

APPM 3010 Final Project: Foraging Patterns in Ants

UNIVERSITY OF COLORADO BOULDER
DEPARTMENT OF APPLIED MATHEMATICS

AUTHOR INFORMATION

Nina Hooper¹

Allison Liu²

Aria Mundy³

¹Chemical Engineering, SID: 108562348

²Applied Mathematics, SID: 106535982

³Mechanical Engineering, SID: 108757957

Contents

1	Introduction	2
2	One-Dimensional Model: Idealized Recruitment of Ants	2
2.1	A 1-Dimensional Model for Ants	2
2.2	Results of the 1-Dimensional Model	4
3	3-Dimensional Model: Lost Ants and Multiple Food Sources	6
3.1	A 3-Dimensional Model for Ants	6
3.2	Results of the 3-Dimensional Model	8
4	Cellular Automata	12
5	Conclusion	14

1 Introduction

Swarm intelligence is the seemingly intelligent behavior that emerges from the collective behavior of a large number of autonomous agents. These emergent behaviors arise from simple rules followed by individual entities, which makes swarm intelligence a complex and fascinating area of study [1].

In biology, swarm intelligence is often studied in insect populations. An impressive example of this collective behavior involves the large-scale traffic control of foraging ants. Analyzing foraging activity provides a lens to better understand the social behavior of ants, and several models have been proposed that attempt to describe their foraging patterns.

In this paper, we will explore two major types of foraging patterns. The first model involves large colonies of ideal foragers exploiting one food source, and applies the logistic equation to model such a scenario. The second model takes into account the fact that foragers can become lost and also exploit multiple food sources, which more accurately represents a realistic physical scenario [2]. We replicate and compare results from *Deneubourg et al.* and explore their 3D model using different initial conditions, focusing primarily on understanding the bifurcation diagrams at different locations over time. Finally, we extend our understanding of the model using cellular automata to visualize specific scenarios identified in the differential equation model.

2 One-Dimensional Model: Idealized Recruitment of Ants

2.1 A 1-Dimensional Model for Ants

Recall that the logistic equation is of the form

$$\dot{x} = rx \left(1 - \frac{x}{K}\right). \quad (1)$$

This is one of the simplest models for growth of organisms in a population, where $x(t)$ is the population at time t , $r > 0$ is the growth rate, and K is the carrying capacity.

Plotting \dot{x} versus x , we can see that the fixed points of the logistic equation occur at $x^* = 0$ and at $x^* = K$ (Figure 1). Analysis of the vector field of the logistic equation reveals that $x^* = 0$ is an unstable fixed point, and $x^* = K$ is a stable fixed point [3].

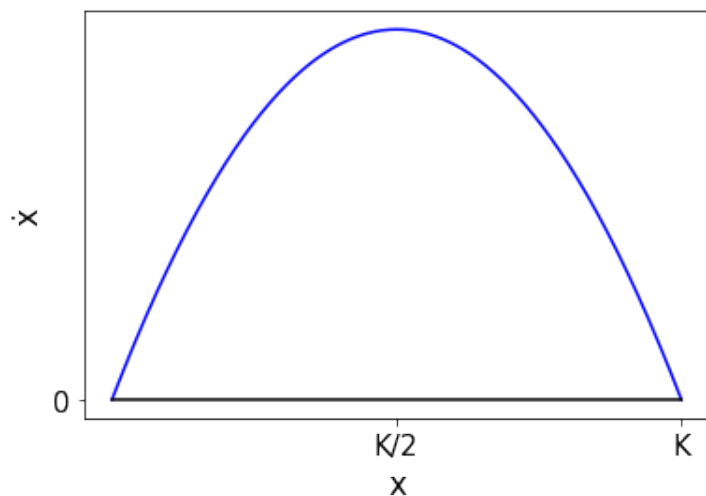


Figure 1: Vector field for logistic model.

Biologically, this implies that a small population will grow exponentially fast from $x = 0$, before reaching an inflection point at which point growth slows. In addition, if the population x is disturbed slightly from K , the disturbance will decay monotonically, and as time goes on, the population will approach K , the carrying capacity [3].

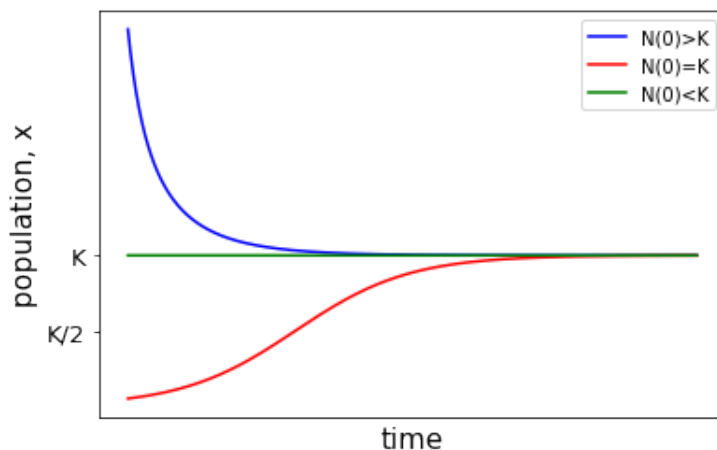


Figure 2: Population size versus time for various initial conditions.

We can plot the population with respect to time for various initial conditions (Figure 2). Note that when $N(0) < \frac{K}{2}$, the population growth initially accelerates until $N(0) = \frac{K}{2}$, and the population growth slows down as it nears the carrying capacity. If $N(0) > K$, then the initial population exceeds the carrying capacity, and it will decrease and approach the carrying capacity. If $N(0) = K$, then the population stays constant.

It is important to note that the logistic model greatly simplifies the actual behavior of populations, and modeling actual population growth of organisms is much more complicated due to behavioral and environmental factors that the logistic model does not take into account. However, the simplicity of the logistic model makes it a fundamental tool for understanding important aspects of population behavior, and thus it is often used to model populations that have a tendency to grow from zero to some carrying capacity K .

A variation of the logistic equation defined in Equation (1) can be used to model the number of ants in a colony that exploit a single food source. Initially, growth is exponential, but after some time, a decrease in the growth rate is observed, as there are less and less ants that have not yet been recruited. The number of ants at the source reaches a plateau value when the rate of recruitment is equal to the rate of departure from the food source. The time evolution of the recruitment can be modeled using the following equation:

$$\dot{Z} = aZY - bZ, \tag{2}$$

where Z is the number of ants around the food source, Y is the number of unrecruited ants, and a and b are rate constants. Note that $Z + Y = N$, where N is the population of the society, which is a finite number [2]. Note that this equation is highly idealized, and the actual behavior of ants is not as deterministic as assumed by the model due to factors such as the random behavior of individual ants, as well as trail-following error.

2.2 Results of the 1-Dimensional Model

Referring to Equation (2), the parameters were experimentally determined by *Deneubourg et al.* to be $a = 8 \times 10^{-4}$ and $b = 72 \times 10^{-3}$, and $N = 270$ [2]. With these parameter values, we can see that Equation (2) exhibits the same behavior as the logistic model, as shown in Figure 3.

The number of ants at the source reaches a plateau value when the recruitment rate, aZY , is equal to the rate of departure from the food source, bZ . With the given parameter values, this occurs at $Z = 180$, and can be regarded as the carrying capacity. Given an initial condition that is greater than this carrying capacity, the rate of departure dominates over the rate of recruitment, and the population at the food source decreases and approaches the carrying capacity. In the physical system, this can be interpreted as slow recruitment due to a low number of recruitable ants. Given an initial condition that is less than the carrying capacity, the rate of recruitment dominates over the rate of departure, and the population at the food source increases and approaches the carrying capacity.

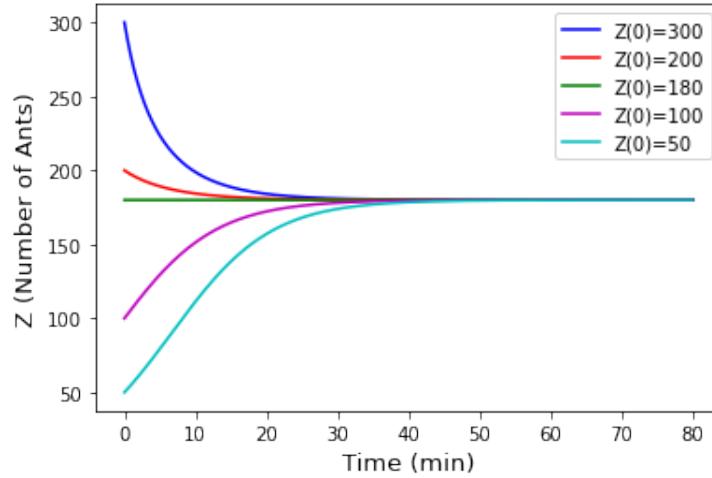


Figure 3: Number of ants at the food source versus time for various initial conditions.

We can analyze Equation (2) to determine where the fixed points occur. Solving for where $f(Z) = aZY - bZ = aZN - aZ^2 - bZ = 0$, we obtain two fixed points: $Z^* = 0$ and $Z^* = N - \frac{b}{a}$. The stability can be characterized by analyzing $f'(Z) = AN - 2aZ - b$. For the fixed point at $Z^* = 0$, $f'(0) = AN - b$, which is stable when $N > \frac{b}{a}$, and unstable when $N < \frac{b}{a}$. For the fixed point at $Z^* = N - \frac{b}{a}$, $f'(N - \frac{b}{a}) = b - AN$, which is stable when $N < \frac{b}{a}$, and unstable when $N > \frac{b}{a}$.

These stability conditions yield the following bifurcation diagram:

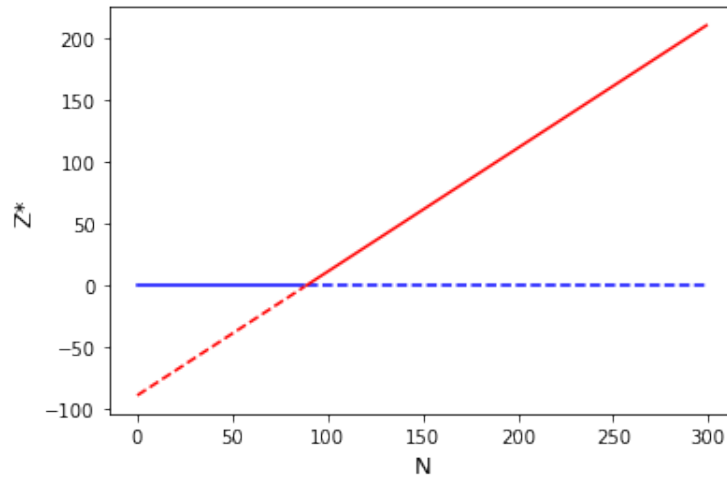


Figure 4: Bifurcation diagram for Eq. (2) with the experimentally determined parameters.

Figure 4 implies that a transcritical bifurcation occurs in this system. Such bifurcations often occur in scientific situations where where a fixed point must exist for all values of a

parameter and never disappear. Transcritical bifurcations are common in logistic models, as there is always a fixed point at zero population, and this fixed point may change its stability when the parameter is varied [3].

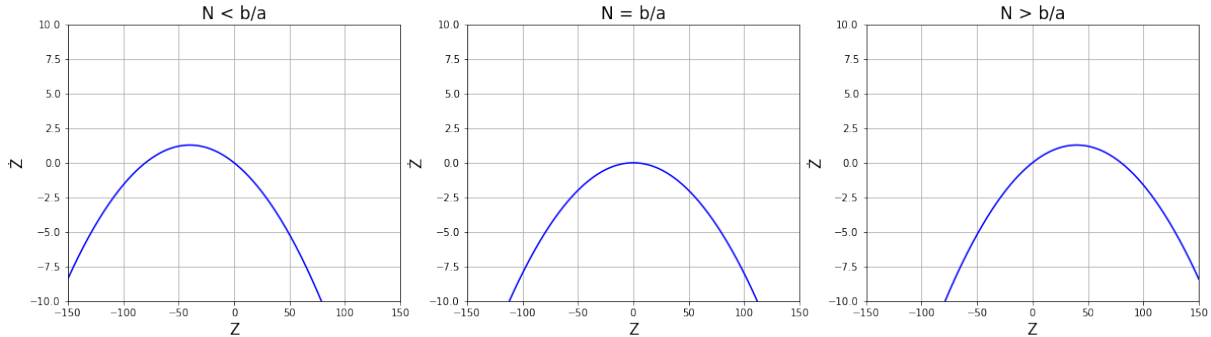


Figure 5: Vector field for Eq. (2) with the experimentally determined parameters as N varies. Note that only fixed points at $Z \geq 0$ are physical.

From Figure 5, we see that the vector field varies as N varies. Note that there is a fixed point at $Z^* = 0$ for all values of Z . Shown on the left subplot is the case where $N < \frac{b}{a}$, in which there is an unstable fixed point at $Z = N - \frac{b}{a}$ and a stable fixed point at $Z = 0$. As N increases the unstable fixed point approaches the origin, and coalesces with it when $N = \frac{b}{a}$, as shown in the middle subplot. Shown on the right subplot is the case where $N > \frac{b}{a}$, where there is a stable fixed point at $Z = N - \frac{b}{a}$ and an unstable fixed point at $Z = 0$. Note that at the bifurcation, the two fixed points essentially switch their stability.

Since the population Z must be greater than or equal to zero, this means that only the fixed points at $Z \geq 0$ are physically possible. Thus, $Z^* = N - \frac{b}{a}$ when $Z^* > \frac{b}{a}$ and $Z = 0$ when $Z^* < \frac{b}{a}$ are the only stable fixed point of the physical system. Thus, $N - \frac{b}{a}$ can be interpreted as the carrying capacity, and thus if the initial population is large enough it increases until reaching its carrying capacity.

3 3-Dimensional Model: Lost Ants and Multiple Food Sources

3.1 A 3-Dimensional Model for Ants

While Equation (2) is a sufficient way to model the foraging behavior of ideal ants given a single food source, one may wish to analyze a more complicated scenario; for example, the behavior of ants when two food sources are introduced. We can also further develop a model

to account for lost recruits, which are ants that have lost the trail, and search the ground for a period of time prior to returning to the nest. Although the lost ants make for a lower efficiency in exploiting the first food source found, wandering ants are critical to discovering other food sources if available. This can often be advantageous to an ant colony.

We will now introduce an attempt to analyze a more complicated three-dimensional model that describes foraging behavior when two identical food sources are offered at the same time to a society. It can be shown that the number of ants around each source grows symmetrically until an abrupt change in kinetics occurs, and consequently, one source becomes more exploited than the other. The dynamics of this system are modeled using the following system of equations:

$$\dot{X}_1 = aX_1f(N - (X_1 + X_2) - E) - bX_1 + cE \quad (3a)$$

$$\dot{X}_2 = aX_2f(N - (X_1 + X_2) - E) - bX_2 + cE \quad (3b)$$

$$\dot{E} = a(X_1 + X_2)(1 - f)(N - (X_1 + X_2) - E) - pE - 2cE \quad (3c)$$

Where X_1 and X_2 represent the number of ants at sources 1 and 2, respectively, E is defined as the number of lost ants, and N is the total number of potential and actual foragers. Model parameters a , b , c , and p stay constant in this report and are summarized in the table below. f is the fraction of ants that successfully find a food source, while the value $(1-f)$ is the fraction that become lost. If f is taken to be constant, this model is symmetric, and Equations (3a) and (3b) are equivalent. However, in reality, this f value is not constant. When ants are following a trail to a food source, they are following a pheromone trail laid out by other ants. The more ants that follow a given trail and release their pheromones, the stronger that trail becomes. Thus, f for a given trail increases with the number of ants on that trail: $f(X_i) = \frac{X_i}{g+X_i}$, where g is a constant specified as 24.3. At high X_i values, f asymptotically approaches 1. Similarly, $f(E) = f(X_1 + X_2) = \frac{X_1+X_2}{g+X_1+X_2}$ [2].

The paper we analyzed only reported asymmetric results of this model [2]. In this report, the model is analyzed both as a symmetric function with f as a constant, and as an asymmetric function with f defined as above. The asymmetric function is compared to the results of [2].

Parameter	Meaning	Value
a	Number of ants recruited per source ant per potential forager	0.001
b	Inverse of average amount of time an ant spends at a source	0.1
c	Probability of lost ants finding another food source per time	0.018
p	Inverse of time before a lost ant returns home	0.033
g	Scaling constant	24.3

3.2 Results of the 3-Dimensional Model

The system of equations describing the ants' movement with multiple food sources present was sufficiently complicated that it was not possible to analyze analytically. Extended attempts were made to solve for fixed points by hand and by use of Mathematica before we concluded that the system would have to be analyzed numerically instead. It was possible to create orbit diagrams by plotting the long-term behavior of this system under different parameters; however, it was not possible to determine unstable fixed points or analytical equations for stable fixed points.

When f is set to a fixed value and the system of equations describing the ants at the two food sources is symmetric, the orbit diagram looks remarkably similar to that of the transcritical 1-dimensional model, as shown in Figure 6. Note that the plots shown are all for an initial condition of $y(0) = [X1, X2, E] = [10, 0, 0]$, and an f value of 0.7. However, the general overall shape of the bifurcation diagram and the trajectories remains the same when changing these values.

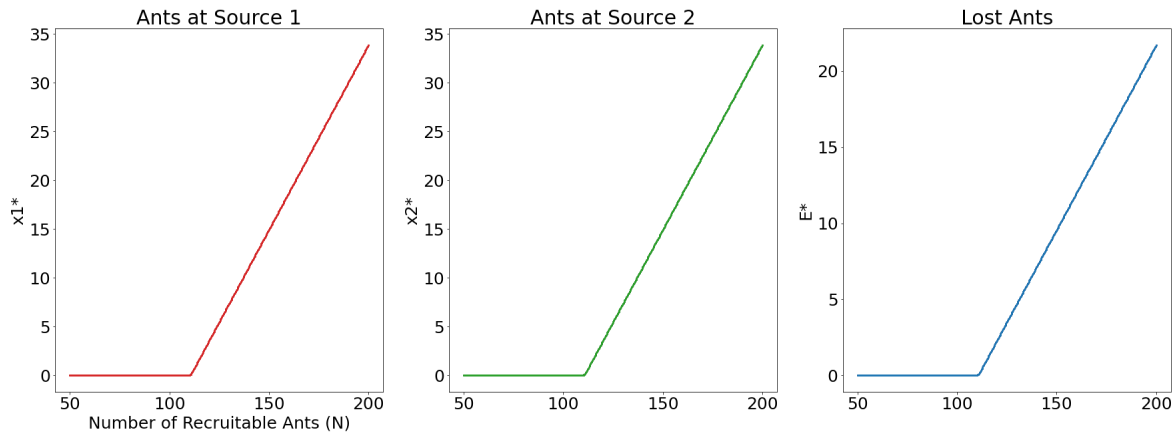


Figure 6: Orbit diagram showing transcritical bifurcation in the stable fixed points of the symmetric 3D model. $y(0) = [X1, X2, E] = [100, 0, 0]$, $f=0.7$

At low N values, there is a stable fixed point at which no ants congregate at any food source ($X1^* = X2^* = E^* = 0$). This occurs when there are few recruitable ants in the colony; ants who know the locations of the food sources are not able to recruit others quickly enough before they all become lost and eventually return home. The trajectories of these ant numbers can be seen in Figure 7b for the case when $N = 100$, before the transcritical bifurcation occurs. Although some lost ants find the second food source, they are also not able to recruit others to that source before getting lost. After the bifurcation, the $X1^* = X2^* = E^* = 0$ fixed point becomes unstable. When the initial condition is greater than 0, the two food sources

ultimately have the same number of ants at them in the long-term with the number increasing approximately linearly with population size. The trajectory of one of these N values is shown in Figure 7a. The symmetry in this model occurs because neither of the food sources has advantage over the other thus the ants end up split evenly between them. Mathematically, it occurs because the \dot{X}_1 and \dot{X}_2 equations are equivalent with regards to their respective X variable.

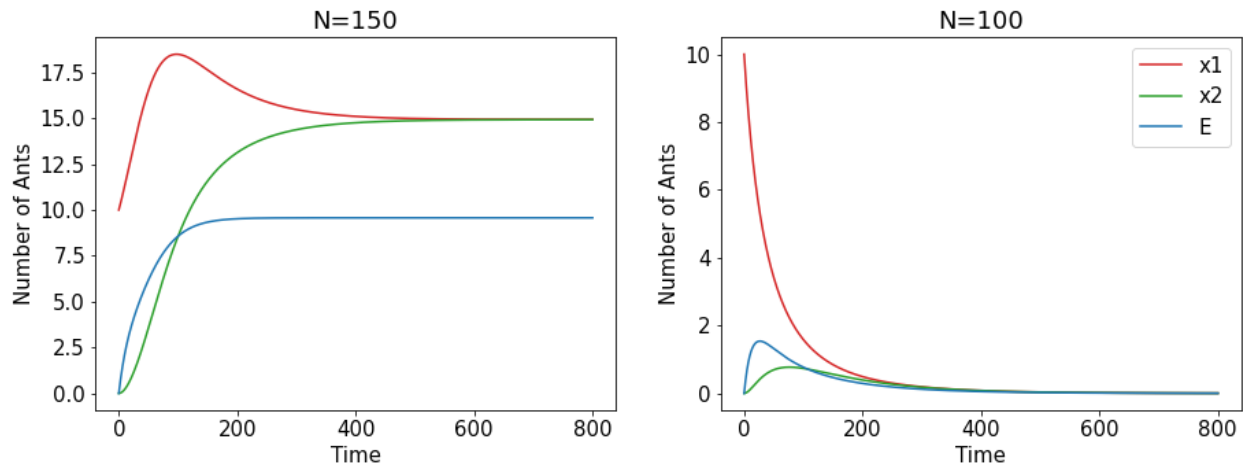


Figure 7: Trajectories of ant populations before the transcritical bifurcation in the symmetric function (right) and after (left). $y(0) = [X_1, X_2, E] = [100, 0, 0]$, $f=0.7$.

When the model takes into account the pheromones of the ants, which decreases the likelihood of ants becoming lost on a well-traveled trail, more interesting behavior emerges. Figure 8 shows the bifurcation diagram when $y(0) = [X_1, X_2, E] = [100, 0, 0]$.

While this initial condition may seem rather extreme, note that this is generally the same behavior that is observed for any initial condition above approximately $y(0) = [5, 0, 0]$. Similar to the symmetrical system, low N values result in a fixed point at which all variables are 0. A bifurcation occurs at just over $N = 190$ that is reminiscent of the transcritical bifurcation seen at just over $N = 100$ in Figure 6. Between about $N = 90$ and $N = 120$, the system remains symmetric; the long-term populations at source 1 and source 2 are the same. This occurs because there are not enough ants to make either pheromone trail significant over the other; in other words, the forces that drive the competition between the food sources are not strong enough to break the symmetry. In fact, it can be seen that the number of lost ants far exceeds the ants at either food source because neither pheromone trail is strong enough to retain many ants.

However, another bifurcation occurs soon after that breaks the symmetry. With the initial condition of $[X_1, X_2, E] = [100, 0, 0]$, this bifurcation occurs at $N = 218$. The pheromone trail to the food source that was discovered first becomes sufficiently stronger than the other

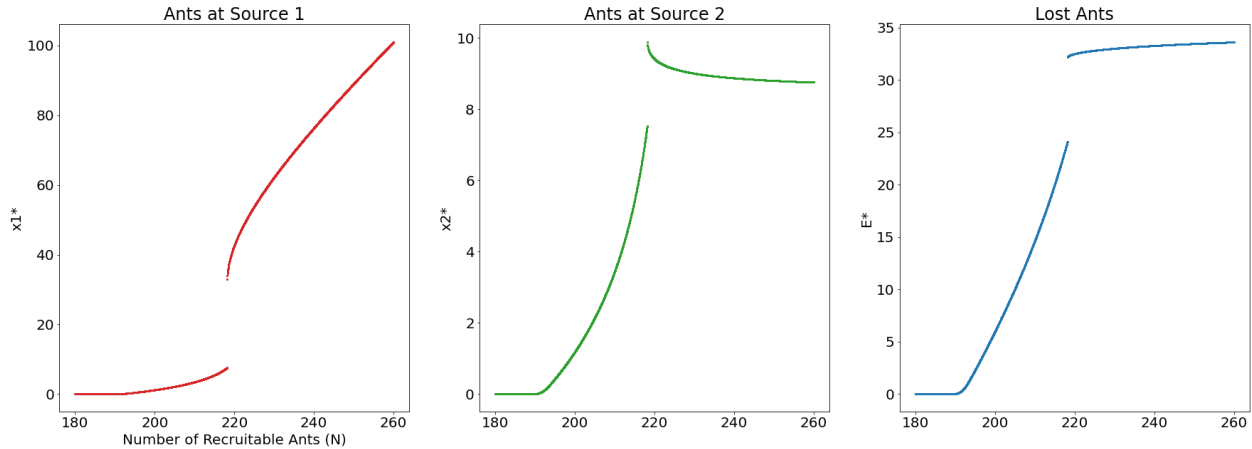


Figure 8: Orbit diagram showing stable fixed points of the asymmetric 3-dimensional model with $y(0) = [100, 0, 0]$. Two distinct bifurcations can be seen.

trail to break the symmetry of the system. In the long-term, more ants always congregate around source 1. A higher N value—more recruitable ants—implies that both pheromone trails are stronger, and thus the forces driving the competition between the two sources are stronger. This asymmetric fixed point existed before $N = 218$; however, it only becomes stable at this point where, presumably, the symmetric fixed point becomes unstable. This is an example of a pitchfork bifurcation, where the top fork is where $X1$ ends up, the bottom fork is where $X2$ ends up, and the middle fork is the unstable symmetric solution.

With most initial conditions, this two-bifurcation orbit diagram is observed. However, when only a small number of ants discover one food source, another feature of the orbit diagram emerges (Figure 9). In the region between $N = 225$ and $N = 236$, the orbit diagram shows three possible fixed points. At first, this appears to be a period-3 orbit. However, an analysis of the trajectories shows that this is not the case, shown in Figure 10.

All trajectories end in a stable, non-oscillatory fixed point. However, the character of this fixed point is extremely sensitive to the number of recruitable ants. N values that lead to each fixed point seem randomly dispersed in this region; two extremely close N values do not necessarily end up at the same fixed point.

Examples of the three fixed points observed in the $N=225$ to $N=236$ region can be seen at $N=230$, $N=233$, and $N=230$ (Figure 10). When $N=230$, the fixed point appears similar to that seen at high initial conditions: the first food source “wins out” and ends up with the majority of the recruited ants while a minority end up at the second food source. The second case, when $N=235$, appears to be the exact reverse: the second food source ends up with the majority of the ants. The final fixed point (seen at $N=233$) continues to follow the

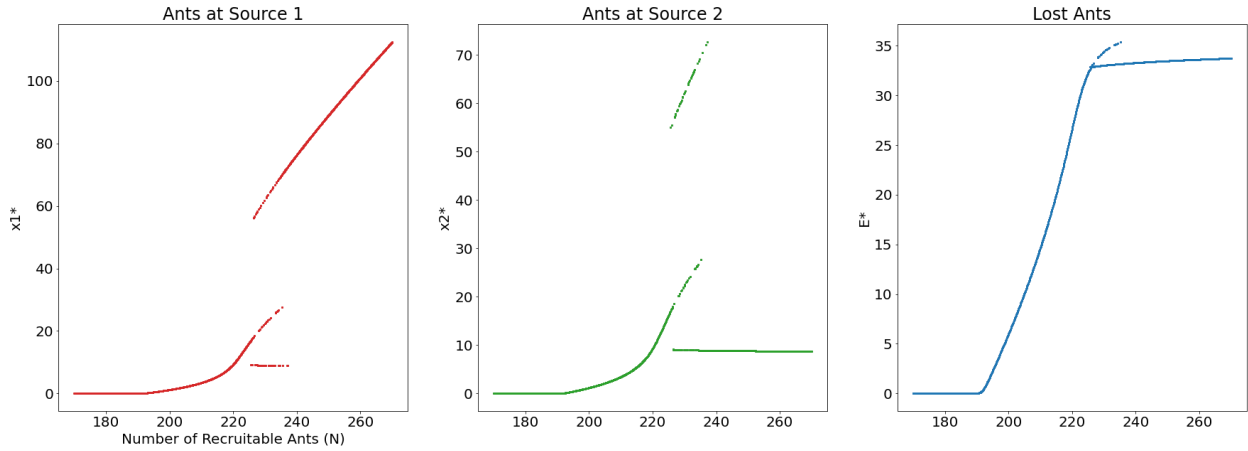


Figure 9: Orbit diagram of asymmetric 3-dimensional function where $y(0) = [1, 0, 0]$.

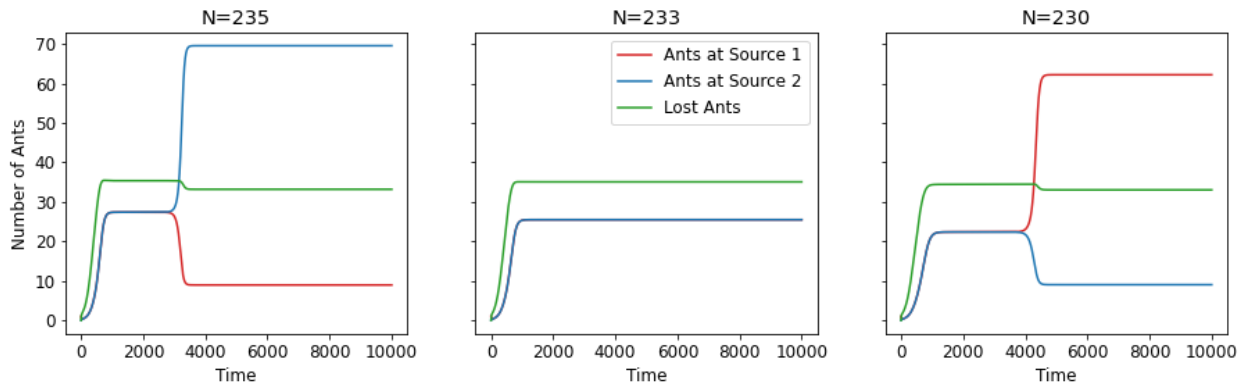


Figure 10: Trajectories of ant populations over time for each fixed point observed in the 3-phase region between $N=225$ and 236 . $y(0) = [1, 0, 0]$.

symmetry seen before $N = 225$; the same number of ants end up at food source 1 as food source 2 and a slightly larger number become lost. Although it is hard to say definitively without an analytical solution for these fixed point curves, they appear to be the same as the symmetry-breaking pitchfork bifurcation seen in Figure 8. The pitchfork bifurcation still exists, but all three branches can be stable solutions for each variable for certain N values.

The reason that the 3-phase region occurs can be explained by the forces present in the model. In this specific region, there is enough driving force in the system to break the symmetry, as shown at high initial conditions. However, because the first food source starts out with so few ants, it does not have a significant advantage over the second food source; their pheromone trails are about the same strength. As can be seen in Figure 10a and Figure 10c, the trajectories appear to retain symmetry until almost 4000 time points, at which point some threshold is crossed and one source finally gains the advantage. Thus, small deviations

in the system can lead to source 2 having more ants, or both sources having the same number.

When N becomes larger than 236 for the $y(0) = [1, 0, 0]$ case, the system returns to the single stable fixed point seen at high initial conditions: the food source first discovered always ends up with a greater population of ants. At this point, the driving forces in the system are great enough to definitively push the system in one direction. The other two fixed points, including the symmetric solution, become permanently unstable. The length of the 3-phase region becomes shorter very quickly as $y(0)$ is increased. The orbit diagram for $y(0) = [2, 0, 0]$ is shown in Figure 11. The range of the 3-phase region in this case only extends from $N = 225$ to $N = 228$. When $y(0) = [3, 0, 0]$, it only consists of a few points.

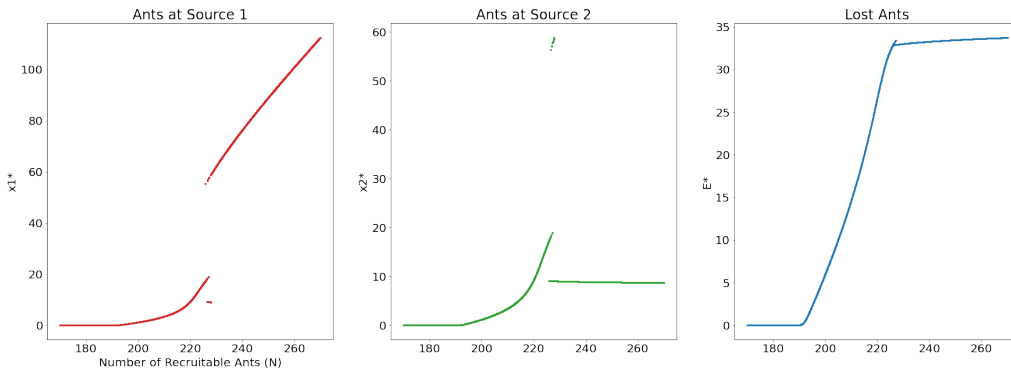


Figure 11: Orbit diagram of asymmetric function with $y(0) = [2, 0, 0]$.

The results of the symmetrical models presented in this report can be compared to those found by *Deneubourg et al.* [2]. The simple pitchfork bifurcation observed at the transition of symmetric to asymmetric stable fixed points at high initial conditions was also reported by *Deneubourg et al.*. However, it should be noted that the concavity of the symmetric region of our bifurcation diagram is opposite that of the paper's. As the paper did not report their methods for obtaining the bifurcation diagram, it is difficult to know why this could be. The paper also did not report the emergence of the three-phase region at low initial conditions.

4 Cellular Automata

Cellular automata (CA) are discrete systems which are useful for modeling complex systems, in particular for specific representations of non-linear dynamics. Each unit of the CA follows a set of rules and can take on only one of a finite set of states at a time. While each cell follows very simple localized rules, in the big picture, complex behavior emerges and patterns arise. CA are well suited to studying swarming dynamics and ant colonies in particular, since

each individual in the colony behaves locally and erratically. CA allow us to visualize the patterns that form in the colony as a whole over discrete time steps.

In these simulations of an ant colony, the orange circle in the center is the nest, and the two blue circles are food sources, each with a limited supply of food. The food sources move to a new location after they have been depleted. The smaller red and green circles represent ants; the red ones represent “scouts” (the ants without food) and the green ones represent ants that have found food and are returning to the nest. In other words, when a scout ant reaches a food source, it turns green and heads back to the nest. When it reaches the nest, it becomes a scout again and turns red. When the ants find food, they begin depositing pheromone that evaporates over time, leaving a path to the source of food for the other ants to follow.

For each time step, it is possible for each ant to move to an adjacent cell that is not occupied by another ant and away from the direction it came from. The code for these simulations was modified from a simple open-source ant colony simulator [4].

We explore different initial conditions and plots specific scenarios of colony behavior below. These scenarios all mimic cases discussed previously and parameters including the life of the pheromone, number of ants, and size of the grid were tuned.

The example in case (a) demonstrates a scenario in which symmetry is broken, as the pheromone trail to the food source discovered first becomes sufficiently stronger. In case (b), the system is symmetric, and the long term populations at the two food sources are approximately the same. In scenario (c), the number of lost ants is very high, because the pheromone trail at either food source is not strong enough to retain many ants.

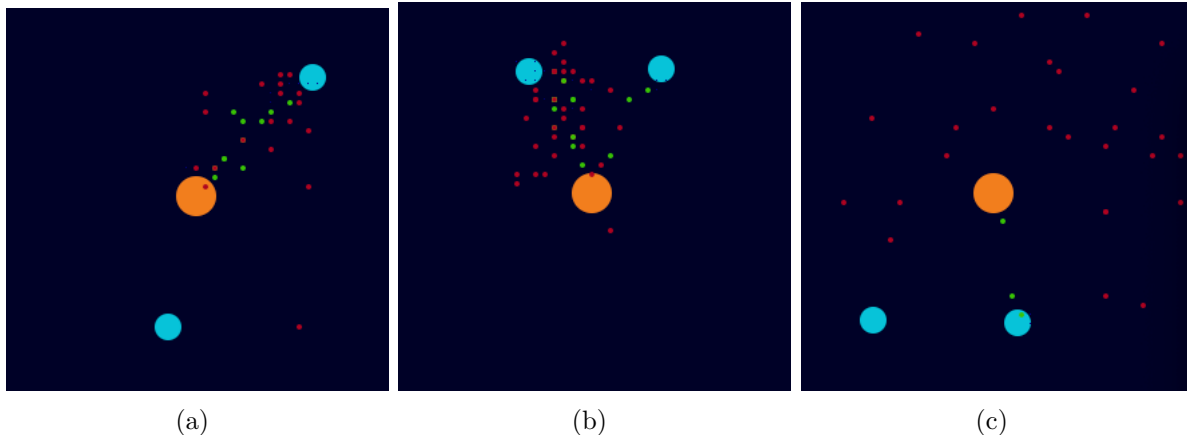


Figure 12: Cellular automata of ant colonies under difference initial conditions (a) Asymmetric system: ants are all going to one food source (b) Symmetric system: ants are going to both food sources approximately equally (c) Symmetric system: lost, hungry ants

5 Conclusion

We replicated results from the idealized one-dimensional model of *Deneubourg et al.* and further explored the bifurcation diagrams which resulted from their 3D model [2]. In the simplified one-dimensional model, we analyze for fixed points and stability and found the carrying capacity using of the system, where ants begin to leave the food source in search of a new one. The three-dimensional model was not solvable using Mathematica or analytical methods known to us. We created orbit diagrams to understand the long-term behavior of this system for a two food-source model. From exploring different initial conditions of the model, we found that at a critical colony size, the symmetry of the system is broken and ants tend to congregate only around a single food source. Finally, we demonstrated that scenarios present in the nonlinear systems could be represented using cellular automata under different conditions, as well.

Given more time, we would continue to explore the three-dimensional model. In particular, we would like to look into how the length of the three-phase region would change as a function of initial condition to better understand the long-term behavior. It would be exciting to replicate the results of the biological experiment and verify the model as well. Additionally, we would further explore the cellular automata models to obtain quantitative results.

Contributions

Nina: Created code to numerically plot 3D model orbit diagram and trajectories. Performed and wrote up analysis of 3D model results based on these plots.

Allison: Cellular Automata Simulation [[CODE HERE](#)], helped with interpretation and code for 3D model, Conclusion, Introduction

Aria: Analysis and code to analyze logistic equation and 1D model, introduction/background information, assistance with 3D model interpretation.

Code for our project can be found in our github repository [[here](#).]

References

- [1] T. L. and, *Biomimetic self-organization and self-healing*, 2021. [Online]. Available: <https://www.sciencedirect.com/topics/mathematics/swarm-intelligence>.
- [2] J. I. Deneubourg, S. Aron, S. Goss, J. Pasteels, and G. Duerinck, “Random behavior, amplification processes and number of participants: How they contribute to the foraging properties of ants,” *Physica D*, vol. 2, no. 1-3, pp. 176–186, 1986, ISSN: 0022-5193. DOI: [https://doi.org/10.1016/0167-2789\(86\)90239-3](https://doi.org/10.1016/0167-2789(86)90239-3). [Online]. Available: <https://www.sciencedirect.com/science/article/pii/0167278986902393?via%3Dihub>.
- [3] S. H. Strogatz, *Nonlinear Dynamics and Chaos*. CRC Press, 2019, ISBN: 9780367092061.
- [4] W. Radji and T. Hesselberg, *Colony ant simulator*, 2021. [Online]. Available: <https://github.com/riiswa/colony-ant-simulator>.