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Agent-Based Modeling of Locust Foraging and Social Behavior

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HARVEY MUDD COLLEGE

Department of Mathematics

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Abstract

Locust swarms contain millions of individuals and are a threat to agriculture on four continents. At low densities, locusts are solitary foragers; however, when crowded, they undergo an epigenetic phase change to a gregarious state in which they are attracted to other locusts. It is believed that this is an evolutionary adaptation that optimizes the seeking of resources. We have developed an agent-based model based on the solitary-gregarious transition and foraging behaviors due to hunger levels. A novel feature of our model is that it treats food resources as a dynamic variable in the environment. We discuss how social interaction strategies influence the efficiency of foraging and the effect of heterogeneous distributions of resources on the solitary-gregarious phase transitions.

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Acknowledgments

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I will always be grateful to my friends and family for their patience and advice as I worked through the many bugs (both metaphorical and literal) I found in my code. Special thanks goes to Tiffany Madruga whose sleep schedule meant she could wake me up at 5am before going to bed and Kailee Lin who edited my thesis and convinced me to include this phrase: "NetLogo is Love, NetLogo is Life".

Chapter 1

Introduction

Locusts are a group of species in the family *Acrididae*, which contains many species of grasshopper and locust, but they can be differentiated from grasshoppers by their ability to change morphology as a response to external factors. Adult locusts also often form cohesive groups (called bands or swarms) as individuals group and travel together. When enough locusts gather in a group in one location, they can form upsurges or even plagues. The United Nations defines a plague of locusts as when two or more regions are simultaneously affected by large swarms of locusts, meaning that plagues could cover up to millions of square kilometers of land (Symmons and Cressman, 2001). According to the United Nations Food and Agriculture Organization, a plague of locusts has the ability to affect 20% of all the Earth's land and could harm the livelihood of 10% of the world's population (Nations, 2019). Because of how detrimental these locusts can be to their habitats, it is important to study them. If we can learn about the patterns and behaviors of locusts, we will be able to work with farmers and other people who may be affected by plagues in order to reach a balance between human and locust habitats.

In order to learn more about how locusts will behave in their habitats, we create an agent-based model and observe the patterns produced by locusts in varying scenarios. In mathematical biology and ecology, agent-based modeling (sometimes referred to as individual-based modeling) is a modeling technique frequently used to assess how individuals behave or interact with their environments. The results of agent-based models can provide insight into how groups of individuals behave, especially in relation to other individuals or their surroundings. This differs from many other methods of modeling which treat an entire group of individuals as one unit, eliminating the ability for different individuals to make independent choices or for the possibility of interaction between individuals of the same group.

In this thesis, we create an agent-based model that considers a variety of factors that control how locusts interact with their environment, including resource availability and distribution as well as interaction between multiple different locusts. This model helps us to understand more about some of the factors that have an influence over locust behavior and how different patterns in behavior may arise.

Chapter 2

Locust Biology

Locusts have been studied by both the mathematical and biological community for a long time. Locusts belong in the family Acrididae, which includes all grasshoppers and locusts. Our research has focused on the Desert locust (*Schistocerca gregaria*), although we have also included research that considers both the Desert locust and the Australian plague locust (*Chortoicetes terminifera*).

Locust species go through a life cycle divided into different phases (Symmons and Cressman, 2001). Locusts go from eggs to nymphs (otherwise known as hoppers) to fully grown adults. This entire life cycle can last anywhere from two to six months. Within the hopper phase, there are five different instars or intermediate stages. With each instar, the locust will grow larger and shed their skin. One important aspect of the transition from the fifth instar to an adult locust is the development of wings. Locusts can only fly once they have matured into an adult. During both the hopper and adult phases locusts will sometimes form groups and move collectively. As an adult, they can create swarms with many flying locusts, but hoppers will create bands or other formations as they collectively move along the ground. In this thesis, our work will focus on locusts in the later hopper stage, typically in their fourth or fifth instar.

2.1 Gregariousness

Locusts can be differentiated from many other species of grasshopper because of their propensity to morphologically change as a response to their surrounding environment. Some of the factors in their environment which may influence their morphology are resource availability and proximity to other locusts. Locust behavior and morphology are both governed by their gregariousness. Biologists define gregariousness as the tendency to seek out interactions with other locusts and an individual who is gregarious is more likely to form bands or swarms with many other gregarious individuals. Gregarious locusts will also occasionally cannibalize other locusts.

An individual who is not gregarious may be solitary, meaning that they prefer to be alone and will actively avoid other individuals. Because solitary locusts typically choose to remain alone, they will not participate in group behavior like forming bands or swarms. The transition from solitary to gregarious is not instant and locusts have the ability to fall somewhere on the spectrum between these two social states. In this thesis, we examine locust social behavior on a scale from solitary to gregarious.

Individuals can become gregarious by a variety of methods, including crowding, stimulation of the hind leg, or the sense of other locusts via sight and smell. Additionally, research shows the importance of serotonin in regulating gregarization. In one study, researchers prevented serotonin from being released and found that locusts would not gregarize, even when presented with different stimuli (Anstey et al., 2009). Additionally, as individuals became more gregarized, the researchers noticed that their serotonin levels were rising, supporting a positive correlation between serotonin and gregariousness (Anstey et al., 2009).

Most research focuses on when locusts move from being solitary to gregarious, but there has also been research done on locusts reversing this direction and changing from gregarious to solitarious, typically when there are very few other individuals around them (Dkhili et al., 2017). For the purposes of our model, most of the locusts will continually gregarize, but we include the ability for individuals to revert back to being solitary if they are isolated from other locusts.

Gregarious locusts moving together have been found to align the direction of their movement with one another. They also move in a pattern known as pause-and-go, in which they pause after every step and occasionally re-adjust their heading. Many previous studies have examined locust behavior based on their levels of gregariousness, specifically examining their movement patterns to see why these might occur. Some researchers have studied how cannibalistic tendencies may lead to a locust's pause-and-go motion or alignment between individuals. Many of these studies have found a positive feedback cycle in which individual locusts are propelled forwards simultaneously towards another locust they could eat and away from predatory locusts behind them (Ariel et al., 2014; Romanczuk et al., 2009; Bazazi et al., 2008). Another group of researchers studied the relationship between density of locusts and swarming or alignment within a group of locusts. Although the researchers were not certain whether or not locusts actively self-regulate their surrounding densities, their laboratory experiments did confirm their beliefs that density regulates locust alignment and order (Buhl et al., 2006).

2.2 Foraging

When in bands or swarms, locusts will travel across vast areas of land, eating most of the plants that they encounter. Even when not in a cohesive group, eating is an important and time consuming part of a locust's life. Many animals utilize the strategy of optimal foraging when looking for food to consume. Optimal foraging helps an individual know where to go in order to get the most food and energy and when they should move on to the next location in order to maximize their own time and energy.

Eric Charnov, an ecologist studying optimal foraging in the 1970s, created the Marginal Value Theorem as a way to explain optimal foraging behavior in a quantitative way. He explained his theorem thusly: "The predator should leave the patch it is presently in when the marginal capture rate in the patch drops to the average capture rate for the habitat" (Charnov, 1976). Charnov showed that individuals would stay foraging in their current position for as long as the energy gain was high enough, but once nutrients were depleted, it made more sense for an individual to leave and forage elsewhere with more food. Although Charnov's mathematical theorem has yet to be strictly proven, many ecologists see quite a bit of support for his ideas and explanations of individuals making decisions about how to gain the most energy.

We can see that locusts also follow this pattern of staying at a food source for as long as it can provide enough food before moving on to the next one. Nonaka and Holme built an agent-based model to determine how clumpiness in food resources could affect an individual's foraging behavior, where clumpiness was defined as heterogeneity or the clustering of food (Nonaka and Holme, 2007). This study compared their model with results from the Marginal Value Theorem in order to verify their models accuracy in predicting how long an individual would stay at a patch of food before moving on to another one. The model found that individuals would stay within one clump of food until most of the food was gone before moving on to another clump of food patches (Nonaka and Holme, 2007). This agent-based model simulation backs up the ideas of the Marginal Value Theorem, but both models are generalized to study any foraging individual, so they ignore other important social factors, like predation, social interaction, or gregariousness.

Chapter 3

Agent-Based Modeling

Agent-based modeling is a method commonly used in mathematical biology or ecology. In an agent-based model, the behavior of individuals is modeled in order to learn about how groups in a specific environment will behave. Agent-based modeling includes two elements: individual agents and the environment.

Individual agents have state variables that they store and which change with internal or external stimuli. State variables can be quantitative or qualitative and can include anything from the color of the agent to a numerical value representing their hunger levels. In addition to dynamic variables, individual agents have a set of rules for decision making. These rules generally stay constant throughout the entire run of the model, although there can be different rules for different scenarios within the model. Rules inform each agent on what their next action should be based on a variety of different variables, often involving agents interacting with other agents or their surrounding environment.

The agent-based model environment does not have rules for decision making because it generally doesn't take action, but it will have state variables that can change. Similar to the individual agents, the environment's state variables can change based on the passage of time or some individual agent catalyzing a change.

3.1 Why Agent-Based Modeling?

Agent-based modeling is often used by ecologists to study groups of organisms because of its unique ability to simulate how groups of individual units interact and behave, instead of considering each group to be one cohesive set. This method of analysis can provide insight into how organisms behave in ways that other modeling methods cannot. This is something that we would like to explore in a locust model because of certain group behaviors. While many previous models have examined behaviors of groups of locusts, we would like to use an agent-based model to learn more about how the behavior of individuals can lead to gregarious locusts and collective decision making.

Agent-based modeling can also incorporate stochasticity into its mechanisms. This randomness means that, although the steady-state behavior of the model will always remain relatively constant, the steps that the model will take to get there can vary quite a bit throughout different simulation runs. Where a different model (e.g. one using differential equations) would only be able to show one possible outcome, agent-based models can demonstrate the variety that is more realistic to nature. One thing that this could add to the discussion of locust modeling is whether different factors or choices as the simulation progress could have an influence on the final results.

3.2 Previous Locust Agent-Based Models

There has been previous work done on locust behavior, using agent-based modeling. One group of researchers chose to build an agent-based model in order to determine why different structures of locusts bands form (Dkhili et al., 2017). This research model paid specific attention to rules of repulsion, attraction, and alignment in locust movement in order to determine how these variables affected the movement and, with little parameter adjustment, they were able to build a model very close to what happens in reality (Dkhili et al., 2017).

Many of the other models look at how resource distribution affects different aspects of locusts' lives, like their ability to optimally forage or change phase. Despland et al. chose an agent-based model to help them determine how resource distribution in different fractal patterns can influence phase change in locusts (Despland et al., 2000). The agent-based model was able to show that there was more gregarization in areas with resources at a higher fractal dimension (Despland et al., 2000). This paper also found that solitarious locusts would group together when necessitated by a patchy distribution of food, which will be useful to know in the agent-based model we create in this thesis.

Another agent-based model specifically highlighted the Marginal Value Theorem as the theory they were trying to examine in their paper (Nonaka and Holme, 2007). These researchers studied how resource clumpiness affected individual animals' ability to optimally forage. After building a model that generally agreed with the principles and results of the Marginal Value Theorem, the study analyzed how individuals would forage on a clump of patches of food, including how much time would pass before an individual would generally move on to the next patch of food (Nonaka and Holme, 2007). Unlike the other models in this section, this model does not specify a species that it is studying, instead taking a general approach; however, it includes many of the same ideas we are exploring in this thesis so it is important to learn about their methods and results so we can expand them to focus specifically on locusts.

All of these agent-based models have attributes that we include in our own model. Despland et al. study how resource distribution affects gregarization, Nonaka and Holme focus on how resource distribution affects foraging behavior, and Dkhili et al. have written a model that studies locust-locust interaction, including attraction, repulsion, and alignment. The model proposed in this thesis has combined the ideas of locust-locust interaction with hunger and resource distribution throughout the environment. This gives us a better idea of the different options that a locust has for actions to take based on their needs at the time and their surrounding environment.

3.3 NetLogo

There are many different ways in which one can build an agent-based model, both with and without using computational techniques. For our agent-based model, we have chosen to work in NetLogo, a program specifically designed to help people build agent-based models. NetLogo is a Scala based language and uses an adapted form of programming as the foundation for how the program works. The program is beneficial because it can provide both visual and numerical outputs. It is possible to edit or understand the code with minimal prior experience and parameters can be easily adjusted if multiple simulation runs require different parameter settings. Many researchers have started to use NetLogo for their models and the program has continued to improve through multiple different versions (Lytinen and Railsback, 2012).

Chapter 4

Model

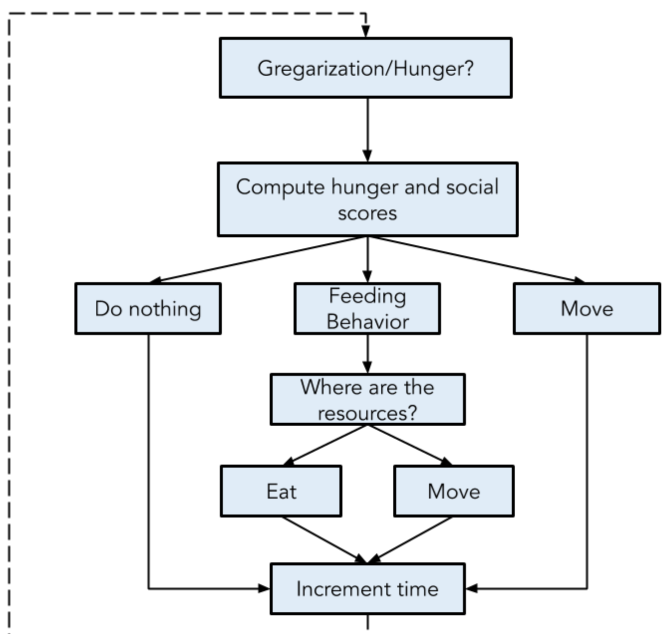
In order to construct our agent-based model, we started by creating an outline of how we wanted the locusts to behave given different circumstances. After coming up with a general idea, we could create mathematical equations that would model the desired behaviors. The mathematical equations and roughly identified parameters were integrated into a NetLogo simulation so we could visualize what we had constructed.

After incorporating the mathematical equations and parameters into the NetLogo simulation, the NetLogo code still needed editing in order to ensure that it behaved in what we considered to be the most biologically accurate way. This involved looking at how certain pairs of state variables interacted with each other and tweaking parameters slightly, based on updated calculations.

4.1 Outline

Based on our literature review, there are five different variables we consider to be important in determining how locusts interact with one another and their resource environment. Gregarization and locust-locust interaction is a large part of the model, so we have three variables that will help us learn more about social interactions. N represents the number of neighbors around each locust, S is the gregarization level of each individual locust, and U is the social contentment score for each locust. Social contentment will determine how happy a locust is with its current social circumstances (e.g. a solitary locust would be unhappy around many other individuals but a gregarious locust would have a bad social contentment score if it were alone). The other important aspect of our model is the inclusion of resources. In order to learn more about how locusts interact with their food resources, we created two more variables. H shows the hunger of each individual locust and R represents the amount of food resources available on a specific patch of the environment.

Figure 4.1 Diagram showing the progression of the model's flowchart



We have created a flowchart which demonstrates how all of the variables work together in the model (Figure 4.1). Gregarization was determined to be the first step in the flowchart, since it would change with each step and it would affect further decisions. This step would reassess how gregarious an individual locust was, based on the level of gregarization in the previous step as well as the number of neighbors surrounding an individual. This step also looks at the hunger level of the locust and re-evaluates based on how much food was consumed in the last time step.

After gregarization and hunger levels were recalculated, the model would compute hunger and social scores. These scores would report how contented each locust was with their current scenario, including how hungry they are and how happy they are with their social surroundings (as described above). These hunger and social scores help the locust determine what they will do next: they could move, if they need to adjust their social environment; they could eat, if they need to prioritize their hunger levels; or they could do nothing if they are already happy. If a locust decides that they need to prioritize their eating behavior, they then must determine if there is any food near them. If a locust is very hungry and there is no food around, its next step is to move in order to find food. If, on the other hand, a locust is very hungry and there is abundant food around, all they need to do is stay where they are and eat the food.

Once the locust has figured out exactly what it will be doing for its next step, time is incremented and hunger and gregariousness are re-evaluated. Then the cycle of the flowchart will repeat until the modeller tells it to stop. The ability to stop the model from running can be determined by a combination of many different attributes chosen by the modeller, including time steps or set value thresholds for state variables.

4.2 Formulation

The flowchart (Figure 4.1) creates a step-by-step framework for how we want the model to behave. This allows us to then create mathematical equations based on transitions between phases in the flowchart. Since many of the variables considered in this model are proportions, the equations often have maxima or minima designed to keep the variables in a range that makes mathematical and biological sense.

Figure 4.2 Table of variables used in model equations and their descriptions

Variable Name	Description	Minimum Possible Value	Maximum Possible Value
N	# neighbors	1 - minimum neighbors (self)	population - maximum neighbors
R	resources on space	0 - no resources	100 - full of food
H	hunger	0 - full	1 - hungry
S	gregariousness	0 - solitary	1 - gregarious
U	social contentment	1 - unhappy	0 - happy

In addition to the five variables described above, we also have some constant parameters in our mathematical model. These constants all have a biological meaning and can be useful in helping to tune the equations to behave in the ways we would expect. In order to implement the equations in NetLogo, we needed to determine possible ranges and starting values for each of the constants. Figure 4.3 shows a table with general ranges of values for each of the parameters as well as a description of what the parameter does.

Later, in the results section of this paper, we will explore the parameters in further detail in order to learn how each of them will affect the model in different ways.

Figure 4.3 Table of parameters used in model equations, their descriptions, and ranges of possible values

Parameter Name	Description	Range of Possible Values
H_i	How much hunger increases each step	[0 , <1]
R_c	Amount of food consumed	[0 , 100]
H_d	How much hunger decreases with eating	[> H_i , 1]
S_t	Gregarization threshold	[>1 , < population]
S_r	Gregarization rate	Varies around 1
P_n	Probability of not eating or moving	[0 , 1]
N*	Neighbor threshold	[1 , 0.5 * population]

Gregarization is calculated as an exponential, so that individuals who are already partially gregarized will become even more gregarized more quickly than if they were not gregarious. Our gregarization equation is a function of the previous time step's gregarization level and the current number of neighbors around an individual. There are also two parameters in this equation: the rate at which an individual gregarizes [S_r] and the gregarization threshold [S_t], which determines the number of neighbors it takes to become more gregarious. Our equation for gregarization includes a bound at 1 such that, if the value from the equation exceeds 1, it will be set to equal 1 instead. This was constructed so that a locust will be entirely gregarized at 1 and will either remain constant at 1 or decrease if there are too few locusts around.

$$S = S * \exp(S_r(N - S_t)) \qquad [0 \leq S \leq 1]$$

Hunger was calculated as a simple function, adding a constant amount of hunger [H_i] to the previous time step's hunger level until there is a maximum of 1, when the locust is as hungry as it can get. Similarly to the method of computing gregarization, if the hunger value calculated from the equation exceeds 1, H will just be set to 1 until the locust eats and the value decreases again.

$$H = H + H_i \qquad [0 \leq H \leq 1]$$

The social contentment score U was calculated so that individuals who are gregarized will have a score of 0 when around other locusts and a score of 1 when isolated. Likewise, a solitary locust will have a score of 1 when around other locusts and 0 when isolated. In order to calculate this, we created another variable Q, which takes into account an exponential of the number of neighbors nearby. When this variable is equal to the gregariousness of a locust, the locust will be completely content with their social environment.

$$Q = 1 - \exp(-N/N^*) \qquad [0 \leq Q \leq 1]$$
$$U = (Q - S)^2 \qquad [0 \leq U \leq 1]$$

In order to use the social contentment score and the hunger score to determine the locusts next action, we formed a probability distribution. The probability of a locust choosing to do nothing, instead of eating or moving, is represented by a constant α divided by the total of α plus the hunger score H and social contentment score U. This probability is called "do nothing".

$$p(\text{do nothing}) = \frac{\alpha}{\alpha + H + U}$$

The probability of a locust choosing to feed next ("feeding behavior") is its hunger score divided by this same sum of the three possible actions.

$$p(\text{feeding behavior}) = \frac{H}{\alpha + H + U}$$

The probability that a locust moves towards or away from other individuals ("move") is its social contentment score divided by the sum of the three possible actions.

$$p(\text{move}) = \frac{U}{\alpha + H + U}$$

Once the locust has chosen its next action, it needs to follow the steps dictated by that action. If a locust decided to move in order to improve their social contentment score, it would calculate the lowest potential social contentment score from the eight neighboring areas and then move to the most desired area (the area with the lowest social contentment score). A locust which chose to do nothing during the next time step would do nothing and then, during the next time step, recalculate the probability of each action and make a new decision.

If a locust needed to eat food next, it would have to determine whether or not there were resources nearby. A locust who has no resources in it's area would then move to a nearby random location. If, however, there is food where the locust is currently located, the locust will eat immediately. This will decrease hunger levels by a constant [H_d], until it reaches 0, when it will level out. These bounds are based on biological principles: a locust cannot be so full that it has negative hunger, so hunger will either stay at 0 or increase if no food has been consumed. In addition to decreasing hunger levels, the resources available in the environment will decrease by a constant [R_c], until they reach 0. For this agent-based model, we have set a maximum amount of food per cell at 100 and a minimum at 0 (when there is no food left) but this maximum could be changed if you wanted to alter the conditions of the world. Additionally, no food grows back in our model, so R can only ever decrease, while H could increase or decrease depending on the frequency of food consumption.

$$H = H - H_d \qquad [0 \le H \le 1]$$
$$R = R - R_c \qquad [0 \le R \le 100]$$

These equations described in this section above form the framework for our exploration of locust behavior. We can now integrate them into NetLogo and simulate different behavioral patterns.

4.3 Simulation

In addition to adding our equations to the NetLogo model, the NetLogo code requires some information about the world, like how many individuals will be inhabiting the space, as well as how large the world is. This aspect of our model does not mirror the "real world" environment of locusts, as their natural world is often not confined to a perfectly square space with an unchanging number of individuals. These variables can be set to values that make it easier to look at other parts of the model. In addition to being able to set the size of the world, we have chosen to have the edges of the world wrap around. This means that a locust who wanders past an edge tile will reappear on the other side of the world, as if all edges are connected.

The NetLogo model is divided so that the world consists of many individual patches, or squares, with coordinates and attributes like resources and color. In order to see more easily how much food is left in each patch, we have color coded the world so that a darker patch will have more food while a white patch has no food left (Figure 4.4). You can also see light pink locusts in the world. In this model, locusts move from one patch to another and are always at the center of their patch. Locusts are seeking out resources to eat as well as patches that either are close to or far away from other individuals, depending on their level of gregariousness. Much like the environment is color-coded to represent the amount of food, locusts are colored such that the darker the locust is, the more gregarious it is, on a scale from light pink [solitary] to dark red [gregarious].

Each time the simulation is run, all of the locusts start out as completely solitary and randomly distributed throughout the world. Each cell in the model has a random number of resources between 0 and 100. A sample initial view is shown below in Figure 4.4. Figure 4.5 shows images of the environment after the locusts have eaten different amounts of the food from the environment.

Figure 4.4 Initial image of the agent-based model simulation

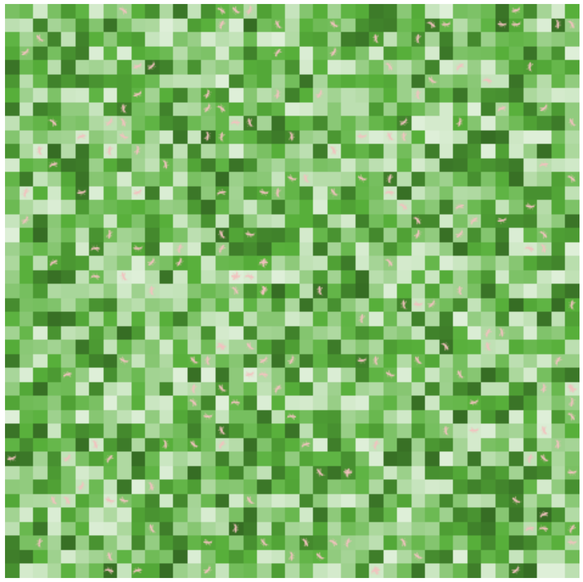
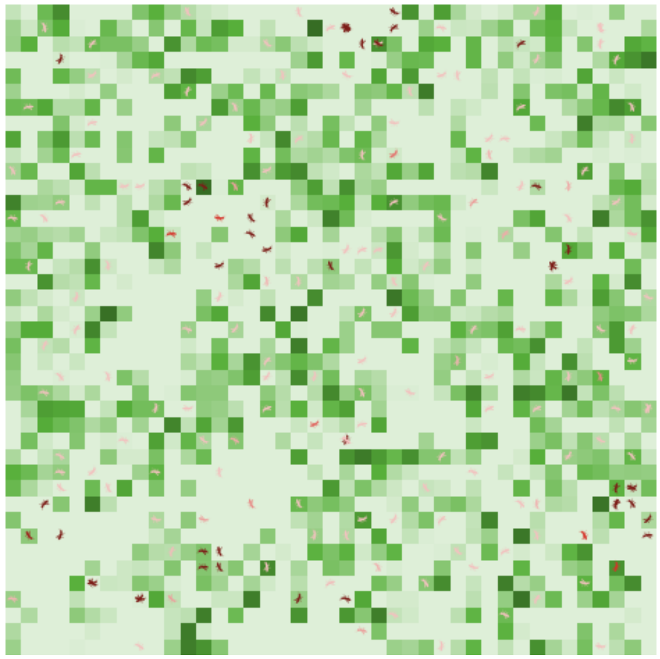
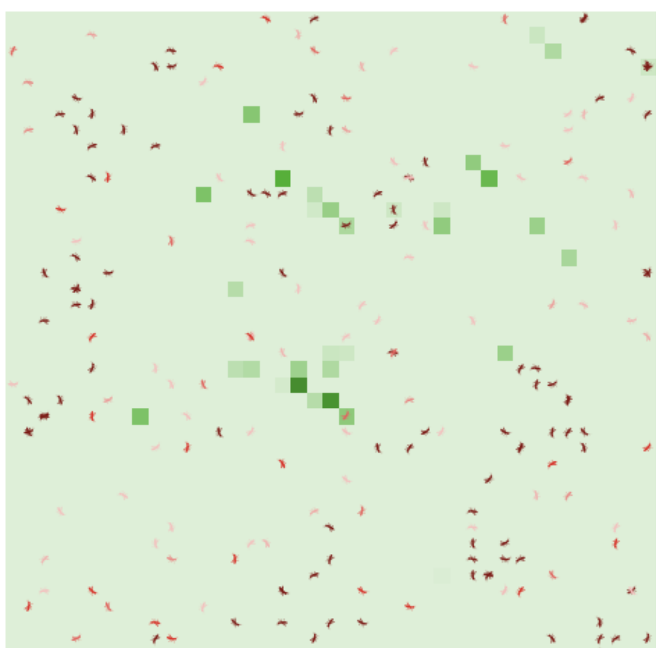


Figure 4.5 Two images of a NetLogo simulation after having run for many time steps

a. Image from part way through the simulation when some locusts are gregarious



b. Image taken when most of the food has been eaten and most individuals are gregarious



4.3.1 Variable Initial Conditions

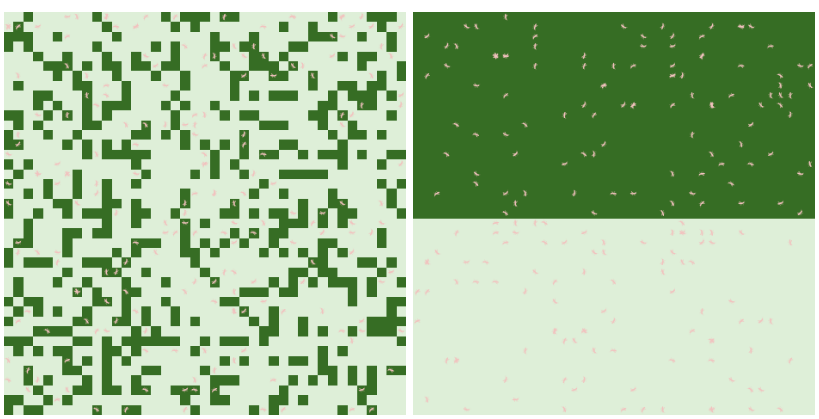
Although the default initial conditions set up the world randomly, we included a few other methods of creating initial conditions that were less random. This allowed us to learn about what the locusts might choose to do in a variety of different worlds. In addition to each cell randomly choosing a resource amount, it is possible for every cell in the world to have the same amount of starting resources, in order to explore a uniform environment.

Many times, in nature, plants will also grow in patches or clumps, which means there will also be large spaces without any plants. In order to simulate this in the NetLogo model, we included the ability to determine how many cells will even have food at the beginning of a simulation. Additionally, there is one initial condition that splits the world into one half that has no food, and one half that has uniform resource distribution. This creates one large patch of food that may attract hungry locusts.

Figure 4.6 Two examples of alternative resource distribution initial conditions (aside from randomly distributed)

a. Starting image from a world where only 30% of cells have food and all cells with food have the same amount

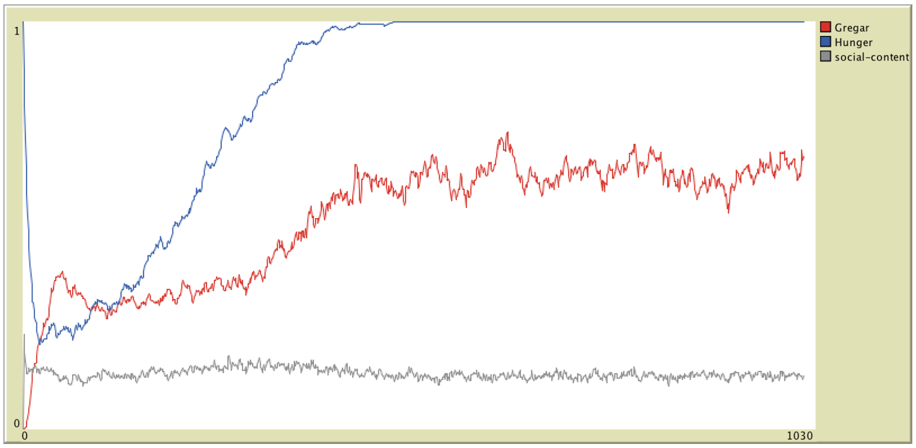
b. Initial conditions where only half of the world has cells with resources. All cells have the same amount of food



4.4 Verification

Before fully analyzing our model in order to arrive at possible conclusions about locust behavior, we spent some time verifying that the model achieves the general behavior that we expected. We started by examining average values for hunger, gregarization, and social contentment over the entire locust population.

Figure 4.7 Graph of average gregarization (red), hunger (blue), and social contentment (grey) for 200 locusts



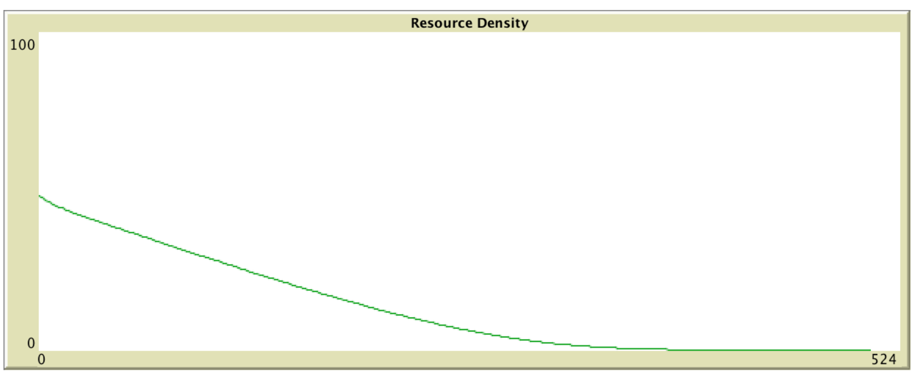
As we expected, the gregarization has a sudden, rapid increase before slowing and gradually rising to a level that it generally maintains for the rest of the simulation. We wouldn't necessarily expect all of the locusts to become gregarized, especially after all of the food has been eaten, because the solitary locusts can continue to roam the environment without having to interact with other locusts. Locusts who have become gregarized tend to stay close to other locusts, so their gregarization will remain high, but there are occasions where they may randomly move in different directions and a locust could become solitary again.

We can also see in this graph that the hunger level goes down very quickly and stays low for a short amount of time. This is the time in the simulation where there is still plenty of food available for all of the locusts, and they can eat without worrying about much else. After the food starts to disappear, the locusts become hungry once again, slowly when there are resources left in the world, and rapidly once the food is gone.

The grey line in Figure 4.7 represents the average social contentment of the locusts. Throughout this entire simulation, the average social contentment is around 1.5. This is relatively low because a high value for social contentment is part of the trigger a locust might get to change its social environment. The social contentment would likely never have an average of zero though, since locusts can only control their own actions and have no ability to know what other locusts nearby might choose to do.

In order to make sure that the model was working correctly, we also looked at average resource density over many time steps. As expected, the resource density decreases in a fairly linear manner. As time goes on and more food has been consumed, there is less food in the environment. This means that it is slightly more difficult for locusts to find food, meaning that the food will be eaten at a slightly slower rate than at the beginning of the simulation. The resource density eventually reaches 0 and stays there, since the environment doesn't grow food back and cannot have less than no resources.

Figure 4.8 Average resource density over time



4.5 Parameter Selection

After writing the equations that determined how the locusts would behave in our model, we briefly identified all of the parameters in the equations and what they represented biologically. The next step, in order to make sure that the model was actually behaving as we wanted, was to come up with more precise values for our parameters. Figure 4.9 shows all of the parameters with descriptions as well as the values we chose to use in NetLogo. Below, we explain how each of these parameter values was chosen.

Figure 4.9 Table showing all identified parameters, descriptions, ranges, and chosen values

Parameter Name	Description	Range of Possible Values	Chosen Value for Simulation
H_i	How much hunger increases each step	[0 , <1]	0.06
R_c	Amount of food consumed	[0 , 100]	5
H_d	How much hunger decreases with eating	[> C1 , 1]	0.21
S_t	Gregarization threshold	[>1 , < population]	1.5
S_r	Gregarization rate	Varies around 1	0.22
P_n	Probability of not eating or moving	[0 , 1]	1/3
N*	Neighbor threshold	[1 , 0.5 * population]	3

4.5.1 Hunger Parameters

There were some parameters which had a wide range of possible values, but when choosing specific values, we had to pay attention to their relationship with other parameters. When choosing H_i (how much hunger increases), although we had determined that it could be anything less than 1, we didn't want H_d (how much hunger decreases) to be a multiple of H_i. If H_d were a multiple of H_i, that would reduce the number of possible values of hunger, effectively making hunger a quantized variable. We also decided, based on biological ideas, that hunger should decrease with food much faster than the naturally increasing hunger rate. Thus, we chose the values $H_i = 0.06$ and $H_d = 0.21$ for these parameters.

The third parameter related to resource consumption was R_c: how much food a locust would eat each time it did decide to eat. Unlike many of the other parameters which deal with locusts directly, this constant affects the world and the resources left after each time step. Because this is the only parameter to affect the environment and initial resources on a cell can vary greatly, we decided to set this parameter to 5.

4.5.2 Gregarization Parameters

There are two parameters in the model which affect how the locusts become gregarized. One parameter, S_r, determines how quickly an individual locust will gregarize, while S_t is more related to the threshold of neighbors over which a locust would become more gregarious. Because S_t represents a threshold of neighbors, we decided that the threshold should be only slightly greater than the average number of neighbors a locust might have throughout the simulation. After running the model many times, the average number of neighbors was estimated to be about 1.3, so we chose S_t to be 1.5.

After choosing a parameter value for S_t, we were able to use the equation for gregarization to estimate a value for S_r. Gregarization is calculated using this equation:

$$S_n = S_c * \exp(S_r(N - S_t))$$

We chose to look at this equation at a time when a locust might be gregarizing quite a bit. In order to do this, we set N (the number of neighbors) to be a value close to the maximum number of neighbors a locust could have (10). We then decided that, when a locust encountered a lot of neighbors, its gregarization rate might increase by 7-fold. This then allowed us to plug in values for all but one variable in the above equation.

$$7 = \exp(8.5 * S_r)$$

Thus, $S_r = 0.223$. Although this isn't a precise number, due to the estimation of other variables in this equation, 0.22 was close enough where the model performed as we hoped it would when we tested it with different conditions.

4.5.3 Other Parameters

There are two other parameters in our system of equations. One parameter helps to determine how socially contented each locust is at every time step. This parameter is the neighbor threshold N^*. We wanted to locusts to be generally happy if they were in the correct social environment. After trying a few different parameter values, we decided that 3 was a roughly good value.

The other parameter left to identify is p_n, the probability of doing nothing. In the original flowchart of the model, there is a third option for locusts who don't want to eat and don't want to move, which is to do nothing. In order to construct this probability model, we decided that approximately $\frac{1}{3}$ of the time, a locust would spend the time step doing nothing.

Chapter 5

Results

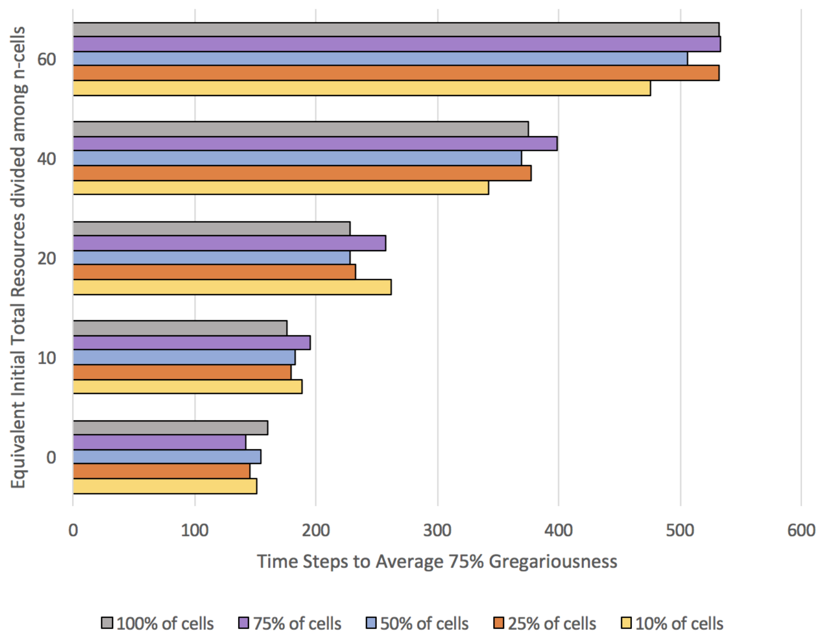
Now that we have both a mathematical model and a simulation in NetLogo which behaves roughly as we expect it to, given initial conditions and chosen parameters, we are able to run the simulation to learn more about how the locusts are behaving under certain specific conditions and how different variables affect their behavior.

5.1 Initial Resource Quantity and Distribution

We examined how some of the initial environmental conditions had an effect on long-term behavior. We wanted to see how, or if, the locusts changed their behavior in response to varying the initial resource conditions, specifically looking at patchiness and the distribution of food throughout the environment as well as quantity of food. We ran one study that chose different percentages of initial cells to distribute food resources among (Figure 5.1).

For each percentage of initial cells with food, the model was run for five different initial resource per cell values. Because we were comparing environments with different percentages of cells with resources, instead of inputting the same number of resources per cell, we compared tests with the same number of total resources in the world, divided among cells that had food. This allowed us to take into account the percentage of cells with resources in them. For example, one could compare a simulation run with all of the cells at 50 food resources to a run where 50% of the cells had 100 food resources. This was done so that we could compare environments where the total quantity of food was the same, so, for each different amount of equivalent resources per cell, the factor that changed was how the food was distributed throughout the environment. There were three replicates of each initial condition combination that were then averaged together to find how long it took for the locust population to reach an average gregariousness threshold.

Figure 5.1 Graph comparing simulations with different percentages of cells with food at various initial resource per cell values. This graph measures how long it takes the locust population to reach an average gregariousness value of 0.75

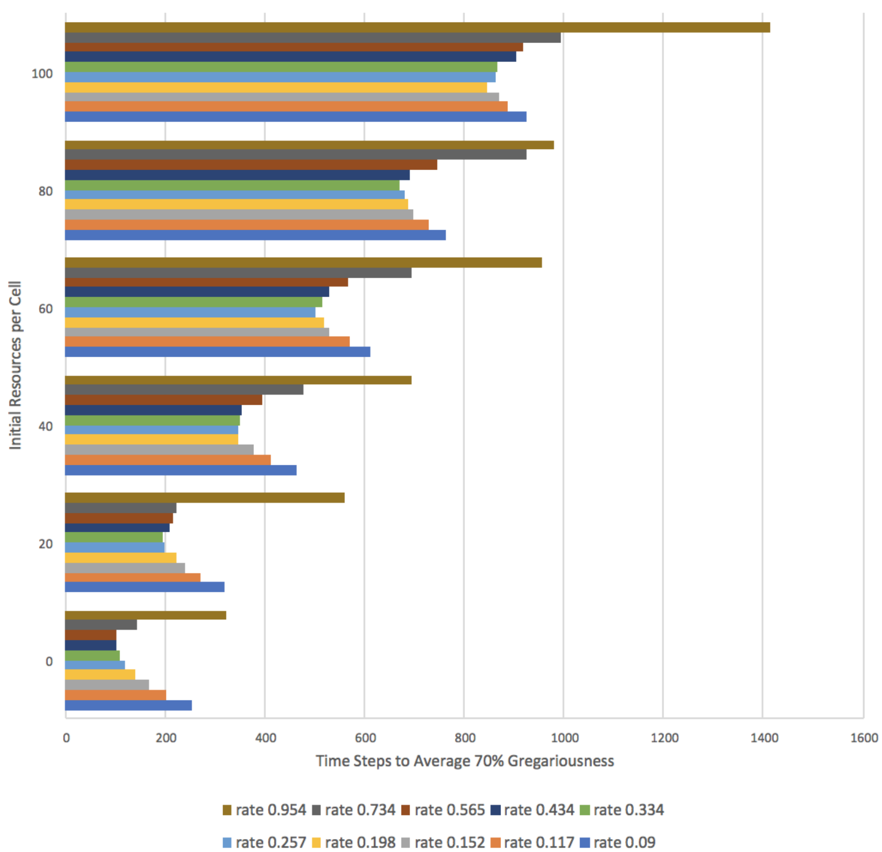


This graph shows, for each initial resource per cell value, the time it takes for the average gregarization of all locusts to reach 75%. All five values for each initial resource per cell value appear to be relatively similar and there isn't a strong pattern for any of the cell percentage groups standing out from the others. This graph shows us that, as long as the total number of resources is the same, the time it takes to reach a population of mostly gregarized locusts is independent of the number of cells that have resources in them. We can also see from this graph that locusts generally take longer to gregarize when there are more resources available to them, as they will spend more time eating food before worrying about their neighboring locusts.

5.2 Initial Resources and Gregarization Rate

We had noticed, while selecting parameters to use in the simulation, that different gregarization rates had a big influence on how each of the locusts behaved and could drastically change what the model looked like after many time steps. In order to further explore this parameter, we performed a study exploring gregarization rate versus time to a gregarization threshold at different amounts of initial resources per cell (Figure 5.2).

Figure 5.2 Graph comparing simulations with different gregarization rates at various initial resource per cell values. This graph measures how long it takes the locust population to reach an average gregariousness value of 0.7



There were ten different gregarization rates studied, evenly spaced on a logarithmic scale between 0.09 and 0.954. Each of these rates was tested at six different initial resource values between 0 and 100 in order to see how they behaved in different environments. We collected data on how many time steps it took for the locust population to reach an average of 70% gregarization. In the study looking at gregarization time and resource distribution, we used an average gregarization threshold of 75%, however, we used 70% in this study because some of the gregarization rates did not have the population reach 75% gregarization. We noticed that there seemed to be quite a bit of noise and variation for each set of gregarization rate and initial resources, so we ran each pair seven times, in order to calculate a smoother average.

In Figure 5.2, as in Figure 5.1, we notice that in environments with more initial resources, it generally takes longer for the average locust population to become gregarized. Additionally, we can see that there is quite a bit of variation between different gregarization values. Smaller gregarization rates like 0.09 tend to take longer to reach the same average gregarization for the population than medium gregarization rates like 0.334; however, the larger gregarization rates like 0.734 and 0.954 generally take the longest time to reach the same average gregarization for the population. This shows us that there is likely a medium gregarization rate for which the time it takes to gregarize a population is a minimum. In Figure 5.3, we can see that the rate which takes the least time to reach 70% average gregarization shifts with different initial resource values. Additionally, simulations with high gregarization rates like 0.954 tend to have a much wider range of times until a majority gregarization. Of the seven runs for the test with 20 initial resources, one run only took 221 steps while another took 1371. Smaller gregarization rates all had much more consistent times.

Chapter 6

Discussion

In this thesis, we have built a system of mathematical equations based on some important biological principles of locusts. This mathematical model takes into account gregarization and social interaction as well as environmental factors like resource distribution. Our model was implemented in NetLogo as an agent-based model and we were able to observe locust behaviors as a result of a wide variety of initial conditions.

We found that locusts generally take more time for the average gregarization of the population to reach a majority threshold when there are more initial resources in the environment, regardless of how the resources are distributed throughout the environment. There are some resource distribution patters we would like to continue exploring, as discussed in our Future Work chapter.

We also found results that suggest that there is a gregarization rate for locusts which has a minimum number of time steps until the population reaches a majority threshold. This gregarization rate may shift depending on environmental initial conditions, like locust distribution and initial resources per cell, but it always lands in the middle, between 0 and 1. Gregarization rates towards both ends of the range (0.09 and 0.954 in our test) tend to take much longer to gregarize.

We also found that high gregarization rates take the longest time to reach a majority gregarization threshold. One observation from watching the locusts forage and interact with each other while running simulations in NetLogo is that locusts with a high gregarization rate tend to start by gregarizing and forming small clumps of nearby locusts, instead of immediately foraging as locusts with lower gregarization rates do. After these initial small groups of gregarious locusts form, they will eventually break up as the locusts choose to eat instead of prioritizing social interaction. Locusts who are initially randomly placed with few other locusts won't form those initial groups and it will take them longer to become gregarized. This situation will take longer for the population to increase its average gregariousness because, while the environment will always have some small groups of gregarious locusts, there will also be other locusts who are separated, foraging, and aren't encountering other locusts as frequently. This scenario differs from a simulation where the gregarization rate is small because, in that environment, all the locusts will forage and generally avoid one another until all the resources are consumed. In both simulations (large and small gregarization rates), it is generally only after all the resources are gone that the populations average gregarization rate will increase past the threshold. This occurrence and explanation was only observed anecdotally so we could not be sure that this is what is causing the relationship between gregarization rate and time until the population's average gregarization reaches the threshold without further study.

Chapter 7

Future Directions

Throughout this project, we have looked at a variety of different resource distributions, including random, uniform, patchy, and a gradient. One agent-based model we found in the literature, written by Nonaka and Holme, explores the idea of clumpiness in the environment and how that may affect different optimal foraging strategies (Nonaka and Holme, 2007). In future work, we would like to combine our model with some of the ideas from this paper to see how large patches or groups of resources clumped together might affect how the locusts behave, forage, and gregarize.

Through some of the parameter identification work conducted in this paper, we thought about both the temporal and spatial scale of the world of the simulation. Unfortunately, this was not something we were able to research thoroughly or connect to the literature and future work could enhance the model by refining both the spatial and temporal scales.

Another element of the simulation that could use more refinement is the orientation of the locusts. Currently, the locusts are given a random orientation at the start of the model and do not change from that position, moving from the center of one cell to the center of a neighboring cell. Unfortunately, we know that this is unrealistic in biology and locusts often align with each other as they are moving or make very small angular changes, so it would be interesting to see how adding orientation into the model would change it. One group of researchers studied how locusts pause between steps and found that they will often slightly alter the direction which they are facing during each pause, causing them to move in a slightly different direction when they next move (Bazazi et al., 2012). We would like to see how this reorientation effect could change locust distribution or movement patterns. Another important element of the locust movement part of our model is repulsion. Much research on locusts discuss the idea of attraction and repulsion from other locusts as two of the fundamental rules of movement (Dkhili et al., 2017). While our model includes attraction, it doesn't have any rules for repulsion, making it likely that gregarized locusts will simply end up piled on top of each other. Future work could explore these nuances in locust movement to see how they might affect how the model predicts locust behavior.

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