

Symmetry Breaking on Density in Escaping Ants: Experiments and Alarm Pheromone Model

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Abstract

As an important concept in many fields, collective behavior in large groups of animals and human is a truly fascinating natural phenomenon. After Helbing et al. (2000) introduced an interesting panic induced collective behavior symmetry breaking, which occurs when crowd pedestrians escape from a closed space with two symmetrically located exits, Altshuler et al. (2005) found that symmetry breaking can even occur in escaping ants and constructed a Vicsek-like model applying alignment rule to explain their results. They also investigated how the total number of escaping ants influences symmetry breaking and their experiments show no measurable results. Our experimental results indicate that the degree of symmetry breaking does not monotonically increase, which does not match the Vicsek-like model, but after a maximum of symmetry breaking it declines as the number of ants increases, which suggests that Vicsek-like model with alignment rule may not be the “right” model for escaping ants. Based on biological facts that ants use pheromones to communicate with each other rather than seeing how other individuals nearby move, we have proposed a simple alarm pheromone model, in which ants deposit and respond to alarm pheromones, to show true fundamental rules of escaping collective behavior in ants.

Introduction

As an important concept in many different fields, such as sociobiology, sociology, even economics and control theory, collective behavior of large groups of animals is a truly fascinating natural phenomenon. Especially when under pressure such as encountering predators, some animals form group and perform amazing patterns for survival (1-2). Apart from collective motion in fish schools (3-5), bird flocks (6-8), etc. in open space,

An interesting panic induced collective behavior is symmetry breaking, introduced by Helbing et al. (2000), which occurs when crowd pedestrians escape from a closed space with two symmetrically located exits, one of them is more used than the other one.(9).

That work was rapidly followed[???]. Altshuler et al. (2005) found that symmetry breaking can even occur in escaping ants instead of pedestrians (10). By introducing a dose of insect-repelling liquid, panic induces high symmetry breaking in escaping ants from a room with two symmetrically located exits, while the low panic groups without insect-repelling liquid produce low symmetry breaking. Inspired by Helbing et al. (2000) (9), they constructed a Vicsek-like model in which the velocity of an individual depends not only on the velocity of itself but also on the average velocity of its neighborhood within its sight range (11). They also investigated how the total number of ants influences symmetry breaking. Their results show that while the model suggests a discrete increase of the asymmetry as the number of ants increases, the experiments

show no measurable dependence on the number of ants (10).

This conclusion that the asymmetry is independent on the density is against the facts reported in the literature that density is an important factor affecting the properties of collective behavior in real biological groups, such as bacterial colonies (12-14), cells (15), insects (16, 17), fish schools (4, 5) and bird flocks (7), as well as in self-propelled particles (SPP) models (11). Hence, it is worthwhile to investigate the interactions inducing asymmetry in the ant group related to density. In this current research, we perform an experiment to explore whether and how symmetry breaking is dependent on the density of ants.

Although Vicsek-like models are successful in a very wide range of collective motion systems, recent experimental researches uncovered that the collective behavior of specific species may not satisfy all the assumptions and rules. Here are some examples. Rather than incorporating homogeneous agents, a well-defined hierarchy has been found in pigeon flocks (8). Different from the assumption that the interaction depends on a fixed metric distance, the starlings in flocks base their interactions on the topological distance (each bird interacts on average with six to seven nearest neighbors)(7); even, some species of fishes tend to follow just one nearest neighbor (18).

For the case of ants, it is well known that most species have poor eyesight, and some ants are nearly blind (20). Rather than seeing how other individuals nearby moves, ants use their antenna to sense their surroundings and use pheromones to communicate with each other. Specifically, when under danger, alarm pheromones are used by social insects and induce responding behavior that they orient osmotactically to the source at low pheromone concentration and at high concentration go into frenzied activity, occasionally attacking the pheromone source (21). Based on these biological facts, we argue that the Vicsek-like model may be unsuitable to describe the ants colony, and we need to construct a model incorporating alarm pheromone to show the underlying rules regulating the panic escape collective behavior in ants.

Experiment

Method

Before the experiments, the field-collected red imported fire ants (*Solenopsis invicta* Buren) from a single nest in South China Agricultural University located in Guangzhou city were fed in laboratory for a few weeks, and the experiments were performed in the period of June 4-24, 2011. The temperature in laboratory is consistently about 25°C. A group of ants were picked up with tweezers and immediately put into a small acquisition bottle, on the internal surface of which PTFE emulsion had been brushed and air dried so that the ants were not able to climb up and could be transferred easily. Just a few seconds later, the ants in the bottle were introduced into the center of a circular cell with two exits symmetrically situated left and right, which were initially blocked. The cell was an acrylic drum of 8 cm diameter and 0.5 cm height with 1 cm wide exits, and rested on several layers, which were a piece of clipped circular filtering paper, a piece of thin plastic paper, and a piece of clipped A4 paper, from up to bottom respectively. After covering the cell with a plastic plate of 0.3 cm thickness, with a hole of 0.3 cm diameter situated at the center of the drum, a dose of 50µL of an insect-repelling liquid (citronella, Labiofam, Cuba)

was rapidly injected into the cell through the hole, producing a disk-shaped spot of the substance at the center of the filtering paper. The two exits were then opened synchronously so that the ants were able to escape. The time from picking up the ants to opening the exits is typically around 30 seconds. The whole setup was rested on a horizontal plastic box without cover of 50 cm length, 40 cm width and 5 cm height, which was divided into two parts symmetrically by plastic walls so that two isolated space formed left and right for retaining and counting the ants escaped. Two desk lamps were placed aside the box symmetrically to keep the light intensity close to uniform, preventing possible moving direction preference of ants induced by uneven light intensity. The whole process was recorded until the end of the escape activity using a video camera situated above the cell.

The experiments were repeated 291 times. In each repetition, a new group of ants collected from the same nest was used, and the layers under the cell including the filtering paper, plastic paper and A4 paper were all replaced by new ones to avoid rudimental of liquid and possible pheromone residue on the equipment.

It should be noted that it was impossible to control precisely the total number of ants in each experiment. The reason is twofold. Firstly, to keep the ants in a high panic situation the ants have to be introduced into the cell quickly enough at the cost of impreciseness of the ants number. Secondly, not every ant can escape because during the escape some of the ants were eventually injured by the immersion in the repellent fluid if they were located under the central hole in the plastic plate at the beginning of the experiment or by accident while escaping. The average proportion of the remained ants at the end of each experiment to the total number of ants at the beginning of each experiment is $(6.3 \pm 0.6)\%$. The total number of ants escaped in the experiments ranged from 6 to 269.

Definition for symmetry breaking

To measure the symmetry breaking, Altshuler *et al.* (2005) [10] used the percentage difference in door use (percentage difference), which is calculated as

$$\frac{|\text{total of ants escaping left} - \text{total of ants escaping right}|}{\text{total of escaping ants}} \times 100$$

This measure, however, did not take into account the natural random difference introduced by a random SPP model. The basic idea is that randomness leads to symmetry while the symmetry breaking if observed should be induced by collective behavior other than randomness. The percentage difference in door use in ref.[xx], however, gets a non-zero value even in a random SPP escape. Take a four particle SPP escape as an example, the total of ants escaping left and right may be (1, 3), (3, 1), (2, 2) and (2, 2). The percentage difference is 25% not zero.

Considering an N particle random SPP model, for an unbiased movement, the possibility of escaping left and right for each particle should be equal, that is $1/2$. After some simple statistical derivations, we get the random difference produced from an N particle random SPP model as,

$$\sum_{i=0}^N \frac{C_N^i}{2^N} \cdot \frac{|2i-N|}{N},$$

where N denotes the total number of escaping ants.

The focus of this current research is to study how the symmetry breaking is influenced by the total number of ants, actually the density when the experiment cell is fixed. Hence, take two experiments with different total ant numbers $N=10$ and $N=100$ as another example, the percentage difference for a random SPP escape is 25(???) and 8.0(???) respectively, as demonstrated in Figure 1. By subtracting the randomness induced part from the percentage difference, we introduce a new measurement to measure the symmetry breaking, *percentage collective asymmetry*, which is given by

$$CA = (\text{difference in door use} - \text{random difference}) \times 100,$$

Hence, the percentage collective asymmetry is given as,

$$CA = \left(\frac{|L-R|}{N} - \sum_{i=0}^N \frac{C_N^i}{2^N} \cdot \frac{|2i-N|}{N} \right) \times 100,$$

where L and R denote the total number of ants escaping left and right respectively. The value of CA may be negative, which means the left and right door use in this specific case is more symmetric than the expectation of a random escape.

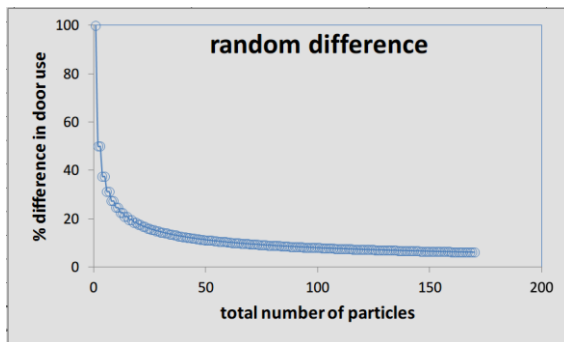


Figure 1: The random difference produced from random SPP model with respect to the total number of particles.

Experiment Results

Experimental results

As mentioned above the total number of ants escaped can not be controlled precisely in each experiment due to the reason that the number of ants introduced into the cell is imprecise and not all the ants are able to escape. It is therefore impossible to test the symmetry breaking by repeating the experiment to get the average of CA with a fixed specific total ant number.

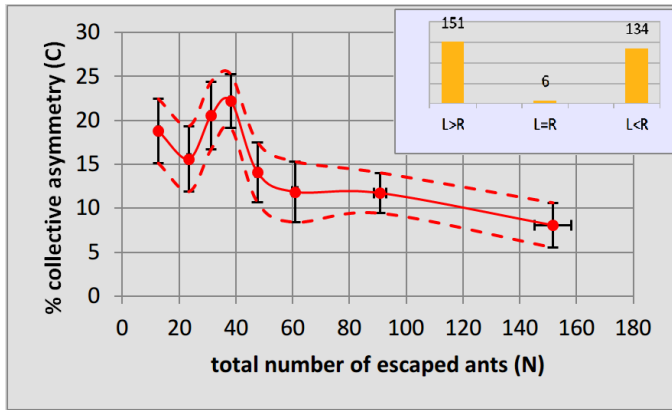
Therefore, a moving average of thirty points is calculated for the CA vs. N curve as illustrated in Figure (???). The two dashed lines above and below the curve are the (standard deviations???) of the moving average. The bin size for the moving average is discussed in the (conclusion and discussion???) to show the robustness of the CA vs. N relationship.

The result shows that there is a nonlinear relationship between the degree of symmetry breaking

and the total number of escaped ants. This curve is featured by a high profile when the number of ants is small as well as a decrease of CA to a low profile as the number of ants is large. (Figure???)

There are totally 291 individual experiments. The number of experiments in which L>R, L<R and L=R is 151, 134 and 6 respectively, as is shown in the inset of Figure (???). This means that there are no hidden biased environmental factors affecting the direction of ant movement.

Figure 2: Moving average of the percentage collective asymmetry (CA) vs. the total number of escaped ants (N). The two dashed lines above and below the curve are the (standard deviations???) of the moving average.



This curve is featured by a high profile when the number of ants is small as well as a decrease of CA to a low profile as the number of ants is large. The inset shows, within the 291 individual experiments, that the number of experiments in which L>R, L<R and L=R is 151, 134 and 6 respectively.

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Model and Analysis

We will show the discrepancy(???) between the results of Vicsek-like model containing the alignment rule and our experiment results presented earlier. Then, we will set up an alarm pheromone model based on ants' biological features and show its greater explanatory power.

Vicsek-like Model

The Vicsek-like model used by Altshuler *et al.* inspired by Helbing *et al.* (2000) suggests a discrete increase of the 'percentage difference in door use' as the number of ants increases [Altshuler, 2005], which does not match our experimental outcome. We perceive the core mechanism for the Altshuler Vicsek-like model is the alignment rule. A simpler model is established that contains the alignment rule and bouncing against the wall, eliminating the interaction among ants and the interaction between ants and the central repellent spot.

A total number of N virtual ants are introduced into a circular cell with two exits like the one used in the experiment. The initial positions and the directions of movement of ants are chosen randomly and they move with a constant absolute velocity u . If an ant gets closer to one of the two exits than a certain critical radius, R_e , it escapes through that door. When an ant hits the wall of the cell, it is reflected, otherwise, the unit vector of velocity of an ant is calculated as

$$\vec{e}_t = \frac{(1-p)\vec{e}_{t-1} + p(\vec{e}_{t-1}^{\text{herd}})}{|(1-p)\vec{e}_{t-1} + p(\vec{e}_{t-1}^{\text{herd}})|}$$

in which, \vec{e}_{t-1} is the unit vector of the ant's velocity at computer step t-1, and $\langle \vec{e}_{t-1}^{\text{herd}} \rangle$ is the average unit vector of the velocities of neighboring ants within a radius R_h from the ant under study at computer step t-1. p is a parameter that determines the tendency of an ant to align with its neighbors.

The main parameters influencing the phenomenon of symmetry breaking are p and R_h . For example, when $p=0$ or $R_h=0$, the ants will behave like random particles and induce low asymmetry. p is assigned as 0.2, 0.5 and 0.8. R_h is assigned as 0.6, 2.0 and 3.75(修改模型). This produces 9 parameter combinations. The radius of the cell $R=4.0$ and $R_e=0.5$ (模型修改), the same as in [Altshuler] and in our experiment. The velocity is set as $u=0.5\text{cm}$ per time step corresponding to the expected value used in [Altshuler] without considering the velocity distribution.

The simulation results suggest a increase of the asymmetry as the number of ant increases as is shown in Figure 3. This simpler model gives the same qualitative results as the Altshuler model does and both can not explain the experimental results which show a significant decline of collective asymmetry when N is large enough. This suggest that the alignment rule is the core mechanism in these two models and it is not suitable to describe the underlying rule of the panic induced collective behavior in ants. That requests a more reasonable model to uncover the underlying rules in escaping ants.

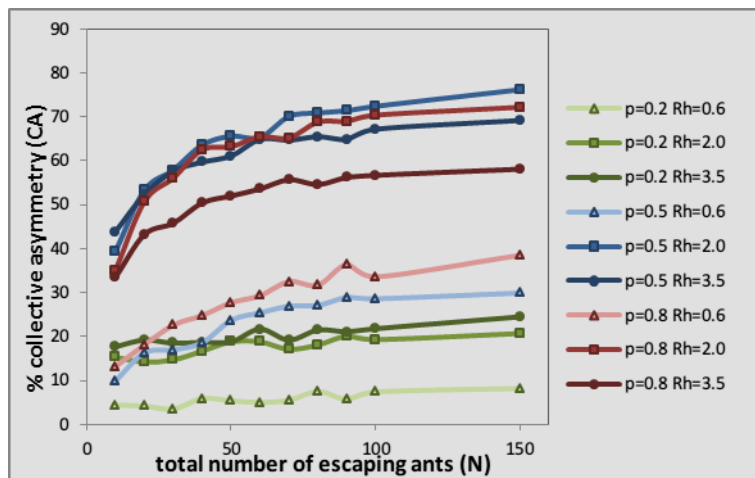


Figure 3: Simulation displayed by Vicsek-like model. p and R_h are set to be low, medium and high value respectively, in which the dark red dots ($R_h=3.75$, $p=0.8$) are corresponding to the [Altshuler's model].

Alarm Pheromone Model

A number of pheromone related models, including the best known ant colony algorithms, have been developing prosperously (22). However, almost all of them are not situated to describe the panic induced collective behavior of ant. On one hand, most of the models are delicately constructed for solving optimization problems rather than exploring biological laws underlying.

On the other hand, nearly all of them are directly inspired by foraging behavior induced by recruitment pheromone, which is different from the alarm pheromone triggered behavior. For example, the ants do not have to move between a source and a sink.

We raise basic questions as follows: 1) how is the pheromone deposited by ants and how does the pheromone evaporate? 2) How do the ants respond to the pheromone? Effective communication of alarm can be critical for social animals so that they are able to deal with threats posed by predators and competitors. Alarm responses can be broadly categorized into two groups (23). Smaller or more vulnerable societies typically exhibit ‘panic’ responses, in which individuals run away from the stimulus, either back into the nest or away from the nest when carrying brood or other non-mobile resources. By contrast, larger or better defended societies, like red imported fire ant (*Solenopsis invicta*) used in our experiments, tend to show an ‘aggressive’ response, in which individuals are attracted to or arrested at the stimulus and attack any detected threats (24). Decades ago, Wilson defined alarm behavior in fire ants, as the rapid, erratic movement of workers toward a disturbed worker (25). Taking inspiration from that and also for simplicity, we assume that when moving under panic an ant deposits a constant amount of alarm pheromone, which then evaporates at a certain rate after being released, and has a tendency orientating to the position where the concentration of alarm pheromone is maximum within its detection range. Moreover, taking into account the limitations of the biological perception, the ability of distinguishing a higher concentration of pheromone cannot be infinite. That is to say, the concentrations of alarm pheromone in two positions within its detection range can both be too high for an ant to “know” which one is even higher.

The rules are described below, and see the schematic diagram in figure 4. We constructed a two-dimensional square lattice $L \times L$.

- 1) Each of the ants occupies one square lattice randomly with a direction vector forward to the center of one of the nearest 8 lattices randomly.
- 2) During simulation, once an ant is located on a lattice, a constant amount of pheromone p_0 is deposited on it obeying linear superposition, and pheromone on each lattice reduces a constant amount of Δp at each time step until it reaches zero.
- 3) The movement of an ant is determined by its detected information. The detection range of an ant is its nearest 8 lattices. When one of the two exits is detected, it goes out immediately. When it meets the boundary, it reflects. Otherwise, the position of each ant updates according to:

$$\begin{cases} x(t+1) = x(t) + \{a_x + p_x^m\} \\ y(t+1) = y(t) + \{a_y + p_y^m\}. \end{cases}$$

Here, x and y denote the x and y component of the position vector of ant respectively. a_x and a_y denote the x and y component of the direction of movement vector, which can only take the value of 1, 0 and -1, meanwhile 0 cannot be assigned for both a_x and a_y . \mathbf{p}^m denotes the vector pointing to the detected maximum pheromone from the ant, and p_x^m and p_y^m are the x and y components of it. The bracket “{}” is defined as the formula below to ensure each ant move exactly one lattice in every time step, and the position of each ant is at the center of one lattice.

$$\{\alpha\} = \begin{cases} 1, & \text{if } \alpha > 0 \\ 0, & \text{if } \alpha = 0 \\ -1, & \text{if } \alpha < 0 \end{cases}$$

Moreover, if any detected amount of pheromone is larger than the given difference threshold p_t , it is treated as the p_t . If more than one positions where pheromone are larger than p_t , an ant selects one from them randomly.

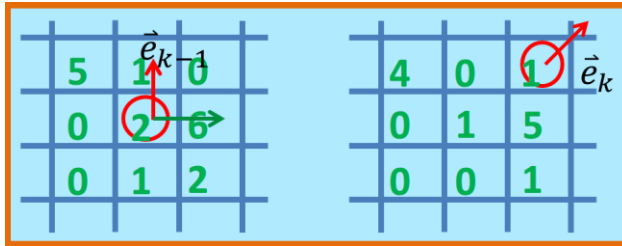


Figure 4: Schematic diagram for the rules of alarm pheromone model. The left and the right schematic diagrams show the updating rules in the model from time step $k-1$ to k . The red circle denotes one ant, and the red arrow denotes its current velocity vector. The green numbers in lattices denote the concentration of pheromone, and the green arrow denotes the vector from the ant to the lattice where the concentration of pheromone is largest within its detection range.

Simulation Results

In the simulation, the following set of parameters is used: $L=20$, $p_t=1$, $p_0=0.25$, $\Delta p=0.006$. We set L to be equal to 20 so that the size of lattice corresponds to the average body length (0.39cm) of the ants we used by means of statistical analysis from the videos of our experiment. Taking into account that the absolute values of p_t , p_0 and Δp are meaningless, but only the relative values make sense, we set the difference threshold p_t be equal to 1 as a reference value. The simulation results compared with experimental results are shown in figure 5. The open blue circles which correspond to the simulation results averaged after 300 runs of a simulation. The simulation result suggests a well agreement with the experiment result.

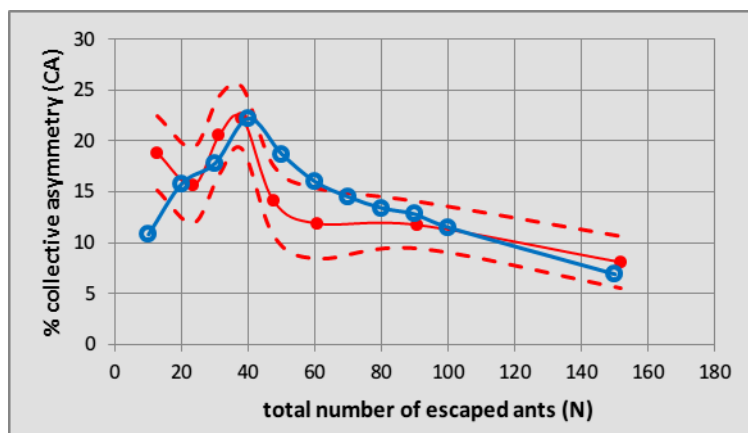


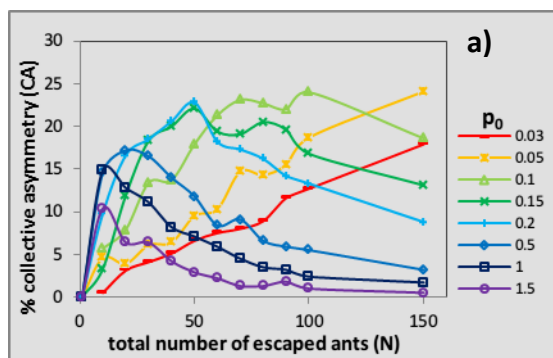
Figure 5: The solid red circles correspond to the experiment result, which is shown in figure 1 in detail. The open blue circles respond to theoretical simulations with the parameters: $L=20$, $p_t=1$, $p_0=0.25$, $\Delta p=0.006$, and be averaged over 300 runs of a simulation.

We can understand the phenomenon from an intuitive point of view. The direction of the movement of ants is affected by pheromones deposited by other ants, which enlarges the asymmetry of directions of movement induced by random fluctuations and eventually leads to the asymmetry of escaping number in the macro level. The interaction occurs locally within a constant detection range, so the density comes to be an important factor. At a very low density, the interaction among the ants can be too weak to produce asymmetry, and when the density increases, the asymmetry may increase accordingly. However, due to the limitations of the biological perception, which is defined for the difference threshold of concentration of pheromone, a too large density of ants can deposit so much pheromone that behavior of ants can be more like random particles. So CA declines monotonously when N is large enough.

Discussion

Instead of vision-based Vicsek-like models, we constructed an extreme simple model, in which ants deposit and respond to alarm pheromones, and successfully explained our experimental results on the symmetry breaking with respect to the density of ants (here we change total number of escaped ants while keeping the area the same).

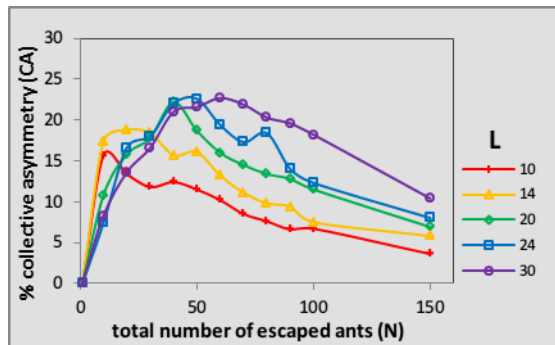
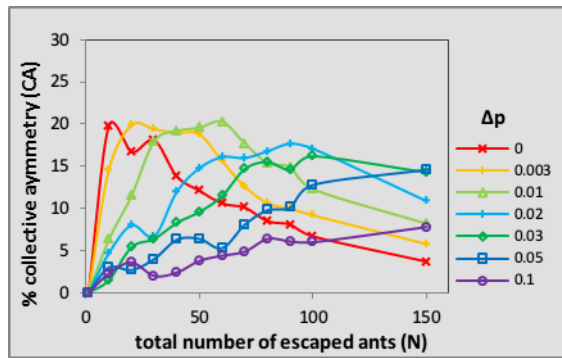
For a deeper comprehension for the model, we then discuss the quantitative simulation results by changing the value of the parameters: p_0 , Δp , p_t , and L . As stated above, p_t is always equal to 1 as a reference value. We set p_0 , Δp , and L as variables respectively while the other two are set as fixed value equal to the set of parameters in figure 3. Each simulation is repeated by 300 times. The results are shown in figure 6. The detailed shape of the curves produced from different sets of parameters can be quite different. Generally, the increasing p_0 plays a role in shifting the maximum of CA left on the X-axis and decreases the maximum. The increasing Δp also decreases the maximum, but shifts the maximum to the right on X-axis. When the area of the cell is enlarged with the increase of L , the maximum is shifted to the right and enlarged.



b)

c)

Figure 6: All points are averaged over 300 times of simulation. a) The fixed parameters are $L=20$ and $\Delta p=0.006$. p_0 discretely ranges from 0.03 to 1.5. b) Δp varies discretely from 0 to 0.1, and $L=20$, $P_0=0.25$. c) $P_0=0.25$, $\Delta p=0.006$, L ranges discretely from 10 to 30.



A good model not only lies in its ability to explain phenomenon but also to make correct predictions. For example, we expect an obviously lower CA by exchanging the cell into a smaller one, according to figure 6, picture C). p_0 and Δp can also be controlled in experiment. The amount of alarm pheromone deposited by an ant is related to the degree of panic, which may be controlled by introducing difference doses of repellent liquid.

Acknowledgement

Author contributions

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Surprisingly, our experimental results indicate that the degree of symmetry breaking does not monotonically increase as shown by the Vicsek-like model performed by Altshuler, etc. (10), but after a maximum of symmetry breaking it declines as the number of ants increases. That the simulation results from the Vicsek-like model do not match our experimental results qualitatively suggests that the Vicsek-like model may not be the “right” model for the collectively escaping ants under panic.

Method 章的语言要改成自己的话。

图：矢量