1.4 How do Ants Form Trails?

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In a joint project with Felix Höfling and Zahra Mokhtari from the Freie Universität Berlin work has been taking place at WIAS to identify simple mathematical models that explain how active particles or agents can interact with each other to form large-scale structures and patterns. In particular, we are studying models that are appropriate on the time and space scales of insects such as ants and where agents interact with each other by depositing chemical messages that can be detected by all agents that pass by in a short period of time. Our initial results suggest that these simple models explain the formation of large-scale trails in a way analogous to phase transitions known in physics.

Fig. 1: *Ant. Photo by Sian Cooper on Unsplash.*

Mathematical insights into collaborative behavior

Ants are well known for their ability for act collectively in order to obtain supplies by forming trails to enable large numbers of ants to visit a food source in close succession with each ant then carrying some of the food back to the colony. This is all achieved without any real-time command and control or long-range communication; however, various species of ants are known to deposit chemical markers, known as *pheromones*, as they move around. At this point, we note that there are many species of ants showing a wide range of behaviors; however, the trail-forming collective behavior seems especially relevant for mathematical study, because it is a good example of distributed self-organization. Studying it serves two purposes: Firstly, to gain mathematical insights into how individuals like ants can collaborate on an equal footing and how external actors might be able to influence the results of such collaborations, and secondly, to develop mathematical methods for studying collaborative motion that arises in other settings.

Key challenges

It is clear that ants and other kinds of agents or active particles do not always move along large-scale trails, but sometimes move in irregular, apparently random ways, for example, when searching for new sources of food. Any useful mathematical model of collective behavior will therefore have to incorporate both uncoordinated idiosyncratic motion and large-scale collaborative trails. Mathematical models that exhibit qualitatively distinct properties depending on the exact values of their parameters are said to have "phase transitions." This means that the goal of the ongoing work is to find a mathematical model that is reasonable given the known physical properties of ants, in particular, their ability to deposit pheromones, and that shows at least one phase transition between disordered motion and trail-based motion. From a mathematical perspective, this topic is closely related to the work of the RG 5 on phase transitions and particle models in physics.

One strand of existing knowledge deals with the Patlak–Keller–Segel equations [1] and applies primarily to physical settings such as micro-swimmers in a fluid, where the pheromones can diffuse quite rapidly, and is not immediately relevant for applications such as ant behavior where pheromone diffusion is expected to be minimal on the time scale of the motion. The Patlak–Keller–Segel equations describe a system of organisms that tend to move towards higher concentrations of a pheromone they produce themselves. Such a model can lead to a phase transition where the organizing effect of the pheromone gradient leads to a large proportion of all the organisms gathering together in a small area despite random dispersive influences; however, it does not seem rich enough to generate collective motion along a "trail," for this one requires a more sophisticated model. A major innovation in the work currently taking place at WIAS and the Freie Universität (FU) Berlin is the use of vector pheromones, that is to say, pheromones that are deposited in a way that gives information about the direction of travel of the ant as it deposited the pheromone.

Pheromones with direction

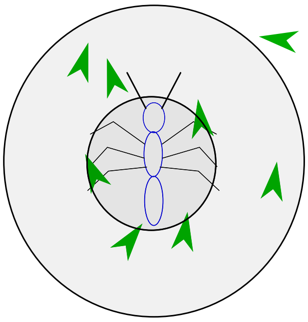

Fig. 2: *Inner disc of radius R_0 represents the ant, the large disc is the sensing radius, and the directed pheromones are shown in green*

As an initial model, we assume that each agent (ant) deposits one pheromone every τ_d seconds and that each pheromone evaporates after τ_p seconds. Each pheromone has an orientation that is the same as the direction of motion of the ant as it deposits the pheromone and does not change until it evaporates. The environment of a single ant can be thought of as shown in Figure 2.

In our model, every ant is treated as a disc of radius R_0 that moves with a constant speed v_0. However, the direction of each ant undergoes diffusion (small random perturbations) on the unit circle with a bias towards aligning with the average orientation of all the pheromones within a sensing radius. After choosing parameters to approximately represent the known physiological properties of the ant *Lasius niger* [2], two important degrees of freedom remain. The first is the ratio of the alignment strength to the orientational diffusion, which we denote s. The second is the concentration of ants or, equivalently, pheromones, which we quantify via the average number of pheromones in the sensing disc of a single ant N_p. Increasing either (or both) of these parameters increases the tendency of nearby ants to move in a common direction.

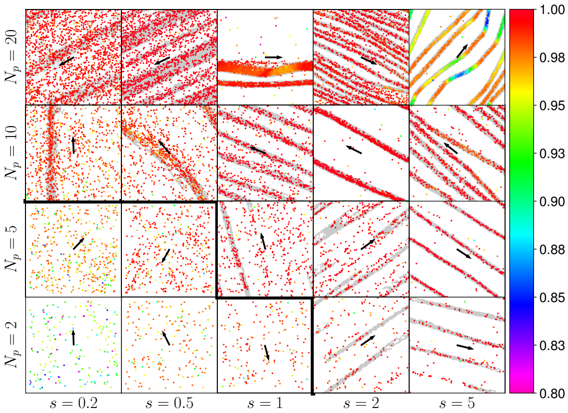

Fig. 3: *Ant positions color-coded by degree of alignment with the global average (black arrow)*

Computer simulations reported in Figure 3 show that this model is capable of capturing both uncoordinated motion (when s and N_p are both small in the bottom left of the figure) and the formation of trails (towards the top and right of the figure where at least one of s and N_p are large). The thick black line in Figure 3 separates the plots with smaller s and MN_p values where there is a drift in a common direction, but no detectable concentration of ants on a trail from the plots where it was possible to identify long trails. The exact position of the thick black line is to some extent a subjective decision, and a more quantitative approach to detecting regimes of trail formation is discussed below; however, the possibility of drawing such a line motivates a more precise mathematical search for a phase transition.

The model introduced above is also capable of reproducing a completely different type of collective behavior, which has long been observed in army ants namely the *ant mill* [5]. In an ant mill, a large rotating disc of ants is formed; this requires a high density of ants in order to produce a very strong pheromone signal and a strong response to the pheromones on the part of the ants, that is, both parameters N_p and s must be relatively large. We were able to observe this phenomenon with $N_p \approx 30$ and $s = 10$ as is shown in Figure 4, where one sees a mill and a mildly undulating trail, which at a later time (not shown) was even absorbed into the mill.

From these initial results, we are able to conclude that our model is capable of reproducing some important and significant features of the collective behavior of ants. They show that changing the parameter values leads to qualitative changes in the collective behavior; it is less clear whether the changes are continuous or abrupt in nature.

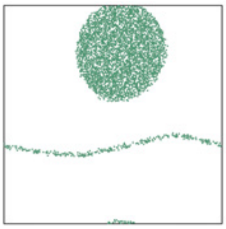

Fig. 4: *Ant positions are shown as green dots on a square domain with periodic boundary conditions*

Quantifying changes in collective behavior

In this section, we concentrate on distinguishing between the uncoordinated motion shown in the bottom left of Figure 3 and the trails visible in the panels towards the top and right of the same figure. The formation of mills as in Figure 4 is neglected as this occurs in a more extreme parameter regime.

Practically, we define a trail to be a region of continuously high pheromone density that extends from one side of the domain to the other. We then consider the ratio

$$p_\infty = \frac{\text{number of pheromones in trails}}{\text{total number of pheromones}},$$

which varies between 0 when there are no trails and 1 when all pheromones (and therefore all ants) are on trails. The value of p_∞ was then sampled repeatedly during simulations with different values of s in order to numerically estimate its probability distribution. The results are shown in Figure 5, which is consistent with Figure 3 in that for $s = 1$ it is rare to find many pheromones in trails (because even small trails are rare), whereas for $s = 10$ it is likely that a significant proportion of pheromones (and therefore ants) are concentrated on trails. The remainder of this highlight article concentrates on attempts to understand which parameter values lead to significant trail formation and which do not.

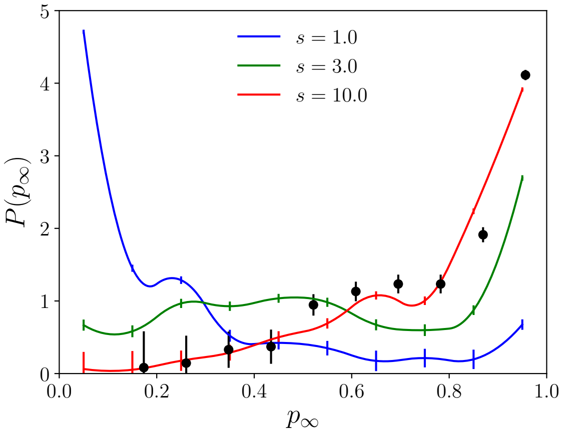

Fig. 5: *Probability distributions for p_∞ sampled with $N_p = 5$ and three different values of s. The black dots are an additional data set for $s = 10$ sampled using an even larger domain.*

The statistics in Figure 5 were derived from simulations carried out by Zahra Mokhtari at FU Berlin and required the development of a complex pipeline of tools to process the simulation results [4]. The image and data processing is not discussed further in this article for reasons of length, although it is an interesting topic in its own right. We note that the trails detected with these methods are shown in light grey in Figure 3.

Critical values for a reduced model

If one passes to the mean field limit on a fixed spatial domain $U \subset \mathbb{R}^2$, that is to say, one looks at the behavior of a very large number of agents leaving very weak pheromones (both scaling with the number of agents), one finds formally the following equations for the evolution in time t of the concentration of agents/ants α and pheromones ϕ on $U \times [0, 2\pi)$ representing position in the plane denoted r and orientation denoted θ:

$$\frac{\partial}{\partial t}\alpha + \nabla_r \cdot (v_\theta \alpha) = -\mu \frac{\partial}{\partial \theta}(\alpha\,(F * \phi)) + D_{\text{rot}} \frac{\partial^2}{\partial \theta^2}\alpha$$

$$\frac{\partial}{\partial t}\phi = -\frac{1}{\tau_p}\phi + \frac{1}{\tau_d}\alpha,$$

where v_θ is the unit vector in direction θ and $[0, 2\pi)$ is given periodic boundary conditions. The parameter μ measures the strength of the aligning force and D_{rot} the strength of the random fluctuations (rotational diffusion) of the ant orientations (the parameter s introduced above is μ / D_{rot}). The function $F = 2\pi \sin\theta$ is an interaction kernel, and $F * \phi$ is the convolution in the orientation variable θ with the pheromone field which gives the local force that the pheromones exert on the ants in order to align their direction with that of the pheromone field.

As an initial step towards identifying critical parameter values for changes in qualitative behavior, one can first consider what happens at a single point in space neglecting the advective part of the above equations. At a single point, the concentration of ants and that of pheromones depends only on their orientation, which is 2π-periodic, and so a Fourier decomposition is natural. The 0-th Fourier mode is simply the total concentration (of ants or pheromones), and the first Fourier mode gives a measure of the existence and prominence of a preferred direction (the direction itself would be given by the phase angle of the mode, which is not studied here). Higher Fourier modes provide a finer description of the distribution of orientations on the circle. Under some simplifying assumptions and extending the approach of [3] to include pheromones, one can derive the following equation for the first Fourier modes of α and ϕ with respect to the orientation variable θ, which are denoted α_1 and ϕ_1, respectively:

$$\frac{\mathrm{d}}{\mathrm{d}t}\begin{pmatrix}\alpha_1\\ \phi_1\end{pmatrix}=\begin{pmatrix}-D_{\mathrm{rot}} & \frac{\mu\alpha_0}{2}\\ \frac{1}{\tau_d} & \frac{-1}{\tau_p}\end{pmatrix}\begin{pmatrix}\alpha_1\\ \phi_1\end{pmatrix}.$$

The basic theory of ordinary differential equations shows that α_1 and ϕ_1 will become large (that is, strong alignment will develop) precisely when $\frac{\mu\alpha_0}{2} > D_{\mathrm{rot}}\frac{\tau_d}{\tau_p}$, a conclusion that is confirmed when the analysis is extended to include the second Fourier modes of α and ϕ.

Conclusions and outlook

The initial phases of this work have established a relatively simple model that qualitatively captures important aspects of the collective behavior of ants and that can be studied using techniques that build on methods extensively used at WIAS. In some simplified situations, we can show that the establishment of a coordinated direction depends critically on the initial concentration of agents (all other parameters held constant).

Along with the colleagues at the FU Berlin, we aim to find improved ways of detecting trail formation in the output of numerical simulations. More importantly, we are trying to find simplified situations where we can assess the stability of a trail and identify the critical parameter values. This means moving beyond the eigenvalue analysis described above, which omits the spatial element and just considers the ability to establish a preferred direction in a small region of space.

References

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