortest path from the nest to the food source. When facing an environment with multiple possible routes to a food source, an ant colony will most of the times choose the shortest one [Sumpter and Beekman, 2003, Bonabeau et al., 1999, Garnier et al., 2009, Goss et al., 1989]. This is rather spectacular since, once again, ants have low cognitive capacities. In particular, there is no central power leading the foraging ants and

only local interactions between them.

Actually, the phenomenon that causes this is rather simple to understand. Assume that there exists two paths connecting a food source to the ants' nest. The shortest path of the two allows ants to bring the food faster so ants walking back and forth on this track will make more travels per unit of time than their counter specifics on the longest path. Therefore, they will make the travel more often and hence leave more pheromones so more ants will be recruited on the shortest track.

This principle has been understood a while ago and has nourished a field of probability theory called "reinforced random walks". One goal of this field is to find geodesics on graphs using random walkers (whose behavior is inspired by ants) on the graph, that use the vertices (with lengths) to go from one node to the other. When walking on a vertex the random walkers (robot ants so to speak) leave a signal (pheromone) giving more weight to this particular vertex, thus, raising the probability that the next ant will choose the same path. So-called "ants algorithms" have proven themselves very efficient to solve optimization problems such as the well-known "salesman problem" [Dorigo et al., 1996, Dorigo and Gambardella, 1997, Stützle and Hoos, 1999] among many others. Moreover, rigorous proofs exist to mathematically establish their efficiency [Jayadeva et al., 2013]. Ants algorithms also prove themselves capable of finding geodesic paths in mazes [Vela-Pérez et al., 2013].

More biologically relevant mathematical models have been introduced to understand the dynamics of trail following. Some one-dimensional models consider a pre-existing trail and focus on the way ants sense the trail [Calenbuhr and Deneubourg, 1992, Calenbuhr et al., 1992, Couzin and Franks, 2003] or the way they regulate traffic [John et al., 2004, Nishinari et al., 2006]. Other models focus on the decision process which leads ants to follow one trail or the other [Beckers et al., 1990, Deneubourg et al., 1990, Edelstein-Keshet, 1994, Goss et al., 1989, Peters et al., 2006, Watmough and Edelstein-Keshet, 1995b]. In these models, the system does not produce the pheromone trails itself.

Most two-dimensional models in the literature consider a walk on a fixed lattice [Ermentrout and Edelstein-Keshet, 1993, Edelstein-Keshet et al., 1995, Beckers et al., 1990, Deneubourg et al., 1990, Rauch et al., 1995, Schweitzer et al., 1997, Tao et al., 2004]. Depending on the model, the ants can leave the pheromones either on the nodes or on the edges of the lattice. Depending on the model, they can be cellular automata or Monte-Carlo models. The one thing they share however, is that they do not consider the system able to self-direct: the pre-existing lattice constraints the directions in which ants can go. In [Rauch et al., 1995] and [Tao et al., 2004], the authors consider ants that are able to depose two different kind of pheromones, depending if they carry food or if they are exploring the environment. We will follow the same approach in this paper.

A two-dimensional model that does not consider a pre-existing lattice is the Boissard-Degond-Motsch model [Boissard et al., 2013]. In this model, ants are able to explore a two-dimensional space. Ants leave one type of pheromones behind them that tell other ants in what direction they were walking when they deposed the pheromone. Their model allows two different interactions: non-polar ones, where ants can distinguish the orientation of a pheromone but not its direction, or polar ones. In the present paper, we will only focus on the second kind of interactions. When considering polar interactions, Boissard, Degond and Motsch observed that the system was able to produce pheromone trails (that is, a large number of aligned pheromones that are oriented in the same direction) that ants would follow preferably. It is, to our knowledge, the first model in which the system was able to create pheromone trails without assuming a pre-existing lattice. Their model however, did not imply a food source.

More recently, Ryan [Ryan, 2016] proposed a two-dimensional model of foraging ants, without a pre-existing lattice. His model considered an ant colony coming out of a nest and looking for a food source within the environment. In his model, once an ant found the food source, it goes directly to the nest using the shortest path, leaving pheromones behind itself to recruit other ants on the trail. The model also includes collective strategies to self-regulate the traffic flow on the path. In Ryan's model, the ants already know the shortest way back to the nest, which is in contradiction with our motivation. This was also assumed in reaction-diffusion equations modeling foraging ants at the macroscopic scale, which were mathematically analyzed in [Amorim, 2015a, Amorim, 2015b, Alonso et al., 2016].

Let us summarize: to our knowledge, all models of geodesic path formation are either on a graph [Vela-Pérez et al., 2013] or assume a pre-existing lattice [Rauch et al., 1995, Tao et al., 2004]. The two-dimensional models that do not consider any pre-existing lattice only consider one type of pheromone. In particular, they either don't consider any food source [Boissard et al., 2013] or consider that the route back to the nest is prescribed [Ryan, 2016, Amorim, 2015a, Amorim, 2015b, Alonso et al., 2016]. In this paper, we will take ideas from those works to build a two-dimensional model with two kinds of pheromones. The crucial assumption of our model is that the ants do not have knowledge of where the food source or the nest is. In particular, the route back to the nest is not prescribed.

Our model is very similar to the Boissard-Degond-Motsch model. We will consider the same mechanism of pheromone deposition, the same mechanism of ant recruitment on trails and we will take the same parameter values. Unlike their model, we will consider two populations: a population of foraging ants and a population of ants coming back to the nest with food. The foraging ants will leave pheromones that indicate their direction to the ants with food. The ants with food will do the same with a second kind of pheromone. As in [Boissard et al., 2013], we will consider only interactions between the ants and the pheromones. In particular, we will not assume that ants can collide with each other or that they directly communicate when bumping into each other. We will also consider polar-interactions between ants and pheromones, which means that ants are able to know in what orientation and in what direction the pheromone is pointing to.

The outcome of our model is that the colony is able to find the food source and to bring it back to the nest, using a short path. The geodesic path (in most situations, the geodesic path will be the straight line between the food source and the nest) is never followed by an ant all the way since it requires that the ant keeps a ballistic trajectory for a very long time (in particular, the geodesic path has a zero-probability to be walked all the way).

Our paper is organized as follows. In Section 2, we precisely describe the model, we explain some assumptions made for the simulations and give our choice of parameter values. In Section 3, we present the outcome of various simulations of the model: with only one food location, with two food locations, with a food source whose location changes and finally, with an obstacle between the food and the nest. In Section 4, we discuss our model and results and give ideas to improve the model from a biological perspective. Finally, we draw a conclusion and give perspectives for future work.

2 The model

We consider a stochastic model of interacting random walkers on a continuous plane, leaving particles carrying information behind them. In view of our motivation, we will call the random walkers "ants"

and the particles "pheromones".

Our model is very similar to the one of [Boissard et al., 2013]. Namely, the way ants move and choose their directions are the same. Unlike [Boissard et al., 2013] though, we consider a food source, two types of pheromones and two types of ants:

- ants that are looking for food,
- ants which have found food and are trying to bring it back to the nest.

Moreover, unlike [Boissard et al., 2013], we consider that pheromones keep the direction of their "parent" ant as an angle in $[0, 2\pi)$ and not as a unit vector. We emphasize that this last modification is purely superficial and does not change the dynamics of trail formation.

The nest is modeled by a disc centered at the origin of radius $R_{nest} > 0$ and the food source by a compact set $\Omega \subset \mathbb{R}^2$ such that $\Omega \cap D(0, R_{nest}) = \emptyset$, which means that the food source and the nest are at two different places.

We consider N ants moving in a 2-dimensional space. Every ant is either a "foraging" ant or an ant "with food" but this status can change. We denote by $N_f(t)$ and by $N_w(t)$ the number of foraging ants and ants with food respectively at time $t \geq 0$. Each foraging ant i is described by its position $x_i \in \mathbb{R}^2$ and the direction of its motion $\theta_i \in [0, 2\pi)$. Each ant with food j is described by its position $y_j \in \mathbb{R}^2$ and the direction of its motion $\omega_j \in [0, 2\pi)$.

We assume that ants are able to depose two types of pheromones: foraging ants depose the first type of pheromones. From now on, we will call those the "green pheromones" out of simplicity. The ants with food on the other hand lay the second kind of pheromones. We will call those the "blue pheromones". We denote by $P_g(t)$ the number of green pheromones and by $P_b(t)$ the number of blue pheromones. Each green pheromone k is described by its position z_k and by its direction $\alpha_k \in [0, 2\pi)$. Each blue pheromone m is described by its position ζ_m and by its direction $\beta_m \in [0, 2\pi)$. The foraging ants are only sensitive to the blue pheromones. Since those pheromones are laid by ants with food, which are going away from the food source, following the direction of this pheromone will make it easier for foraging ants to find the food source. The same mechanism with green pheromones will enable the ants with food to find their way back to the nest.

Once a pheromone is laid, it remains active (in other words, detectable by an ant) for an exponential time with parameter $\frac{1}{T_p}$, where $T_p > 0$ is the mean activity time of pheromones. We assume that the pheromones have no spatial dynamics: until it is no longer active, a pheromone stays where it is.

Unlike the pheromones, the ants do move. Every ant follows a so-called "Run & Tumble" motion (or velocity-jump process). During the running phase, we assume that an ant goes in a straight line with velocity $c > 0$ in the direction given by its angle θ or ω such that the motion dynamics of foraging ants and ants with food is given by

$$\dot{x_i}(t) = c \cdot \begin{pmatrix} \cos\theta_i(t) \\ \sin\theta_i(t) \end{pmatrix}, \tag{2.1}$$

$$\dot{y_j}(t) = c \cdot \begin{pmatrix} \cos\omega_j(t) \\ \sin\omega_j(t) \end{pmatrix}. \tag{2.2}$$

The "Tumble" is an instantaneous phase of velocity redistribution process which is different depending on the status of the ant and on the pheromones' concentration. We explain this process in details in the next two subsections. We assume that the radius of detection of an ant is $R > 0$

regardless of the pheromone type or the ant's status. This means that the ant is sensitive to a pheromone if and only if the Euclidean distance between the pheromone and the ant is less or equal to R.

2.1 Foraging ants

After the end of its running phase, a foraging ant chooses a new direction in $[0, 2\pi)$ depending on the pheromones' concentration.

Random velocity jumps: If there is no blue pheromone within the radius of detection of the ant, we assume that the new direction θ_i' of the ant is chosen randomly such that

$$\theta_i'(t) \equiv \theta_i(t) + \varepsilon_i(t) \mod(2\pi), \tag{2.3}$$

where $\theta_i(t)$ is the current direction of the ant and $(\varepsilon_i(t))_{i,t}$ is an independent family of Gaussian random variables with zero mean and variance $\sigma^2 > 0$.

Once a foraging ant has chosen this direction, it keeps it for an exponential time of parameter $\lambda_f > 0$ and then, a new tumble occurs.

Trail recruitment jumps: If there are blue pheromones within the radius of detection of the foraging ant, the ant chooses one of these pheromones uniformly and aligns its direction with the chosen pheromone such that its new direction θ_i' is

$$\theta_i'(t) = \beta_{M_i}, \tag{2.4}$$

where M_i is uniformly distributed in $\{m \in \mathbb{N},\ \|x_i(t) - \zeta_m\| \leq R\}$, where $\|\cdot\|$ is the standard Euclidian norm on $\mathbb{R}^2$.

After the ant has made a trail recruitment jump, the next velocity jump occurs after a random exponentially distributed time with parameter $\lambda_b \cdot |\{m \in \mathbb{N},\ \|x_i(t) - \zeta_m\| \leq R\}|$, where t is the time of the trail recruitment jump and $|\cdot|$ is the cardinal of the set. This means that the higher the number of blue pheromones within the detection zone, the shorter the time until the next tumble.

Laying pheromones: We assume that, with a rate $\nu_g > 0$, the foraging ants lay green pheromones, which means that each foraging ant lays a green pheromone at every ticking of an exponentially distributed clock with parameter ν_g. When a foraging ant i lays a green pheromone at time t, a green pheromone k is created with the same position as the ant but in the opposite direction

$$z_k = x_i(t), \qquad \alpha_k \equiv \pi + \theta_i(t) \mod(2\pi). \tag{2.5}$$

Finding the food source: When a foraging ant finds the food source, *i.e.* $x_i(t) \in \Omega$, a tumble instantaneously occurs: the ant's location does not change but the ant turns in the opposite direction and becomes an ant with food, which means that its new orientation $\omega_j'(t)$ is given by

$$\omega_j'(t) \equiv \pi + \theta_i(t) \mod(2\pi), \tag{2.6}$$

where $\theta_i(t)$ is its current direction. The next tumble will occur as was previously planned by the ant.

2.2 Ants with food

The random motion of the ants with food is pretty similar to the one of the foraging ants but ants with food only lay blue pheromones and are sensitive only to green pheromones. After its running phase, an ant with food chooses a new direction in $[0, 2\pi)$ depending on the pheromones' concentration.

Random velocity jumps: If there is no green pheromone within the radius of detection of the ant, we assume that the new direction ω_j' of the ant is chosen randomly such that

$$\omega_j'(t) \equiv \omega_j(t) + \varepsilon_j(t) \mod(2\pi), \tag{2.7}$$

where $\omega_j(t)$ is the current direction of the ant and $(\varepsilon_j(t))_{j,t}$ is an independent family of Gaussian random variables with zero mean and same variance $\sigma^2 > 0$ as the foraging ants.

Once an ant with food has chosen this direction, it keeps it for an exponential time of parameter $\lambda_w > 0$ and then, a new tumble occurs.

Trail recruitment jumps: If there are green pheromones within the radius of detection of the ant with food, the ant chooses one of the pheromones uniformly and aligns its direction with the chosen pheromone such that its new direction ω_j' is

$$\omega_j'(t) = \alpha_{K_j}, \tag{2.8}$$

where K_j is uniformly distributed in $\{k \in \mathbb{N},\ \|y_j(t) - z_k\| \leq R\}$.

When the ant makes a trail recruitment jump, it chooses a random exponentially distributed time with parameter $\lambda_g \cdot |\{m \in \mathbb{N},\ \|x_i(t) - \zeta_m\| \leq R\}|$ and will not make a velocity jump until this time. As for the foraging ants, this means that the tumbles occur more often when there are many green pheromones.

Laying pheromone: We assume that with a rate $\nu_b > 0$, the ants lay blue pheromones. When an ant with food j lays a blue pheromone at time t, a blue pheromone m is created with the same position as the ant but in the opposite direction

$$\zeta_m = y_j(t), \qquad \beta_j \equiv \pi + \alpha_j(t) \mod(2\pi). \tag{2.9}$$

Finding the nest: When an ant with food finds the nest, *i.e.* $y_j(t) \in D(0, R_{nest})$, a tumble instantaneously occurs: the ant chooses a new direction uniformly on $[0, 2\pi)$ and becomes a foraging ant. Its new direction $\theta_i'(t)$ is therefore distributed as

$$\theta_i'(t) \sim \text{Unif}\left([0, 2\pi)\right). \tag{2.10}$$

The next tumble will occur as was previously planned by the ant.

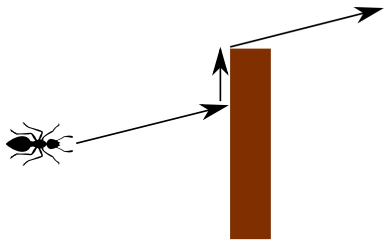

Figure 1: *Illustration of the behavior of an ant facing an obstacle (one example). When arriving at the foot of the obstacle from the left, the ant starts to walk around the obstacle. In this example, the ant was going to the East-North-East direction so the ant walks around the obstacle going north. When the ant no longer faces the obstacle, it keeps the direction that it had before it encountered the obstacle (unless a tumble occurred in between).*

2.3 Dealing with an obstacle

In some simulations, we will consider the existence of an insuperable obstacle. We model this obstacle by a rectangle $[O_l, O_r] \times [O_d, O_u]$ in the plane such that $([O_l, O_r] \times [O_d, O_u]) \cap D(0, R_{nest}) = \emptyset$ and $([O_l, O_r] \times [O_d, O_u]) \cap \Omega = \emptyset$, which means that the obstacle is not located at the same place as the nest or the food source. We describe here the dynamics of an ant, regardless of its status, when it encounters an obstacle. The ant tries to walk around the obstacle. This means that the spatial dynamics of the ant is not described by the running phase ((2.1) or (2.2)) anymore but rather by this "walking around" phase:

$$\dot{x_i}(t) = c \cdot \begin{cases} (0, \text{sign}(\sin\theta_i(t))), & \text{if } x_i(t) \in \{O_l, O_r\} \times [Od, Ou], \\ (\text{sign}(\cos\theta_i(t)), 0), & \text{if } x_i(t) \in [O_l, O_r] \times \{O_d, O_u\}, \end{cases} \tag{2.11}$$

$$\dot{y_j}(t) = c \cdot \begin{cases} (0, \text{sign}(\sin\omega_j(t))), & \text{if } y_j(t) \in \{O_l, O_r\} \times [Od, Ou], \\ (\text{sign}(\cos\omega_j(t)), 0), & \text{if } y_j(t) \in [O_l, O_r] \times \{O_d, O_u\}. \end{cases} \tag{2.12}$$

This means that an ant will systematically translate to its left or right when located at the foot of the obstacle. It will choose left or right according to its current orientation. It then gets back to a normal run phase when the obstacle is away. The Figure 1 gives a simple illustration of the behavior of an ant at the foot of the obstacle.

We emphasize that a tumble can still occur during this phase but that the dynamics will be determined by (2.11)-(2.12) until the ant is away from the obstacle.

2.4 Simulations parameters

For the sake of simulations, we add more parameters to our model.

Discrete time Model We use time steps of size $\Delta t > 0$ and we make any time related random variables T discrete by considering $\Delta t \cdot \lceil \frac{T}{\Delta t} \rceil$ instead, where $\lceil \cdot \rceil$ is the upper integer part. We stop the simulation at a final time T_f.

Table 1: Model parameters and their values

Parameter	Interpretation	Value
c	Instantaneous speed of ants	2cm/s
λ_f	Random jump frequency of foraging ants	2s^{-1}
λ_w	Random jump frequency of ants with food	10s^{-1}
σ	Standard deviation of orientation changes	0.1
λ_b	Trail recruitment jump frequency of foraging ants	2s^{-1}
λ_g	Trail recruitment jump frequency of ants with food	2s^{-1}
ν_g	Green pheromones deposition rate	0.2s^{-1}
ν_b	Blue pheromones deposition rate	0.6s^{-1}
T_p	Pheromones mean lifetime	100s
R	Detection radius	1cm
R_{nest}	Radius of the nest	1cm
Ω	Food source	
O_l, O_r, O_d, O_u	Dimensions of the obstacle	

"Initial" conditions At $t = 0$, we assume that a single foraging ant leaves the nest at position $(0, 0)$ with a direction chosen uniformly on $[0, 2\pi)$. Then, every second, a new foraging ant leaves the nest at position $(0, 0)$ with the same direction probability distribution until the maximal number of ants N is reached.

Boundary conditions We restrict our study to the square box $[-\frac{l}{2}, \frac{l}{2}] \times [-\frac{l}{2}, \frac{l}{2}]$. When an ant reaches the boundary of the box, we suppose that it dies, regardless of its status. It is then instantaneously replaced by a new foraging ant, which comes out of the nest with direction chosen uniformly on $[0, 2\pi)$.

Maximal number of pheromones To keep the computations affordable, we impose a maximal number of pheromones that the system can support. When the maximal number $P_b^{\max}$ of blue pheromones or the maximal number $P_g^{\max}$ of green pheromones is reached, the corresponding ants stop deposing those pheromones until the disappearance of other pheromones allow them to produce some more.

2.5 Choice of parameters

We recap here all the parameters of our model and specify what values we choose for them. The Table 1 shows the values of the model parameters and the Table 2 shows the values of the simulations parameters. When specified in the tables, this parameter value is chosen in all simulations shown in Section 3. When not specified, the parameter value depends on the simulation and will be specified in the corresponding subsection.

We emphasize that, when such correspondence can be made, we systematically choose the same parameter values as in [Boissard et al., 2013]. We discuss the biological relevancy of such choices in Section 4.

Table 2: Simulations parameters and their values

Parameter	Interpretation	Value
T_f	Duration of the simulation	
Δt	Time increments	0.1s
l	Dimension of the box	100cm
N	Maximal number of ants	200
$P_b^{\max}$	Maximal number of blue pheromones	1000
$P_g^{\max}$	Maximal number of green pheromones	1000

3 Results

3.1 Typical dynamics of the system

We show in Figure 2 the outcome of one simulation with $T_f = 200$ seconds and where Ω is a disc of radius 2 centimeters centered at point $(0, 40)$. The so-called green pheromones are represented by green sticks showing in which direction the pheromone is oriented and the blue pheromones by blue sticks. Black squares represent foraging ants and red squares represent ants with food. The nest is represented by a black circle and the food source by a red circle. After 30 seconds, there were 31 foraging ants in the environment, which were all making random velocity jumps and deposing green pheromones. No ant found food yet. After 56.20 seconds, one foraging ant found food and became an ant with food. The ant then proceeded to come back to the nest following the green pheromones that it left when it was still foraging. When it didn't find any pheromones ahead, it started to make random velocity jumps again, and made a detour but the green pheromones in the square $[-10, 0] \times [0, 10]$ put it back on track (see the middle-left part of the figure and more specifically, the blue pheromones). It took the ant 22.2 seconds to walk from the food source back to the nest, whereas the geodesic (*i.e.* the straight line which is 37 centimeters long) would have taken $37/c$=18.5s. After 100 seconds, there were two ants with food, taking a different (presumably shorter) path to get back to the nest. After 200 seconds, there were 24 ants with food and the overall pattern was that ants with food walked on the straight line from the food source to the nest.

3.2 Geodesic path from the food source to the path

From now on, for a better understanding of the simulations, we only represent the pheromone trails and do not represent the ants in our figures.

We study the long time behavior of the system and we investigate the ability of the ants to optimize their food transport, that is, to find the geodesic that links the food source to the nest. In order to measure the length of a path, we adopt the following perspective: given that all ants constantly walk with speed c=2cm/s, we let the ants with food keep a memory of the time spent since they encountered the food source. When they finally find their way back to the nest and start foraging again, we call "path followed by the ant" the trajectory of this ant. In other word, a "path followed by an ant" is a set of the form

$$\{y_j(t) \mid T_0 \leq t \leq T_1,\ y_j(T_0) \in \Omega,\ y_j(T_1) \in D(0, R_{nest})\} \tag{3.13}$$

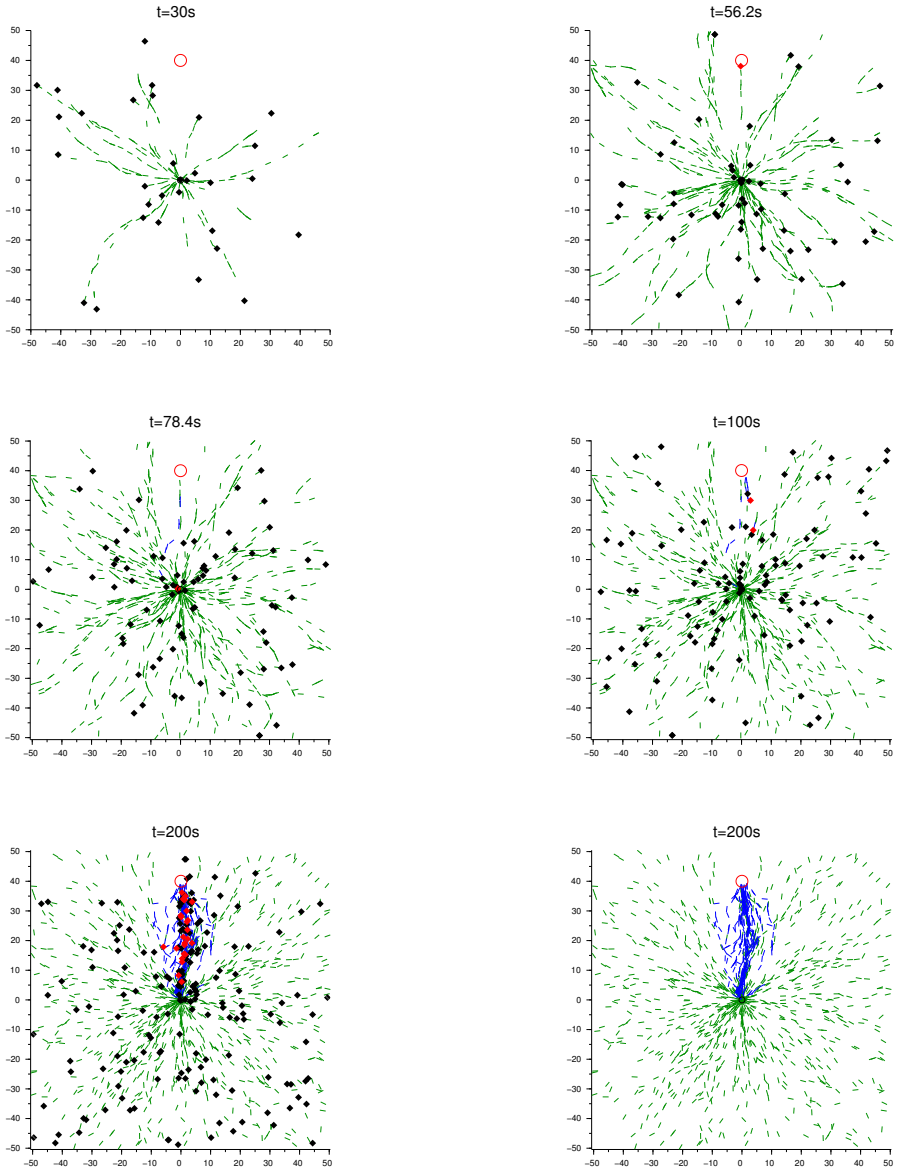

Figure 2: *One simulation of the model where the food source is a disc of radius 2cm centered at* $(0, 40)$. *Top left: Outcome of the simulation after 30s. Top right: Outcome of the simulation after 56.20s (discovery of the food source by one ant). Middle-left: Outcome of the simulation after 78.4s (when the first ant with food found its way back to the nest). Middle-right: Outcome of the simulation after 100s. Bottom-left: Outcome of the simulation after 200s. Bottom-right: Outcome of the simulation after 200s (only the pheromones' locations are shown and blue pheromones are shown in priority over the green ones). Black circle at the origin: Nest. Red circle: Food source. Black squares: foraging ants. Red squares: ants with food. Green sticks: "green pheromones" (left by foraging ants). Blue sticks: "blue pheromones" (left by ants with food).*

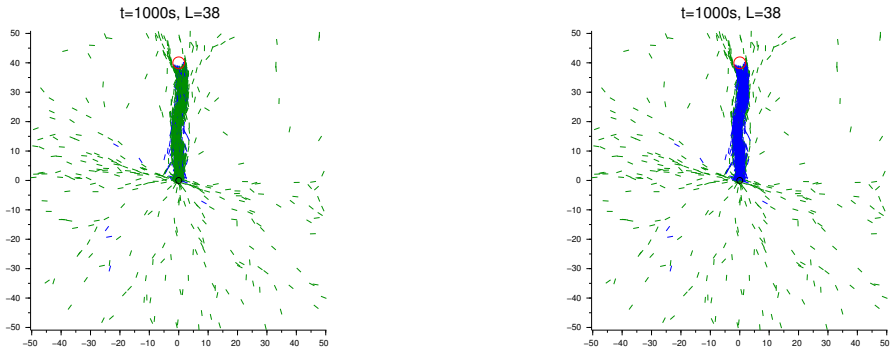

Figure 3: *Simulation of the model with* $T_f = 1000s$. Ω *is a disc of radius 2cm centered at* $(0, 40)$. *The left figure shows the "green pheromones" in priority and the right figure shows the "blue pheromones" in priority. Black circle: nest. Red circle: food source.*

and the length of this path is defined as

$$L := c\,(T_1 - T_0)\,. \tag{3.14}$$

We show in Figure 3 and Figure 4 the typical outcome of a simulation after $T_f = 1000$ seconds when Ω is a disc of radius 2 centimeters centered at $(0, 40)$. We first notice that there exists a "pheromone highway", that is, a high concentration of pheromones next to the geodesic. The shortest recorded path followed by an ant is 38 centimeters long, which is close to the 37 centimeters of the geodesic (there is 40cm between the two centers of the food source and the nest and the radii are 1cm and 2cm long). We represent in the bottom-right corner of Figure 4 the evolution of the shortest recorded path's length. The upper-left corner of Figure 4 shows evidence of a phase transition. It represents the mean-value of $(\sin \alpha_k)_k$, where $(\alpha_k)_k$ is the orientation of all green pheromones. Since the food source is located North to the nest, we expect many green pheromones to be oriented to the South and therefore, we expect the sine of this orientation to be close to -1. We can see that, between 0 and 200 seconds, the mean sine of the green pheromones orientation first gathers around the mean value 0 of the sine of the uniform law on $[0, 2\pi)$, as predicted by the strong law of large numbers (let us recall that the direction of the foraging ants is initially uniformly distributed). But after 200 seconds, due to the presence of ants with food (see the bottom-left corner for comparison), the green line stabilizes around the middle of 0 and -1. We emphasize that it does not stabilize around -1 due to our boundary conditions. Indeed, when foraging ants reach the boundary, they die and are replaced with an ant whose orientation is uniformly distributed in $[0, 2\pi)$. The blue line, as we can see in the upper-right corner of Figure 3, stays close to 1, which means that most of the blue pheromones are oriented in the North direction.

3.3 Disconnected food source

From now on, we will show the outcome of our simulations by representing the green and blue pheromones but we will show the blue pheromones in priority, in the same fashion as in the right-hand side of Figure 3. We emphasize that, where there is a

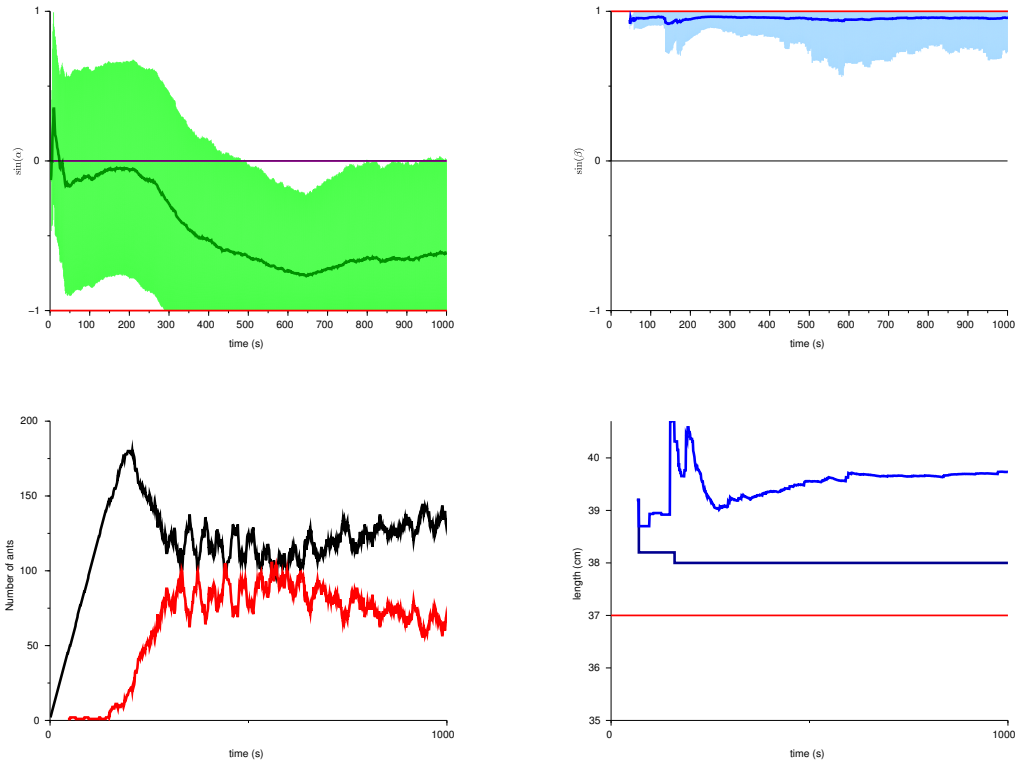

Figure 4: *Evidence of a phase transition. Top-left: dark green line: mean orientation of the green pheromones, green zone: standard deviation around the mean-value, red line: orientation of the geodesic going from the food source to the nest, magenta line: Mean value of the uniform distribution on* $[0, 2\pi)$. *Top-right: dark blue line: mean orientation of the blue pheromones, light-blue zone: standard deviation around the mean-value, red line: orientation of the geodesic going from the nest to the food source. Bottom-left: black line: number of foraging ants. Red line: number of ants with food. Bottom-right: deep blue line: mean paths length, dark blue line: minimal path length, red line: geodesic length.*

high concentration of blue pheromones, there is also a high concentration of green pheromones, even though they may not appear in the figures.

In these simulations, we assume that the food source is disconnected, namely that it is the reunion of a disc of center $(30, 30)$ with radius 2 centimeters and an other disc of center $(-a, a)$ and same radius. From now on, we will call the first disc "the North-East food location" and the second disc "the North-West food location". We take different values for $a > 3$ (let us notice that the food source and the nest have a non-empty intersection when $a \leq 3$). Given what happened in the previous simulations, we would expect the ant colony to select the shortest path, *i.e.* to have more pheromones oriented in the North-West direction when $a < 30$ and and more pheromones oriented to the North-East when $a > 30$. This is indeed the case for the simulations shown in Figure 5, when $a = 5, 10, 15, 20, 35, 40$ but as, we can in the case $a = 25$, the probability that the colony does not privilege the shortest path is non-zero. In some situation, like the simulation with $a = 45$, the colony goes to both food locations.

We show in Figure 6, the probability that the North-West food location (*i.e.* the disc centered at $(-a, a)$) is chosen over the North-East one (*i.e.* the disc centered at $(30, 30)$) as a function of a. For this, we develop the following statistical approach.

For each $a \in \{5, 10, 15, 20, 25, 30, 35, 40, 45, 50\}$, we simulate our model 500 times. Since this is a rather large number of simulations, we need to reduce the computational cost of all simulations. Hence, for the purpose of drawing Figure 6 and for this purpose only, we fix $P_b^{\max} = 200$ and $P_g^{\max} = 600$ and we stop the simulation once the maximal number of blue pheromones is attained. We call this stopping time τ. We then count the number of blue pheromones whose orientation lies in $\left[0, \frac{\pi}{2}\right)$ and consider them as pheromones pointing to the North-West quadrant. We also count the number of blue pheromones whose orientation lies in $\left[\frac{\pi}{2}, \pi\right)$ and consider them as pheromones pointing to the North-East quadrant:

$$P_b^{NE}(\tau) := \left| \{\beta_m \mid 1 \leq m \leq P_b(\tau)\} \cap \left[0, \frac{\pi}{2}\right) \right|, \tag{3.15}$$

$$P_b^{NW}(\tau) := \left| \{\beta_m \mid 1 \leq m \leq P_b(\tau)\} \cap \left[\frac{\pi}{2}, \pi\right) \right|. \tag{3.16}$$

We estimate that the colony chose the food location in the North-West quadrant over the North-East one if and only if $P_b^{NW}(\tau) > P_b^{NE}(\tau)$. We estimate the probability that the colony privileges the Nort-West quadrant food by counting how many times this event occurred among the 500 simulations. The results are shown in Figure 6. The simulations show that when a increases, the probability that the colony will choose the food located next to $(-a, a)$ decreases linearly.

3.4 Dynamical food source

In these simulations, the food source's location varies. There are two steps. Between 0 and $T_f/2 = 500$ seconds, the food source is located at one place and between $T_f/2 = 500$ seconds and $T_f = 1000$ seconds, it is located at a different place. We simulate this model in a situation where the two locations and the nest are nearly aligned (Figure 7), one where the two locations and the nest form a right-angle (Figure 8) and finally, one where the two locations and the nest form an acute angle (Figure 9). We systematically represent the pheromone trail every 100 seconds after the 500th one. What these simulations show is that, after a small transition, the ants are able to find the second food source, even though they were first misled. The pheromone trail keeps memory of the first part of the simulation, as we clearly see in Figure 9. Indeed, even though the geodesic to the second

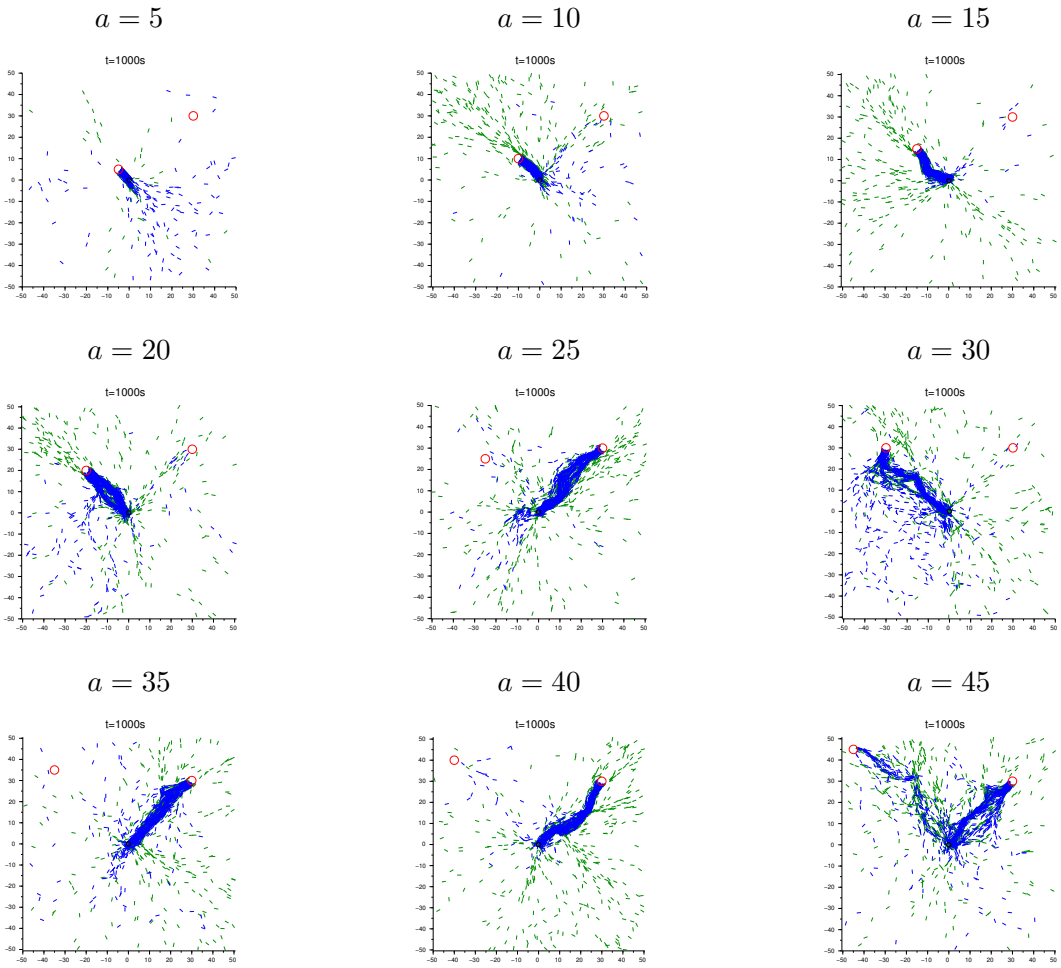

Figure 5: *Nine simulations of the model with disconnected food source. The food source is simultaneously located at the reunion of the disc of radius 2cm centered at* $(30, 30)$ *and the disc with same radius centered at* $(-a, a)$ *for* $a = 5, 10, 15, 20, 25, 30, 35, 40, 45$*. In all above simulations but the ones obtained with* $a = 25$ *and* $a = 45$*, the colony clearly favored the shortest path to the food source. For* $a = 25$*, the colony did not choose the shortest path and for* $a = 45$*, the colony brings food from the two locations, with a preference for the closest one. Green sticks: "green" pheromones. Blue sticks: "blue" pheromones. Red circle: food source. Black circle: nest.*

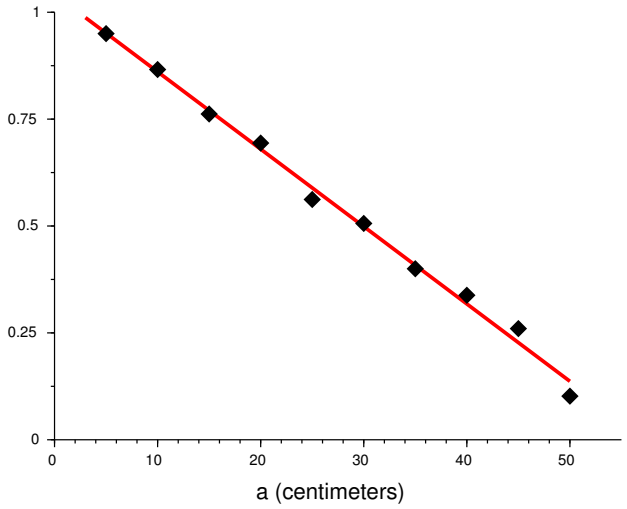

Figure 6: *Estimated probability that the colony chooses the food location located at a disc of radius 2cm and center* $(-a, a)$ *over one located at a disc of radius 2cm and center* $(30, 30)$ *as a function of* a*. Red line: linear regression* ($y = -0.0181(x - 3) + 0.9874$).

food location is a straight path, the ant colony follows an S-shaped trail because of the history of the simulation.

3.5 Dealing with an obstacle

In these simulations, we set $T_f = 1000$ seconds and consider that the food source is a disc of center $(0, 40)$ and of radius 2 centimeters. We assume that there is a an obstacle of constant width (O_l=20, O_r=22) but with various lengths. The Figure 10 shows that if the obstacle is short enough, the colony is able to find the food source and to bring food back to the nest. As in the first simulations, we compute the length of the shortest trail by collecting the times spent by the ants with food. What this study shows is that the colony is able to find a path that is close to the shortest path. Let us emphasize that the shortest path is very unlikely to be followed by an ant since it requires to have a nearly ballistic trajectory from the food to the obstacle and from the obstacle to the nest but to make two sharp turns: one when arriving at the obstacle, one when leaving it.

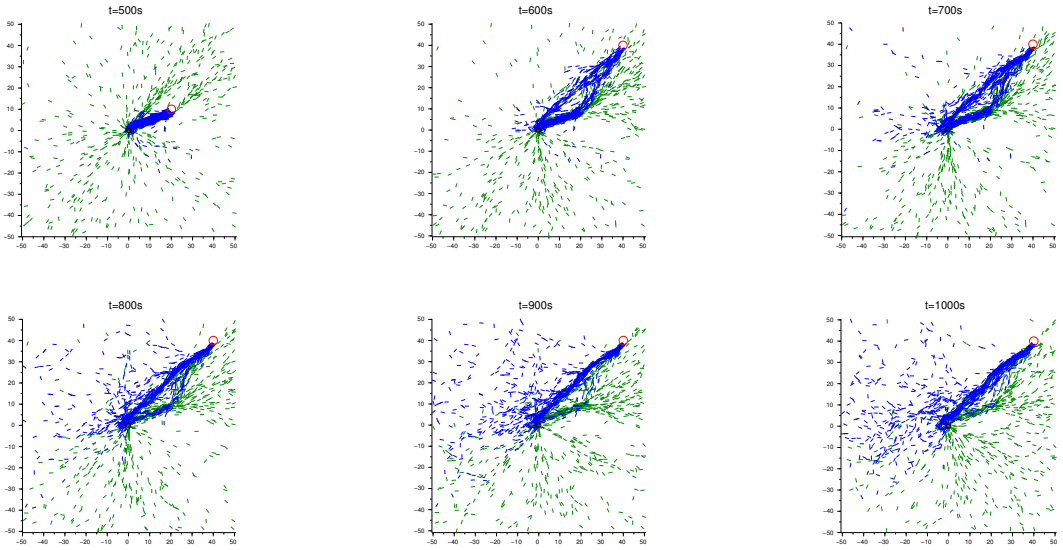

Figure 7: *One simulation of the model with a dynamical food source. The food source is a disc of radius* $2cm$ *centered first at* $(20, 10)$ *and then at* $(40, 40)$ *after 500s. Blue sticks: "blue" pheromones. Green sticks: "green" pheromones. Red circle: Food source. Black circle: nest.*

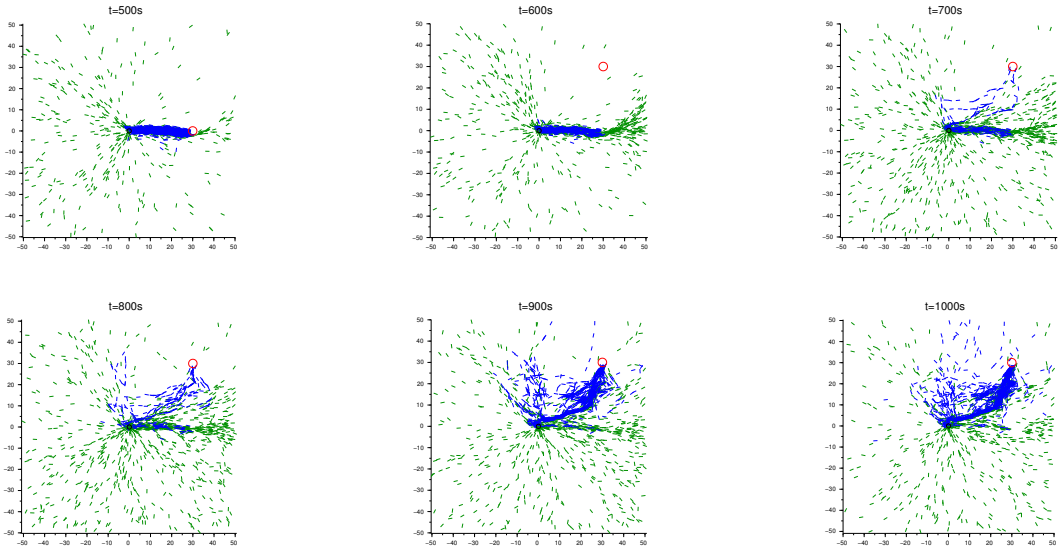

Figure 8: *One simulation of the model with a dynamical food source. The food source is a disc of radius* $2cm$ *centered first at* $(30, 0)$ *and then at* $(30, 30)$ *after 500s. Green sticks: "green" pheromones. Blue sticks: "blue" pheromones. Red circle: food source. Black circle: nest.*

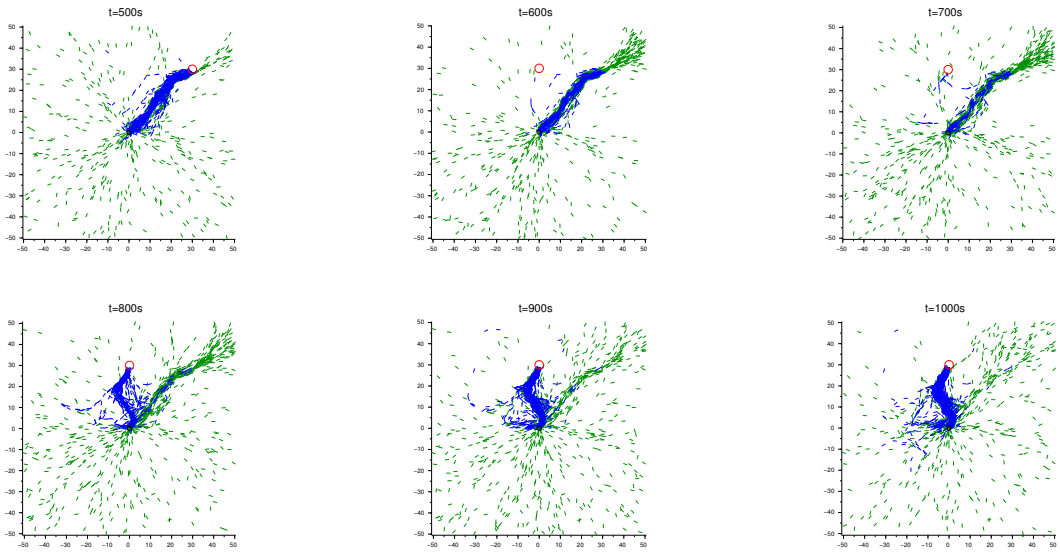

Figure 9: *One simulation of the model with a dynamical food source. The food source is a disc of radius* $2cm$ *centered first at* $(30, 30)$ *and then at* $(0, 30)$ *after 500s. Blue sticks: "blue" pheromones. Green sticks: "green" pheromones. Red circle: Food source. Black circle: nest.*

4 Discussion

Our model is rather simple but it has proven itself very effective to localize a food source and to bring it back to the nest in a quite optimal way. When no obstacle is involved, the colony tends to concentrate on a "highway" located on the straight line linking the food source to the nest. When two food locations are involved the colony tends to favor the closest one. Sometimes, the colony does not the closest food location (Figure 5, $a = 25$) but the probability to choose the "wrong" food location decays almost linearly as its distance increases (*cf* Figure 6). Hence, the colony makes "big mistakes" (choosing a food location far away when one is much closer) with a rather small probability. Even when the location of the food changes, the colony is able to find the new location quite rapidly. In this scenario, the pattern keeps a memory of the history of the experiment and the colony can follow non-straight paths (*cf* Figure 9). The colony is also able to find an optimal trail when an obstacle is involved. Let us now discuss the biological relevancy of our model.

Regarding the modeling of directed pheromones of Boissard, Degond and Motsch, a discussion about the biological relevancy was already conducted in [Boissard et al., 2013]. We summarize it here but an interested reader should read it (see [Boissard et al., 2013], Section 3.6) since it contains many arguments supporting the hypothesis of directed pheromones. A mechanism called "osmotropotaxis" described in [Calenbuhr and Deneubourg, 1992,Calenbuhr et al., 1992,Couzin and Franks, 2003] could explain how ants can sense the orientation of a pheromone drop. There are two possible hypothesis to explain the sensitivity of ants to the direction of a pheromones drop: either ants leave long continuous pheromone drops or they leave several small drops one after an other. In the case of continuous pheromones drop modeled in [Bossert and Wilson, 1963], the pheromone drop has an oval shape with higher chemical concentration in the middle. In this scenario, the

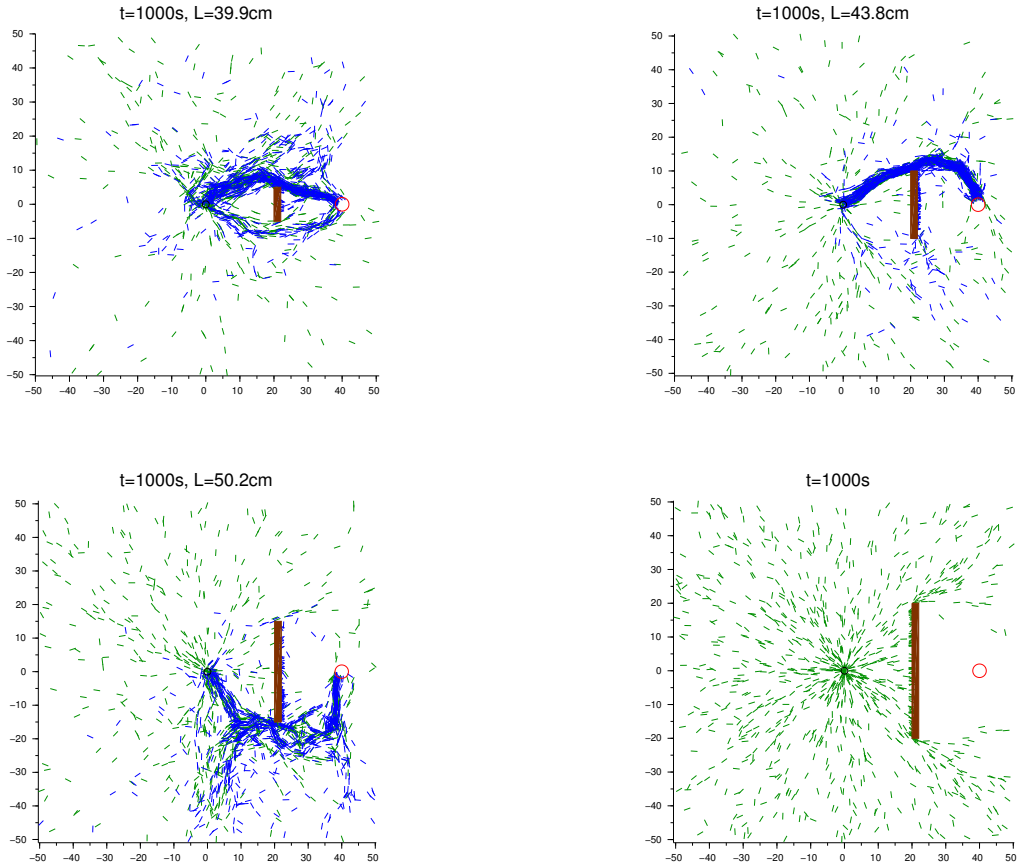

Figure 10: *Four simulations of the model with an obstacle. Top left simulation: obstacle*$=[20,22]\times[-5,5]$*, shortest path followed by one ant: 39.90cm, actual geodesic length between the food source and the nest:* $\approx$*38.30cm. Top right simulation: obstacle*$=[20,22]\times[-10,10]$*, shortest path followed by one ant:* $\approx$*43.80cm, actual geodesic length between the food source and the nest: 41.95cm. Bottom left simulation: obstacle*$=[20,22]\times[-15,15]$*, shortest path followed by one ant: 50.20cm, actual geodesic length between the food source and the nest:* $\approx$*47.43cm. Bottom right simulation: obstacle*$=[20,22]\times[-20,20]$*, no ant found the food source. Green sticks: "green" pheromones. Blue sticks: "blue" pheromones. Red circle: food source. Black circle: nest. Brown rectangle: obstacle.*

ants are able to sense the orientation of the crest line of higher concentration. In the case of discontinuous drops modeled by [Haefner and Crist, 1994], a diffusion process must be taken into account to homogenize the pheromone drop. A quantitative study of this homogenization process with realistic parameter value was conducted in the appendix of [Boissard et al., 2013].

A second issue regarding the pheromone modeling is our choice of polar interactions. More precisely, our modeled pheromones keep information of the orientation and the direction of the "parent" ant. Non-polar interactions seem more biologically accurate since no evidence of polar oriented pheromone exist to our knowledge. In [Vincent and Myerscough, 2004], the authors modeled these interactions as follows: when an ant walks with orientation θ and encounters a pheromone of orientation θ', the ant can either pick the orientation θ' or $\theta' \pm \pi$ but chooses the closest angle to its current orientation. This way, the trajectory of the ant does not make acute angles. We emphasize that such a choice might interfere in the process of selection of the shortest path since much information is lost compared to the polar interaction scenario.

Our choice of parameters was made to match the one from [Boissard et al., 2013] when a connection could be made. We refer to this reference and to [Bernadou and Fourcassié, 2008, Casellas et al., 2008, Beckers et al., 1992a] for a motivation of this choice of parameter values for *Lasius niger*.

Our model considers two types of pheromones. There is evidence showing that some ants, such as the Pharaoh's ant [Beekman et al., 2001, Fourcassié and Deneubourg, 1994, Jackson et al., 2007, Jackson and Châline, 2007, Jeanson et al., 2003, Sumpter and Beekman, 2003], can lay different type of chemicals using different glandes to produce them. Other ants species, such as the big headed ant *Pheidole megacephala* [Dussutour et al., 2009] vary the concentration of deposed pheromones to vary the pheromonal information. Other mathematical models also exist where two types of pheromones are used to differentiate trail that are exploring the field from the ones that are coming back to the nest [Rauch et al., 1995, Tao et al., 2004]. We emphasize that, since our model is adapted from the Boissard-Degond-Motsch model, our choice of parameter values is adapted to the black garden ant *Lasius niger*, even though this species can only lay one type of pheromone [Beckers et al., 1992b, Beckers et al., 1993, Dussutour et al., 2004, Nicolis and Deneubourg, 1999].

One assumption of our model, which is physically irrelevant, is the absence of collisions between ants. As was previously observed in experiments and models [Ryan, 2016, Dussutour et al., 2004, Couzin and Franks, 2003], this issue is crucial since a large number of ants can be at the same time on a narrow track. Reduction of traffic congestion is very important to optimize the food transport by ants. Physical interactions between ants can be modeled using a repulsive Lennard-Jones repulsive operator in the same spirit as Ryan's work [Ryan, 2016]. We could also consider communication between ants when a collision occurs. As was observed in many biological experiments (see [Gordon et al., 1993, Mailleux et al., 2010] among many others), antennas contacts between individuals is a key element to understand how complex tasks are achieved by ants societies. Taking these into account is likely to improve the capacity of the model to optimize food transport since exchange of informations is the key to the ants' complex social structures. On the other hand, taking physical interactions, like Ryan did, does not slow the foraging process as was observed in [Ryan, 2016] but we expect that it will raise the computational cost of the simulation since interactions between a large number of ants would have to be taken into account.

5 Conclusion

We have presented a model of foraging and pheromones deposing ants with two types of pheromones. The model has two strengths:

1. It is rather simple. Indeed, the local interactions between ants and pheromones is very simply described and the pheromones' lifetime process as well.

2. It allows the modeled colony to find the food source and to bring it back to the nest in a quite optimal way.

We then showed the outcome of simulations of the model in various situations, namely: simulations with one or two food locations, simulations with one food source which location that changes during the experiment and simulations with an obstacle between the food source and the nest. We showed that even in these situations, the ants were capable of finding a way to bring the food back to the nest, using an optimal path. The actual geodesic path is never followed by ants since, in those cases, it requires the ant to have a nearly ballistic trajectory.

Throughout our discussion of the model, we underlined that the model can be improved from the biological perspective by letting ants communicate with each other and by considering a model with physical interactions between ants.

There are other perspectives for future work. A possible sequence of this work is to derive the kinetic equations that describe the dynamics of the system at the mesoscale. Such a (formal) derivation was conducted in Boissard Degond and Motsch's article [Boissard et al., 2013] as well as a hydrodynamic limit of the equation. The purpose of such a derivation is to get a kinetic partial differential equation whose numerical resolution is faster than the simulation of our model. In a recent work [Amorim, 2015a], Amorim established a description of a chemotactic model of foraging ants at the macroscopic scale. He further analyzed the corresponding system of diffusive equations along with Alonso and Goudon in [Alonso et al., 2016]. Amorim's numerical resolution shows the emergence of a trail from the food source to the nest [Amorim, 2015b]. We emphasize that, in Amorim's description, the ants know the shortest way to get back to the nest. As a perspective for future work, we could do the same kind of analysis: we could derive (formally or rigorously) the kinetic Kolmogorov equation of our model and solve it numerically. This can be challenging since there will be 4 structure variables: the time variable, the two space variables and the orientation variable θ. From the reading of the present paper, we expect that this numerical simulation gives an algorithm that approaches the geodesic between the food source and the nest by spotting the high concentrations of pheromones.

In conclusion, the purpose of this work is to open perspectives in two different fields. From the biology perspective, we presented a model in which a colony of ants finds optimal paths to bring food back to the nest without assuming any pre-existing lattice, which seems more naturally accurate than the previous models. We hope that this work will get attention from the biology community and that it will help understanding the behavior of some insects. From the mathematics perspective, we hope to have set a first stone towards a kinetic partial differential equation method to find geodesics on a plane.

References

[Alonso et al., 2016] Alonso, R., Amorim, P., and Goudon, T. (2016). Analysis of a chemotaxis system modeling ant foraging. *Mathematical Models and Methods in Applied Sciences*, 26(09):1785–1824.

[Amorim, 2015a] Amorim, P. (2015a). A continuous model of ant foraging with pheromones and trail formation. *Pro. Series of the Brazilian Society of Applied and Computational Mathematics*, 3(1).

[Amorim, 2015b] Amorim, P. (2015b). Modeling ant foraging: A chemotaxis approach with pheromones and trail formation. *Journal of Theoretical Biology*, 385:160–173.

[Beckers et al., 1992a] Beckers, R., Deneubourg, J. L., and Goss, S. (1992a). Trail laying behaviour during food recruitment in the ant Lasius niger (L.). *Insectes Sociaux*, 39(1):59–72.

[Beckers et al., 1992b] Beckers, R., Deneubourg, J. L., and Goss, S. (1992b). Trails and U-turns in the selection of a path by the ant Lasius niger. *Journal of Theoretical Biology*, 159(4):397–415.

[Beckers et al., 1993] Beckers, R., Deneubourg, J. L., and Goss, S. (1993). Modulation of trail laying in the ant Lasius niger (Hymenoptera: Formicidae) and its role in the collective selection of a food source. *Journal of Insect Behavior*, 6(6):751–759.

[Beckers et al., 1990] Beckers, R., Deneubourg, J. L., Goss, S., and Pasteels, J. M. (1990). Collective decision making through food recruitment. *Insectes Sociaux*, 37(3):258–267.

[Beekman et al., 2001] Beekman, M., Sumpter, D. J. T., and Ratnieks, F. L. W. (2001). Phase transition between disordered and ordered foraging in Pharaoh's ants. *Proceedings of the National Academy of Sciences*, 98(17):9703–9706.

[Bernadou and Fourcassié, 2008] Bernadou, A. and Fourcassié, V. (2008). Does substrate coarseness matter for foraging ants? An experiment with Lasius niger (Hymenoptera; Formicidae). *Journal of Insect Physiology*, 54(3):534–542.

[Boissard et al., 2013] Boissard, E., Degond, P., and Motsch, S. (2013). Trail formation based on directed pheromone deposition. *Journal of Mathematical Biology*, 66(6):1267–1301.

[Bonabeau et al., 1999] Bonabeau, E., Dorigo, M., and Theraulaz, G. (1999). *Swarm intelligence: from natural to artificial isystems*. Oxford University Press, New York.

[Bossert and Wilson, 1963] Bossert, W. H. and Wilson, E. O. (1963). The analysis of olfactory communication among animals. *Journal of Theoretical Biology*, 5(3):443–469.

[Brady, 2003] Brady, S. G. (2003). Evolution of the army ant syndrome: The origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. *Proceedings of the National Academy of Sciences*, 100(11):6575–6579.

[Calenbuhr et al., 1992] Calenbuhr, V., Chrétien, L., Deneubourg, J. L., and Detrain, C. (1992). A model for osmotropotactic orientation (II). *Journal of Theoretical Biology*, 158(3):395–407.

[Calenbuhr and Deneubourg, 1992] Calenbuhr, V. and Deneubourg, J. L. (1992). A model for osmotropotactic orientation (I). *Journal of Theoretical Biology*, 158(3):359–393.

[Cammaerts and Cammaerts, 1980] Cammaerts, M. C. and Cammaerts, R. (1980). Food recruitment strategies of the ants Myrmica sabuleti and Myrmica ruginodis. *Behavioural Processes*, 5(3):251–270.

[Casellas et al., 2008] Casellas, E., Gautrais, J., Fournier, R., Blanco, S., Combe, M., Fourcassié, V., Theraulaz, G., and Jost, C. (2008). From individual to collective displacements in heterogeneous environments. *Journal of Theoretical Biology*, 250(3):424–434.

[Couzin and Franks, 2003] Couzin, I. D. and Franks, N. R. (2003). Self-organized lane formation and optimized traffic flow in army ants. *Proceedings of the Royal Society B: Biological Sciences*, 270(1511):139–146.

[Deneubourg et al., 1990] Deneubourg, J.-L., Aron, S., Goss, S., and Pasteels, J. M. (1990). The self-organizing exploratory pattern of the argentine ant. *Journal of Insect Behavior*, 3(2):159–168.

[Detrain et al., 2001] Detrain, C., Natan, C., and Deneubourg, J.-L. (2001). The influence of the physical environment on the self-organised foraging patterns of ants. *Naturwissenschaften*, 88(4):171–174.

[Dorigo and Gambardella, 1997] Dorigo, M. and Gambardella, L. M. (1997). Ant colony system: a cooperative learning approach to the traveling salesman problem. *IEEE Transactions on Evolutionary Computation*, 1(1):53–66.

[Dorigo et al., 1996] Dorigo, M., Maniezzo, V., and Colorni, A. (1996). Ant system: optimization by a colony of cooperating agents. *IEEE Transactions on Systems, Man, and Cybernetics, Part B (Cybernetics)*, 26(1):29–41.

[Dussutour et al., 2004] Dussutour, A., Fourcassié, V., Helbing, D., and Deneubourg, J.-L. (2004). Optimal traffic organization in ants under crowded conditions. *Nature*, 428(6978):70–73.

[Dussutour et al., 2009] Dussutour, A., Nicolis, S. C., Shephard, G., Beekman, M., and Sumpter, D. J. T. (2009). The role of multiple pheromones in food recruitment by ants. *The Journal of Experimental Biology*, 212(Pt 15):2337–2348.

[Edelstein-Keshet, 1994] Edelstein-Keshet, L. (1994). Simple models for trail-following behaviour; Trunk trails versus individual foragers. *Journal of Mathematical Biology*, 32(4):303–328.

[Edelstein-Keshet et al., 1995] Edelstein-Keshet, L., Watmough, J., and Ermentrout, G. B. (1995). Trail following in ants: individual properties determine population behaviour. *Behavioral Ecology and Sociobiology*, 36(2):119–133.

[Ermentrout and Edelstein-Keshet, 1993] Ermentrout, G. and Edelstein-Keshet, L. (1993). Cellular Automata Approaches to Biological Modeling. *Journal of Theoretical Biology*, 160(1):97–133.

[Fourcassié and Deneubourg, 1994] Fourcassié, V. and Deneubourg, J. L. (1994). The dynamics of collective exploration and trail-formation in Monomorium pharaonis: experiments and model. *Physiological Entomology*, 19(4):291–300.

[Franks et al., 1991] Franks, N. R., Gomez, N., Goss, S., and Deneubourg, J. L. (1991). The blind leading the blind in army ant raid patterns: Testing a model of self-organization (Hymenoptera: Formicidae). *Journal of Insect Behavior*, 4(5):583–607.

[Garnier et al., 2009] Garnier, S., Guérécheau, A., Combe, M., Fourcassié, V., and Theraulaz, G. (2009). Path selection and foraging efficiency in Argentine ant transport networks. *Behavioral Ecology and Sociobiology*, 63(8):1167–1179.

[Gordon et al., 1993] Gordon, D. M., Paul, R. E., and Thorpe, K. (1993). What is the function of encounter patterns in ant colonies? *Animal Behaviour*, 45(6):1083–1100.

[Goss et al., 1989] Goss, S., Aron, S., Deneubourg, J. L., and Pasteels, J. M. (1989). Self-organized shortcuts in the Argentine ant. *Naturwissenschaften*, 76(12):579–581.

[Haefner and Crist, 1994] Haefner, J. W. and Crist, T. O. (1994). Spatial Model of Movement and Foraging in Harvester Ants (Pogonomyrmex) (I): The Roles of Memory and Communication. *Journal of Theoretical Biology*, 166(3):299–313.

[Hangartner, 1969] Hangartner, W. (1969). Trail laying in the subterranean ant, Acanthomyops interjectus. *Journal of Insect Physiology*, 15(1):1–4.

[Jackson and Châline, 2007] Jackson, D. E. and Châline, N. (2007). Modulation of pheromone trail strength with food quality in Pharaoh's ant, Monomorium pharaonis. *Animal Behaviour*, 74(3):463–470.

[Jackson et al., 2007] Jackson, D. E., Martin, S. J., Ratnieks, F. L. W., and Holcombe, M. (2007). Spatial and temporal variation in pheromone composition of ant foraging trails. *Behavioral Ecology*, 18(2):444–450.

[Jayadeva et al., 2013] Jayadeva, Shah, S., Bhaya, A., Kothari, R., and Chandra, S. (2013). Ants find the shortest path: a mathematical proof. *Swarm Intelligence*, 7(1):43–62.

[Jeanson et al., 2004] Jeanson, R., Deneubourg, J.-L., Grimal, A., and Theraulaz, G. (2004). Modulation of individual behavior and collective decision-making during aggregation site selection by the ant Messor barbarus. *Behavioral Ecology and Sociobiology*, 55(4):388–394.

[Jeanson et al., 2003] Jeanson, R., Ratnieks, F. L. W., and Deneubourg, J.-L. (2003). Pheromone trail decay rates on different substrates in the Pharaoh's ant, Monomorium pharaonis. *Physiological Entomology*, 28(3):192–198.

[John et al., 2004] John, A., Schadschneider, A., Chowdhury, D., and Nishinari, K. (2004). Collective effects in traffic on bi-directional ant trails. *Journal of Theoretical Biology*, 231(2):279–285.

[Khuong et al., 2016] Khuong, A., Gautrais, J., Perna, A., Sbaï, C., Combe, M., Kuntz, P., Jost, C., and Theraulaz, G. (2016). Stigmergic construction and topochemical information shape ant nest architecture. *Proceedings of the National Academy of Sciences*, 113(5):1303–1308.

[Mailleux et al., 2010] Mailleux, A.-C., Buffin, A., Detrain, C., and Deneubourg, J.-L. (2010). Recruiter or recruit: who boosts the recruitment in starved nests in mass foraging ants? *Animal Behaviour*, 79(1):31–35.

[Nicolis and Deneubourg, 1999] Nicolis, S. and Deneubourg, J. (1999). Emerging Patterns and Food Recruitment in Ants: an Analytical Study. *Journal of Theoretical Biology*, 198(4):575–592.

[Nishinari et al., 2006] Nishinari, K., Sugawara, K., Kazama, T., Schadschneider, A., and Chowdhury, D. (2006). Modelling of self-driven particles: Foraging ants and pedestrians. *Physica A: Statistical Mechanics and its Applications*, 372(1):132–141.

[Peters et al., 2006] Peters, K., Johansson, A., Dussutour, A., and Helbing, D. (2006). Analytical and numerical investigation of ant behavior under crowded conditions. *Advances in Complex Systems*, 09(04):337–352.

[Rauch et al., 1995] Rauch, E. M., Millonas, M. M., and Chialvo, D. R. (1995). Pattern formation and functionality in swarm models. *Physics Letters A*, 207(3-4):185–193.

[Robinson et al., 2008] Robinson, E. J. H., Ratnieks, F. L. W., and Holcombe, M. (2008). An agent-based model to investigate the roles of attractive and repellent pheromones in ant decision making during foraging. *Journal of Theoretical Biology*, 255(2):250–258.

[Ryan, 2016] Ryan, S. D. (2016). A model for collective dynamics in ant raids. *Journal of Mathematical Biology*, 72(6):1579–1606.

[Schweitzer et al., 1997] Schweitzer, F., Lao, K., and Family, F. (1997). Active random walkers simulate trunk trail formation by ants. *Biosystems*, 41(3):153–166.

[Stützle and Hoos, 1999] Stützle, T. and Hoos, H. (1999). The Max-Min ANT System and Local Search for Combinatorial Optimization Problems. In *Meta-Heuristics*, pages 313–329. Springer, Boston, MA.

[Sumpter and Beekman, 2003] Sumpter, D. J. T. and Beekman, M. (2003). From nonlinearity to optimality: pheromone trail foraging by ants. *Animal Behaviour*, 66(2):273–280.

[Tao et al., 2004] Tao, T., Nakagawa, H., Yamasaki, M., and Nishimori, H. (2004). Flexible Foraging of Ants under Unsteadily Varying Environment. *Journal of the Physical Society of Japan*, 73(8):2333–2341.

[Vela-Pérez et al., 2013] Vela-Pérez, M., Fontelos, M., and Velzquez, J. (2013). Ant foraging and geodesic paths in labyrinths: Analytical and computational results. *Journal of Theoretical Biology*, 320:100–112.

[Vincent and Myerscough, 2004] Vincent, A. D. and Myerscough, M. R. (2004). The effect of a non-uniform turning kernel on ant trail morphology. *Journal of Mathematical Biology*, 49(4):391–432.

[Vittori et al., 2006] Vittori, K., Talbot, G., Gautrais, J., Fourcassié, V., Araújo, A. F., and Theraulaz, G. (2006). Path efficiency of ant foraging trails in an artificial network. *Journal of Theoretical Biology*, 239(4):507–515.

[Watmough and Edelstein-Keshet, 1995a] Watmough, J. and Edelstein-Keshet, L. (1995a). Modelling the Formation of Trail Networks by Foraging Ants. *Journal of Theoretical Biology*, 176(3):357–371.

[Watmough and Edelstein-Keshet, 1995b] Watmough, J. and Edelstein-Keshet, L. (1995b). A one-dimensional model of trail propagation by army ants. *Journal of Mathematical Biology*, 33(5):459–476.

[Whitehouse and Jaffe, 1996] Whitehouse, M. E. A. and Jaffe, K. (1996). Ant wars: combat strategies, territory and nest defence in the leaf-cutting antAtta laevigata. *Animal Behaviour*, 51(6):1207–1217.

[Wilson, 1962] Wilson, E. O. (1962). Chemical communication among workers of the fire ant Solenopsis saevissima (Fr. Smith) 1. The Organization of Mass-Foraging. *Animal Behaviour*, 10(1):134–147.

[Witte and Maschwitz, 2002] Witte, V. and Maschwitz, U. (2002). Coordination of Raiding and Emigration in the Ponerine Army Ant Leptogenys distinguenda (Hymenoptera: Formicidae: Ponerinae): A Signal Analysis. *Journal of Insect Behavior*, 15(2):195–217.

[Wyatt, 2003] Wyatt, T. D. (2003). *Pheromones and animal behaviour: communication by smell and taste*. Cambridge University Press, Cambridge, UK ; New York.