Phase Transitions in Insect Populations

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Abstract

Abstract: This paper will examine recent work on the phase transitions that appear in collective behavior of insect populations. Basic models will be defined and then compared with experimental results. These results indicate that the collective behvior can be predicted without having to model the complexity of the individual biological entity.

I   Introduction

Physicists have long been familiar with the concept of magnetism, the ability of a non-magnetic material to become and remain magnetized after it is exposed to an externally applied field [1]. It has also been shown that a material will develop a magnetic moment as it is cooled below some critical temperature even in the absence of an external magnetic field. This is a simple, everyday example of a system with an emergent property. Recently, the concept of emergent properties in biological systems has become an area of increased study. Biologists have documented these phenomena and tried to explain them in terms similar to those that describe physical systems. The key concept is that the patterns or behavior of the group can be described by considering the interactions between individuals or the interaction between an individual and the environment without having to consider the complexity of the animal [1].

This paper will look at the emergent properties of animal populations, specifically insects [2],[3]. Ants, termites, wasps and locusts exhibit such behavior when foraging, migrating, or building a nest. Experimental results have not only demonstrated the existence of these phases and their transitions, but have also demonstrated some of the factors that lead to the particular group behavior.

The first section will examine recent papers that document the behavioral phases and transitions in ant colonies. Recent models will be discussed and compared with experimental results. The second section will address recent work on the phase transitions of marching patterns that have been observed in locust populations. Also, a simple theoretical model that attempts to explain the aggregation of locusts will be considered and its basic concepts discussed. In the final section, we will consider how these results may be applied to existing practical problems.

II   Ant Trail Formation

To watch a solitary ant, it is hard to imagine that there is any pattern to its motion. A single ant will wander wildly across its environment, but the popular image of a column of ants marching between a food source and their nest is common in our society. How is it that ants can form a stable marching pattern when the natural tendency of every ant is to follow a random walk?

Biology has already provided part of the answer. As an ant moves, it leaves behind a chemical (commonly called a pheromone) trail that other ants can detect [1]. Other ants can pick up this trail and follow it, all the while leaving behind their own pheromones, reinforcing the trail, and subsequently making it easier for even more ants to detect the trail.

At first glance, this would appear enough to explain the ordered pattern of marching ants. However, several factors work against a trail being sustained.

The chemical the ants lay down to create the trail is volatile and will evaporate quickly if it not reinforced by another ant [1]. In order to reinforce the trail, another ant must first locate the trail while it is walking about randomly. If the population is too sparse it is unlikely that another ant will discover the trail before it vanishes and the trail will be lost. Likewise, there is also a probability that an ant will lose a trail that it is following. This probability is greater on a lesser reinforced trail [3]. These are factors that must be included in even the simplest models of ant trail formation.

MODELS

An active walker model for trail formation was developed by Helbing, *et al.* and has proven to be useful in describing the formation of complex structures, biological aggregates and directed motion [4]. The particles in this system are initially assumed to follow a random walk. However, an active walker is distinguished from a random walker by its interaction with the environment. Active walkers are able to change the environment within a particle's local region. In the case of ants this is done by leaving a chemical substance to mark the trail. This marking can then be picked up by other active walkers and allow a trail to be formed and strengthened.

Several adjustments were made to account for environmental factors that limit trail formation. These include (1) the use of two chemicals to mark trails depending on whether an ant is looking for food or has already found a food source, (2) the possibility of an ant not reacting to a marker, (3) an inertia to keep an ant moving in its current direction, and (4) the volatility of the chemicals. Taking account of these physical behaviors, the active walker model is shown to agree with observed trail formation of ant colonies [4].

The second model that is considered was developed by Beekman *et al.* and is designed to predict the increase in the number of ants that are foraging at a food source [3]. In this model, the increased number of ants, x, foraging at a source which has a trail leading to it is determined as a function of the following parameters:

1) the total number of individuals in the ant colony (n)

2) the probability per unit time that an individual ant discovers the food source randomly (α)

3) the probability per unit time that an individual ant discovers the food source by following a trail (βx)

4) the probability per unit time that an individual ant loses the trail is given by s/(s+x)

Here α, β, and s are all constants related to characteristics of the environment and individual ants. From this information, Beekman *et al.* were able to write down a mean field equation (Eq.1) for the time rate of change of x. In seeking equilibrium solutions dx/dt was set to zero and Eq. 2 was found [3].

$$\frac{dx}{dt} = (\alpha - \beta x)(n - x) - \frac{sx}{s + x} \tag{1}$$

$$\beta x^3 + (\beta s + \alpha - \beta n)x^2 + (s(1 + \alpha - \beta n) - \alpha n)x - \alpha ns = 0 \tag{2}$$
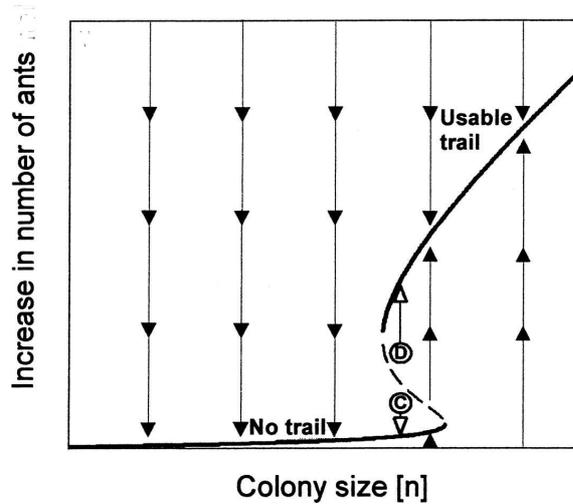
Figure 1: Increase in ants at the feeder [x] vs. Colony size[n], from model [3]

Immediately, it is clear that the number of ants, x, at the food source is a nonlinear function of the colony size, n. The behavior of x is dependent on the values chosen for α, β, and s. Specifically, for Eq. 2, there will be either one solution or three solutions depending on the values of the given parameters. Through observational data, realistic values for α, β, and s can be assigned.

If the equation for the increased number of ants at the feeder has only one solution then the increase in the number of ants is continuous and the phase transition is second order. However, as seen in Fig. 1, for the situations where Eq. 2 has three solutions there are two equilibria that are stable (solid lines) and one that is unstable (dashed line). The effect is that the phase transition is first order. These results are tested in the Beekman *et al.* paper and will be discussed in the following section.

EXPERIMENTAL RESULTS

The focus of this section is on the work done and published by Beekman *et al.* The experiment was set up in the laboratory so that colony size could be controlled and easily varied. Pharaoh's ants were placed in a nest box within a large plastic box that replicated a foraging environment. A single feeder was placed in the box 50cm away from the nest box and filled with a sugar solution. The reader is directed to the original article for the specific details of the setup and the reasons for the choice of Pharaoh's ants. For a given colony size, measurements were made of the number of ants at the feeder at fixed time intervals so as to determine the increased number that were foraging. A control measurement was made without the feeder in place to determine an approximate value for α, the probability of a random discovery of the food source.

The purpose of the experiment was to determine the ability of an ant colony to create and sustain a foraging trail as a function of the number of individuals

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size	N	mean	variance	prop.
100	23	0.49	0.57	0.48
200	23	0.85	1.25	0.17
300	23	0.56	1.65	0.3
400	23	0.42	2.01	0.43
500	34	0.79	1.36	0.35
600	36	0.48	1.03	0.28
700	30	2.56	3.29	0.33
800	69	4.09	3.24	0.16
900	36	5.27	6.61	0.14
1000	33	9.44	10.00	0.06
1100	33	7.23	11.58	0.15
1200	30	5.60	4.24	0.2
1500	36	12.27	7.98	0.03
1700	15	12.44	4.05	0
2000	18	18.99	10.92	0
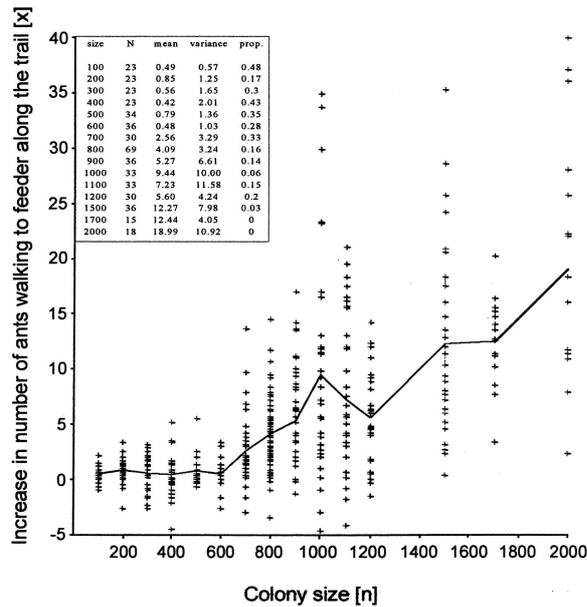
Figure 2: Increase in ants at the feeder [x] vs. Colony size[n], from experiment [3]

in the colony. It is important to note that, unlike the model, not all the ants in the colony are looking for food. As expected from reason and theory, an increase in colony size leads to an increase in the number of ants feeding at the source. The results from this experiment are shown in Fig. 2.

For colonies of fewer than 600 ants, no increase in the number of individuals feeding at the source is seen. This indicates that these small colonies are unable to sustain a trail that leads to the feeder. In this scenario the only means for the nest to locate food is by chance.

For colonies with more than 600 individuals, the results shown in Fig. 2 show that the number of ants at the feeder is increasing. These larger colonies are capable of producing and sustaining a trail; however, as can be seen from the results of the single trials (the crosses in Fig. 2) the existence of a trail is not guaranteed just because the colony is larger than a critical size. Is this evidence of the unstable equilibrium, and first order phase transition, predicted by the theory and seen in Fig. 1B? Can the variability of the path stability be explained in terms of other factors?

As mentioned earlier, in this experiment the number of ants foraging for food was not necessarily the same number as ants in the colony. If the randomly chosen nest for a given trial was constituted of a higher (lower) percentage of foragers than average then the nest would be more (less) likely to form a trail than on average. This variability in the makeup of the nest could be a cause of the observed instability of trail formation in intermediate sized colonies. Likewise, the theory predicts that there is a range of colony size that is in an unstable equilibrium. The tendency of the trail to form or disappear

for these colonies is dependent on the initial conditions. In other words, a trail should form if sufficiently many ants locate the source at the beginning. It is unable to determine if the above results are conclusive proof of a first-order phase transition in the foraging behavior of the ants. However, a second experiment was performed by Beekman *et al.* to ascertain whether the behavior of the colony exhibits a phase transition.

Beekman *et al.* directly compared the trail building of small (300 ants) and intermediate (700 ants) sized colonies in trials with varying initial conditions. The experimenters chose to adjust was the number of ants that initially discover the food source. In order to do so, the feeder was initially placed next to the nest box and remained there until a sufficient number of ants (20-40) were feeding. At this point, the feeder was removed to the original distance of 50cm and all subsequent measurements were the same as described above. By positioning the feeder close to the nest and then moving it away the ants are able to form an initial trail before resuming their normal foraging behavior. The results of this experiment were then compared to the above results when the ants discovered the food source randomly to determine if any phase transitions were occurring.

The results for both colonies are shown in Fig. 3. In the small colony, no statistically significant increase in the number of ants at the feeder was observed when helped to start a trail. This is the same result as was seen in the original setup when the ants discovered the feeder by chance. These results indicate that a small colony is unable to either form a trail or sustain an existing trail.

Intermediate colonies, though, display a different behavior. When helped to form an initial trail, the number of ants at the feeder increase by an average of 4.6±3.3. However, without an initial trail the increase was only 2.6±3.3. As well, a similar effect can be seen by the distribution shown in Fig. 3. The reader is again urged to read the original article for a discussion of the statistical methods used to analyze the data.

The results of the trials done on intermediate sized colonies seem to indicate that trail formation and maintainability are dependent on the initial conditions. These colonies exhibit two stable foraging equilibria indicating both a first order phase transition between disordered (no trail) and ordered (sustained trail) feeding. The dependence on initial conditions are also indicative of hysteresis, although this could be true for smaller or larger colonies if the values of α, β, and/or s were different. (The theoretical prediction is that hysteresis would occur for any system which has three solutions to Eq. 2.) In this experiment, the results obtained by Beekman *et al.* confirm the predictions made by the theory that was described above.
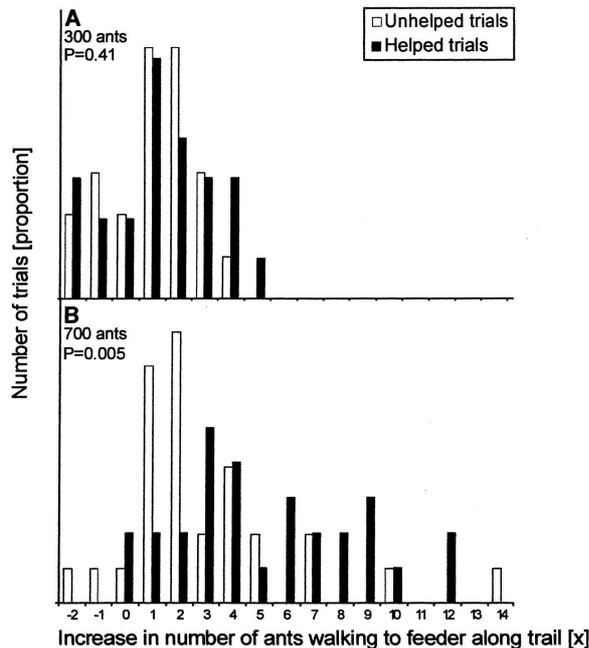
Figure 3: Distribution of [x] values for many trials [3]

III Locust Swarms

A solitary locust is an inconsequential pest to mankind. These solitary locusts also prefer a state where they avoid other locusts. However, a change can occur in locust behavior where the solitary phase is abandoned in favor of a gregarious state. In this state, locusts are actively looking for one another and large ($\sim 10^9$ individuals) swarms form. Plagues of locusts are capable of destroying vegetation on the scale of tens to thousands of kilometers and wreaking environmental and economic damage [5].

The discussion that follows will focus not so much on the processes that cause these large swarms, but more so on how these large swarms are able to migrate in such a uniform pattern. The first discussion will detail some of the properties of a model that describes the self-ordered motion of a group of individuals [6]. These individuals are commonly referred to as self-propelled particles (SPPs). The last section will look at an experiment that was designed to test the ordering of moving locusts. The phases were examined as a function of density and the results compared to the predictions of the SPP model.

MODEL

The following model was developed by Vicsek *et al.* to describe systems with particles undergoing interactions defined by basic biological rules. For the model considered here, the behavior of the individual particles are governed by a predetermined rule with fluctuations taken into account. This rule is defined as follows: "[A]t each time step a given particle driven with a constant absolute velocity assumes the average direction of motion of the particles in
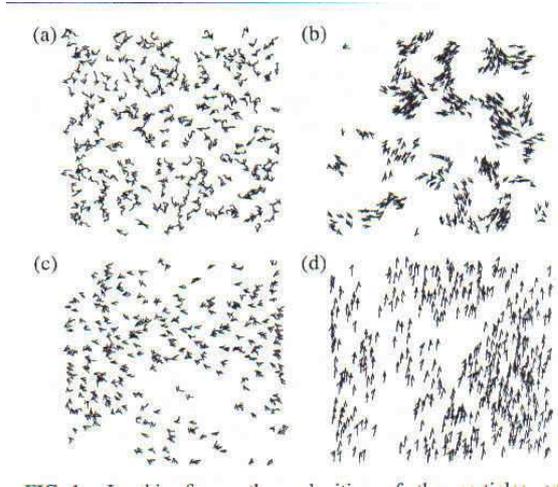
Figure 4: Simulated collective behavior for varying densities, noise [6]

its neighborhood of radius r with some random perturbation added." (Vicsek *et al.*)

This rule, although simplistic, is analogous to the one that governs the spin magnets described in the introduction. At low temperatures, the magnetic spins tend to align in the same direction. In the SPP model, also, the fluctuations are to be in analogy to random perturbations in the spin magnets resulting from temperature.

Several simulations were run and reported by Vicsek *et al.* Their work is based on the following equations:

$$\mathbf{x}_i(t+1) = \mathbf{x}_i(t) + \mathbf{v}_i(t)\Delta t \tag{3}$$

$$\theta(t+1) = <\theta(t)>_r + \Delta\theta \tag{4}$$

where v_i is the velocity of given particle, which has a fixed speed v for all times and a direction given by θ. The quantity $\langle\theta(t)\rangle_r$ is the average direction of all particles that are a distance r or less away from particle i . $\Delta\theta$ is the fluctuation term and is randomly chosen such that $|\Delta\theta| \leq \frac{\eta}{2}$. The simulations were done on systems of particles in a two-dimensional environment of area L^2 with periodic boundary conditions. The density of the system $\rho = \frac{N}{L^2}$ is constant and η is the noise in the system. By varying these quantities during the trials collective motion can be examined.

Fig. 4 [6] shows the results of several simulated trials for a system described by the above parameters. All these figures represent systems with N=300 particles where the particles current position and velocity are given by the arrow and its recent path is the drawn curve. Fig. 4(a) is a representative initial state with a random pattern of positions and velocities. Fig. 4(b)-(d) show the system's pattern after some time has elapsed for various density and noise values. For a system of low density and low noise (Fig. 4(b)) the particles form
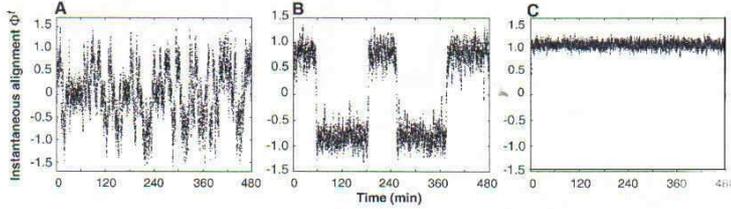
Figure 5: Predicted alignment as a function of time from SPP model [2]

small, coherent groups. However, the groups are not correlated to each other. The behavior of dense populations with large fluctuations (Fig. 4(c)) the particles are moving randomly. Lastly, in Fig. 4(d), populations with a high density but with only small fluctuations exhibit correlated motion throughout the entire population. This is the ordered state of collective behavior.

This model, its basic features, and predictions are the starting point for the work done by Buhl *et al.*. The experimental setup and results of this paper will be discussed below. Their model differs from the SPP model described above in that this simulation is one-dimensional and the rules are given by [2]:

$$x_i(t+1) = x_i(t) + v_0 u_i(t) \tag{5}$$

$$u_i(t+1) = \alpha u_i(t) + (1-\alpha)G(<u(t)>_i) + \zeta_i \tag{6}$$

$$G(u) = \frac{u}{2|u|}(u+1) \tag{7}$$

where a particle's position is x_i, its dimensionless velocity is u_i, α is a weighting factor, ζ is the noise term, and G is a function that defines the adjustment of the velocity to the neighboring particles. The results of running this simulation are shown in Fig. 5 [2]. The quantity $\Phi^t = \langle u(t) \rangle$ is used to measure the ordering of the system and allows for experimental comparisons later. Fig. 5(A) shows that the predicted behavior of a low density population is no sustained collective motion (disordered state). For systems of intermediate density, Fig. 5(B), an aligned motion is expected. However, the direction of alignment is predicted to randomly change. As seen if Fig. 5(C), high density populations should exhibit a stable, aligned collective motion (an ordered state). These conclusions are directly tested below.

EXPERIMENTAL RESULTS

Buhl *et al.* used desert locust confined to a ring-shaped environment to test for the ordered and disordered states and any phase transitions between the two. The locust were then observed over a period of time and the position and orientation of each locust analyzed with computer tracking software. To measure the alignment of the locusts the orientation angle had to be rigorously defined. This angle, χ, is defined as the angle between the line from the center of the ring to x(t) and the line from x(t) to x(t+1). The alignment is then
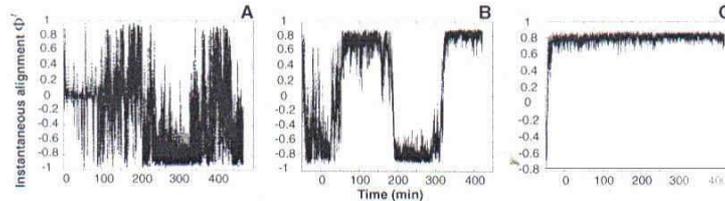
Figure 6: Observed alignment as a function of time [2]

defined (where m is the number of moving locusts) as:

$$\Phi^t = \frac{2}{m\pi}\Sigma_{i=1}^m \chi_i^t \tag{8}$$

The locusts were observed and at each time step the alignment was calculated. The results are shown in Fig. 6(A)-(C) [2] for low, intermediate, and high densities, respectively. At low densities, the locusts do not exhibit any sustained alignment. As the density increases the locust begin to display collective motion. However, at these intermediate densities, the alignment will spontaneously switch direction. At even higher density, though, the locust have an aligned collective motion with a lifetime greater than the length of the trials.

A comparison of the experimental results of Fig. 6 to the model simulations (Fig. 5) seem to indicate that the model is an accurate prediction of locust aggregation. However, much like the results of Beekman *et al.* , further analysis was done in order to determine if observed transition between ordered and disordered marching agreed with the SPP model predictions. To this end, Buhl *et al.* generated the plots shown in Fig. 7 [2]. The experimental (A,B) and theoretical (C,D) results are all in good agreement as the density increases. Specifically, the distribution of the mean alignment (Fig. 7 A,C) clearly move from a continuous spectrum to two well-defined peaks as density is increased. It is clear that high density populations are strongly aligned in either the clockwise or counterclockwise direction. Likewise, the time that is spent in coherent motion (Fig. 7 B,D) should be longer than the observation length.

In light of the experimental results published by Buhl *et al.* the validity of the SPP model has been demonstrated for locusts and can be applied to other societies that are governed by rules similar to those defined above. It is therefore expected that other species will exhibit phase transitions between disordered and ordered motion as density is increased.
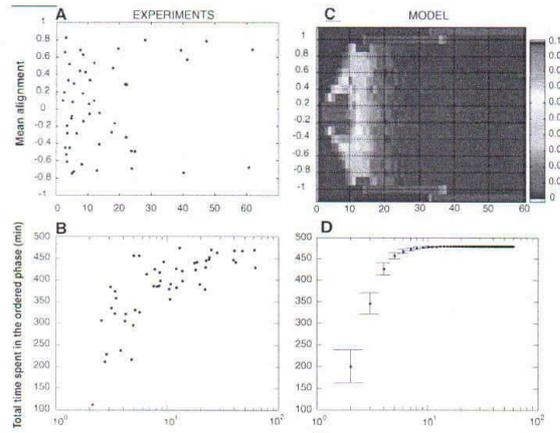
Figure 7: Mean alignment (A,C) and Time spent in aligned state (B,D) for observed and modelled locust populations as a function of density [2]

IV   Conclusion

The results of the work done by Beekman *et al.* and Buhl *et al.* verified that the models in use are accurate predictors of phase transitions and ordered behavior in insect colonies. The practical applications of these results are two-fold. The active walker models can be extended to human traffic and can be applied to pedestrian pathways in urban environments [4]. Likewise, the SPP model has demonstrated that the collective motion of dense populations is more predictable over time than the motion of smaller populations. The predictability of denser populations may aid in identifying and controlling locust destruction and allowing for better use of resources [5].

In a greater sense, the success of these experiments have shown the ability of simple models to predict complex patterns and emergent behaviors. Most notably, in the same way that one does not have to resort to quantum effects to explain the emergence of magnetization, we have not had to account for the ability of animals to think or use other complex biological behaviors in order to explain the observed phase transitions mentioned above [1]. Perhaps, despite the complexity of its members, biological systems can soon be understood in terms of physical systems that are now familiar.

V   References

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