Simulating Pollinator Decline: How pesticide affects bumble bees and the plants that they pollinate

A Major Qualifying Project
Submitted to the Faculty of
Worcester Polytechnic Institute
in partial fulfillment of the requirements for the
Degree in Bachelor of Science
in
Bioinformatics and Computational Biology
By

Rachel I Blakely

Professor Elizabeth F Ryder, Major Advisor

Professor Robert J Gegear, Co-Advisor

Abstract

Pesticides may contribute to recent large declines in pollinator populations. Many kinds of pesticides impact learning and memory in bees in the laboratory. To determine whether these sub-lethal effects could impact bee populations over time, I created an agent-based simulation using virtual bees and flowers. The simulation assumes that pesticides reduce the bees' memory capacity for floral rewards. The resulting prediction was that pesticide-impaired bees forage less efficiently, resulting in a decline in both the bee and flower populations. In addition to serving as a research tool that can predict the effects of pesticide impairment, this simulation will be able to act as an educational tool for the general population to learn about potential detrimental effects of pesticide usage.

Table of Contents

1 Introduction & Background

Pollinators have been decreasing in number for years in multiple regions of the world. These declines are not only harming the pollinators, they also raise serious concerns about agriculture and the animals that rely on plant pollination for food (Potts et al., 2010). Five different environmental pressures are widely considered to be the primary causes of pollinator decline: agricultural intensification, climate change, invasive species, landscape alteration, and pathogens (González-Varo, 2013). Although there has been much research on how these environmental stressors affect individual pollinators, there has not yet been significant investigation into the long-term effects. As a result, the mechanisms of pollinator decline remain unclear.

Each of these environmental pressures has a negative impact on pollinators, but when the pollinators are faced with more than one pressure, the effects can be intensified, added to each other, or one pressure can even negate the effects of another (González-Varo, 2013). It can be difficult to obtain an accurate understanding of these effects in a controlled lab environment, especially over a long period of time. On the other hand, conducting a field study introduces difficulties with tracking the pollinator populations and their changes. Traditional approaches to conducting research into long-term effects of pressures can be very impractical and time consuming. In order to circumvent the difficulties with lab and field methods, this project will use a computational modeling approach to investigate pressures and their effects on the bumble bees and plants over a period of multiple seasons. A computational model could potentially include multiple species, both pollinators and the species that rely on them, and multiple environmental pressures. For this initial project, however, I intend to create an accurate agent-based simulation of bumble bees and flowering plants in an environment in which the bees are impaired by pesticide. This simulation will focus on how the pesticide affects the the foraging bees' behavior, and how that in turn affects the colony's output and the plants that rely on the foragers' performance.

1.1 Bumble Bees

Bumble bees have natural behaviors, which are affected by environmental pressures in different ways. Depending on the bees' responses, the pressures can have different, usually harmful, effects. In some cases, the bee may not respond appropriately causing the pressures to have an even greater impact.

1.1.1 Life and Behavior of Bumble Bees

A bumble bee colony is created when a single queen awakens in the spring from her winter hibernation (figure 1; *The bumblebee lifecycle,* BBCT). She immediately begins to consume nectar to build up her energy so that she can search for a nest site and begin to construct her nest. A bumble bee nest site can be anywhere that provides appropriate shelter for the colony. It can be aboveground, belowground, an existing burrow, or a new construction. Once she has developed a nest she collects pollen and lays the eggs that will begin to populate her colony (figure 1). In early summer, the first group of worker females hatch (there are no males at this point). Some of the workers in the nest and others will become the foragers that collect nectar and pollen to sustain the colony. At this point in the life cycle the queen remains inside the nest at all times and lays more eggs. Throughout the summer foragers continue collection and the queen continues to lay eggs, which produce more workers for inside and outside of the nest (figure 1).

Near the end of the summer eggs hatch more than just workers. These eggs produce males and queens, which are females that have been fed significantly more than others. The new male bees leave the nest to mate and usually do not return. Soon after the males leave the nest, the queens leave the nest and the males they meet have to compete to mate with them (figure 1). After a queen has been mated, she stores energy by feeding on nectar and pollen. In the meantime, the original colony dies out as summer ends. The young mated queens find a place to hibernate for the winter and are the only members of the colony to survive into the next spring, at which time they start the cycle again by creating a new nest and laying eggs.

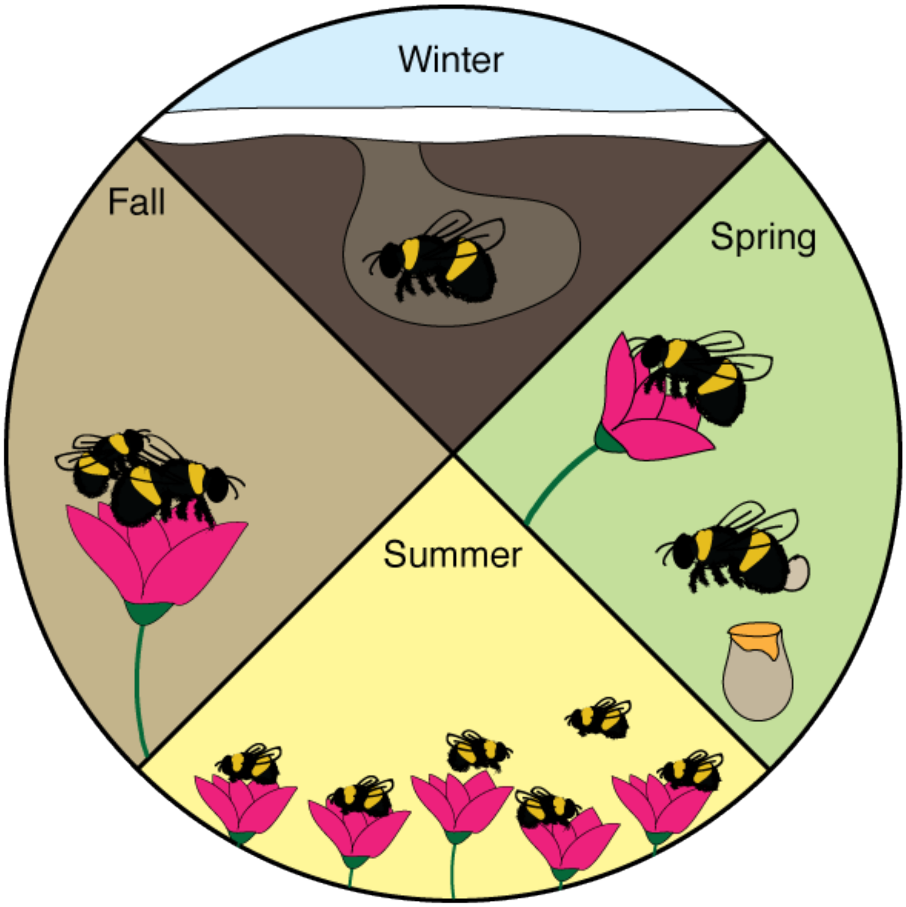


Figure 1. The bumble bee life cycle In winter the queen hibernates. In spring the queen collects pollen to start her colony and lays the first eggs. In summer the foragers work during all daylight hours. In fall the males mate with queens so that the queens will be ready to begin a new colony in the following year.

Foragers play a critical role in the colony as they are responsible for collecting the food that allows the colony to continue to survive. They work during every minute that there is light outside. Because the whole colony is relying on the foragers for survival, foraging strategies must be optimized as much as possible. Although bumble bees fall into the category of generalists because they can visit many different flowers, some of these flowers are more rewarding than others (Goulson, 1999). Some flowers simply hold more nectar than others or regenerate nectar at a faster rate than others. Additionally, flowers can vary in shape so that nectar can only be reached by bees with certain tongue lengths and shapes, thus making the flower less rewarding to bees that can't reach the nectar and more rewarding to those that can.

Because not all flowers are created equal, foragers tend to develop a preference for those that have been more rewarding as part of their foraging strategy (Goulson, 1999). In order to use the best foraging technique, foragers need to be able to maximize their chances of visiting the most rewarding flowers. To do this they must ensure that they are sampling different kinds of flowers yet still focusing on the flower that has been most rewarding in the recent past. Over time the floral resources vary so the bees also have to be able to track the change over time and account for them in their behavior. To succeed foragers require a good memory and strong decision making skills. As a result, bumble bees have evolved memory and decision-making ability to perform foraging tasks well. Individual bees that have reduced memory or an inability to make appropriate adaptive forging decisions will bring fewer floral resources back to the colony. This change reduces the reproductive output (male and queen production) of the colony. The number of reproductives in the fall determines how many bees are in the population the following year; thus, foraging success or failure of individuals has a direct effect on the population dynamics.

1.1.2 Effects of the Environmental Pressure Pesticide

The five environmental pressures that impact bumble bees are agricultural intensification, climate change, invasive species, landscape alteration, and pathogens (González-Varo, 2013). Agricultural intensification includes increased usage of pesticide, change in fertilizers, change in farm size, and other alteration in agricultural practices. Climate change primarily includes warming, which can affect the timing of the seasons and flower life cycles. Invasive species can involve a new pollinator species, a new plant species, or a new predator. Landscape alteration occurs when the natural habitat is degraded or destroyed causing the landscape or community to be changed. Lastly, pathogens can infect the bees and spread to the hive or even the whole population. Of all these pressures, this project focused only on the effects of pesticides.

It has been noted that pesticides have multiple individual and colony-wide impacts on bumble bees (Gill et al., 2012). Bees are exposed to these pesticides when the pesticide is sprayed on the flower from which they collect nectar. Foragers get the most exposure, but the rest of the colony is exposed as well when they consume the pesticide-filled nectar, which has been brought back to the hive. While effects are generally sub lethal in the individual, there can be an increased mortality rate among the workers due to the behavioral impairments that they suffer. Over time pesticide can reduce the number of bees by leading foragers to act inefficiently and depriving the colony of the resources needed to survive. Thus there will be less brood development and the colony will have decreased success (Gill et al., 2012). Observations have also demonstrated that along with a slower colony growth rate, there is a decrease in queen production, which means fewer colonies in the seasons to follow (Whitehorn et al., 2012). This in turn decreases the reproduction of the crops on which the pesticide was initially sprayed. By harming the bumble bees, crop pollination is also at risk (Kremen et al., 2002). With reduced pollination, plants will produce fewer seeds and so there will be fewer plants in the next season. With exposure to more than one pesticide, the effects are increased.

Different types of pesticide will affect the foragers differently, but all of these effects are detrimental. Some of these effects include reproduction complications, malformations in new bees, and a variety of foraging behavior impairments (Thompson, 2003). Neonicotinoid pesticides have increasingly become the preferred pesticide choice. This type of pesticide affects bees by impairing learning and memory (Williamson and Wright, 2013). The pesticide can harm formation of long-term memories. Without long-term memory, the bees have difficulty learning what they need to in order to make foraging decisions. The bee's ability to learn also relies on the bee's ability to identify flowers by odor and other cues (Thompson, 2003). Some pesticides impair the foragers' ability to detect odor and thus harms their ability to learn about their environment well.

The literature shows that many pesticides affect the bees by impairing the learning and memory of the foragers. Because of this, I chose to approach this project with the assumption that pesticide impacts the bees by reducing the size of their memory. To do this, I needed to be able to control the foragers' access to pesticide, control how the pesticide affects the bees, and collect data on the memory and behavior of the bees. This is an experiment that would be very difficult if not impossible to conduct with living bees. A more appropriate method for this investigation was to create a computational simulation. Even though real bees would provide much more realistic data, an agent-based simulation offers the opportunity for measurement and control that would be impossible with living bumble bees. In my simulation I planned to model accurate foraging behavior and then include pesticide that reduces the size of forager memory. With this simulation I planned to obtain a prediction of how the pesticide would affect the bees and flowers. This prediction provides a basis to suggest that the sub-lethal effects of pesticide would have important long-term effects on the populations of bees and flowers.

1.2 Agent-Based Simulations

Agent-based simulations, also known as agent-based models (ABMs) or individual-based models (IBMs) have been increasing in recognition and popularity over the last few years (Railsback and Grimm, 2011). Because ABMs are a relatively recently accepted tool, they have only begun to be regularly used in the last couple of years. As a result, there have not yet been many models developed to address questions about pollinators.

1.2.1 Reasons For Using Agent-Based Simulations

An ABM is a computational model with a visual interface. The interface has buttons, sliders and graphs so that the user can alter variables in the simulation, which is seen as visual agents moving in a window. The movement, behavior, numbers, and traits of the agents are determined in the code. In ABMs individual agents react with each other and their environment. The agent can be anything from a molecule to an animal. Thus ABMs are most useful for investigating how certain patterns emerge in any system from behavior of the individuals over time (Railsback and Grimm, 2011).

ABMs provide an easy and low-cost way to conduct studies on a large variety of agents and topics. Many useful studies with human agents can be conducted using ABMs. These studies can include topics in social patterns, spread of disease, and cooperation in social dilemmas (Goldstone and Janssen, 2005). These same types of ABMs apply to species other than humans as well. An agent can really be anything that has programmable characteristics. The largest scale agent could be a population of humans (or other species), and the smallest scale agent may be an atom or molecule. ABMs simulate a system, so anything that is part of a system can be an agent.

Prior to the introduction of ABMs, most models were purely mathematical equation-based models. Many of the behaviors that are simulated in ABMs would be difficult to accurately model mathematically. ABMs implement more complex factors, allowing for more detailed models (Railsback and Grimm, 2011). ABMs are able to include more complex features by using computational and software concepts in addition to mathematics. An equation may have to be very complex before it can come close to accurately representing the behavior of a living organism. On the other hand, ABMs can model behavior through decision rules and logic operations that more accurately resemble the actual thought processes that living organisms follow (Helbing, 2012). Programmed this way, the model also becomes much more flexible. For example, it is significantly easier to vary traits of individual agents within the population. These factors make ABMs more appropriate for handling populations of living organisms.

There are many languages specifically designed for creating ABMs. The most popular of these languages are NetLogo, MASON, Repast, and Swarm. Because these languages are specifically designed for creating simulations, they provide all of the necessary tools in an easy to use manner. NetLogo is the most commonly used of these languages and is considered to be the most comprehensive (Railsback and Grimm, 2011). The NetLogo graphical interface has three tabs. The first tab is the one that contains all of the visuals. The visuals are the simulation itself and any buttons, sliders, graphs, or switches that have been programmed into the simulation. The second tab is the info tab in which any type of useful information can be written. The final tab is the code tab in which the author writes the code that creates and controls everything that can be seen in the first tab. NetLogo code is written in the NetLogo language, which is specifically designed for coding an ABM.

Because ABMs have been demonstrated to be a useful tool with numerous advantages, this is the method that this project will use to investigate environmental pressures on bumble bees. This project will be programmed in NetLogo because it is one of the best tools for creating ABMs.

1.2.2 Existing Pollinator Simulations

Thus far, ABMs have not been a common tool for investigating pollinator decline. There have been a few studies about pollinators and bees that use ABMs, but only one that investigates some of the environmental pressures. These existing simulations provide a starting point from which this project was developed.

A 2013 study *A spatially explicit agent-based simulation platform for investigating effects of shared pollination service on ecological communities* investigates how pollination by multiple species affects ecological communities (Qu et al., 2013). This simulation allows the user to define traits of plants such as growth, mortality, and seed production as well as traits of pollinators such as the abundance and spatial configuration of each species. This model specifies different traits for each species of pollinator, and then the pollinators service the individual plants. The pollinators in this simulation have the ability of perception, memory, and learning. Plants go through a cycle from seed to sapling to full sized plant, with growth rates and mortality calculated with mathematical models. One interesting aspect of this team's approach to their simulation is that they chose to program the model in C++ rather than use an agent-based modeling language such as MASON, NetLogo, Repast, or Swarm. This simulation was proven to be a successful tool for predicting effects of shared pollination services and can be used for an array of scientific projects.

Honey bees have been the topic of a few simulations such as the one described in the study *Dynamic modelling of honey bee (Apis mellifera) colony growth and failure,* also from 2013 (Russell et al., 2013). The aim of this simulation is to model the dynamics of a honey bee colony in order to better investigate reasons for colony collapse. The simulation is based on multiple mathematical models for different points in the bee life cycle. As a more mathematically-based model, this is not exactly an ABM, however it is still an appropriate example of a pollinator model. Findings indicated that forager mortality, food availability, and the age at which workers become foragers are the details that have the greatest impact on the success or failure of the colony.

Another study, *A-Bees See: A Simulation to Assess Social Bee Visual Attention During Complex Search Tasks,* focuses on the search methods that foragers use to avoid wasting time at unrewarding flowers (Bukovac et al., 2013). Two different scan methods were used in a variety of environments to thoroughly observe the differences between the two techniques. The bees in this simulation have the ability to detect flowers and remember them. This allows them to use the same data as a real bee in order to make educated decisions. The two types of scanning methods that were compared in this study were the honey bee serial scan and the bumble bee parallel scan. The simulation indicated that the honey bee method was more effective in environments where there were not distractors (unrewarding flowers) interspersed among the rewarding target flowers and that the bumble bee method was more effective when the distractors and targets were mixed. This simulation provides a solid framework for simulating foraging strategies in future bee models.

BEEHAVE: a systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure is an ABM programmed in NetLogo, which considers two of the environmental pressures and their effects on honey bees (Becher et al., 2014). In this simulation, pathogens are the foremost issue that is investigated by including varroa mites. In addition, the effects of landscape alteration can be explored if different landscapes are uploaded into the simulation. This model tracks the bees in a single colony from egg to death and maintains an accurate record of the different stages of bees in the colony, the mites, and the nectar and pollen counts. In addition to the colony, this simulation can include a beekeeper, which can treat the colony for the mites as well as perform a few other beekeeping tasks. The primary finding of this simulation is that the mites cause serious damage to the performance of the colony, but if treated by the beekeeper, the bees will recover and perform just as well as they did before infection.

Although it is using an agent-based modeling language, the *BEEHAVE* simulation takes a slightly different approach to using the NetLogo program. A typical ABM includes programmed agents that each appear as a visual object in the simulation. In the case of this simulation most of the agents are not visually moving and interacting on the screen, most of them are behind the scenes. The visuals that are provided are instead used to track numbers of agents and the well-being of the colony over time. This approach to the model is an interesting way to present data. Unfortunately, at the same time, it also makes the simulation's visuals significantly less intuitive. *BEEHAVE* provides a unique example of how the ABMs can really be used in a large variety of ways.

1.2.3 The Simulation Approach in this Project

The aforementioned simulations have some useful traits and some limitations. The *A-bees see* simulation includes foraging behaviors similar to what is necessary for this project. The *BEEHAVE* model is limited by its unconventional use of visuals that makes the simulation less intuitive. Because it is addressing a different question, there are a number of differences between this simulation and the previously existing examples. This simulation includes a detailed memory for each bee that the other simulations do not have. Also, this simulation, unlike the others, explores the effects on flowers. One of the biggest differences between the approach of this project and the existing simulations is that for this project I wanted to create a simulation that would also serve as an educational tool. I have not seen any prior case of a simulation being created with the intent of increasing awareness of a biological problem. However, ABMs provide the opportunity to create intuitive visuals and real-time graphs that are appropriate for demonstrating biological concepts. By taking an educational approach, my simulation can not only explore questions related to the effects of pesticide on bumble bees, but it can also act as a tool to demonstrate these effects to the general population.

1.3 Project Goals and Objectives

The primary purpose of this project was to explore long-term effects of pesticides on the bumble bee population and how that then affects the seed output of the plants. This was done by creating a simulation, which could also serve as an educational tool. By having made this simulation educational, it will help spread the message that pesticide is harming the bees as well as plant species that rely on their pollination efforts.

The first goal was to demonstrate the individual effects of the incorporated environmental pressure: pesticide. The simulation has the ability to demonstrate accurately the effects of pesticide on the bee population and, in turn, the plant population. The second goal was to demonstrate these effects over a period of multiple seasons so that colony output could be calculated and used to demonstrate the overall performance of different colonies on a realistic time scale. This would demonstrate whether or not the effects of the pesticide continue to effect the bees and plants over time. The third goal was to demonstrate that the colony behaviors had an effect on plant species that the bees visit, not just the bees themselves. The fourth and final goal was to provide an educational tool for people of varying interests and ages. To reach this goal, the simulation needed to have an intuitive interface that anyone could comfortably use and understand. It must also have clear visuals so that those who view the running simulation could easily comprehend what they are looking at. Overall the simulation must clearly demonstrate the above goals so that people of all ages can understand and learn from it.

2 Methodology: Overview, Design concepts, Details (ODD)

The ODD is an ABM documentation method recognized in the agent-based simulation community (Grimm et al., 2006). In the case of this project, programming the simulation is the methodology and so the ODD provides a standardized way of explaining the simulation.

2.1 Purpose

This model is designed to serve as an accurate representation of the effects of pesticide on the performance of the bumble bee population and the seed production of flowering plants in surrounding environment. It includes the behaviors that are involved in the bees visiting flowers, collecting nectar, and bringing it back to the hive. The bees have memory, which helps them decide which flowers to visit. When exposed to pesticide the memory is impaired. When the bees visit flowers of the same species, they pollinate them, enabling the flowers to generate seeds. When a season passes, new bees and flowers are generated based on nectar collection and seed production.

The reason for creating this model is to demonstrate how pesticide affects bees at the individual and population levels as well as how the impaired behavior of the bees affects the flower species that rely on them. This model shows multiple seasons on a shorter time frame so that the user will be able to see the effects that would be difficult to observe in a real life situation.

2.2 Entities, State Variables, and Scales

The model has three different collectives of individuals: bees, flowers, and hives. There are no spatial units or environment in this simulation. The flowers each have only a few state variables, which are its nectar content, whether or not it is occupied, its species, and whether or not it has pesticide on it. The hives only have one nectar content variable. A bee is characterized by its location, heading, the flowers it can see, whether or not it is on a flower, its memory (the last flowers it visited and the reward it got from them), the amount of nectar it has collected, and what it wants to visit next.

Entity	State Variables	Possible Values
Globals	hive-1	Location of hive 1
	hive-2	Location of hive 2
	monitor-bee-1	Identity of a random bee for monitoring
	monitor-bee-2	Identity of another random bee
	Seed-total-*x*	Number of seeds in species *x* population
	Number-of-species-*x*	Current number of species *x* flowers
	Run-time	Number of ticks simulation can run
	Number-bees	Current number of bees this season
	Hive-1-bees	Current number of bees in hive 1
	Hive-2-bees	Current number of bees in hive 2
	Reset-time	Number of ticks before season resets
Sliders	**Hive Sliders:**	
	number-of-hives	The number of colonies in the simulation
	Hive-nectar-label?	Toggle nectar label on hives
	Bee Sliders:	
	number-of-bees	Number of bees at start
	bee-nectar-max	Max amount of nectar a bee can hold
	bee-nectar-label?	Toggle nectar label on bees
	Normal-memory-size	Size of a normal bee's memory

	Impaired-memory-size	Size of an impaired memory
	Sample-frequency	How often bee samples random species
	Percent-affected	Percent of bees affected by pesticide
	Flower Sliders:	
	flower-nectar-max	Max amount of nectar a flower can contain
	flower-nectar-label?	Toggle nectar label on flowers
	Start-num-species-*x*	Number of flowers of species *x* (*x* = 1-4)
	Regeneration-rate-*x*	Rate of nectar regeneration in species *x*
	Percent-pesticide	Percent of flowers with pesticide
Bee	on-flower?	Is the bee on a flower?
	hive-belongs-to	Number of the hive bee belongs to
	nectar-collected	Amount of nectar bee has
	time-on-flower	Amount of time bee has been on flower
	flowers-in-view	List of flowers in view
	species-seen	List of flower species bee can see
	chosen-flower	ID of flower bee is going to
	have-chosen?	Has the bee chosen a flower?
	Total-visits-*x*	Number of visits bee has made to species *x*
	Visit-frequency-*x*	Frequency of visits to species *x*
	Visit-frequencies	List of all visit frequencies
	Species-*x*-visited	List of species *x* flower IDs visited
	Species-*x*-rewarded	List of species *x* rewards gotten
	Max-memory	Maximum memory size for this bee
	Oldest-memory-*x*	Oldest memory in list for species *x*

	Visit-chance-*x*	Chance bee will visit species *x*
	Visiting-chances	List of all visiting chances
	Species-wanted	Species type bee wants to visit next
	Update-time-*x*	Last time species *x* lists were updated
	Impaired-memory?	Is the bee's memory impaired
	Susceptible?	Is this bee susceptible to pesticide
	Last-species	The species of the last flower visited
Flower	flower-nectar-content	Amount of nectar in flower
	occupied?	Are there any bees on this flower?
	Species	Species number of this flower
	Has-pesticide?	Does this flower have pesticide?
	Max-seeds	The max number of seeds possible
	Seeds-pollinated	Number of pollinated seeds so far
Hive	hive-nectar-content	Amount of nectar in hive

2.3 Process Overview and Scheduling

Each tick, the bees move once in no particular order. Based on where the bee is, it calls different functions. Additionally, each tick, the three breeds update their variable values to account for nectar transfer and seed pollination if it occurs.

In this simulation, 10 ticks are equivalent to 1 second. When a bee is on a flower, it stays on the flower for a number of ticks that is equal to the units of nectar in the flower giving a transfer rate of one unit of nectar per tick. A real bee is expected to remain on a flower for up to 4 seconds (40 ticks) thus the flowers in the simulation have a maximum of 40 units of nectar, because transferring 40 units of nectar would take 4 seconds. This nectar is refilled based on the rate set by the sliders for each species. A real bee is expected to visit up to 20 flowers before it has to return to the hive thus the simulated bee can hold up to 800 units of nectar. The number of flowers visited can vary significantly, however, depending on how full or empty the flowers are.

A bee is calling search and visit procedures until it reaches its maximum amount of nectar, at which point it calls the procedure to deliver nectar to the hive. The search procedures involve identifying the flower species that it sees which would be best to visit based on the memory of the bee's previous visits. From this point the bee selects a specific flower to visit and heads to it. While the bee is on the flower it calls the collect nectar procedure. Once the bee has finished visiting a flower it records the reward it got from the flower and the ID of the flower using the memory procedures. If a bee encounters pesticide this leads to the impair memory procedure, which reduces the maximum size of the bee's memory.

A season ends and a new one begins after a set amount of ticks. This amount of time is determined based on the number of bees and flowers present. Flowers are produced based on the number of seeds generated in the previous season. Because of this, a season has to be long enough for the flowers to finish generating seeds. Bees are produced based on the rate of nectar collected in the previous season rather than the final amount of nectar. The season must be long enough to calculate an accurate rate, however, the length of the season should not largely impact the number of bees produced. The time a season lasts is shorter than a real season would be based on the time schedule in this simulation, however, it is calculated to be a time that will not impact the numbers of flowers and bees produced in the next season.

The length of a season is specifically calculated based on the ratio of flowers to bees at the start. This is done with the following formula where start-num-species-x is the number of species x flowers at the start and number-of-bees is the number of bees at the start: $500 \times \frac{start-num-species-1+start-num-species-2+start-num-species-3+start-num-species-4}{number-of-bees}$.

2.4 Design Concepts

2.4.1 Basic Principles

This model simulates only the daylight hours the bees are out collecting nectar from flowers. To choose a flower, the bee determines which flower species are in its view. The bee has calculated visit chances from its memory, which it associates with the species in its view. The bee determines which species to visit by choosing the species in view with the highest visit chance. Every thousand ticks (almost 2 minutes in real time), the bee samples other species to maintain awareness of the fluctuations in reward. When the bee chooses what to sample, it chooses the flower in view with the lowest visit chance rather than the highest. When the bees have obtained the maximum amount of nectar that they can hold, they bring it back to the hive.

During the flower visit, bees commit the visit to memory so that they can calculate visit chances for future visits. When the bee lands on a flower, if it came from the same kind of flower, it brings with it the right kind of pollen and so the flower produces a seed. If the bee came from a different kind of flower then the pollen it brings blocks the flower's ability to produce a seed. If the flower has pesticide when the bee lands on it, the pesticide impairs the bee's memory so that it has fewer previous visits to calculate into the visit chances.

2.4.2 Objectives

In this model, the bees' objective is to collect the maximum amount of nectar and bring it back to its hive.

2.4.3 Learning

The bees are able to remember which are the last flowers they have just visited and how rewarding the flowers were so that they can calculate which species gives the best reward. This memory allows the bees to learn where they have been and what is best to visit so that they can make educated choices.

2.4.4 Prediction

The bee predicts that a flower of the same species from which it has previously received the best reward will most likely also have a good reward and so visiting that species would be a good choice.

2.4.5 Sensing

The bees have a cone of sight, which they use to see nearby flowers in the direction in which they are heading. They are able to tell which of these are closest and what species they all are. Bees also know where their own hive is so that they can return to it.

2.4.6 Interaction

When the bee is on the same patch as the flower it has targeted, it is assumed that the bee "lands" on that flower and gathers all of its nectar. This is demonstrated by the bee staying on that patch for one tick per unit of nectar it drains and the entire nectar quantity transferring from flower to bee. If the flower has pesticide, the bee's memory becomes impaired. The last thing that happens during interaction is seed production. If the bee has come from the same species of flower, the number of seeds-pollinated in the flower increases by one. If the bee came from a different species, then the number of max-seeds decreases by one.

The bees do not interact with each other, although they can cross paths. If another bee is already on the flower a bee has targeted, the second bee will not land there to avoid conflict. The only interaction bees have with the hive is to visit the hive and deliver nectar in the same way that they take the nectar from the flowers.

2.4.7 Stochasticity

At the beginning of the simulation the flowers are placed at random provided no two flowers are in the same location.

The direction in which the bee heads is somewhat random if it has not found a flower to go towards. In this situation, the bee moves forward one with a random degree of turn within the range of -30 to 30 degrees. With this variability, the bees all land on flowers in a different path and thus have different flowers and rewards stored in memory.

2.4.8 Collectives

The individual bees are all part of a colony and all colonies are part of the population. The activity of the individual contributes to how the whole population is doing.

2.4.9 Observation

The data collected shows how much nectar the hive has over time, how much nectar the bees have over time, and how much nectar the flowers have over time. Also data is collected to demonstrate how many times each flower gets visited. There are graphs to show total nectar collected, as well as total numbers of bees, flowers, and seeds.

2.5 Initialization

Upon clicking the setup button, a number of flowers, as designated by the *number-of-species* sliders, should be generated in random coordinates on the screen. If the *number-of-hives* slider is set to one, one hive will be put in the middle of the screen; if the number is set to two, one will be in the top right corner and one in the bottom left corner. The bees will be generated in the location of their hive. The number of bees generated in each hive is determined by the *number-of-bees* slider so that if there is one hive, it has all the bees, and if there are two hives, the bees are divided in half between the hives.

2.6 Input Data

There is no input data in this model.

2.7 Submodels

There are three submodels that make up this model: the Basic Bee model, the Memory model, and the Pesticide model.

2.7.1 Basic Bee Submodel

The basic bee submodel consists of the bees, hives, and flowers. The bees visit the flowers, collect the nectar, and bring it back to the hive. The hives accumulate the nectar. The flowers calculate their seed counts based on where the bees that visit came from.
This submodel affects the variables in the table below.

Entity	**State Variables**	**Possible Values**
Globals	hive-1	Location of hive 1
	hive-2	Location of hive 2
	monitor-bee-1	Identity of a random bee for monitoring
	monitor-bee-2	Identity of another random bee
	Seed-total-*x*	Number of seeds in species *x* population
	Number-of-species-*x*	Current number of species *x* flowers
	Run-time	Number of ticks simulation can run
	Number-bees	Current number of bees this season
	Hive-1-bees	Current number of bees in hive 1
	Hive-2-bees	Current number of bees in hive 2
	Reset-time	Number of ticks before season resets
Sliders	**Hive Sliders:**	
	number-of-hives	The number of colonies in the simulation
	Hive-nectar-label?	Toggle nectar label on hives
	Bee Sliders:	

	number-of-bees	Number of bees at start
	bee-nectar-max	Max amount of nectar a bee can hold
	bee-nectar-label?	Toggle nectar label on bees
	Sample-frequency	How often bee samples random species
	Flower Sliders:	
	flower-nectar-max	Max amount of nectar a flower can contain
	flower-nectar-label?	Toggle nectar label on flowers
	Start-num-species-*x*	Number of flowers of species *x* (*x* = 1-4)
	Regeneration-rate-*x*	Rate of nectar regeneration in species *x*
Bee	on-flower?	Is the bee on a flower?
	hive-belongs-to	Number of the hive bee belongs to
	nectar-collected	Amount of nectar bee has
	time-on-flower	Amount of time bee has been on flower
	flowers-in-view	List of flowers in view
	species-seen	List of species bee can see
	chosen-flower	ID of flower bee is going to
	have-chosen?	Has the bee chosen a flower?
	Total-visits-x	Number of visits bee has made to species x
	Visit-frequency-x	Frequency of visits to species x
	Visit-frequency	List of all visit frequencies
	Last-species	Last-species
Flower	flower-nectar-content	Amount of nectar in flower
	occupied?	Are there any bees on this flower?
	Species	Species number of this flower

	Max-seeds	Max-seeds
	Seeds-pollinated	Seeds-pollinated
Hive	hive-nectar-content	Amount of nectar in hive

2.7.2 Memory Submodel

The memory submodel consists of the bee's memory. Each bee has eight lists. These lists consist of a reward list and a flower ID list for each species. When the bee visits a flower, the memory lists are updated. The bee records how much reward it got from each of the last ten flowers, and the ID of that flower. This way, the bee can calculate which species it is getting the best reward from. Visiting chances are calculated based on these memories. To calculate the visit chances the rewards in each of the reward lists are averaged to obtain four numbers. These numbers are then normalized so that the largest number is a 1 and the other three numbers are proportionally lower with a minimum of zero. When the bee decides what species to visit next, it picks the species with the highest visiting chance of the species within the bee's cone of view. Because of this the bee will tend to specialize on the same flower species when it has memory. This is why there is a sample frequency to tell the bee to sample a random species periodically to make sure that another species is not now better. The variables below are involved in this submodel.

Entity	State Variables	Possible Values
Sliders	Normal-memory-size	Size of a normal bee's memory
	Impaired-memory-size	Size of an impaired memory
	Sample-frequency	Frequency bees sample random flower
Bee	Species-x-visited	List of species x flower IDs visited
	Species-x-rewarded	List of species x rewards gotten
	Max-memory	Maximum memory size for this bee
	Oldest-memory-x	Oldest memory in list for species x
	Visit-chance-x	Chance bee will visit species x
	Visiting-chances	List of all visiting chances
	Species-wanted	Species type bee wants to visit next
	Update-time-x	Last time species x lists were updated

2.7.3 Pesticide Submodel

The pesticide model puts pesticide on the flowers and affects the bees simply by reducing the size of their memory. Pesticide can be placed on all or just some of the flowers. Also, it is possible to change the percent of bees that can be affected by the pesticide. This is done by affecting the variables in the table below.

Entity	**State Variables**	**Possible Values**
Sliders	Percent-affected	Percent of bees affected by pesticide
	Percent-pesticide	Percent of flowers with pesticide
Bee	Impaired-memory?	Is the bee's memory impaired
	Susceptible?	Is this bee susceptible to pesticide
Flower	Has-pesticide?	Does this flower have pesticide?

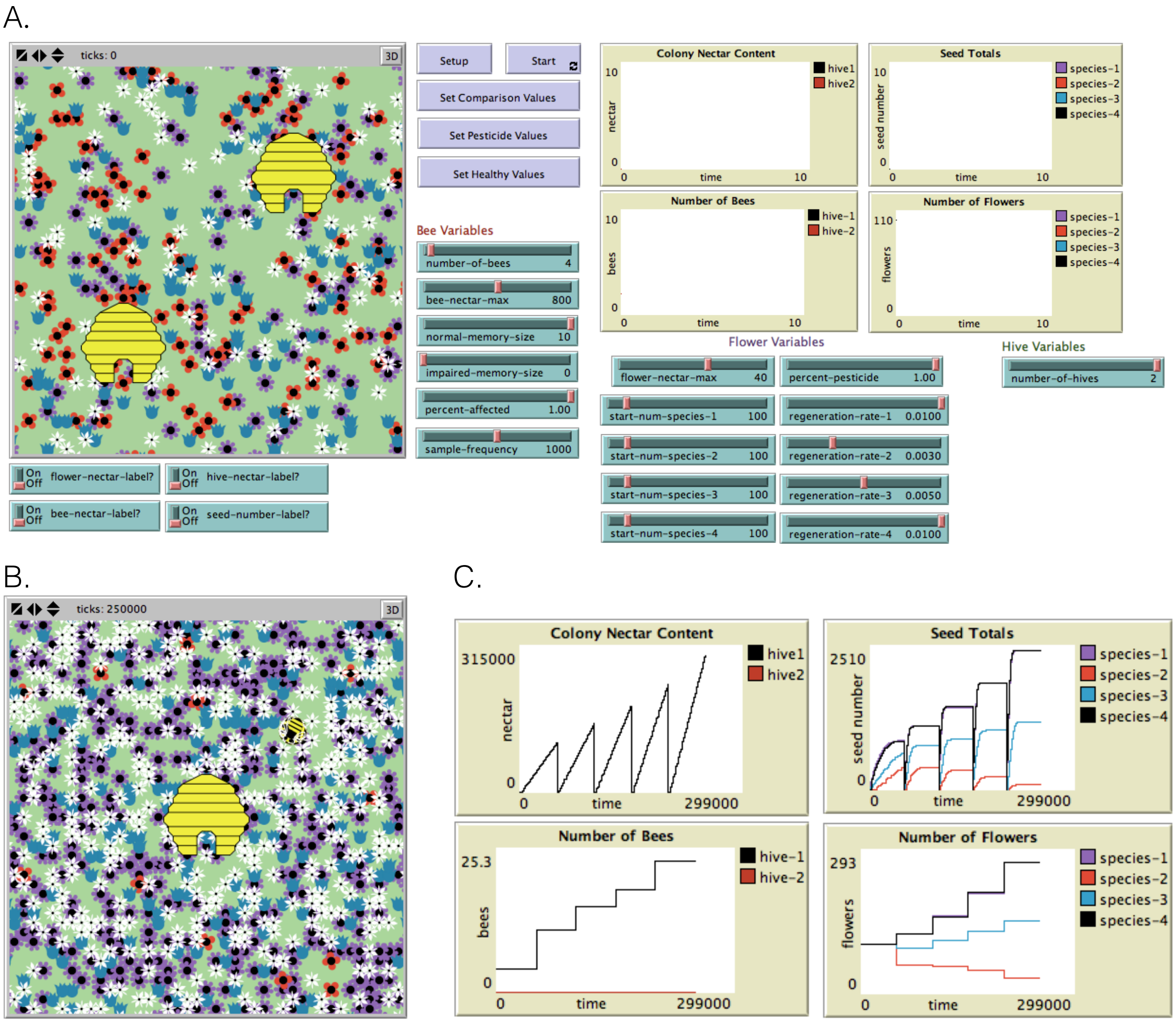
3 Results

3.1 The Simulation

The simulation that I have developed includes bees, which each belong to a colony, and four species of flowers. The bees fly around and visit flowers. They choose which flower to visit based on what species they have calculated to provide the best reward. When a bee lands on a flower it takes all of the nectar in the flower. If the flower has pesticide, the visiting bee becomes impaired by contact with the pesticide. With the default values, a normal bee has a memory of ten and an impaired bee has a memory of zero. The simulation runs over multiple seasons. In this simulation seasons do not reflect an accurate time period; they instead last for a period of time that is long enough to calculate accurate data (for more details see the methods section).

The completed simulation includes a visualization of the agents, four graphs for tracking progress, and many sliders for altering variables as desired. These variables include the number of bees, flowers, and colonies, the regeneration rates of the flowers, the amount of nectar that flowers and bees can hold, the frequency with which bees sample flowers, the normal and impaired memory sizes, the percent of flowers with pesticide, and the percent of bees susceptible to the pesticide. An image of the entire simulation interface is shown in figure 2A. When the simulation is run, the interface updates to show the progress. The visualization shows the bees going from flower to flower and delivering the nectar to the hive. When a new season begins, the starting number of bees and flowers is calculated based on the amount of nectar and number of seeds at the end of the previous season. The visualization redraws the flowers and regenerates the bees to have the correct numbers. Over time there will be visible differences as demonstrated by figure 2B.

As the simulation progresses, the graphs are continuously drawn. Over time trends will be visible like in figure 2C. The first graph shows the amount of nectar in the colony. Each season it starts over at zero. For the simulation conditions shown in figure 2C it becomes apparent that in each season more nectar is collected, though this trend does not always hold true. The rate at which the nectar is collected directly translates to the number of bees generated in the next season. As more nectar is collected in each season and each season is the same length, more bees can be generated each season leading to the increase of bees seen in figure 2C. The seed totals, like the nectar, are reset to zero each season. Each flower has a limit to how many seeds it can generate, so once all of the seeds are generated the totals become constant. In figure 2C it is apparent that in most cases the seed totals reach their maximum long before the season ends. The seed totals directly lead to the number of flowers generated in the next season.



Bee Variables

number-of-bees 4

bee-nectar-max 800

normal-memory-size 10

impaired-memory-size 0

percent-affected 1.00

sample-frequency 1000

Flower Variables

flower-nectar-max 40

percent-pesticide 1.00

start-num-species-1 100

regeneration-rate-1 0.0100

start-num-species-2 100

regeneration-rate-2 0.0030

start-num-species-3 100

regeneration-rate-3 0.0050

start-num-species-4 100

regeneration-rate-4 0.0100

Hive Variables

number-of-hives 2

On Off flower-nectar-label?

On Off hive-nectar-label?

On Off bee-nectar-label?

On Off seed-number-label?

Figure 2. Simulation Interface The simulation interface includes multiple sliders and graphs with the visualization. A. The entire interface at setup. There is no data in the graphs because the simulation has not yet run. B. The visualization after five seasons. The number of flowers and bees has changed over time. C. The graphs after five seasons with healthy values set. The nectar and seed numbers drop to zero as they are reset at the beginning of each season. The bee and flowers numbers remain constant through a season and only change when a new season begins.

When I collected data from the simulation I kept most variables constant, although a user may change them if they so choose. When I ran tests, at the start of the simulation there were always four bees and 100 of each flower species (400 total). The healthy bee memory size was set to ten and the impaired size was set to zero. For all trials, the bee nectar max was set to 800 and the flower nectar max to 40. Lastly, the sample frequency stayed at 1000 ticks. Everything else was changed depending on what hypothesis was being tested.

Using the simulation, I investigated the following questions: 1) How do pesticide-induced impairments to an individual's memory capacity affect that individual's behavior, 2) how do these impairments to the individual affect the bees and plants on the population level, 3) how do different degrees of memory reduction affect the bee and plant populations, and 4) how does the impairment affect the bee and plant populations when different percentages of the bees are impaired.

3.2 Memory capacity alters the bee's behavior

During development of the memory aspects of the simulation, I needed to explore whether or not the model functioned as expected. I started exploring functionality when the simulation had only two flower species and one bee. By removing the interference brought on by including many bees, I was able to observe that a single bee has all of the expected behaviors. To obtain these observations I had the simulation generate graphs to show what a bee was visiting and what the bee's visit chances were at any given time. These graphs are shown in figure 3.

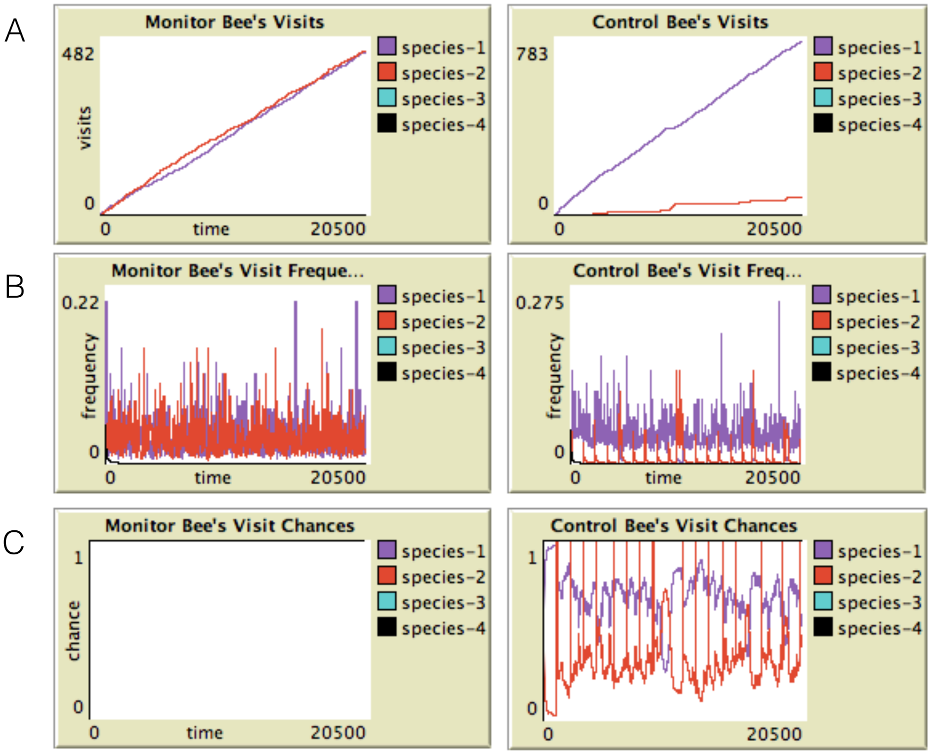


Figure 3. Memory Testing Graphs from an early version of the simulation to demonstrate memory functionality. Monitor bee is a random impaired bee and control bee is a random healthy bee. A. The total number of visits the bee made to each flower species. The impaired bee made a similar number of visits to each type, the healthy control bee visited much more of the more rewarding species 1 than the less rewarding species 2. B. The frequency with which each bee visited the flower species at a given time. The healthy control bee showed a large

preference for species one flowers that the impaired bee did no show. C. The visit chances each bee had calculated for each flower species at one time. The impaired bee always calculated a 1 for each flower; the healthy bee usually had a higher chance for species one than two, unless it was sampling (every 1000 ticks).

Figure 3 demonstrates that there is a clear difference in the memory of a healthy bee with a memory of size 10 and an impaired bee with no memory. Part C shows that the impaired bee just set its visit chances for each species to one because it had nothing in memory to calculate an accurate value from. On the other hand, the healthy bee calculated chances that reflected its experiences, which showed that species one was the better flower species. The graph also shows that in these calculations every 1000 ticks the visit chances were set to one so that the bee would sample randomly. The differences in the visit chances were reflected in the bees' visiting behaviors in parts A and B of figure 3. In part A it is clear that because of the equal visit chances, the monitor bee was visiting the flowers randomly and relatively equally. The control bee visited far more species one flowers than species two flowers. Part B demonstrates in another way that the healthy bee was visiting species one flowers much more frequently. There were only a few times in when the monitor bee was visiting the species two flowers. Most of these appear to be a single visit from sampling. There was one point when the bee switched briefly to visiting species two, but it was not long before the bee returned to species one. As expected, without its memory, a bee cannot make educated calculations and thus does not specialize on the better flower type.

3.3 Bee populations and rewarding flower populations grow over time when bees are healthy

When the bees are healthy, the simulation should resemble a situation in the real world when the bees and flowers are doing well and there is no interference with the system. The expectation is that, with these parameters, the bee population will thrive. With a well functioning bumble bee population, the flowers should also thrive, but the more rewarding flowers should do better than the less rewarding.

To confirm this hypothesis, I ran the simulation ten times with no pesticide. I gathered the output averages from the four graphs to show the trends the agents in the simulation follow over five seasons in figure 4.

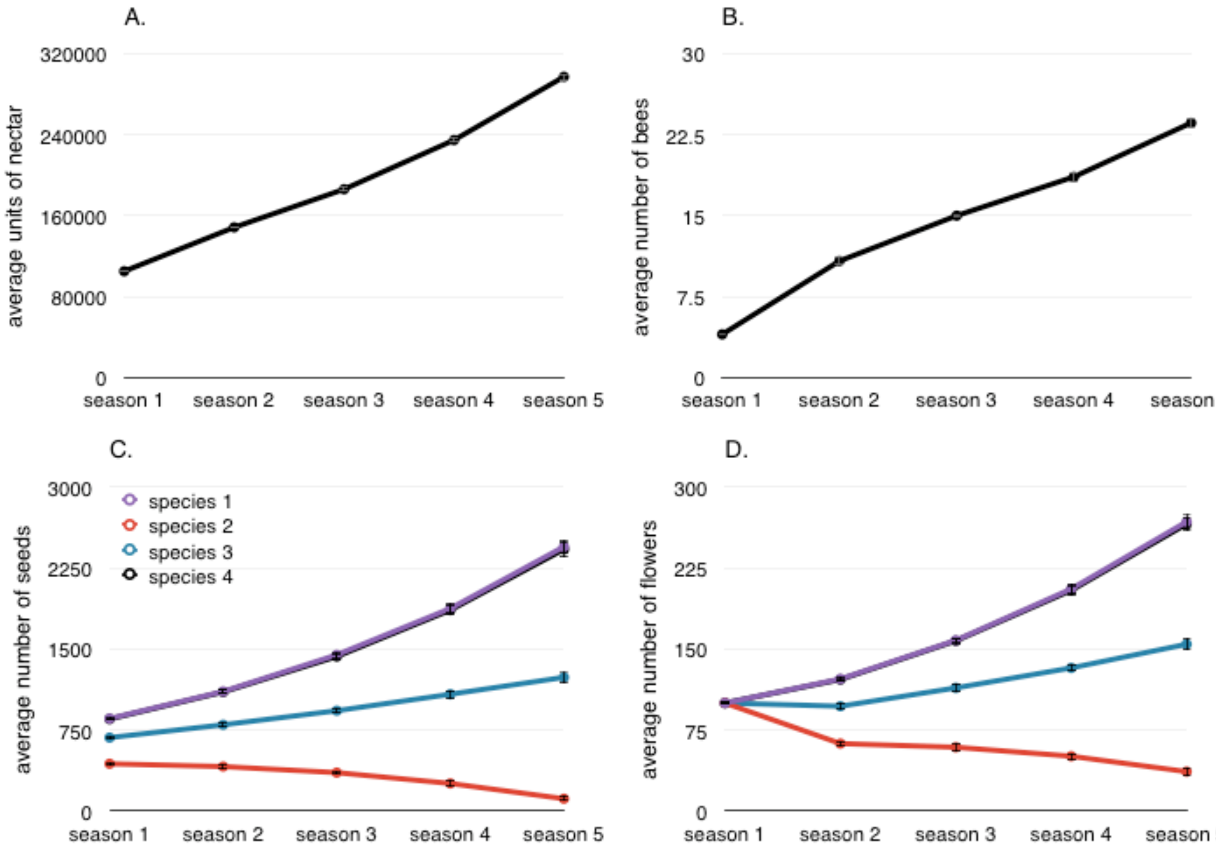


Figure 4. Healthy bees with memory of 10 Bees and strong flower species increased every season, weak flower species decreased each season. Numbers are averages over ten runs of the simulation with the same settings. A. The amount of nectar collected each season. B. The number of bees present in each season. C. The number of seeds produced by each flower species during each season. D. The number of flowers of each species present during each season.

As the healthy bees visited flowers, they could efficiently collect nectar by specializing on the most rewarding flowers as demonstrated by the control bee in figure 3. In this situation, each season with the increase of bees and flowers, the colony collected more nectar. The result was a fairly steady increase in the amount of nectar collected each season as seen in figure 4A. Because the amount of nectar collected directly relates to the number of bees in the next season, the same increase can be seen in figure 4B, which shows the number of bees in each season. When the bees had full memory, they were specializing their visits on the more rewarding flowers. Figure 4C demonstrates that the bees' behavior lead to a variation in numbers of seeds produced by each flower species based on the reward the species produced. The two flower species that produced the most reward were able to produce an increasing number of seeds each season, the flower species that produced the least reward produced a decreasing number of seeds each season, and species 3 had only a slight increase in seeds produced each season. Because the seed number directly translates to the flower number in the following season, figure 4D shows the same trend in the number of flowers as in the number of seeds in figure 4C.

The results from this figure demonstrate that when all of the bees in the simulation are healthy with a memory of size ten, the colony grows each season (Fig. 4A,B). In addition, the three flower species that provide better reward increase their population sizes each season. The flower species that provides very little reward do poorly (Fig. 4C,D).

3.4 There is significant reduction in all bee and flower populations when bees are impaired

In this simulation, pesticide affects the bees by reducing their memory. Adding pesticide to the simulation reduce the bees' memories causing them to lose the ability to appropriately judge which flowers are best. With pesticide, the bee colony should not perform as well. For this trial, the impaired bee memory is reduced to zero. The visiting choices should become random and so the flowers will no longer be distinguished by reward. The flowers will also produce fewer seeds because the bees are switching between species more frequently.

To test this hypothesis I ran the simulation ten times with percent pesticide on the flowers at 100 percent and the percent of bees affected at 100 percent so that all bees would be impaired by pesticide immediately. I averaged the output from the four graphs in figure 5.

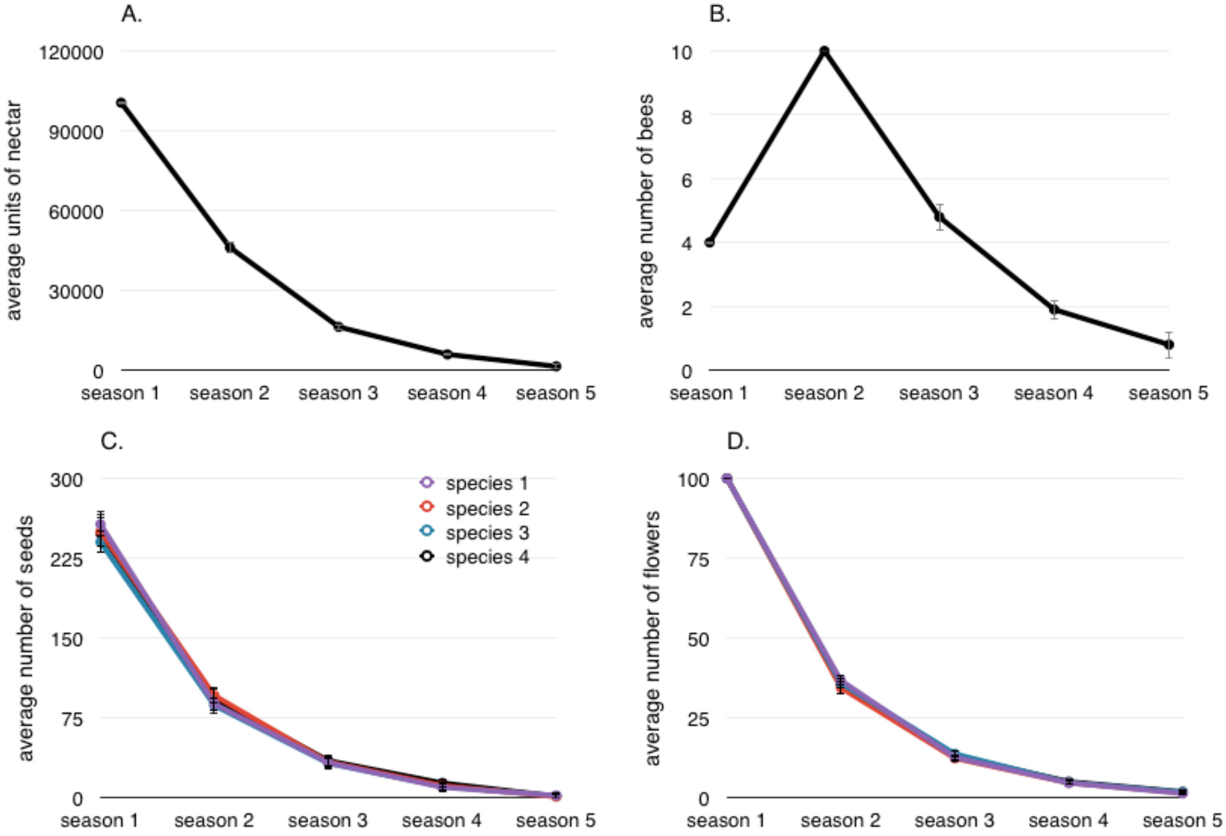


Figure 5. Impaired bees with memory of zero Bees and all species of flowers decreased in number over time when bees had no memory. Numbers are averages of ten runs of the simulation with the same settings. A. The amount of nectar collected each season. B. The number of bees present in each season. C. The number of seeds produced by each flower species during each season. D. The number of flowers of each species present during each season.

As the impaired bees visited flowers, they lost their ability to specialize on the better flower, like the monitor bee in figure 3. As a result, they were unable to collect as much nectar as healthy bees. This lead to a decreasing trend in the amount of nectar collected each season as seen in figure 5A. Because the amount of nectar collected directly relates to the number of bees in the next season, the same decrease can be seen in figure 5B after the first season. With no memory, the bees were visiting flowers at random. Figure 5C demonstrates that the bees' behavior caused the distinction between species seen in figure 4 to disappear. All of the flowers were generating roughly the same number of seeds each season with a decreasing trend. Because the seed number directly translates to the flower number in the following season, figure 5D shows the same trend in the number of flowers as in the number of seeds in figure 5C.

The results from this figure demonstrate that when all of the bees in the simulation are impaired with a memory of size zero, the colony decreases each season to the point of having no bees remaining (Fig. 5A,B). The only exception to this is the first season where the bees do better than the following season because there are so many flowers in the environment. The subsequent reduction in flowers then leads to the drop in bee numbers. In addition, the flower species are all decreasing at equal rates until they are all gone after five seasons (Fig. 5C,D)

3.5 Reducing bee memory size causes reduction in bee populations and improvement in less rewarding flower populations

Having established the effects of full memory and no memory in bees, I chose to investigate the full range of memory sizes. The larger memory size should allow bees to make more accurate judgments, so as the memory size decreases, the number of bees should decrease. This hypothesis is based on the assumption that the bees are collecting nectar less efficiently. If their collection is less efficient, the number of flowers would be expected to reduce because the bees would be switching between species more frequently.

To confirm these hypotheses, I ran the simulation with no pesticide. To change the memory size, I changed the value of healthy memory size. I ran ten trials at each memory size and averaged the trials together to obtain the data in figure 6.

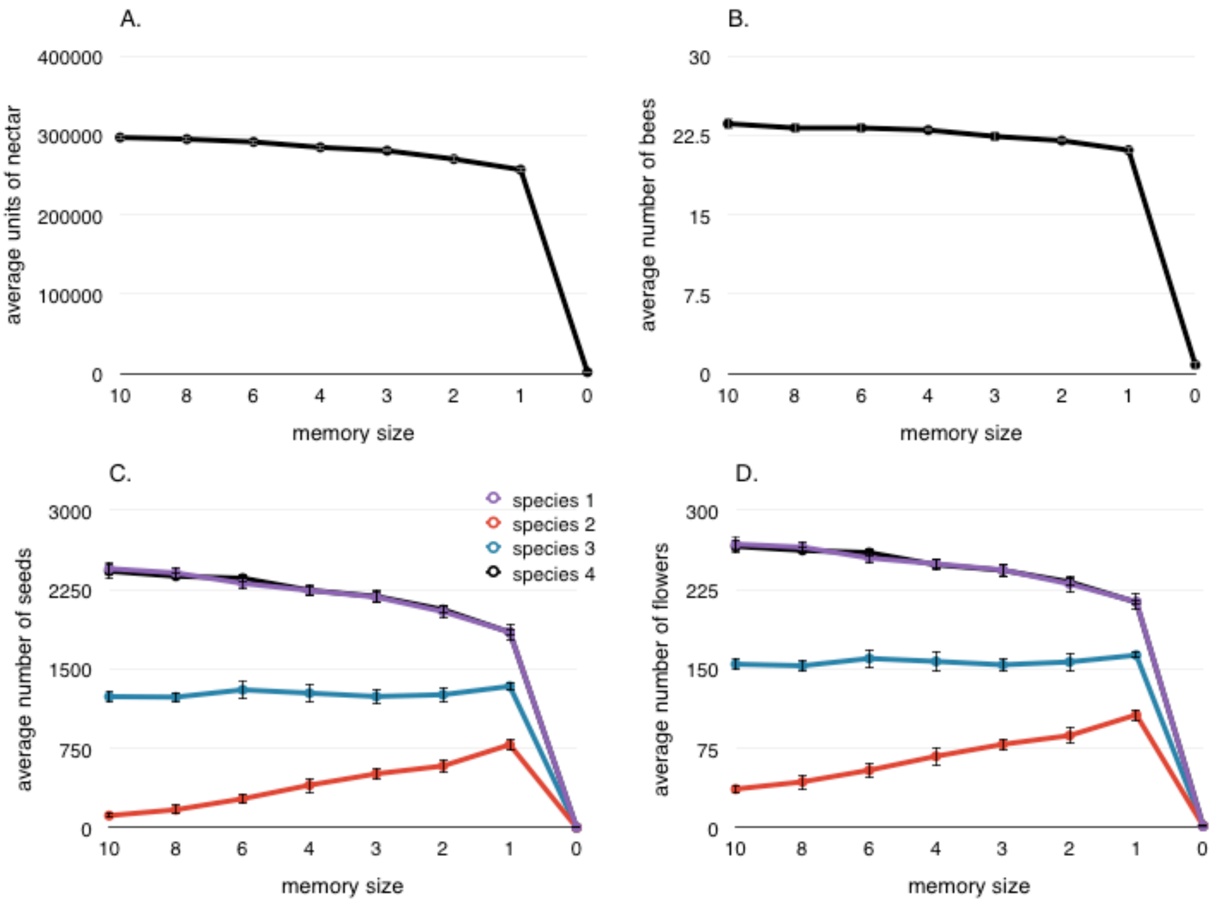


Figure 6. Effects of reducing bee memory Bees and rewarding flowers decreased in number as memory was reduced, less rewarding flowers benefitted from the memory reduction. Numbers are averages of ten runs of the simulation with the same settings. A. The amount of nectar collected in the fifth season at each memory size. B. The number of bees present in the fifth season at each memory size. C. The number of seeds produced by each flower species in the fifth season at each memory size. D. The number of flowers of each species present in the fifth season at each memory size.

When the size of a bee's memory decreased, it had fewer flowers on which to base its visit chance calculations. This means that the bee was less likely to specialize appropriately. As a result, there was a decreasing trend in the amount of nectar collected with the decrease in memory size as seen in figure 6A. The decrease in nectar amount lead to the same decrease in figure 6B for the number of bees. The small changes in the bee's calculations as their memory decreased changed their flower visiting behavior enough to impact the numbers of different flower species produced. Figure 6C demonstrates that the bees' behavior caused the distinction between species seen in figure 4 to lessen slightly as the memory size got smaller. The more rewarding flowers were decreasing in number, and the least rewarding flower was increasing in number. Because the seed number directly translates to the flower number in the following season, figure 6D shows the same trend in the number of flowers as in the number of seeds in figure 6C.

The results from this figure demonstrate that as the size of the bees' memory decreases, the colony decreases slightly and drops suddenly to zero when the memory is removed completely (Fig. 6A,B). In addition, the flower species are converging to more equal numbers with the total number of flowers keeping relatively constant as there is a decrease in memory size. The more rewarding flowers are decreasing and the least rewarding are increasing. When the memory is completely removed all flowers are reduced to zero (Fig. 6C,D).

3.6 Increasing the percentage of impaired bees directly harms the performance of the population and decreases flower numbers

In previous trials, all of the bees have had the same memory size at all times. To investigate the effects of combining impaired and healthy bees, I ran multiple trials with different percentages of pesticide-impaired bees in the colony. Combining healthy and impaired bees will result in numbers between what was seen with the healthy bees in figure 3 and the impaired bees in figure 4. As the percentage of impaired bees increases, the impaired bees should have a larger impact on the numbers of both bees and flowers. All graphs should show a decreasing trend with the increase of impaired bees.

For these trials all healthy bees had a memory of ten, and impaired bees had no memory as in the other trials. Pesticide was present on all flowers. The variable that changed was the percent of bees that are susceptible to pesticide. As before, ten trials were done at each variable setting and the output was averaged in figure 7.

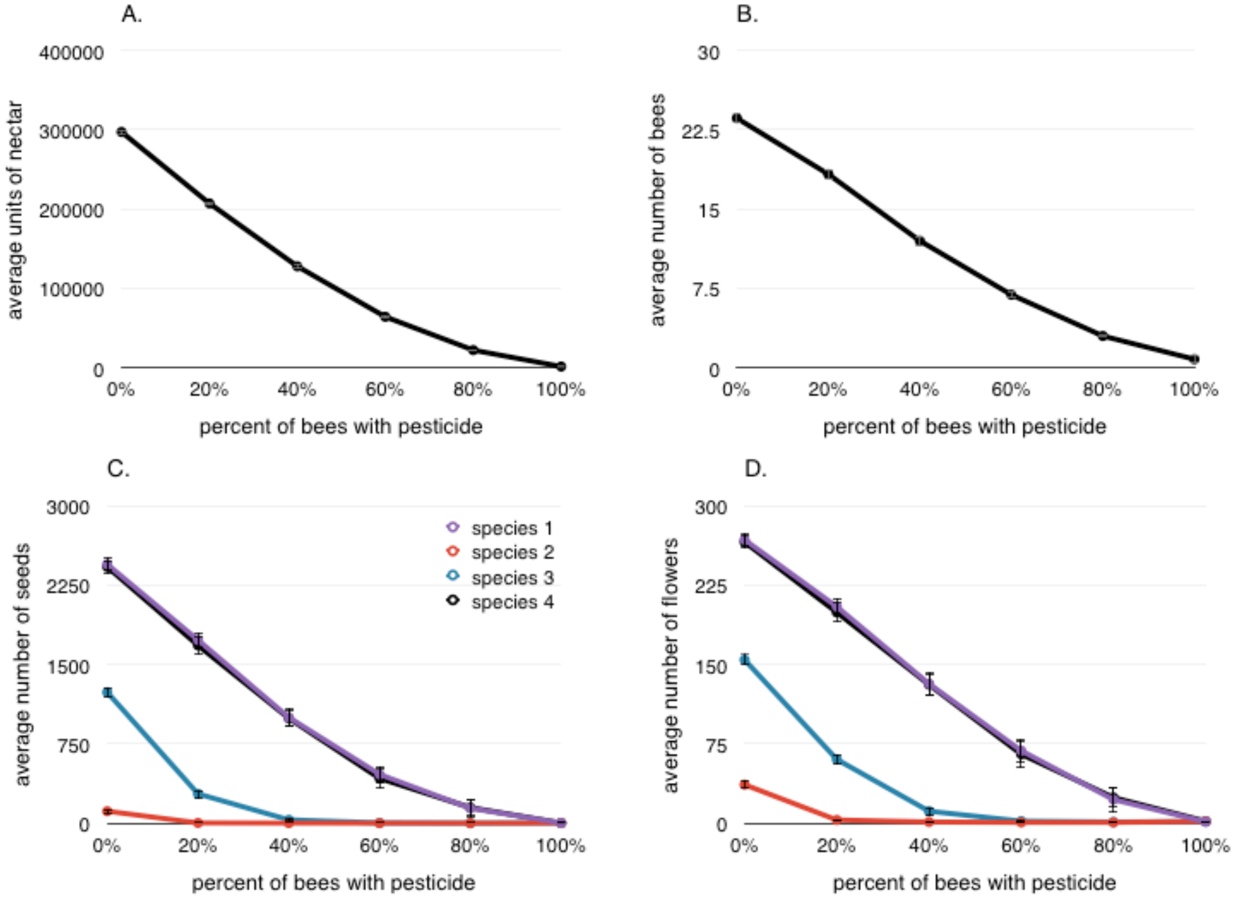


Figure 7. Effects of reducing bee memory Bees and flowers decreased in number as percent of impaired bees was increased. Numbers are averages of ten runs of the simulation with the same settings. A. The amount of nectar collected in the fifth season at each percentage. B. The number of bees present in the fifth season at

each percentage. C. The number of seeds produced by each flower species in the fifth season at each percentage. D. The number of flowers of each species present in the fifth season at each percentage.

Increasing the percentage of bees meant that more of the bees in the colony were acting inefficiently and fewer were making smart decisions. This meant that as more of the bees were impaired, less nectar was being collected as seen in figure 7A. The decrease in nectar amount lead to the same decrease in figure 7B for the number of bees. The impaired bees were visiting flowers at random, so as more of the bees were impaired, there was more switching between flower species. Switching between flower species caused the flowers to produce fewer seeds. Figure 7C demonstrates that the bees' behavior caused a decrease in the number of seeds produced by all of the flower species. The decreasing trend in seed number directly translates to the flower number in the following season. Figure 7D shows the same decrease in the number of flowers as in the number of seeds in figure 7C.

The results from this figure demonstrate that as the percentage of impaired bees increases, the colony collects less nectar and has fewer bees each season (Fig. 7A,B). In addition, all four flower species are experiencing a decrease in seed production and a loss in number regardless of reward (Fig. 7C,D).

4 Discussion & Conclusions

The results explored above introduce many new questions. In this section I will attempt to explore some of the reasons for these results, and draw conclusions. There are many aspects of the existing simulation that could still be explored and there are many ways the simulation could be expanded upon in the future. I will propose future steps for this project in the final section.

4.1 Discussion of Results

This simulation has the ability to explore many areas of pesticide effects, however, it is important to bear in mind that the results from the simulation may not exactly reflect the patterns found in nature. The simulation is limited by the size of the field in which the bees can forage, in the complexity of the bees' behaviors, in the ways that pesticide can affect the bees, and in a number of other areas. Even so, it is possible to draw some conclusions from the simulated bees so that we can begin to form an understanding of the effects of pesticide.

From the results it is evident that impaired bees cause reductions in the number of bees and in the numbers of flowers in the system. To analyze the reasoning behind this I first considered figure 3. In this figure, it is apparent that impaired bees visit flowers randomly and healthy bees make educated decisions.

From this data we can fairly easily understand the impaired bees. An impaired bee never remembers any flowers it has visited. As a result, its visit chances are all one at all times. A bee chooses which flower to visit by picking the species in its view that has the best visit chance. In this case, because all flowers are the same, the bee will pick a species that it sees at random. Once it decides to visit that species, the bee will pick a random one of the flowers of that species that it sees. In short, the selection process is completely random when all of the visit chances are one. In this situation all of the flower species are being visited equally so it can be assumed that they are all experiencing relatively equal nectar draining from the bees. In this situation the flowers with slower regeneration rates will definitely have less nectar than those with faster regeneration rates. By visiting randomly, the bees are not getting as much nectar as they could because they are visiting the flowers with less nectar as much as the flowers with more nectar. With less nectar brought back to the colony, fewer bees will be present in the next season.

When there are four flower species, the impaired bee has an equal chance of picking each species. Three of those species will be different from the one that the bee just visited, and one of those is the same species. This means that there is only a 25% chance that a bee will have come from the same species and give the flower a seed. There is a 75% chance that a bee will come from a different species and block a seed. This means that with impaired bees, all flower species will only produce about one quarter of the potential number of seeds. Because they are producing so few seeds, there will be a significantly reduced number of flowers in the next season. This is why impaired bees cause large reductions of flowers.

In the case of a healthy bee, memory contains up to the last ten flowers visited of each species. This is up to 40 flowers total. To calculate the visit chances, the bee averages all ten of the rewards it obtained from each species. In this way the bee will know which species is best. When the healthy bee needs to choose a flower to visit, it determines which of the species in its cone of view has the highest visit chance. It then selects a random one of the flowers in its view of that chosen species. In this way, the healthy bee is visiting the most rewarding flowers most of the time. By doing this, it is avoiding flowers with less reward and so it is able to collect a maximum amount of nectar for the colony and more bees are produced in the next season.

The healthy bees are spending most of their time visiting the most rewarding flower species. For this species, this is a good thing because the bees are usually coming from the same species and so many seeds can be produced and many flowers will be present in the next season. If a healthy bee visits one of the less rewarding species, it is usually because the bee is sampling. In this situation, the bee is most likely coming from another species and so it blocks a seed. The other situation during which a healthy bee visits the weaker flower species is when the bees have spent so much time specializing on the strong flowers that all of the strong flowers are drained and the weaker flower is better. In this situation the bee specialized on the weak species so a few seeds can be produced, but it is not long before the bee will switch back to the stronger flower type. With this pattern of visiting, the weaker flower species do not produce many seeds and thus see a reduction in flower number in the following season. This is why the stronger flowers will likely increase in number and the weaker flowers will likely decrease in number.

The trend seen in figure 7 shows that as the proportion of impaired bees in the colony increases, the numbers of bees and flowers will decrease. This is the result of the combined efforts of the impaired and healthy bees. While the healthy bees are specializing on the better flowers and collecting the maximum amount of nectar for the colony, the impaired bees are collecting less efficiently and thus reducing the amount of nectar in the colony from what it would be with all healthy bees. From the flowers' perspective, the impaired bees' random visits are reducing the number of possible seeds from what it would be with only healthy bees. As a result, the higher the ratio of impaired bees to healthy bees becomes, the lower the numbers of all bees and flowers will be.

The most interesting trend is seen in figure 6 with the changes in memory. The first interesting detail is that, while reducing memory does decrease the number of bees, it is a very small decrease. The bees seem to manage fairly well even with a memory of size one. The second interesting detail is that reducing the memory does not seem to harm the flowers. The most rewarding flowers only see a very slight decrease and the least rewarding flowers see a fairly significant increase in number. All of these trends show relatively small changes until the memory is removed completely, at which point the numbers are reduced to zero.

The best explanation for these trends has to do with the fact that larger memory will take into account flowers that were visited some time ago, while smaller memory will only take into account the most recently visited flowers. Because bees with memory specialize on better species, there are times when the better species are all drained of nectar from being visited too frequently. At such times, the less rewarding species are mostly full and thus contain the greater reward. During such a period of time, a bee with a small memory is likely to switch to the weaker flower species, which has become more rewarding. On the other hand, a bee with larger memory will still account for the times when the stronger species were not drained and so these bees are less likely to switch flower species.

This affects the flower population because, when the bee memory gets shorter, the weaker flowers experience more specialization and so are able to produce more seeds. The stronger flowers experience a little more switching and so they produce slightly fewer seeds. The bees with shorter memory are more flexible about switching to a temporarily better flower species. While it might seem logical that this flexibility allows the bee to get the most reward more efficiently, that is not the case. The bees that are more flexible are actually doing slightly worse than those that have larger memory. This is most likely because the bees with larger memory will stick with the stronger flowers. Even if the stronger species is temporarily drained, it will quickly replenish to be the better choice. The bee with smaller memory will switch to the weaker flower species when it is temporarily the more rewarding species. This weaker species will very quickly return to being the less rewarding choice and then the bee will not be doing as well. Thus, the bee with larger memory does slightly better than the bee with smaller memory.

4.2 Conclusions

As stated in the introduction, the first objective of this project was to demonstrate the individual effects of pesticide on bees. Figure 3 demonstrates that the bee takes on very different visiting behaviors when it loses its memory. The bee loses its ability to calculate visit chances and thus its ability to make good choices about which flower to visit. From this figure, I drew the conclusion that when pesticide removes a bee's memory, there is a clear change in the bee's visit choices and behaviors. By comparing part A of figures 4 and 5, it is clear that these behavioral differences in the impaired bees lead to a significant decrease in the amount of nectar collected by the whole colony. From figure 6 I concluded that the effects of pesticide are significantly greater if the pesticide completely removes the bee's memory. This is a case where the simulation revealed information that was not otherwise obvious: just reducing the memory has a much smaller impact on the bee than on the plants, although there is still a negative impact.

This leads to the second objective, which was to demonstrate the effects of pesticide impairment over multiple seasons. Figure 5 demonstrates the effects of pesticide over five seasons. From this figure I concluded that a pesticide that completely removes the bee's memory would, if used for multiple seasons, eventually severely harm not only the bee populations, but all of the flower populations as well. While the simulation shows all populations dying out entirely after the fifth season, I cannot conclude that this would happen in a real environment where other pollinators and species would be impacting the system. Additionally, figure 6 leads me to conclude that all populations will endure the pesticide much better if only a portion of the bees are impaired.

The third objective of this project was to investigate the effects that pesticide impaired bees had on the plant species that they visited. By comparing the numbers of seeds and plants in parts B and C of figures 4 and 5, I concluded that the changes in the bees' behaviors harm all flower species because, when the bees have no memory, they switch between species more frequently. In this way, the pesticide causes the flowers to produce fewer seeds and thus their populations reduce in number each season.

Figure 7 also demonstrates that the harmful effect that the impaired bees have on flowers is still present when there is a mix of healthy and impaired bees. If there aren't many impaired bees, the effect is not large, but as the proportion of impaired bees increases, the impact they have on the flowers increases as well. From the results of figure 6, I concluded that reducing the bees' memory but not removing it entirely is not necessarily harmful to the flowers. The weaker species will even see a benefit from the reduction. With reduced memory, the bees will be more likely to switch between species with the fluctuations in reward. This will slightly harm the better flower species because they will see more switching, but it will also help the weaker species because they will be visited more.

The fourth and final objective of this project was to make a simulation that could serve as an educational tool. The simulation is intended to demonstrate, for educational purposes, the effects of pesticide on the bees and the flowers. I have concluded that the simulation accomplishes this because, as discussed above, the data the simulation outputs clearly shows that there is a negative impact on the bees and flowers when the bees are impaired by pesticide. In order for the simulation to be as clear as possible so that the target audience may understand it well, I created visuals for flowers, bees, and colonies that children and users that are unfamiliar with bees will understand and recognize. I also included graphs that will help users follow what is happening over time while the simulation runs. From this, I have concluded that the simulation will be able to serve as an educational tool to demonstrate the effects of pesticide on bees and flowering plants.

4.3 Proposed Future Steps

There are many potential directions for this project to take from this point onward. With the existing simulation, there are many questions that could still be explored. There are also aspects of the functionality that could still be improved. Lastly, there are many things that could be added to the simulation to explore additional avenues.

I focused my exploration of the simulation primarily on the effects of memory size and percentage of impaired bees. While this demonstrates multiple aspects of how impaired bees affect the colony and the flowers they visit, there are always more details to be explored. Some investigations that would be of interest include doing further explorations with impaired bees having a memory of size one instead of zero. This would demonstrate very different results because even with as little memory as size one, the bee can make some educated judgments that it could not with no memory. Another interesting direction to explore would involve including different combinations of flowers and observing the impacts of the changed environment. Flowers with more similar or more differentiated nectar regeneration rates will show different behaviors in the bees.

While the simulation as is can demonstrate many different situations, it could still be improved. One aspect that could use some improvements is the memory. Perhaps it would be more realistic for memory to fade over time rather than having a fixed size. There could also be some improvements to the bees' behavior to make certain details a little more realistic. For example, the way a bee decides when and what to sample could be improved. Currently a bee is told to sample every 1000 ticks by the visit chances for each flower species being altered. The last thing that could potentially be improved is the way in which bees calculate visit chances.

Currently the bees take all the data in their memory and calculate averages to determine what is the best species. There are more factors that bees could take into consideration when making these calculations that might make the values more realistic. One possibility would be to consider how long it has been since flowers were visited, because some data in its memory might be very old.

In addition to small improvements, this simulation could use multiple additions to explore new questions. There are more environmental pressures that harm bees aside from just pesticide. Adding more of these pressures would allow the simulation to explore long-term effects of each pressure individually. By including more than one pressure in the simulation, combined effects of different pressures could also be investigated. In addition to adding to the environmental pressures, there could be additions to the species included in the simulation. For example, birds that eat seeds from the flowers would be affected by impaired bees along with the flowers. Including the birds and other impacted species in the simulation would allow for exploration into effects on the whole food chain rather than just one or two species. By adding to this simulation, it could develop into a tool that will answer many questions that have been difficult to investigate with field and lab studies in the past.

5 References

Aizen MA, Morales CL, Morales JM (2008). Invasive mutualists erode native pollination webs. PLoS Biology 6(2): 396 – 403.

Arundel J, Oldroyd BP, Winter S (2013). Modelling estimates of honey bee (*Apis spp.*) colony density from drones. Ecological Modelling 267: 1 – 10.

Becher MA, et al. (2014). BEEHAVE: a systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure. Journal of Applied Ecology 51: 470 – 482.

Brown MJF, Paxton RJ (2009). The conservation of bees: a global perspective. Apidologie 40: 410 – 416.

Bukovac Z, Dorin A, Dyer AG (2013). A-Bees See: A simulation to assess social bee visual attention during complex search tasks. ECAL 12: 276 – 283.

Cameron SA, et al. (2011). Patterns of widespread decline in North American bumble bees. PNAS 108(2): 662 – 667.

Chautá-Mellizo A, et al. (2012). Effects of natural and artificial pollination on fruit and offspring quality. Basic and Applied Ecology 13: 524 – 532.

Didham RK, et al. (2007). Interactive effects of habitat modification and species invasion on native species decline. TRENDS in Ecology and Evolution 22(9): 489 – 496.

Dyer AG, et al. (2014). Bee reverse-learning behavior and intra-colony differences: simulation based on behavioral experiments reveal benefits of diversity. Ecological Modelling 277: 119 – 131.

Gill RJ, Ramos-Rodriguez O, Raine NE (2012). Combined pesticide exposure severely affects individual – and colony – level traits in bees. Nature 491: 105 – 109.

Goldstone RL, Janssen MA (2005). Computational models of collective behavior. TRENDS in Cognitive Sciences 9(9): 424 – 430.

González-Varo JP, et al. (2013). Combined effects of global change pressures on animal-mediated pollination. Cell 28(9): 524 – 530.

Goulson D (2003). Effects of introduced bees on native ecosystems. Annual Review of Ecology, Evolution, and Systematics 34: 1 – 26.

Goulson D (1999). Foraging strategies of insects for gathering nectar and pollen, and implication for plant ecology and evolution. Perspectives in Plant Ecology, Evolution and Systematics 2: 185 – 209.

Grimm V, et al. (2005). Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310: 987 – 991.

Grimm V, et al. (2006). A standard protocol for describing individual-based and agent-based models. Ecological Modelling 198: 115 – 126.

Helbing D (2012). Agent Based Modeling. Social Self-Organization 25 – 70.

Kremen C, Williams NM, Thorp RW (2002). Crop pollination from native bees at risk from agricultural intensification. PNAS 99(26): 16812 – 16816.

Potts SG, et al. (2010). Global pollinator declines: trends, impacts, and drivers. 25(6): 345 – 353.

Qu H, et al. (2013). A spatially explicit agent-based simulation platform for investigating effects of shared pollen service on ecological communities. Simulation Modelling Practice and Theory 37: 107 – 124.

Railsback SF, Grimm V (2011). Agent-Based and Individual-Based Modeling: A Practical Introduction. Princeton University Press.

Russell S, Barron AB, Harris D (2013). Dynamic modeling of honey bee (*Apis mellifera*) colony growth and failure. Ecological Modelling 265: 158 – 169.

Sih A (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. Animal Behaviour 85: 1077 – 1088.

The bumblebee lifecycle. Bumblebee Conservation Trust. Viewed on Oct 25, 2014. http://bumblebeeconservation.org/about-bees/lifecycle/.

Thompson HM (2003). Behavioural Effects of Pesticides in Bees – Their Potential for Use in Risk Assessment. Ecotoxicology 12: 317 – 330.

Williams NM, et al. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation 143: 2280 – 2291.

Williamson SM, Wright GA (2013). Exposure to multiple cholinergic pesticides impairs olfactory learning and memory in honeybees. The Journal of Experimental Biology 216: 1799 – 1807.

Whitehorn PR, et al. (2012). Neonicotinoid Pesticide Reduces Bumble Bee Colony Growth and Queen Production. Science 336: 351 – 352.