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

Nils Caillerie *

February 13, 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 oriented 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 various simulations of our model and we investigate the ability of the colony to select the shortest path from the nest to the food source. We introduce a system of kinetic equations that can describe the dynamics of this model at the mesoscopic scale and leave its rigorous derivation for future work. Finally, we discuss the biological relevancy of our assumptions by comparing the behavior of our individually-based model with the one of various species of ants as described in the biology literature and we give ideas to improve the model from the optimization perspective.

Key-words: velocity-jump process, foraging ants, geodesic, Self-propelled particles, pheromone deposition, pattern formation, alignment interactions.

AMS Class. No: 92D50, 35Q80, 35L60, 82C70

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 stocking and sometimes harvesting. Very simple interactions between individuals with low cognitive capacities can achieve very complex tasks, such as building a nest for the colony [43], developing war strategies to protect the nest [61], following routes and regulate the traffic to reduce congestion [18, 25] or find food and bring it back to the nest using a very optimal route in the process [32, 34]. It 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 [34]. In this paper, we are interested in the issue of food localization and optimization of the transport by a colony of ants.

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The formation of trails in ant colonies has been understood a while ago. There is already a wide biological literature on the subject [4, 18, 21, 26, 27, 59, 60]. The general observation is that the formation of trails is a result of simple local interactions, such as brief antennae contacts [33, 44] or distant communication, *via* deposition of chemical markers called pheromones. We will only focus on this last strategy in this paper.

The principle of pheromone communication is simple. One ant leaves a pheromone signal using the sting on its abdomen [4, 36, 37, 40, 62, 63]. The ant then keeps walking but the pheromone remains where the ant left it. When a new ant arrives on site, it obtains the information that an ant was formerly here, but biologists argue that the pheromone drop carries much more information. The ant can indeed gain qualitative information about the concentration of pheromones and the orientation of the ants which laid the pheromone through a mechanism called osmotropotaxis [14, 15, 18] or about the chemical composition of the pheromone [64]. For example *Myrmica sabuleti* specimens can leave different pheromones depending on the food they found [16], the Pharaoh's ant *Monomorium pharaonis* is also able to deposit attractive or repellent pheromones [49]. The ant which originally laid the 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 [8, 30, 37, 38, 41, 54] or for the big headed ant *Pheidole megacephala* [24]. Other species such as the Argentine ant *Iridomyrmex humilis* [20, 32, 58], the black garden ant *Lasius niger* [5, 6, 25, 45] and the Army ant *Eciton burchelli* [13, 18, 31], on the other hand, are known to lay only one type of pheromone. These signals carry simple informations (location and orientation of the ant, chemical concentration, chemical type...) but through multiplication of large numbers of such signals, the colony as a whole is able to deal with more complex informations and, in particular, to form patterns such as trails.

One remarkable observation about those pheromone trails in colonies of foraging ants 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 two possible routes to a food source, an ant colony will most of the times choose the shortest one [11, 32, 34, 54]. 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. In fact, the phenomenon that causes this is rather simple to understand. The shortest paths allow ants to bring the food faster so an ant that goes the path back and forth will make more travels per unit of time and will therefore leave more pheromones on this path than ants on the longer paths. Theoretically, the colony will finally prefer the shortest path since it is marked by more pheromones than the other.

This principle has been understood a while ago and has engendered a complete field of probability theory called "reinforced random walks". The idea is to find geodesic on graphs using random walkers (whose behavior is inspired by ants) on the nodes, that use the vertexes (with lengths) to go from one node to the other. When going on a node or a vertex (depending on models) the random walkers (robot ants so to speak) leave a signal (pheromone) giving more weight to this particular node or vertex. So-called "ants algorithms" have proven themselves very efficient to solve optimization problems such as the well-known "salesman problem" [22, 23, 53] among many others. Moreover, rigorous proofs exist to mathematically establish their efficiency [39]. Ants algorithms also prove themselves capable of finding geodesic paths in mazes [56].

More biologically relevant mathematical models have been introduced to understand the dynamics of trail following. One-dimensional models consider a pre-existing trail and focus on the way

ants sense the trail [14, 15, 18] or the way they regulate traffic [42, 46]. Other models focus on the decision process which leads ants to follow one trail or the other but in these models, the system does not produce the pheromone trails itself either [7, 20, 26, 29, 34, 47, 60].

Most two-dimensional existing models consider a walk on a fixed lattice [7, 20, 27, 28, 48, 52, 55]. 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 indicates what direction ants are supposed to go to. In [48] and [55], 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 [10]. In this model, ants are able to explore a whole two-dimensional space without bias. Ants leave one type of pheromones behind them that tell other ants that they were here and what direction they were going to when they deposited 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 this 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 or foraging ants.

More recently, Ryan [50] 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. Once an ant found the food source, it would go directly to the nest using the shortest path, leaving pheromones behind itself to recruit other ants on the trail. The model also takes collective strategies to self-regulate the traffic flow on the path in consideration. 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 [1–3].

Let us summarize: to our knowledge, all models of geodesic path formation are either on a graph [56] or assume a pre-existing lattice [48, 55]. True unbiased two-dimensional models only consider one type of pheromone. In particular, they either don't consider any food source [10] or consider that the geodesic path is already known by the system [1–3, 50]. In this paper, we will take ideas from those works to build a two-dimensional model of short paths formation with two pheromones between a food source and a nest.

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. Contrary to 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 the ants with food how to go back to the nest and the ants with food will leave pheromones that indicate where the food is. As in [10], 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 facing 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).

Similarly to [10], we will formally derive a kinetic description of the model at the meso-scale. Kinetic equations are often used in biology to describe the dynamics of self-propelled individuals, like bird flocking in the Cucker-Smale [19] model or to study how *chemotaxis* allow bacteria (such as *Escherichia coli*) to find locations of high nutrient concentration [51], among many other examples.

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 parameters. 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 that changes location and finally, with an obstacle between the food and the nest. In Section 4, we formally derive a kinetic description of the model. In Section 5, we discuss our model and results and give ideas to improve the model from a biological perspective and from the optimization perspective. Finally, we draw a conclusion and give perspectives for future work.

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2 The model

We consider a stochastic model of interacting random walkers on a 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 [10]. Namely, the way ants move and choose their directions are the same. Contrary to [10] though, we consider a food source, two types of pheromones and two types of ants: the ones that are looking for food and the ones which have found food and are trying to bring it back to the nest. Moreover, we do not consider that pheromones keep the direction of their "parent" ants as a unit vector, but rather as an angle in $[0, 2\pi)$. 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 2-dimensional space. Every ant is either a "foraging" ant or an ant "with food" but this status can change in time. We denote by $N_f(t)$ and by $N_w(t)$ the number of foraging ants and food with ants 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 deposit two types of pheromones: foraging ants are able to deposit pheromone that are pointing to the nest while ants with food are able to deposit pheromone

pointing to the food source. Let us recall that the ants never know where the nest and the food source are. Hence, the pheromones do not point directly to the nest or the food source but rather tell in which direction the ant was going when it left the pheromone. We denote by $P_g(t)$ the number of pheromones left by foraging ants and by $P_b(t)$ the number of pheromones left by ants with food. Each pheromone k left by a foraging ant is described by its position z_k and by its direction $\alpha_k \in [0, 2\pi)$. For the sake of simplicity, we will call those pheromones the "green pheromones". Each pheromone m left by an ant with food is described by its position ζ_m and by its direction $\beta_m \in [0, 2\pi)$. Once again, out of simplicity, we call those the "blue pheromones".

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 a pheromone. 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 in the plane. Every ant follows a so-called "Run & Tumble" motion. 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 and ants with food is given by

$$\dot{x}_i(t) = c \cdot \begin{pmatrix} \cos \theta_i(t) \\ \sin \theta_i(t) \end{pmatrix}, \quad (2.1)$$

$$\dot{y}_j(t) = c \cdot \begin{pmatrix} \cos \omega_j(t) \\ \sin \omega_j(t) \end{pmatrix}. \quad (2.2)$$

The "Tumble" is an instantaneous phase of velocity redistribution process which is different depending on the status of the ant and on the pheromone concentration. 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 sensible 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 pheromone concentration.

Random velocity jumps: If there's 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

$$\theta'_i(t) \equiv \theta_i(t) + \varepsilon_i(t) \pmod{2\pi}, \quad (2.3)$$

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

$$\theta'_i(t) = \beta_{M_i}, \quad (2.4)$$

where M_i is a 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 .

When the ant makes a trail recruitment jump, it chooses a random exponentially distributed time with parameter $\lambda_b \cdot |\{m \in \mathbb{N}, \|x_i(t) - \zeta_m\| \leq R\}|$ and will wait that long before making a new velocity jump. This means that the higher the number of pheromones within the detection zone is, the shorter the time until the next tumble will be.

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 opposite direction

$$z_k = x_i(t), \quad \alpha_k \equiv \pi + \theta_i(t) \pmod{2\pi}. \quad (2.5)$$

Finding the food source: When the foraging ant find the food source, *i.e.* $x_i(t) \in \Omega$, a tumble instantaneously occurs: the ant makes U-turn and becomes an ant with food, which means that its new velocity $\omega'_j(t)$ is given by

$$\omega'_j(t) \equiv \pi + \theta_i(t) \pmod{2\pi}, \quad (2.6)$$

where $\theta_i(t)$ is its current direction.

2.2 Ants with food

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

Random velocity jumps: If there's 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

$$\omega'_j(t) \equiv \omega_j(t) + \varepsilon_j(t) \pmod{2\pi}, \quad (2.7)$$

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 align its direction with the chosen pheromone such that its new direction ω'_j is

$$\omega'_j(t) = \alpha_{K_j}, \quad (2.8)$$

where K_j is a uniformly distributed in $\{k \in \mathbb{N}, \|y_j(t) - z_k\| \leq R\}$, where $\|\cdot\|$ is the standard Euclidean norm on \mathbb{R}^2 .

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 the tumbles occur all the more often when there are many 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 opposite direction

$$\zeta_m = y_j(t), \quad \beta_j \equiv \pi + \alpha_j(t) \pmod{2\pi}. \quad (2.9)$$

Finding the nest: When the 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 ion $[0, 2\pi)$ and becomes a foraging ant. Its new direction $\theta'_i(t)$ is therefore distributed as

$$\theta'_i(t) \sim \text{Unif}([0, 2\pi)). \quad (2.10)$$

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

2.3 Dealing with an obstacle

In certain simulations, we will also 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 "run around" phase:

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

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

this means that an ant will systematically go left or right when facing an obstacle. It will choose left or right according to its current orientation. It then gets back to a normal running phase when the obstacle is away.

We emphasize that tumbling can still occur during this phase but that the direction of the ant will only matter when the obstacle is away. Then, the direction of the ant (and not only the sign of its cosine or sine) is used to determine the new position of the ant according to (2.1) or (2.2).

2.4 Simulations

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

Discrete time Model We keep the spatial continuity of our model but we make the time structure discrete. We use time steps of size $\Delta t > 0$ to do so 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 .

"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 a 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 $[0, 2\pi)$ and next tumble occurring in a random exponentially distributed time with parameter λ_f .

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 depositing 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. When specified in the table, this parameter value is chosen in all simulations shown in Section 3. When unspecified, the parameter depends on the simulation.

We emphasize that, when such correspondence can be made, we systematically choose the same parameter values as in [10]. We discuss the biological relevancy of such choices in Section 5.

The Table 1 shows the chosen values for the model parameters and the Table 2 shows the chosen values for the simulations parameters.

3 Results

3.1 Typical dynamics of the system

We show in Figure 1 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 diamonds represent foraging ants and red diamonds represent ants with food. The nest is represented by a black circle and the food source by a red circle. After 30 seconds, there are foraging 31 ants in the environment, which are all making random velocity jumps and depositing green pheromones. No ant found food yet. After 56.20 seconds, one ant found food and became a ant with food. The ant then proceeded to come back to the nest following the pheromone that it (most probably) left. When it didn't find any pheromones ahead, it started to make random velocity

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 ants random velocity jumps	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 pheromone deposition rate	$0.2s^{-1}$
ν_b	Blue pheromone deposition rate	$0.6s^{-1}$
T_p	Pheromone 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	

Table 2: Simulation 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

jump again, and made a detour but the green pheromones in the square $[-10, 0] \times [0, 10]$ put it back on track. 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 $37/c=18.5$ s. After 100 seconds, there are now two ants with food, taking a different (presumably shorter) path to get back to the nest. After 200 seconds, there are now 24 ants with food and the overall pattern is that ant with food follow paths that are close to the geodesic.

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 $c=2$ cm/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 set of the form

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

and the length of this path is defined as

$$L := \frac{T_1 - T_0}{c}. \quad (3.14)$$

We show in Figure 2 and 3 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 gathering of many pheromone next to the geodesic. The shortest path followed by ant has length 38 centimeters, which is close to the 37 centimeters of the geodesic. We represent in the bottom-right corner of Figure 3 the evolution of the path length. The upper-left corner of Figure 3 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 all new ants are directed according to this law). 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 , as expected. 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 which 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 clue pheromones are oriented in the right direction.

3.3 Disconnected food source

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

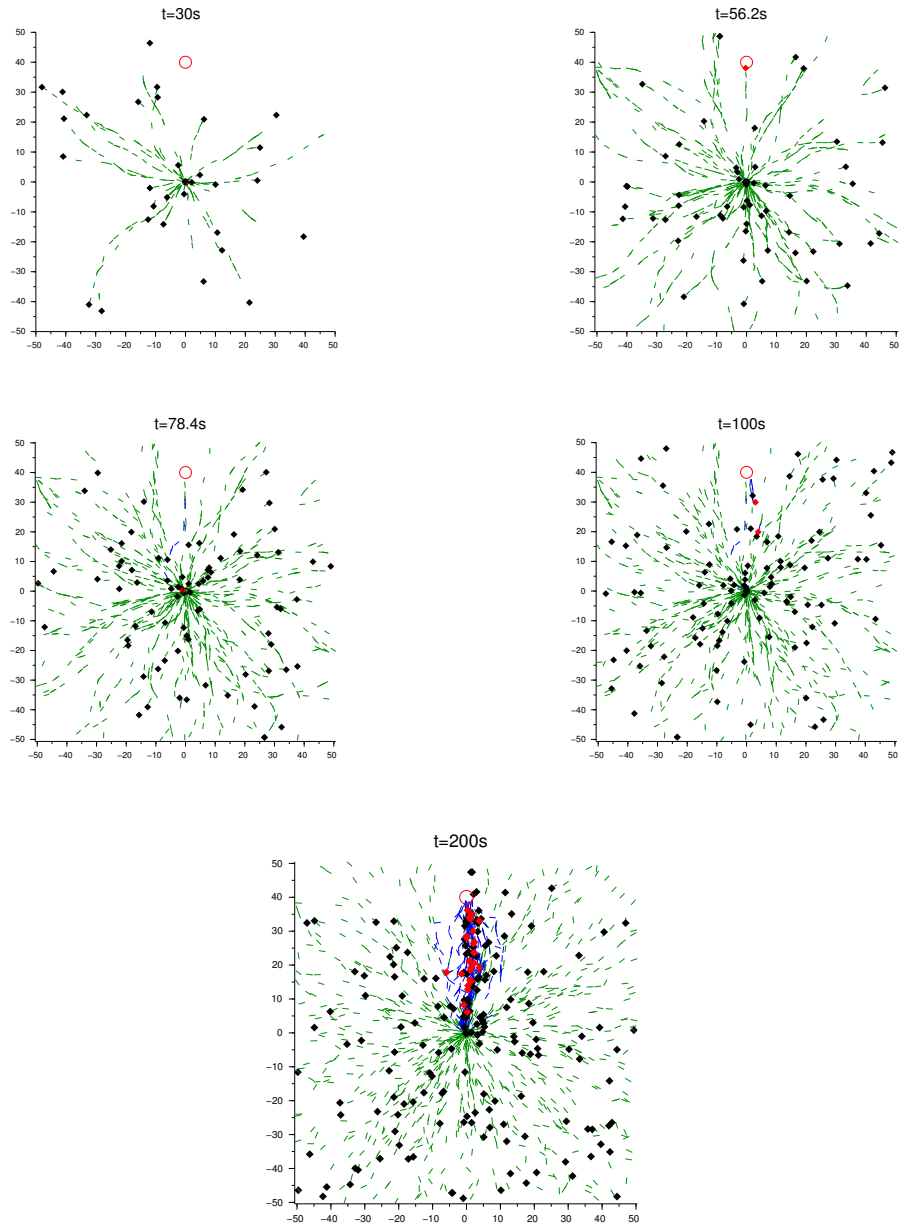


Figure 1: One simulation of the model where the food source is a disc of radius 2cm centered at $(0, 40)$. Top left: Outcome of the simulation after 30s. Top right: Outcome of the simulation after 56.20s (when the first ant finds the food source). Middle-left: Outcome of the simulation after 78.4s (when the first ant with food found its way back to the nest). Middle-right: Outcome of the simulation after 100s. Bottom: Outcome of the simulation after 200s. Black circle: Nest. Red circle: Food source. Black diamonds: foraging ants. Red diamonds: ants with food. Green sticks: "green pheromones" left by foraging ants. Blue sticks: "blue pheromones" left by ants with food.

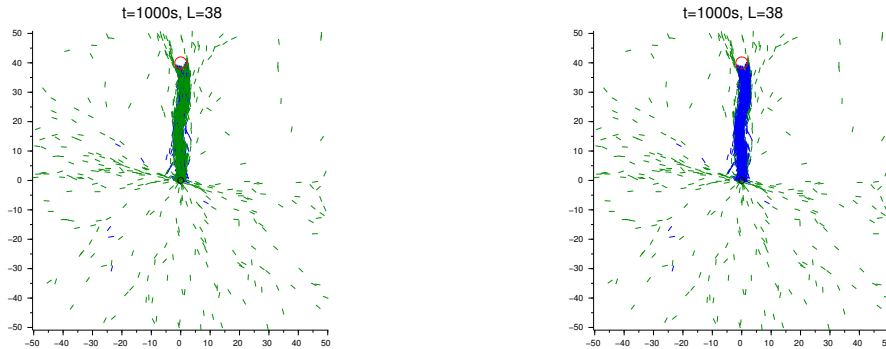


Figure 2: Simulation of the model with $T_f = 1000s$. Ω is a disc of radius 2cm centered at $(0, 40)$. The left figure shows the "green pheromones" in priority and the right figure shows the "blue pheromones" in priority. Black circle: nest. Red circle: food source.

radius and we take different values for $a > 1$. 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 4, when $a = 5, 10, 15, 20, 35, 40, 50$ 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 5, the probability that the North-West food location is chosen as a function of a . For this, we develop the following statistical estimation. We fix $T_f = 100$ seconds and for different values of a , we simulate the random process 100times. We then count the number of blue pheromones the oriented in the North-East and in the North-West direction:

$$P_b^{NE}(100) := \left| \{ \beta_m \mid 1 \leq m \leq P_b(100) \} \cap \left[0, \frac{\pi}{2} \right) \right| \quad (3.15)$$

$$P_b^{NW}(100) := \left| \{ \beta_m \mid 1 \leq m \leq P_b(100) \} \cap \left[\frac{\pi}{2}, \pi \right) \right| \quad (3.16)$$

and estimate that the colony chose the food in the North-West quadrant over the North-East one if $P_b^{NW}(100) > P_b^{NE}(100)$. We estimate the probability that the colony privileges the North-West quadrant food by counting how many times the situation occurred among the 100 simulations. The results are shown in Figure 5. The simulations show that when a increases, the probability that the colony will choose the food located next to $(-a, a)$ decreases.

3.4 Dynamical food source

In these simulations, the food source is dynamical and has 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 6), one where the two locations and the nest form

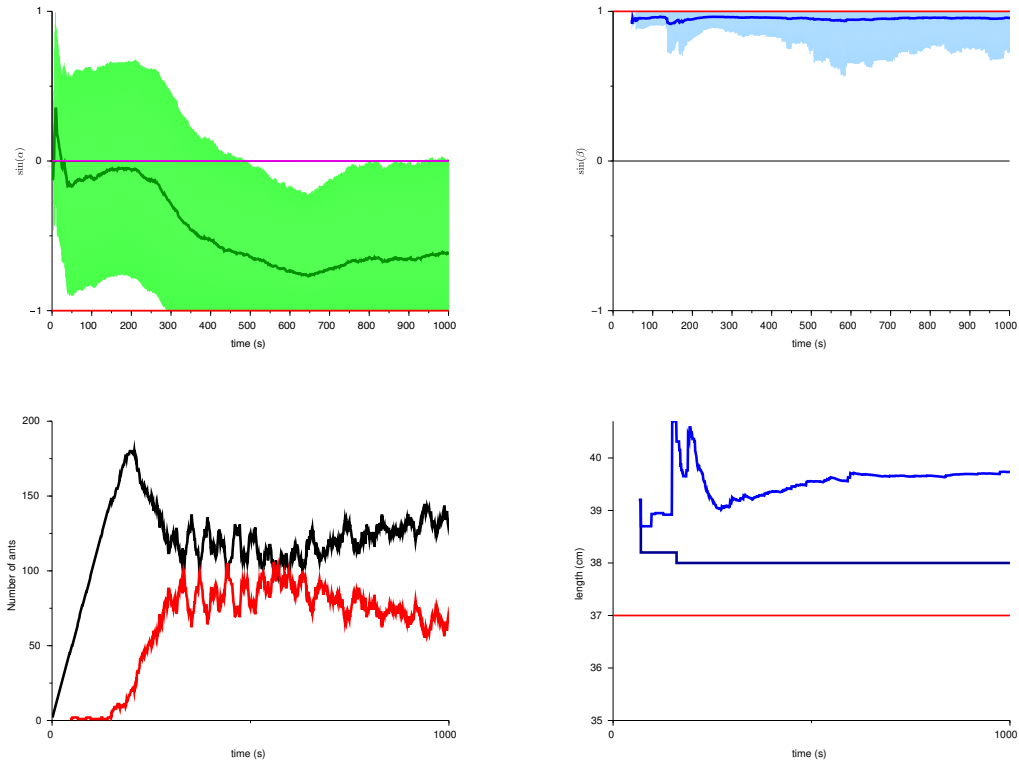


Figure 3: Top-left: dark green line: mean orientation of the green pheromones, green zone: standard deviation around the mean-value, red line: orientation of the geodesic going from the food source to the nest, magenta line: Mean value of the uniform distribution on $[0, 2\pi)$. Top-right: dark blue 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.

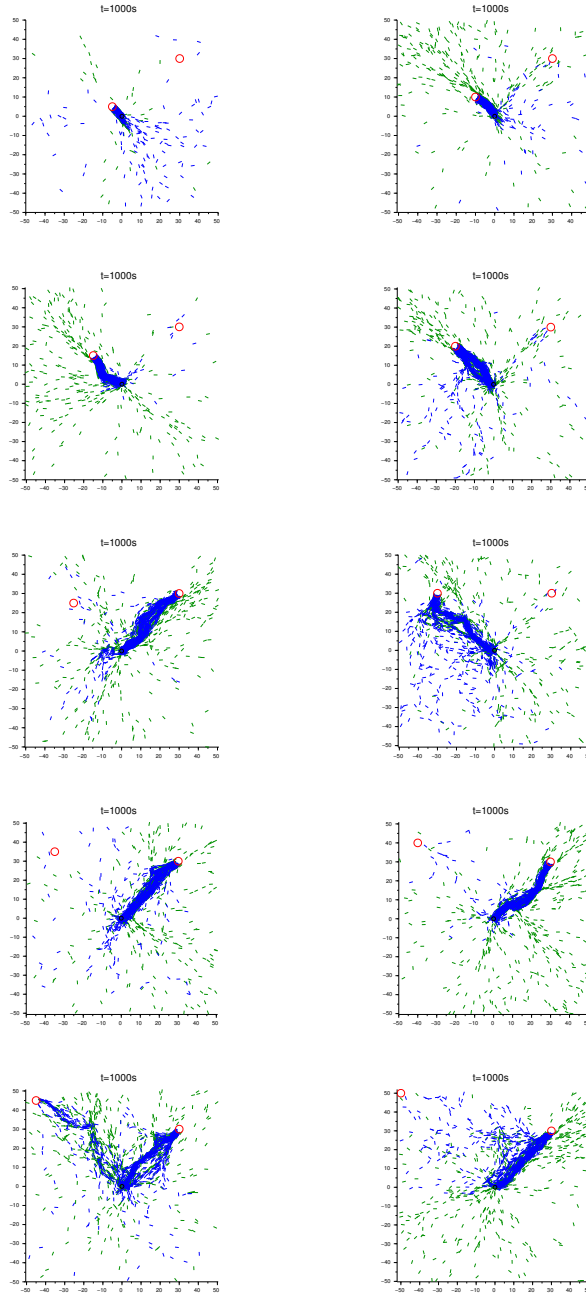


Figure 4: Ten simulations of the model with disconnected food source. The food source is simultaneously located at the reunion of the disc of radius 2 centered at $(30, 30)$ and the disc with same radius centered at $(-k, k)$ for $k = 5, 10, 15, 20, 25, 30, 35, 40, 45, 50$. In all shown simulations but $k = 25$ and $k = 45$, the colony clearly favored the shortest path to the food source. For $k = 25$, the colony chose the wrong path and for $k = 45$, the colony does not discriminate between the two locations, with a preference for the closest one though. Green sticks: "green" pheromones. Blue sticks: "blue" pheromones. Red circle: food source. Black circle: nest.

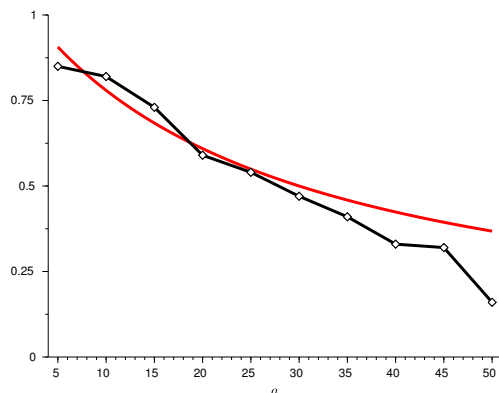


Figure 5: White diamonds: probability to choose the food location located at $(-a, a)$ over the one located at $(25, 25)$ as a function of a . Red line: $a \mapsto \frac{L_a}{L_{25} + L_a}$, where L_{25} is the length of the geodesic between the nest and the food located at $(25, 25)$ and L_a if the food located at $(-a, a)$.

a right-angle (Figure 7) and finally, one where the two locations and the nest form an acute angle (Figure 8). 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 shortest path from the second food source to the nest, even though the first food source first misled them.

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 9 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 at the right angles at the obstacle.

4 Kinetic description of the model

In this section, we propose a mesoscopic description of the ant and pheromone dynamics. Since the kinetic description of the model with one pheromone and no food source has already been done in [10], we will be brief and refer to this paper for further explanations.

Variables Since there are two types of ants and two types of pheromones, we will consider four state variables: F , W (respectively the density of foraging ants and ants with food), G and B (respectively the density of green and blue pheromones). Each of these are functions of the structure

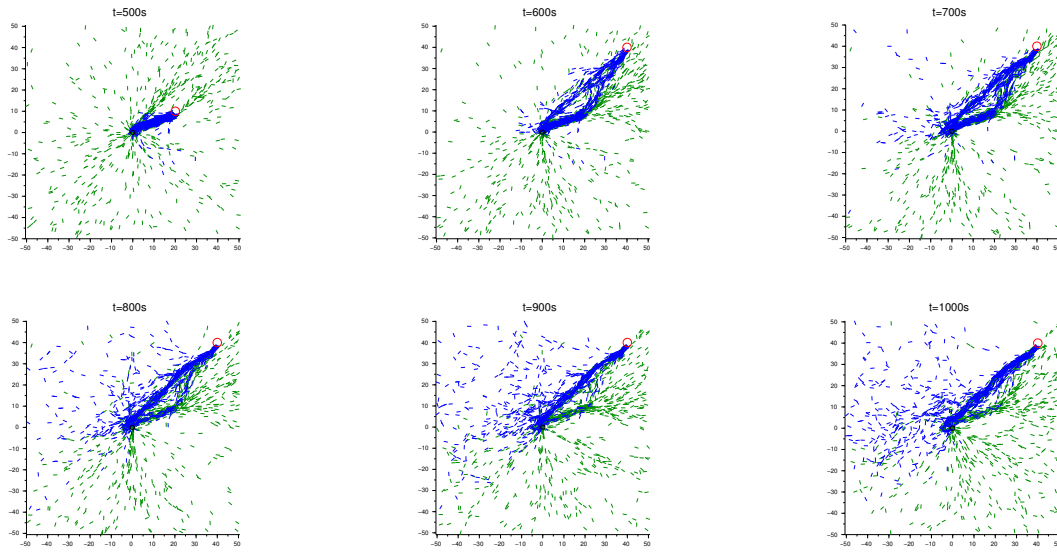


Figure 6: One simulations of the model with dynamical food source. The food source is a disc of radius 2 centered first at $(20, 10)$ and then at $(40, 40)$. Blue sticks: "blue" pheromones. Green sticks: "green" pheromones. Red circle: Food source. Black circle: nest.

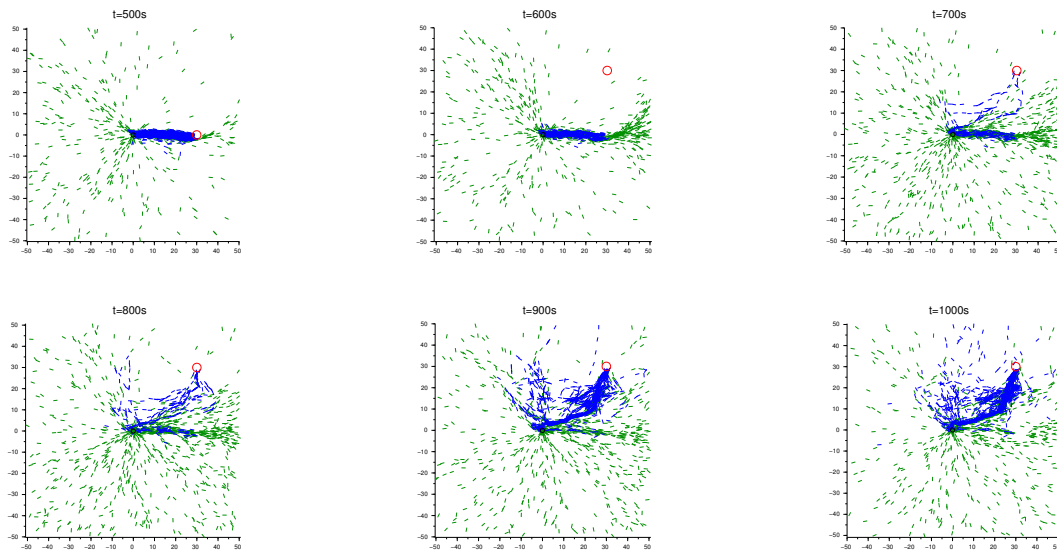


Figure 7: One simulation of the model with dynamical food source. The food source is a disc of radius 2 centered first at $(30, 0)$ and then at $(30, 30)$. Green sticks: "green" pheromones. Blue sticks: "blue" pheromones. Red circle: food source. Black circle: nest.

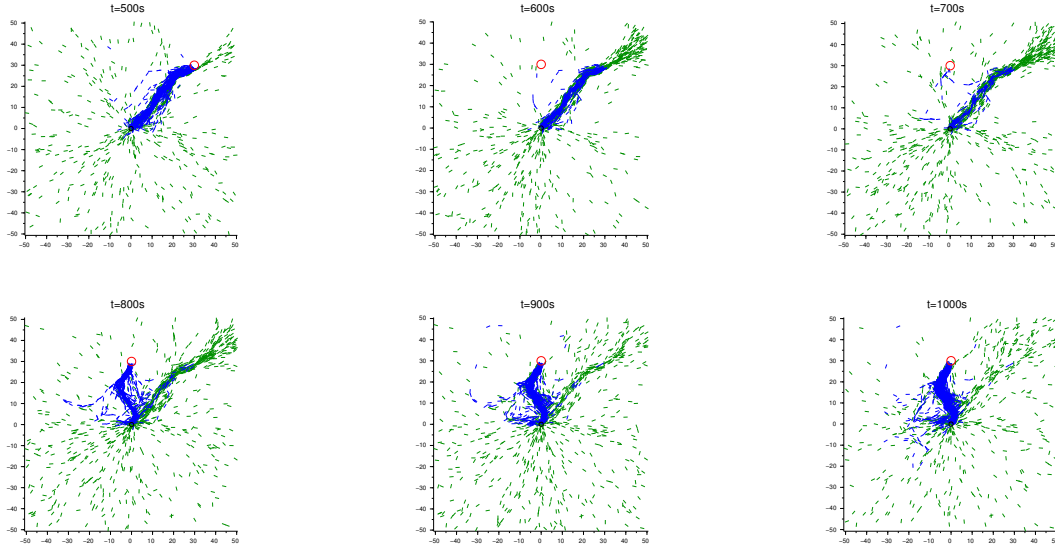


Figure 8: One simulation of the model with dynamical food source. The food source is a disc of radius 2 centered first at $(30, 30)$ and then at $(0, 30)$. Blue sticks: "blue" pheromones. Green sticks: "green" pheromones. Red circle: Food source. Black circle: nest.

variable $t > 0$ (time), $x \in \mathbb{R}^2$ (space) and $\theta \in 2\pi\mathbb{T}$ (orientation), where \mathbb{T} is the one-dimensional torus. We emphasize that, contrary to the microscopic description of the model, we use the same variable x and θ for all ants and pheromones regardless of their status.

We model the food source Ω and the nest Γ as a subsets of \mathbb{R}^2 . In our situation, we always set

$$\Gamma := D(0, R_{nest}).$$

Pheromone dynamics Green pheromones of orientation θ are deposited by foraging ants of orientation $\theta + \pi$ with a rate ν_g and disappear with a rate of $1/T_p$. The equation for the green pheromone deposition is therefore

$$\partial_t G(t, x, \theta) = \nu_g F(t, x, \theta + \pi) - \frac{1}{T_p} G(t, x, \theta), \quad (4.17)$$

and similarly the equation describing the blue pheromones dynamics is

$$\partial_t B(t, x, \theta) = \nu_b W(t, x, \theta + \pi) - \frac{1}{T_p} B(t, x, \theta), \quad (4.18)$$

Ant dynamics The equation governing the ant dynamics is a kinetic equation with a Boltzmann-type conservative operator:

$$\partial_t F + cv_\theta \cdot \nabla_x F = Q(F), \quad (4.19)$$

$$\partial_t W + cv_\theta \cdot \nabla_x W = Q(W), \quad (4.20)$$

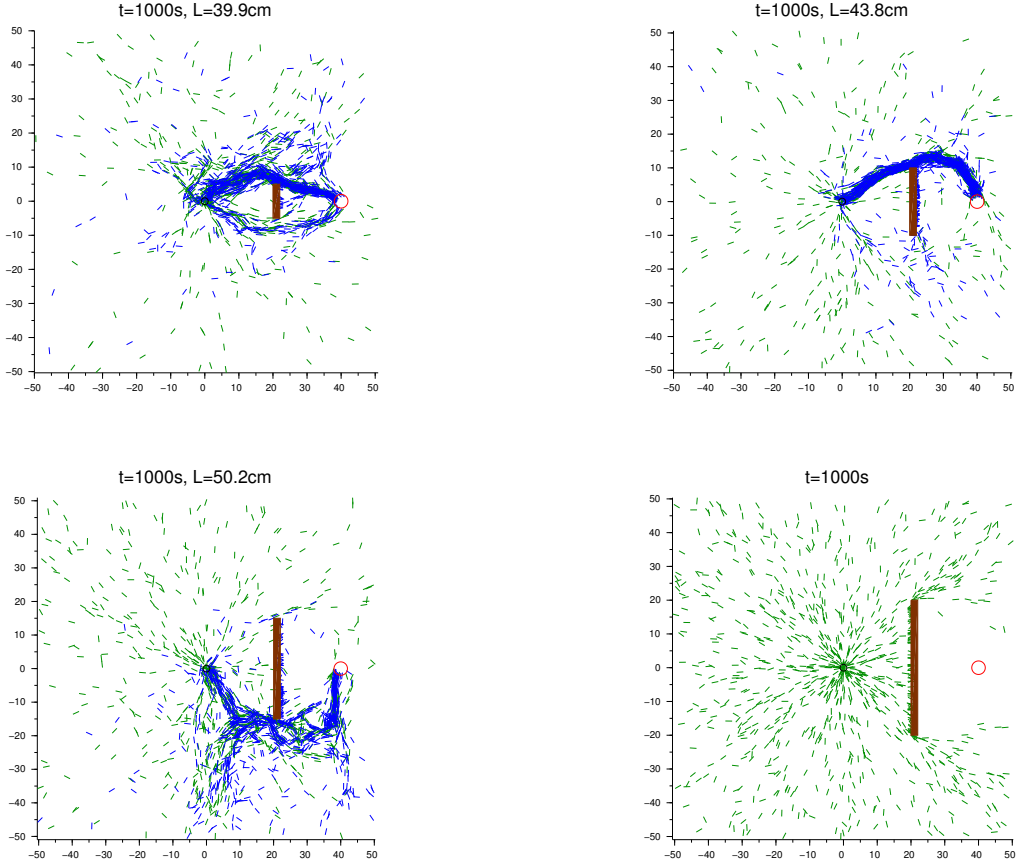


Figure 9: Four simulations of the model with an obstacle. Top left simulation: obstacle= $[20, 22] \times [-5, 5]$, shortest path followed by one ant: 39.90cm, actual geodesic length between the food source and the nest: ≈ 38.30 cm. Top right simulation: obstacle= $[20, 22] \times [-10, 10]$, shortest path followed by one ant: ≈ 43.80 cm, 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: ≈ 47.43 cm. Bottom right simulation: obstacle= $[20, 22] \times [-20, 20]$, no ant found its way from the food source to the nest. Green sticks: "green" pheromones. Blue sticks: "blue" pheromones. Red circle: food source. Black circle: nest. Brown rectangle: obstacle.

where

$$v_\theta := (\cos \theta, \sin \theta). \quad (4.21)$$

The left hand-side of both equation, the free-transport term, describes the straight motion with speed c orientated with angle θ (the "run") and the right-hand side, the Boltzmann operator, describes the direction change dynamics (the "tumble"). Since direction changes can happen during a random velocity jump (with rate λ_f and λ_w respectively) or a trail recruitment jump (with rate λ_b and λ_g respectively), both operator are decomposed in two:

$$Q := Q_r + Q_p, \quad (4.22)$$

$$\mathcal{Q} := \mathcal{Q}_r + \mathcal{Q}_p, \quad (4.23)$$

with

$$Q_r(F)(\theta) := \lambda_f \left(\int_{\mathbb{T}} \phi(\theta, \theta') F(\theta') d\theta' - F(\theta) \right), \quad (4.24)$$

$$\mathcal{Q}_r(W)(\theta) := \lambda_w \left(\int_{\mathbb{T}} \phi(\theta, \theta') W(\theta') d\theta' - W(\theta) \right), \quad (4.25)$$

where $\phi(\theta, \theta')$ is the probability density distribution to select a new orientation θ , given the present one θ' , in our situation, the Gaussian:

$$\phi(\theta, \theta') := \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(\theta' - \theta)^2}{2\sigma^2}}, \quad (4.26)$$

and with

$$Q_p(F)(x, \theta) := \lambda_b \int_{\mathbb{T}} \int_{\|x-x'\| \leq R} B(x', \theta') d\theta' dx' \left(\frac{\int_{\|x-x'\| \leq R} B(x', \theta) dx'}{\int_{\mathbb{T}} \int_{\|x-x'\| \leq R} B(x', \theta') d\theta' dx'} \rho_F(x) - F(x, \theta) \right), \quad (4.27)$$

$$\mathcal{Q}_p(F)(x, \theta) := \lambda_g \int_{\mathbb{T}} \int_{\|x-x'\| \leq R} G(x', \theta') d\theta' dx' \left(\frac{\int_{\|x-x'\| \leq R} G(x', \theta) dx'}{\int_{\mathbb{T}} \int_{\|x-x'\| \leq R} G(x', \theta') d\theta' dx'} \rho_W(x) - W(x, \theta) \right), \quad (4.28)$$

where

$$\rho_F(x) := \int_{\mathbb{T}} F(x, \theta') d\theta', \quad (4.29)$$

$$\rho_W(x) := \int_{\mathbb{T}} W(x, \theta') d\theta'. \quad (4.30)$$

These Boltzmann operator are conservative since one can check that $\int_{\mathbb{T}} Q_p(F) = 0$ and $\int_{\mathbb{T}} \mathcal{Q}_p(W) = 0$.

One can find detailed and precise explanations of these operators in [10], section 4.2 but let us give a short motivation hereafter. We focus on the operator acting on foraging ants. The left hand-side term $\lambda_b \int_{\mathbb{T}} \int_{\|x-x'\| \leq R} B dx' d\theta'$ describes how the rate of trail recruitment jumps raises as the total number of green pheromones raises within the radius of detection R of the ant, λ_b is the constant rate of trail recruitment jumps. The new orientation of is then described by the probability distribution function given by

$$M(\theta) := \frac{\int_{\|x-x'\| \leq R} B(x', \theta) dx'}{\int_{\mathbb{T}} \int_{\|x-x'\| \leq R} B(x', \theta') d\theta' dx'},$$

which explains the form of the operator of Boltzmann type: $M(\theta)\rho_F - F$.

Collecting and leaving food

We finally model the conversion of foraging ants to ants with food (and *vice versa*) with boundary conditions. In a way, a foraging ant walking to the food source vanishes and is replaced by an ant at the same position with food, walking in the opposite direction. Therefore, our boundary condition at the food source is

$$F(t, x, \theta) := 0, \quad \forall x \in \overset{\circ}{\Omega}, \quad (4.31)$$

$$W(t, x, \theta) := F(t, x, \theta + \pi), \quad \forall x \in \partial\Omega, \quad (4.32)$$

where $\overset{\circ}{\Omega}$ is the interior set of Ω and $\partial\Omega = \Omega \setminus \overset{\circ}{\Omega}$ is its border.

Using the same ideas, recalling that an ant with food drops its food and chooses a new orientation uniformly on $[0, 2\pi)$, the boundary condition at the nest is

$$W(t, x, \theta) := 0, \quad \forall x \in \overset{\circ}{\Gamma}, \quad (4.33)$$

$$F(t, x, \theta) := \frac{1}{2\pi}, \quad \forall x \in \partial\Gamma, \quad (4.34)$$

We emphasize that we could also impose that ants with food make a U-turn when they drop the food. In that case, the boundary condition would become

$$F(t, x, \theta) := W(t, x, \theta + \pi), \quad \forall x \in \partial\Gamma.$$

Complete model

Gathering the pieces (4.17) to (4.34) of our model, we obtain a kinetic model with boundary conditions. We emphasize that our derivation of the model is based only on formal considerations and that a rigorous derivation of this model is still an open question.

As a last note, we would like to emphasize that a macroscopic limit of our model can be performed. We refer to [10], section 4.3 where such a limit was performed in the case with no food source.

5 Discussion

Our model is rather simple. There are immediate biological flaws that one can think of (the fact that ants do not collide with each other, for instance). On the other hand, as we saw in certain simulations, the colony does sometimes use unnecessarily long paths to go to the food source and back. This makes us think that the model can be improved from both the biological and the optimization perspective. The tricky part might be to improve it on both levels at the same time.

5.1 Biological Relevancy

Regarding the modeling of oriented pheromones of the Boissard-Degond-Motsch model, a critical of the biological relevancy was already written in [10]. We summarize it here but an interesting reader should read it there for more details. A mechanism called "osmotropotaxis" and described in [14, 15, 18] could explain how ants can sense the orientation of a pheromone drop. In the case of a continuous drop (*i.e.* the ant which left the pheromone left a continuous trace while keeping walking) modeled in [12], the pheromone drop has an oval shape with higher chemical concentration in the middle. The ant is able to sense where the crest line of higher concentration which is oriented the same way the previous ant was. In the case of discontinuous drops (the ant leaves several little pheromone drops one after another) modeled by [35], a diffusion process must be taken into account to homogenize the pheromone drop. A quantitative study of this study with realistic parameter value was conducted in the appendix of [10].

A second issue regarding the pheromone modeling is our choice of polar interactions. Namely, our modeled pheromones keep information of the angle of the ant which left it. This gives the second ant an information about the orientation (on what route should I walk?) but also on the direction (*e.g.* should I walk the route to the East or to the West?). Non-polar interactions seem more biologically accurate since no evidence of polar oriented pheromone exist to our knowledge. In [57], 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 [10] when a connection could be made. We refer to this reference and to [4, 9, 17] for a motivation of this choice of parameter values for *Lasius niger*.

Our model considers two types of pheromones. There are evidence showing that some ants, such as the Pharaoh's ant [8, 30, 37, 38, 41, 54], can lay different type of chemicals using different glandes to produce them. Other ants species, such as the big headed ant *Pheidole megacephala* [24] vary the concentration of deposited 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 [48, 55].

One assumption of our model, which is rather physically than biologically irrelevant is the absence of collisions between ants. As was previously observed in experiments and models [18, 25, 50], this is crucial factor to optimize the food collection by ants. Physical interactions between ants can be modeled using a repulsive Lennard-Jones repulsive operator in the same spirit as in Ryan's work [50]. We could also consider communication between ants when an encounter occurs. As was observed in many biological experiments (see [33, 44] among many others), antennas contacts

between individuals is a key element to understand how complex tasks are achieved by ants societies. One important thing we would like to emphasize is that this biologically relevant modification is likely to improve the model from the optimization perspective since exchange of informations is the key to ants complex achievements. On the other hand, taking physical interactions as Ryan did does not slow the foraging process as was observed in [50] but it is likely to raise the computational cost of the simulation since interactions between a large number of ants would have to be taken to account.

5.2 Optimize the model

As we saw in our various simulations, our model can sometimes select quite non-optimal paths or worth, it may not be able to locate the food source. There are ways we can improve the model in this perspective. Off course, one could let the ants be aware of all existing paths at all time but that would take us out of our framework, since we only want to consider local interactions. Even considering only local interactions, we can speculate that some modifications might improve the model.

For instance, one think we immediately think of is communication between ants. In our simulations, we let the ants with food know how much time passed since they collected the food. We could improve the model by allowing those ants to communicate this time with foraging ants. This way, when facing two different pheromone trails, a foraging ant would select one over the other based on informations from ants coming back. This could probably improve the shortest path selection but seem biologically irrelevant since no such time memory was observed on ants.

We could also let the colony have "cleaner ants". In this scenario, blue pheromones do not only keep memory of the orientation of the ant, but also of the time spent since the food discovery. When ants with food come back to the nest, they tell cleaner ants how long it took them to get beck to the nest. Cleaner ants then have knowledge of the current time record and go clean every blue pheromone that was left after this current critical time. At first, cleaner ants will only clean pheromones that are close to the nest, therefore foraging ants will not be led on misleading path but after a while, cleaner ants will come closer to the food source and leave only the "best" pheromones traces. Once again, no such behavior was observed on ants to our knowledge so this modification might be contradictory with biological relevancy.

We could also let all ants be aware of the time record when they come back to the nest. This way, if an ant with food realizes that it has passed this record, it stops leaving blue pheromones. This way, no long paths are created. In our two previous scenarios, we kept the hypothesis that only local interactions occur but we allowed ants to have a "memory" which weakens the model from the biological perspective.

6 Conclusion

We have presented a model of foraging and pheromones depositing 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 pheromone activity process too
2. It allows the modeled colony to find a food source and to bring it back to the nest in a quite optimal way

We then showed the outcome of a simulation of the model in various situations, namely: simulations with two food locations, simulations with one food location that changes location 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.

We then formally derived a kinetic description of the model at the meso scale. Rigorous derivation of the kinetic equations and performing the macroscopic limit are still open questions.

Throughout our discussion of the model, we underlined that the model can be improved from the biological perspective by taking more realistic parameters, by letting ants communicate with each other and by considering a model with physical interactions. On the other hand, the model can be improved from the optimization perspective by considering "more intelligent" particles which are able to privilege the shorter paths of two. It is likely, however, that those two perspectives conflict each other.

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