Team Control Number

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Problem Chosen

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HiMCM

Summary Sheet

Our paper models honey bee colonies over time through differential equations and activation functions. The model predicts honey bee populations over time for a basic bee hive. To fully achieve this goal, we model each of the main stages in a bee's life and the different roles bees take in a hive. This allows us to analyze the dynamics of a hive and the interactions between these stages. Beyond this, we mimic the inner workings of a real hive by modeling not just population but also pollen and nectar stores, which feeds back into bee populations and is a key indicator of hive failure. The differential equations used in our model's code grants us the power to analyze our variables day by day. We use this to create hypothetical scenarios based on real issues experienced by bees, which provides insight into what parameters have the greatest effect on the survival chances of a hive. Our activation functions, which take inputs from the various differential equations at previous time steps and outputs values used in the current time step, are essential to modeling a real bee hive. One example of this are the recruitment functions, which determines how bees should be assigned to the different available roles in the hive. This directly mirrors how the roles of different bees in beehives are decided. We then constructed multiple scenarios with accurately chosen parameters and in depth sensitivity analysis to find a solution to the widely debated question:

How many bee colonies should be placed on a farm?

We discovered that the optimal number of colonies is 1 to 2 colonies per acre. The range of 1-2 comes with reasoning - 1 hive insures the survival of the bees as there is abundant food and a lack of competition. On the other side is 2 hives; while full pollination is more likely when given 2 hives, the competition generated by this extra colony can lead to mutual destruction. Despite this, 2 hives is optimal for short periods of time (such as those during specific bloom seasons of crops).

Contents

1 Introduction

European Honeybees, or *apis mellifera*, are vital pollinators in both commercial farms and nature. However, honeybee colonies across the world have experienced massive drops in populations, also known as **Colony Collapse Disorder**, causing concerns about the future of food safety, economies, and ecosystems. Although there is no one cause of CCD, modeling bee colonies provides insight into how to keep colonies alive and what factors have the greatest effect on bees. The life cycle of bees is complicated, with three main stages - the uncapped brood, the capped brood, and the bees. Analyzing the dynamical interactions between these 3 stages, as well as intrastage fluctuations, allows us to understand the ways in which bees are vulnerable and how to prevent the collapse of colonies. This knowledge also allows for a estimate on how many hives are necessary to sustain a farm of a given size. We use differential equations and activation functions to model the change in bees, pollen, nectar, and brood over time, and determine the optimal number of hives to pollinate a farm. Differential equations are the best choice in this scenario as as they represent the change of a variable over time, directly addressing the problem.

2 Definitions, Assumptions, and Variables

2.1 Definitions

Bee: *apis mellifera*, the European Honeybee.
Uncapped brood: Larva and eggs.
Capped brood: The pupa which are capped in a cocoon-like cell.
Larva: The immature form of a bee that is in between the stages of being an egg and pupa.
Drone: A male bee.
Forager: A female bee that forages for pollen or nectar.
Hive Bee: A worker bee that cleans the hive and tends to the uncapped brood.
Colony/Hive: A collection of bees, capped brood, uncapped brood, drones, and the queen.

2.2 Assumptions and Justifications

Assumption 1: Bee colony size is not capped.
Justification 1: A domesticated bee colony tends to have multiple human-created bee hives. A large enough bee colony in our model could, hypothetically, be split into multiple smaller colonies with no major effect on hive dynamics.

Assumption 2: Each type of bee is one homogeneous entity. The survival function treats a group of bees as a homogeneous, single entity. A fraction of all living, available bees transition between two states at once (i.e. every day, $\frac{1}{12}$ of the capped brood transitions to hive bees).
Justification 2: At a large scale, individual differences between each bee are insignificant, and considering only the collective total of a group of bees is a accurate approximation.

Assumption 3: The crops in the land are homogeneously distributed *prunus dulcis* (almond trees) with the same number of flowers per tree.
Justification 3: Almond trees are the second highest fruit or nut tree produced commercially in the US. Additionally, they can only be pollinated by honeybees and have a high dependence on pollinators to reproduce (1).

Assumption 4: The given parcel of land will have sufficient variation in almond tree species to allow for cross pollination.
Justification 4: Almond trees are always grown with other plants or species of almond trees that will allow for cross pollination.

Assumption 5: Pollen and nectar provide all required nutrients for the bee's survival (unless otherwise specified).
Justification 5: Almond pollen contains all required nutrients and is homogeneous (2).

Assumption 6: Consumption from drone bees and the queen bee is negligible.
Justification 6: In total, the drones and queen account for an insignificant portion of the colony, and do not produce anything but eggs (which are accounted for).

Assumption 7: All bees in our model are *apis mellifera*, the European Honeybee.
Justification 7: *apis mellifera* are the most common type of honeybee in North America.

Assumption 8: Pollen and nectar is available year-round.
Justification 8: The bees are placed in an open environment with various species of plants that are often found living together. Because all of these plants benefit from having pollen, they have evolved over time to release their pollen and nectar at various points across the year.

2.3 List of Variables

Variables	Meaning
L	number of eggs laid per day
s_H	survival function sensitivity to hive bees
s_p	survival function sensitivity to pollen
s_n	survival function sensitivity to nectar
r_p	recruitment function sensitivity to pollen
r_n	recruitment function sensitivity to nectar
r_I	recruitment function sensitivity to social inhibition
b	baseline recruitment rate
u_0	inverse of days as uncapped brood
c_0	inverse of days as capped brood
m_c	capped brood mortality
m_p	pollen forager mortality
m_n	nectar forager mortality
c	pollen gathered ($\frac{grams}{bee}$)
p_U	capped brood pollen consumption (grams)
p_H	hive bee pollen consumption (grams)
n_U	capped brood nectar consumption (grams)
n_W	adult bee nectar consumption (grams)

3 Bee Colony Model

In this section we present a mathematical model of a bee colony that calculates the number of different types of bees each day as a function of the hive's population the previous day and the food that was collected by the foragers throughout the day. Starting from the initial larva state, moving to pupa, then to capped brood, then to hive bees, and finally to a forager bee, a certain proportion of the bees in each state dies and the rest moves on to the next state after a certain period of time. We don't explicitly include the queen or the drones in the model. The queen is included implicitly though, through the eggs that are laid every day. The drones are also included only implicitly through the laid eggs. Thus the model explicitly captures the number of larva, pupa, capped brood, and worker bees. The dynamics of bee population are represented by differential equations, one equation per bee type. In particular, we are interested in the following vector:

$$\text{hive}(t) = [U(t), C(t), H(t), P(t), N(t), p(t), n(t)]$$

where

$U(t)$	number of uncapped brood bees at time t
$C(t)$	number of capped brood bees
$H(t)$	number of hive bees
$P(t)$	number of pollen foragers
$N(t)$	number of nectar foragers
$p(t)$	amount of pollen stored in the colony at time t
$n(t)$	amount of nectar stored in the colony at time t

There are two decisions embedded in these definitions:

1. Eggs and larvae are combined together into the uncapped brood variable $U(t)$ while capped larva/pre-pupal stage and pupae are combined into the capped brood variable $C(t)$. This is done to explicitly separate the brood into a stage where food is consumed, drawing on the resources of the hive and figuring into colony's allocation of food resources, and a stage where pupae are not consuming any food. Hive bees are required to attend to pupae but no food is spent on them.

2. Foragers are split into pollen foragers and nectar foragers. Because pollen and nectar play complementary roles in a colony's life we want to capture the dynamics that influence how hive bees are transformed into foragers and, possibly, back to hive bees. These decisions are made based on the colony's needs at a given time and, in turn, influence food collection. Recruitment rates create a feedback mechanism since different relative amounts of pollen and nectar foragers affect the nutrition provided to the uncapped brood. The self-regulating mechanisms that allow bees to adapt to different conditions are important in modeling a colony and require these feedback connections.

In the sections below we go through each differential equation and provide justification for the model. The general approach of using differential equations (without explicitly modeling pollen/nectar separation) is used in a paper by Khoury (3) and extended to specific scenarios dealing with artificial feeding (4), pollen consumption (5), bee stress (6), and bee infection (7). There are also alternative mathematical frameworks in papers by Russell (8) and Schmickl (9). Our framework is based on Khoury (3) in terms of using differential equations to model bee state transitioning but we created our own activation functions for modeling survival probabilities and recruitment rates.

3.1 Equation for uncapped brood

Uncapped brood is defined by the following equation:

$$\frac{dU(t)}{dt} = L \cdot S(\text{hive}(t)) - u_0 U(t) \tag{1}$$

Here, L denotes the number of eggs that the queen lays daily. $S(\text{hive}(t))$ is the activation function that models the survival probability of a laid egg as a function of the hive: amount of food available and the number of hive bees available to take care of the eggs and larvae. This function will be defined in a later section. Every day, the number of uncapped brood is increased by the number of the laid eggs that survived and decreased by the proportion u_0 of the existing population of uncapped brood. This decrease is due to uncapped brood transitioning to the capped brood state. In the base case scenario we take $L = 2000$, which is consistent with the number of eggs laid by a queen in a strong colony when conditions are especially favorable. This number is deflated by the survival activation function so that the number of eggs/larvae that survive can be quite a bit smaller and will, on average, reflect the realistic egg laying rates while increasing the variability of the number of uncapped brood moving on to the capped state under different environmental conditions. The value for u_0 is taken to be $u_0 = 1/9$ to account for the 9 days (3 for eggs and 6 for larva) spent in the uncapped brood state. In principle, the model could keep track of the uncapped brood population of every age, day 1 to 9, but in practice the difference in uncapped brood population of different ages is negligible. Over time this population can increase or decrease greatly based on the dynamics; the evolution of the differential equation will capture these population changes.

3.2 Equation for capped brood

Capped brood is defined by the following equation:

$$\frac{dC(t)}{dt} = u_0U(t) - (c_0 + m_C)C(t) \tag{2}$$

In this equation, the term $u_0U(t)$ corresponds to the surviving uncapped brood that turned into capped brood. The term $-c_0C(t)$ is the proportion of capped brood population that turns into hive bees. Since it takes 12 days for this process to complete, $c_0 = 1/12$. The last term, $-m_CC(t)$, is the mortality rate of capped brood. Under normal conditions this mortality rate is very low in practice - pupae are well protected and not dependent on what happens to the colony. We set $m_C = 0$ in our base scenario. But there are also situations where external factors like Varroa mites will make this mortality rate high both directly and through introducing viruses and infections.

3.3 Equation for hive bees

Hive bees are defined by the following equation:

$$\frac{dH(t)}{dt} = c_0C(t) - R_p(\text{hive}(t))H(t) - R_n(\text{hive}(t))H(t) \tag{3}$$

In this equation, $c_0C(t)$ represents the surviving capped brood that matured and turned into hive bees. $R_p(\text{hive}(t))H(t)$ and $R_n(\text{hive}(t))H(t)$ represent the proportions of hive bees that are recruited to become pollen and nectar foragers, respectively. Although all foragers are capable of collecting both pollen and nectar, there is specialization within the colony to optimize food collection under specific conditions. Some of this specialization is found to be genetic (10), but most of it is in response to the current needs of the colony. The important point is that the recruitment rates are not constants but rather complicated functions of the state of the hive. These functions work in both directions: when the colony has a shortage of, for example, pollen foragers, a large portion of hive bees will be promoted to specifically pollen foragers. When the number of foragers of both types is sufficient, fewer hive bees will become foragers. This happens through the process of "social inhibition" and is regulated by a pheromone produced by foragers (18). The process also works in the other direction, allowing for some foragers to go back to hive bee duties if there is a shortage of hive bees in the colony.

3.4 Equations for foragers

Both pollen and nectar foragers follow similar equations:

$$\frac{dP(t)}{dt} = R_p(\text{hive}(t))H(t) - m_p P(t) \tag{4}$$
$$\frac{dN(t)}{dt} = R_n(\text{hive}(t))H(t) - m_n N(t) \tag{5}$$

Both types of foragers gain membership from recruitment of hive bees and both types of foragers die off at a given mortality rate.

3.5 Equations for pollen and nectar accumulation

Food is gathered by foragers and brought back to the hive. Part of the collected food goes to feed the colony with the differences in roles played by pollen and nectar described above, and the rest is stored for future use. These factors translate into the following equations:

$$\frac{dp(t)}{dt} = \mu_p(t)cP(t) - p_U U(t) - p_H H(t) \tag{6}$$
$$\frac{dn(t)}{dt} = \mu_n(t)cN(t) - n_U U(t) - n_W(H(t) + P(t) + N(t)) \tag{7}$$

The first term in each equation corresponds to the amount of food collected per forager, pollen and nectar respectively. This amount is modeled as a product of a fixed amount c multiplied by a function $\mu(t)$. The role of this function is to account for the seasonal variation in the amount of food available. It has a sinusoidal shape with the maximum corresponding to the peak of the blooming season for pollen and nectar season for nectar (11). These peaks are not assumed to coincide so that even though the functional form for pollen and nectar seasonality is the same, the phase shift is different. The difference in phase shift plays an important role in the dynamics of hive evolution.

The rest of the parameters highlight the differences in the roles played by nectar and pollen. Hive bees consume both pollen and nectar. Larvae are fed royal jelly that is secreted from hypopharyngeal glands and mandibular glands of hive bees after they consume pollen, and then move to pollen and nectar. This underscores the importance of pollen and the feedback structure of the system: pollen is the ingredient necessary for creating royal jelly and feeding young larvae and the queen, but jelly is produced by hive bees who need both pollen and nectar to survive. The colony adjusts its foraging process to maximize the chance of colony survival.

Foragers only consume nectar, thus the term in the nectar store equation that subtracts the amount consumed by the foragers.

It is surprisingly difficult to get precise estimates for the magnitudes of p_U, n_U, p_H, and n_W. Most of the calculations we came across were based off methodologies that computed the total amount of pollen/nectar collected over a long period, computing how much pollen/nectar was left in the hive, and dividing the difference by the approximate number of bees. Even these results had a lot of variation due to the fact that what really matters to colony survival is not the gross amount of pollen/nectar but rather the amount of sugar, protein, and amino acids (vital for larvae development) that is contained in pollen/nectar. But conversion of raw food to its chemical components seems to depend greatly on the food itself. Just like for humans, two meals of the same weight can have vastly different nutritional values. It is noted that colonies, just like humans, benefited from a diet that has variety and complexity (12). For example, pollen from maize has roughly half the nutrients of mixed pollen. Just like humans, bees don't benefit from food with high corn syrup content (13). One difference, however, is that for bees, digestive efficiency must be taken into account as well: since the colony fights for survival every day, food that is easier to digest takes less energy and thus less of that food is required to get sufficient energy (14). Without doing deep research on this topic our base case assumptions are $p_H = n_W = 7$mg per day and $p_U = n_U = 18$mg per day.

3.6 Differential equation for hive

Using $\text{hive}(t) = [U(t), C(t), H(t), P(t), N(t), p(t), n(t)]$ we can collect equations from the previous sections to write one vector equation for the evolution of the hive. First we construct a matrix for the dynamics

$$M(t) = \begin{bmatrix} -u_0 & 0 & 0 & 0 & 0 & 0 & 0 \\ u_0 & -(c_0 + m_C) & 0 & 0 & 0 & 0 & 0 \\ 0 & c_0 & -(R_p(t) + R_n(t)) & 0 & 0 & 0 & 0 \\ 0 & 0 & R_p(t) & -m_p & 0 & 0 & 0 \\ 0 & 0 & R_n(t) & 0 & -m_n & 0 & 0 \\ -p_U & 0 & -p_H & \mu_p(t)c & 0 & 0 & 0 \\ -n_U & 0 & -n_W & -n_W & \mu_n(t)c - n_W & 0 & 0 \end{bmatrix}$$

and a vector for adding eggs

$$v(t) = \begin{bmatrix} L \cdot S(t) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

Combining the two terms we get an equation for the hive dynamics

$$\frac{d\text{hive}(t)}{dt} = M(t) \cdot \text{hive}(t) + v(t) \tag{8}$$

keeping in mind that both $M(t)$ and $v(t)$ are explicit functions of hive(t) through the activation functions.

3.7 Activation functions for the model

In this section we describe the activation functions for survival, recruitment, and seasonal food availability.

Function	Meaning
$S(H, p, n)$	survival function
$R_p(H, P, N, p, n)$	pollen forager recruitment function
$R_n(H, P, N, p, n)$	nectar forager recruitment function
$\mu_p(t)$	pollen availability function
$\mu_n(t)$	nectar availability function

3.7.1 Survival function

The survival function for uncapped brood depends on three parameters: nectar, pollen, and number of hive bees. It is logical that when each of this parameters increases the survival rate goes up:

1. Additional pollen is beneficial in three ways: (1) through increasing the lifespan of hive bees who consume it, (2) through production of royal jelly that is fed to larvae, and (3) through increased feeding of uncapped broods that moved on from royal jelly to pollen and nectar.

2. Additional nectar is beneficial in two ways: (1) through increasing the lifespan of hive bees who consume it and (2) through increased feeding of uncapped broods that moved on from royal jelly to pollen and nectar.

3. Additional hive bees are beneficial because there is more attention paid to uncapped broods, thus increasing their chance of surviving.

We assume that the survival function has the following form:

$$S(H, p, n) = 0.9 \cdot (1 - e^{-s_H H}) \cdot (1 - e^{-s_p p}) \cdot (1 - e^{-s_n n}) \tag{9}$$

Survival is capped at 90% while the weights s_H, s_p, s_n allow for different relative importance to be assigned to each of the three components. When any of the variables are close to 0, the survival corresponding to that variable is nearly linear.

3.7.2 Recruitment function

Recruitment functions determine what proportion of hive bees remain as hive bees, what proportion becomes pollen forager, and what proportion becomes nectar forager. When there is a shortage of hive bees, “social inhibition” takes place where foragers can transition back to hive bees; this should happen when the total proportion of hive bees relative to all worker bees is small. When there is shortage of nectar relative to pollen more hive bees will transition to nectar foragers; conversely, more hive bees will transition to pollen foragers when there is not enough pollen. The recruitment functions have the following forms:

$$R_P(H, P, N, p, n) = b \cdot (1 - \frac{1}{2}e^{-r_p \frac{p}{p+n+0.01}})(1 - e^{-r_I \frac{H}{H+P+N}}) \quad (10)$$

$$R_N(H, P, N, p, n) = b \cdot (1 - \frac{1}{2}e^{-r_n \frac{n}{p+n+0.01}})(1 - e^{-r_I \frac{H}{H+P+N}}) \quad (11)$$

Here, b is the baseline recruitment rate, and r_p and r_n are the weights for determining how seriously the imbalance $\frac{p}{p+n+0.01}$ and $\frac{n}{p+n+0.01}$ should be treated (0.01 is added for numerical stability). The last term, $1 - e^{-r_I \frac{H}{H+P+N}}$ represents social inhibition where if the number of hive bees is small relative to the overall number of workers, fewer hive bees are converted to foragers. r_I is the weight for social inhibition.

3.7.3 Seasonal food availability multiplier

Seasonal food availability multiplier accounts for different amounts of pollen and nectar that are available during different seasons. In most parts of the United States, winter will have few, if any, blooming flowers and no nectar flow. Spring is expected to be optimal for both blooming and nectar flow. Summer can be good as well, depending on the geographical location and the specific climate.

Seasonal multipliers have the following form:

$$\mu_P(t) = \sin(\frac{\pi t}{180} + \frac{\pi}{4}) + 1 \quad (12)$$

$$\mu_n(t) = \sin(\frac{\pi t}{180} + \frac{\pi}{8}) + 1 \quad (13)$$

Here, t is measured in days so that $\frac{\pi t}{180}$ represents one year when $t = 360$. The phase shift for the pollen multiplier is $\frac{\pi}{4}$, which means that the maximum pollen availability is at $t \approx 45$ days. This roughly corresponds to mid-February which is the typical start of the pollination season for California almonds, the crop that we consider in later sections. Note that for nectar, the phase is $\frac{\pi}{8}$ to account for the lag between the peak of pollination and the peak of nectar flow (also for California almonds). During the peak, the amount of food is twice the average amount, and during winter this amount goes to 0 for wild honeybees in a typical climate.

3.8 Parameter values for activation functions

Parameter	Standard Value	Parameter	Standard Value
L	2000	s_H	0.00005
s_p	0.005	s_n	0.005
r_p	1	r_n	1
r_I	0.4	b	0.25
u_0	$\frac{1}{9}$	c_0	$\frac{1}{12}$
m_p	$\frac{1}{3*7}$	m_n	$\frac{1}{3*7}$
m_c	0	c	0.07
p_U	0.018	n_U	0.018
p_H	0.007	n_W	0.007

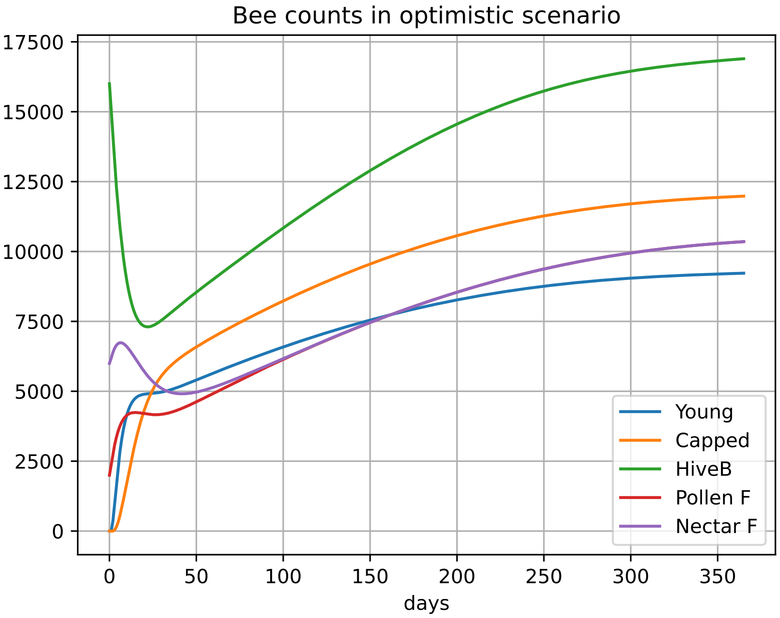
4 Scenarios and Sensitivities

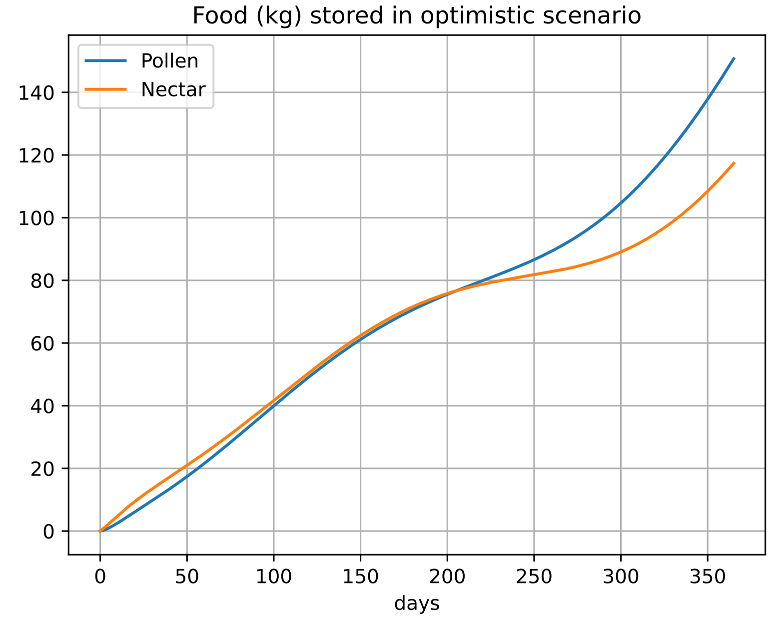
In this section we present the results of running the model defined in the previous section through various scenarios. Our objective is to develop the intuition about how hives operates and what parameters create the most sensitivity to the hive dynamics. Each simulation scenario below outputs two graphs and a table of derivatives (sensitivities) to model parameters. The first graph displays the daily numbers of bees in each of the five states that are modeled: Young (eggs/larvae), Capped (capped brood/pupae), HiveB (hive bees), Pollen F (pollen foragers), and Nectar F (nectar foragers). The second graph displays the total amount of nectar and pollen (in kgs) that has been accumulated by the hive up to the given day. The starting point of each scenario has 16,000 hive bees, no pollen or nectar foragers, and no brood. We think of this as a "clean slate" that allows the colony to start optimizing its content on day 1 without taking into account what happened before. As mentioned earlier, day 0 corresponds to mid-February and it is assumed that blooming season starts around that time (and nectar season a couple of weeks later). Below the graphs is a table with 18 rows and 7 columns. The entry in row i and column j represents the derivative of the variable in column j calculated at the end of the year-long simulation with respect to the parameter in row i. To make it easier to compare derivatives across different parameters, each derivative is scaled by 1% of the parameter value. For example, if the derivative of HiveB with respect to parameter eggs is 470.2 this means that the exact derivative of the number of hive bees after 365 days of simulation with respect to the number of eggs laid by queen daily is 470.2/20. The factor of 20 is due to the fact that, as specified above, the assumption for parameter L, the number of eggs laid by the queen daily, is 2000, so that 1% of that number is 20. In other words, each derivative is meant to be interpreted as answering the question of how much each of the output variables would change if that parameter was increased by 1%. The last two columns, Pollen and Nectar, are expressed in grams even though the graphs are expressed in kg: the scales are different since the graph shows the cumulative amount of food while the table shows the change.

The model was implemented using pyTorch, a software package used for deep learning with built-in automatic differentiation capability. This allows us to calculate every derivative **exactly** - differential equations that govern hive dynamics contain coefficients that are either constants or differentiable activation functions. Each simulation updates the hive 365 times, each time calling differentiable functions to obtain output for that day and then using that output as input for the next day and calling the same function but with different arguments. The hive vector that results from 365 days of simulation is a function of the original parameters, and pyTorch is able to compute the exact derivatives of 365 function calls.

4.1 Optimistic Scenario

The "Optimistic" scenario shows what happens when everything goes very well: there is plenty of pollen and nectar (up to seasonal variation) and the distance between the hive and the source of food is small. In this scenario bees work very hard and bring in a lot of food but don't exceed their total flight distance. A common assumption is that bee's total lifetime mileage doesn't exceed 800km, and in this scenario this constraint is not violated. Since the starting point is mainly hive bees only with very few other bee types, there is a big shift at the beginning of the simulation as many hive bees are recruited to become foragers, dipping the number of hive bees initially. As the time progresses, the ranks of hive bees get filled up again by the brood.





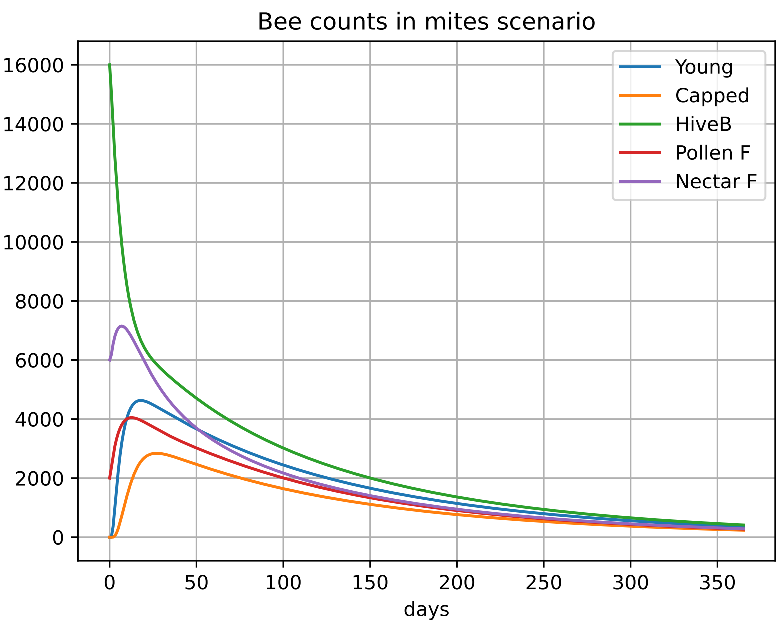
	Young	Capped	HiveB	Pollen F	Nectar F	Pollen	Nectar
eggs	256.2	333.7	470.2	291.1	291.1	3075.3	2050.4
brood_surv_hive	169.3	221.5	315.6	196.7	196.7	2255.7	1530.1
brood_surv_pollen	0.2	0.3	0.6	0.4	0.4	28.7	23.9
brood_surv_nectar	0.0	0.1	0.1	0.1	0.1	4.6	3.8
recruit_pollen	-15.8	-20.6	-45.5	-6.3	-29.4	117.0	-312.7
recruit_nectar	-8.3	-10.8	-23.7	-21.0	2.1	-328.2	194.3
recruit_soc_in	-100.0	-130.6	-286.7	-114.7	-114.7	-940.1	-543.1
recruit_base	-109.7	-143.3	-314.5	-125.9	-125.9	-1035.1	-598.7
1/larva_duration	-88.7	5.0	9.3	5.5	5.5	699.4	657.9
1/capped_duration	7.5	-106.3	20.9	13.5	13.5	363.5	287.2
pollen_eaten_per_brood	-4.2	-5.4	-12.1	-4.5	-4.5	-22.1	-501.9
nectar_eaten_per_brood	3.7	4.8	10.5	4.2	4.2	-466.8	12.7
pollen_eaten_per_hiveb	2.5	3.2	7.0	2.8	2.8	-333.7	-0.7
nectar_eaten_per_worker	-6.3	-8.1	-18.1	-6.7	-6.7	-41.8	-760.9
food_gathered_per_worker	4.6	5.9	13.4	4.7	4.7	2404.8	2452.1
mortality_capped	-3.8	-7.7	-10.8	-6.7	-6.7	-76.8	-54.1
mortatiliy_pollen	-9.4	-12.1	-27.2	-112.7	-10.3	-2206.8	139.0
mortality_nectar	-43.5	-56.5	-125.2	-48.3	-150.7	-314.3	-2172.9

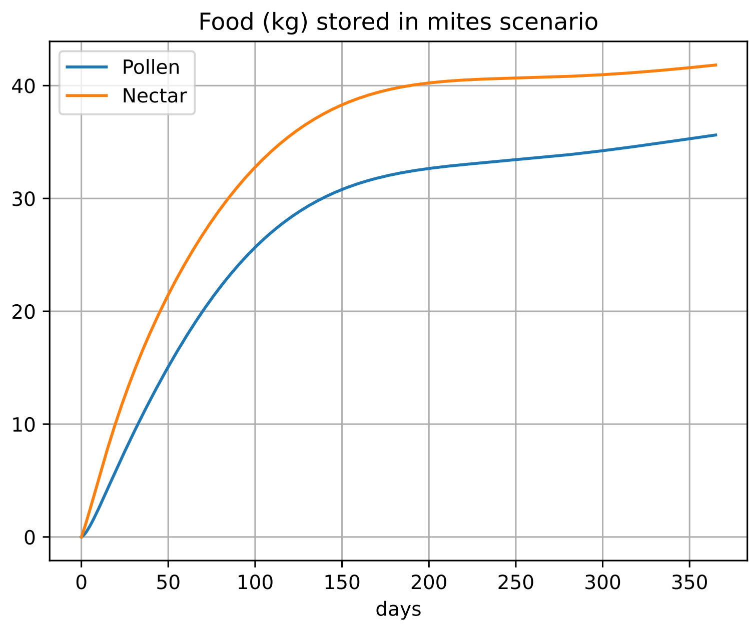
Because there is a lot of food available, the stores of both nectar and pollen go up continuously and end up at roughly 140kgs of both nectar and pollen after a year. The colony is healthy and grows in size quickly during the first half of the year and stabilizes after that. The total size of the colony ends up at about 60,000 bees, including brood. Foragers represent about 1/3 of the total colony. Interestingly, this ratio is pretty consistent across the different scenarios that we try below, suggesting that this ratio may somehow be near optimal across a wide range of scenarios.

Since there are plenty of resources, the number of eggs laid per day is one parameter to which all output variables have the highest sensitivity. The other parameter with a high positive derivative is brood_surv_hive, which is the exponential weight attributed to the survival probability due to the number of hive bees. In general, in this scenario the hive bees are the bottleneck: there is a high negative probability due to the social_inhibition parameter and to the base recruitment rate, meaning the colony has to balance making more hive bees into foragers to bring in more food against keeping hive bees as nurse bees so they can help create more worker bees. There is sensitivity to the 9 day period spent in egg/larvae state as well as in the capped state; the numbers for the variables representing the number of bees in those states are negative because the parameters are the inverses of the average number of days spent in those state and they go into the corresponding equations [1] and [2] with negative signs, i.e. they represent the rates at which bees are leaving those states. But this is also the reason why they have positive sensitivities to pollen and nectar storage: if bees could mature quicker, they could get to work quicker and produce more for the colony. Food gathered per worker bee has large positive sensitivity for the amount of pollen and nectar stored. This is straightforward: everything else being equal, if foragers bring in more the colony ends up with more. The same goes for the mortality rates: if foragers die quicker there is less food.

4.2 Mites and Viruses Scenario

The "Mites and Viruses" scenario was created to compare what happens when conditions are still favorable but there is non-zero mortality of capped brood due to mites/viruses or other adverse circumstances. The parameters are the same as in the "Optimistic" scenario except mortality rate of capped brood is 4%. Even though this mortality rate is low, it causes drastic negative changes to the colony. The colony survives in terms of storing nectar and pollen but the number of bees in the colony shrinks dramatically, stabilizing at about 3,000 bees of each type except for hive bees that stabilize at a little over 4,000. If the mortality rate goes up to 8% then the colony dies. This high sensitivity to a negative external factor shows just how fragile the equilibrium of a colony is even when there is plenty of food. If the amount of food decreases, for example because the colony is competing with other nearby colonies, this can result in a very quick deterioration of the colony.



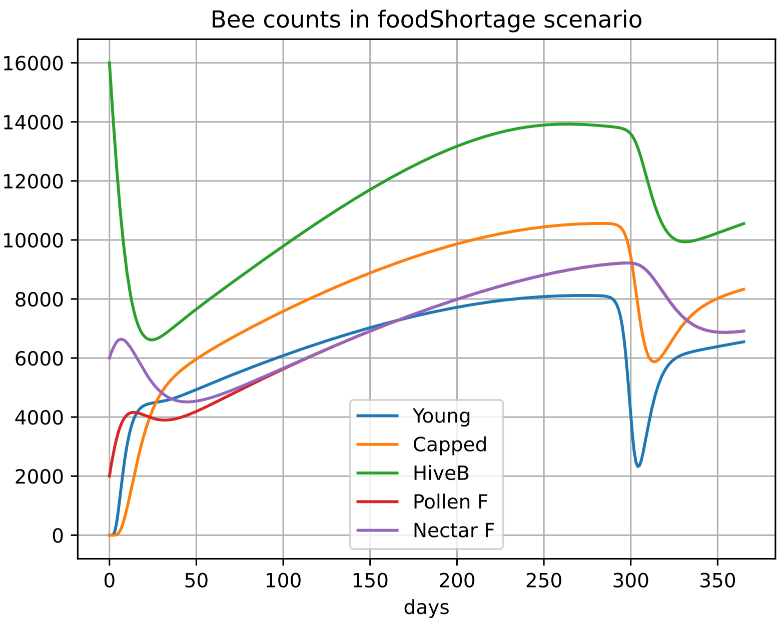


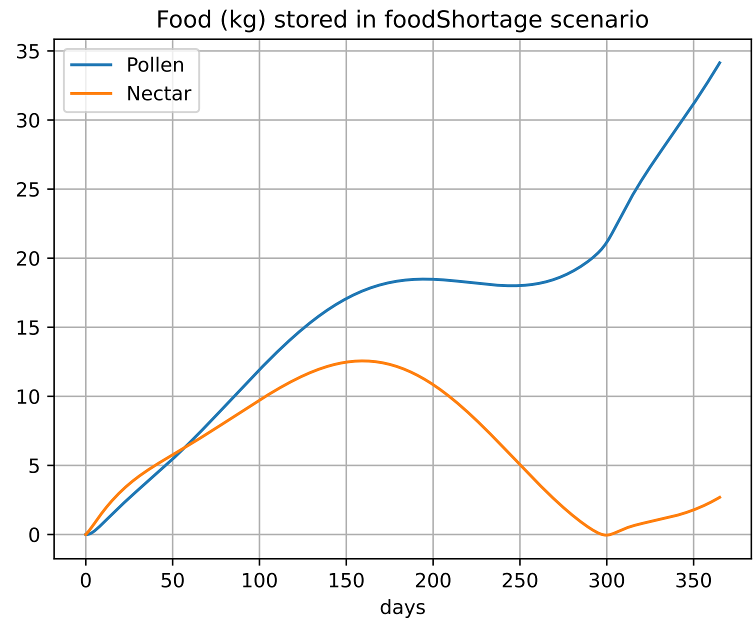
	Young	Capped	HiveB	Pollen F	Nectar F	Pollen	Nectar
eggs	26.6	17.5	28.0	17.7	18.2	294.7	230.6
brood_surv_hive	25.3	16.6	26.5	16.7	17.2	257.7	197.9
brood_surv_pollen	0.1	0.0	0.1	0.1	0.1	5.8	5.7
brood_surv_nectar	0.0	0.0	0.0	0.0	0.0	0.9	0.9
recruit_pollen	-1.9	-1.3	-2.3	-0.9	-1.7	47.0	-65.5
recruit_nectar	-2.1	-1.4	-2.6	-1.8	-1.1	-80.0	58.9
recruit_soc_in	-17.2	-11.3	-20.9	-11.6	-12.0	-100.9	-74.2
recruit_base	-18.8	-12.3	-22.8	-12.6	-13.1	-110.2	-81.5
1/larva_duration	-4.9	-0.9	-1.5	-0.9	-1.0	129.4	125.5
1/capped_duration	11.6	6.4	14.1	8.9	9.2	217.7	181.0
pollen_eaten_per_brood	-0.0	-0.0	-0.0	0.1	-0.1	8.2	-120.5
nectar_eaten_per_brood	0.0	0.0	0.0	-0.1	0.1	-123.3	12.3
pollen_eaten_per_hiveb	-0.0	-0.0	-0.0	-0.1	0.1	-82.0	12.0
nectar_eaten_per_worker	-0.0	-0.0	-0.1	0.1	-0.2	16.8	-163.1
food_gathered_per_worker	0.1	0.1	0.2	0.1	0.2	543.1	684.1
mortality_capped	-12.4	-9.4	-15.0	-9.5	-9.8	-207.5	-170.4
mortality_pollen	-5.2	-3.4	-6.3	-7.2	-3.0	-572.9	78.4
mortality_nectar	-6.1	-4.0	-7.4	-3.6	-8.0	19.7	-683.5

In this scenario there is high sensitivity to the mortality rates of pollen and nectar foragers, as well as food gathered per worker. Since fewer bees reach adulthood, it is important that the ones who survived their capped stage go on living as long as possible to be able to provide for the colony, and that they collect as much food as possible. There is still high sensitivity to the number of eggs laid every day; again, when fewer bees reach adulthood it is important to start out with as many eggs as possible. This sensitivity, together with the survival parameters due to the number of hive bees, were higher than sensitivity to forager mortality rates in the Optimistic scenario because in that scenario, with everything going well and survival probability high, number of eggs and number of workers were related by a higher multiplicative factor than in the current scenario. When this factor decreases the longevity of foragers becomes more important to the colony's survival, making the sensitivity higher.

4.3 Food Shortage Scenario

In this scenario we explore what happens to the colony when the food supply dwindles. Now the assumption is that the total amount of food collected per forager per day is just over 50% of the value in the "Optimistic" scenario. Because of the low amount of food, pollen and nectar stores at the end of the year are much lower than in the previous two scenarios. Now the difference between nectar and pollen is even more noticeable: pollen store keeps going up, although there is a flat growth period that corresponds to the season where there is very little food to forage. This flat period corresponds to the period where the number of eggs/larvae stops growing. In the same period, the amount of nectar starts decreasing and this decrease causes a crisis in the colony around day 300. Shortly after day 300, the number of all types of bees drops abruptly; the number of eggs/larvae almost goes to the number of eggs laid every day - the survival function drops, causing eggs to die. The crisis does not kill the colony - the number of bees decreases but they need less food as well. The capped brood does not need any food and as it starts developing into worker bees, the food supply starts coming back up and the colony is on its way back to survival. The crisis is averted and the colony survives the year, but its nectar supply at the end of the year is very low relative to the size of the hive.



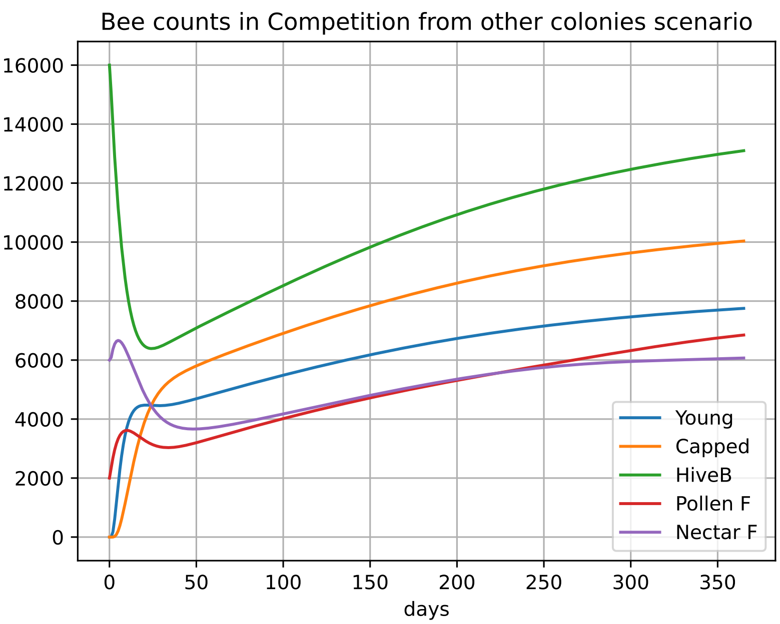


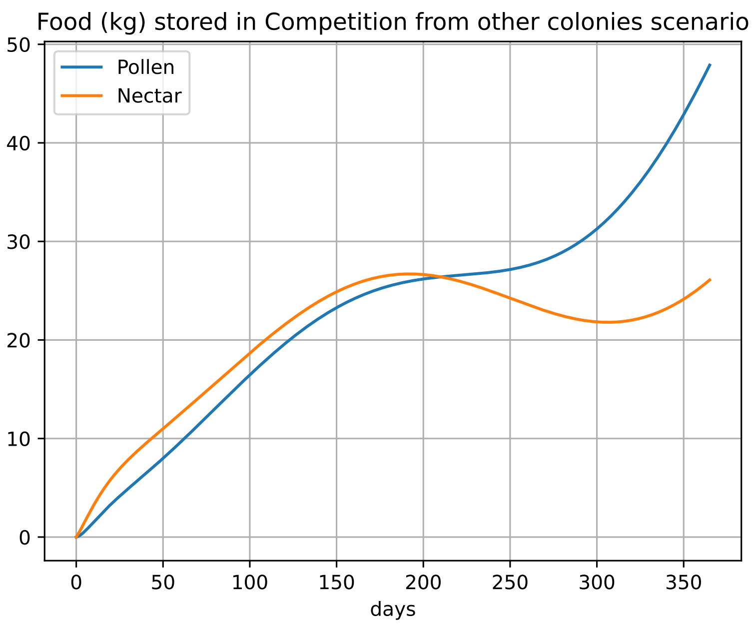
	Young	Capped	HiveB	Pollen F	Nectar F	Pollen	Nectar
eggs	-12.6	-33.6	-133.9	-133.2	-133.2	160.4	-115.2
brood_surv_hive	-2.1	-15.6	-87.0	-90.2	-90.2	143.7	-83.9
brood_surv_pollen	2.7	3.7	5.4	4.0	4.0	17.3	2.0
brood_surv_nectar	3.0	4.5	6.0	3.9	3.9	1.9	-2.1
recruit_pollen	-38.5	-50.8	-79.2	-40.7	-56.4	86.3	-31.1
recruit_nectar	66.3	89.9	131.5	94.1	109.8	-11.8	65.5
recruit_soc_in	112.3	158.0	212.0	215.9	215.9	292.7	139.0
recruit_base	123.5	173.6	233.3	237.0	237.0	320.2	152.1
1/larva_duration	171.5	317.5	474.0	343.5	343.5	770.9	192.1
1/capped_duration	17.2	-56.7	35.9	24.4	24.4	108.9	11.7
pollen_eaten_per_brood	-211.6	-283.1	-425.0	-307.5	-307.5	-280.4	-185.9
nectar_eaten_per_brood	-11.7	-15.6	-23.1	-18.4	-18.4	-438.0	-8.8
pollen_eaten_per_hiveb	-14.5	-19.3	-28.8	-22.1	-22.1	-336.0	-10.6
nectar_eaten_per_worker	-337.9	-453.5	-678.5	-488.6	-488.6	-428.4	-280.8
food_gathered_per_worker	581.3	779.6	1166.8	844.5	844.5	1843.4	512.8
mortality_capped	-3.1	-5.7	-6.7	-4.0	-4.0	-18.5	-1.6
mortality_pollen	84.6	116.2	166.9	62.6	134.6	-831.1	94.2
mortality_nectar	-377.7	-504.4	-762.8	-528.5	-600.6	-419.5	-349.2

The sensitivities are interesting. The biggest sensitivity is from parameters that specify the amount of food gathered per worker to the variable that represents pollen storage at the end of the year. Somewhat surprisingly, the sensitivity of nectar stores is more than 3 times smaller than the "Optimistic" scenario. This suggests that in this scenario there is just not enough food to sustain the colony adequately in the first year. Despite this lack of food, the colony survives that year and has a relatively successful second year (not shown). There is still an increase followed by a decrease for nectar storage, but it is not as pronounced and there is no abrupt drop in the number of bees. Another interesting point is that the sensitivity for the number of bees with respect to social inhibition and recruitment base changes sign and becomes positive. There is not enough food but foragers still bring in more than they eat, so it now makes sense for the bees to have relatively more foragers and relatively less brood. But of course, less brood now means fewer foragers in the future so there is a balancing act that the colony must perform to keep the number of bees low enough to be able to feed everyone, number of foragers high to compensate for low food per forager, and brood numbers relatively low but not so low as to kill the colony in the long run.

4.4 Competition from Other Colonies Scenario

The "Competition from Other Colonies" scenario looks at what happens when the beehive is competing for food against other colonies so foragers have to spend more time looking for available flowers, extract smaller amount of nectar/pollen from each flower, spend more time flying, accumulating more mileage, and eventually dying. This scenario is realistic in the context of pollination of crops, considered in the next section, where farmers want to ensure there are enough bees to pollinate. The scenario assumes that there is plenty of both pollen and nectar to be collected but bees from each colony get less of it because they are competing with bees from other colonies. In order to reach the flowers, bees work extra hard, increasing the number of hours they forage while bringing 25% less food than in the "Optimistic" scenario. The cost of increased workload is in the mileage that accumulates much quicker and induces higher mortality. Compared to the "Optimistic" scenario, the colony now stores less than a third of the pollen and nectar than when there is no competition. The number of bees in the colony decreases as well and foragers become the smallest group by population. Overworked foragers shift all other population segments downward as well: there are many fewer hive bees because now hive bees must convert to foragers sooner. Fewer hive bees means the brood is not taken care of as well. This in turn decreases the brood population through the survival function of the uncapped brood that depends on the number of hive bees as well as food. Otherwise, the colony is healthy, and storage of pollen and nectar is sufficient to support a somewhat smaller colony.



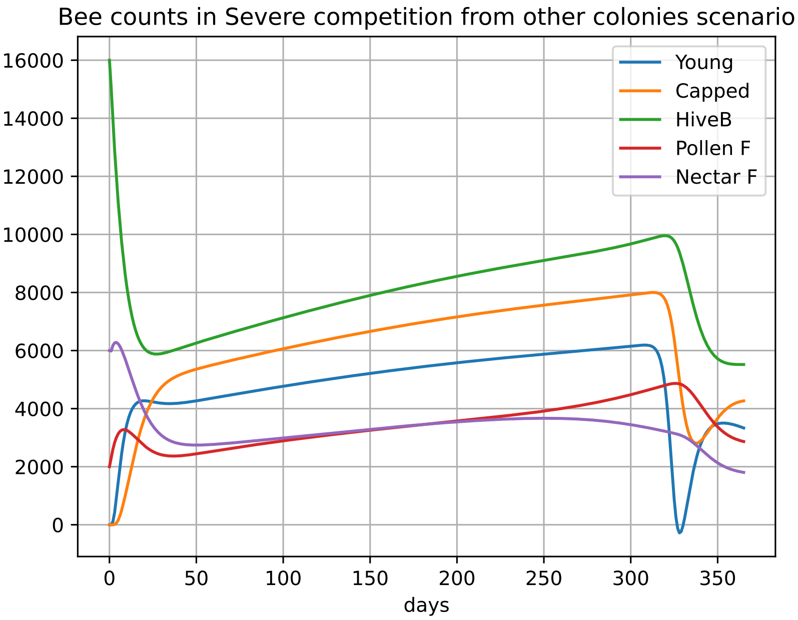


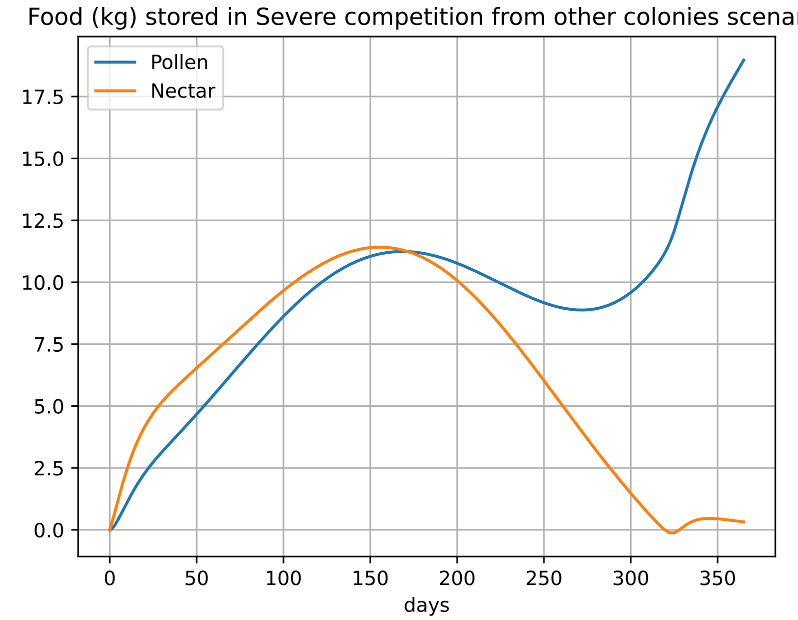
	Young	Capped	HiveB	Pollen F	Nectar F	Pollen	Nectar
eggs	271.1	351.3	461.1	252.2	199.9	1029.8	64.1
brood_surv_hive	199.5	259.6	343.2	188.5	149.3	809.7	66.7
brood_surv_pollen	0.5	0.7	1.1	0.6	0.6	15.3	9.9
brood_surv_nectar	0.1	0.1	0.2	0.1	0.1	2.5	1.7
recruit_pollen	-14.2	-18.5	-33.9	1.2	-25.0	165.8	-166.2
recruit_nectar	-14.6	-19.0	-34.7	-28.0	3.4	-235.1	217.3
recruit_soc_in	-120.9	-156.9	-287.7	-114.5	-87.4	-252.5	167.4
recruit_base	-133.9	-173.9	-318.8	-126.9	-96.8	-279.6	185.5
1/larva_duration	-73.7	5.4	7.5	0.2	9.0	469.8	456.6
1/capped_duration	9.6	-84.5	22.1	12.2	10.4	142.4	71.3
pollen_eaten_per_brood	1.8	2.0	4.8	15.8	-14.6	126.9	-533.2
nectar_eaten_per_brood	-1.3	-1.5	-3.4	-10.9	9.9	-524.1	114.1
pollen_eaten_per_hiveb	-1.5	-1.8	-3.6	-8.5	6.5	-376.4	82.9
nectar_eaten_per_worker	2.3	2.5	6.1	20.7	-19.3	175.0	-697.7
food_gathered_per_worker	-0.8	-0.4	-2.6	-16.4	18.1	1095.2	1306.3
mortality_capped	-4.4	-8.0	-10.5	-5.6	-4.7	-30.8	-9.9
mortality_pollen	-32.9	-41.7	-79.5	-126.9	9.7	-1460.5	509.1
mortality_nectar	-24.1	-32.2	-56.0	13.6	-119.2	312.9	-1326.3

Although the graphs and sensitivities are directionally similar to the "Optimistic" scenario, there are some interesting differences. For example, the number of eggs laid per day remains an important sensitivity to the amount of pollen and nectar but it lags behind the forager mortality rate sensitivity: conditions are not as favorable, so simply laying more eggs will not fix the high mortality problem. This sensitivity decline is especially noticeable for nectar storage where it is now smaller than the larva_duration sensitivity. This makes sense: if foragers are dying quicker, then if the brood could develop quicker to replenish the ranks of foragers everything would be better. This would essentially speed up the life cycle of the hive, making the lifespan of each individual bee shorter, but, as a whole, the colony would be healthy and look almost identical to the "Optimistic" scenario. We also see more sensitivity, relatively speaking, to how hive bees are contributing to the brood survival. Just like before, the model makes the dual role of hive bees very clear: they take care of the brood but they also create foragers. The two roles are competing: the colony wants hive bees to stay in the hive to ensure a higher percentage of brood surviving and the colony wants hive bees out of the hive so they can collect food and feed everyone.

4.5 Severe Competition from Other Colonies Scenario

The "Severe Competition from Other Colonies Scenario" shows how bad having too many hives in the pollination area can be for the bees. In this scenario severe competition reduces food gathered per worker by half relative to the "Optimistic" scenario and now bees have to travel even further to get to this food than in the "Competition from Other Colonies" scenario. This places a heavy strain on foragers, causing them to get to their lifetime mileage limit very quickly. Due to less food and shorter life span the hive dies after the amount of food starts seasonally decreasing. There is a small amount of pollen that is left available, but nectar starts decreasing even when there is food available because workers can't get replaced fast enough to feed the colony. The reason that the pollen is not exhausted is because the number of eggs/larvae stays sufficiently low (because their survival rate goes down) for the hive bees to create enough royal jelly to feed the youngest larvae and enough pollen to feed the older ones. Even though older larvae consume a lot of pollen, because there are relatively few of them there is still enough. Despite this, there is not nearly enough nectar and the hive dies after six months. There are small bumps visible on the graphs around day 150 where the numbers of bees start decreasing and there is a slight increase in the amount of nectar, similar to the "Food Shortage" scenario. Unlike the "Food Shortage" scenario where colony rebounds after this bump, the population in this scenario does not decrease fast enough to match the rate at which food is declining, causing the colony to eventually die.





5 Pollination of a 20 acre parcel of land

This section provides a model for the pollination of a 20 acre field of bee pollination reliant plants. As stated in the assumptions section, the crop modeled in these scenarios is the almond tree. For a 20 acre parcel of land with exclusively almond trees planted on it, a minimum of 20 (at least 16,000 total bees) beehives is necessary to successfully pollinate all flowers required in a full harvest. This number can be potentially increased to 30 beehives but our scenarios in the previous section show that more that 35-40 beehives could introduce competition between different colonies leading to deterioration of each individual beehive. Although it is important to try to get all almond trees pollinated, the high sensitivity to competition and mites/infections/viruses means that the number of beehives used should be conservative.

5.1 Pollination mechanism for almond trees

Almond trees rely exclusively on pollination provided by bees. There are roughly 100 almond trees per acre of farmland. Each almond tree has approximately 20,000 flowers, of which about half will become almonds after pollination. At any given time during the pollen collection period, half of the bees will be actively collecting pollen from flowers and the other half will either be flying back to the hive or to more flowers. Bees visit on average 10 flowers a minute (this depends heavily on how much pollen is in each flower, as more pollen per flower means bees visit less flowers per trip and less pollen per flower results in up to 20 flowers per minute). Due to weather conditions, bees are only able to work for about 4 hours a day (from 10am to 2pm), severely limiting the amount of pollen that can be collected during bloom season. Because of their efficiency in harvesting pollen, bees will often finish all actively blooming flowers in a day, causing them to revisit flowers throughout the bloom period. Almond flowers produce pollen mainly in the first two days after they open up, but residual pollen can still be collected for up to two more days. All two million flowers will bloom in 3-10 days, with longer, staggered bloom periods allowing the bees to collect more pollen. Adding more pollen to an already pollinated flower speeds up growth and is therefore beneficial to the overall health of the trees. After almond flowers are no longer receptive to pollen, they begin producing nectar, resulting in an increase in activity for nectar forager bees (15). Given the relatively short amount of time that almond trees are "active" (producing either pollen or nectar), bees are forced to seek out different plants to provide food. Our simulation runs only for the period of time that almond trees are active, with the assumption that after the almond blooming season concludes a farmer would transfer the bees to a different parcel of land containing other pollen-reliant crops.

5.2 Calculations

About 25% of bees in a hive at any given time are pollen foragers (16) (this is also supported by the results from our model). Given a hive with 16,000 total bees, this means 4,000 bees are specifically pollen forager bees. As previously stated in the pollination mechanism subsection, at any given time about half of these 4,000 bees will not be gathering pollen. This leaves us with 2,000 bees. At 100 trees per acre, this means 20 bees will be pollinating each tree. 20 bees gathering pollen from 10 flowers a minute means in one working day (4 hours), these bees can visit 48,000 flowers total, meaning each flower will be visited over two times in a single day. Almond flowers produce 0.7 to 1.2 mg of pure pollen (this value is doubled, as the pollen used by bees contains "glue" that accounts for 50% of the total mass) throughout the entire blooming period. This means one acre of almond trees can produce up to 4.8 kilograms of usable pollen in one season (15). In the 2 days that flowers are most active, each one will be visited almost 5 times (although consecutive visits provide diminishing pollen returns), meaning additional days of blooming allows for pollination redundancy. This means that an entire acre of almond trees can be pollinated by a single strong bee hive even given the worst case scenario where blooming is not staggered and bees have to complete pollination within 3 days. Additional hives may be beneficial, as more pollen stimulates flower growth. There is a limit though, as after 1.5-2 hives per acre, the competition between colonies due to lack of food causes critical, unsustainable damage to the bee populations. The balancing of supply (pollen from flowers) and demand (bee colonies) also depends on how long the hives remain on this land. It may be sustainable to have 2 hives on the same acre of land for up to 300 days, but diminishing pollen will eventually kill both hives if left unattended beyond this period of time.

$$\text{pollen foragers: } 16000 \text{ bees} * 25\% \text{ foragers} = 4000$$

$$\text{actively foraging: } \frac{4000 \text{ bees}}{2} = 2000$$

$$\text{bees per tree: } \frac{2000 \text{ bees}}{100 \text{ trees}} = 20$$

$$\text{flowers per minute (one tree): } 20 \text{ bees} * 10 \text{ flowers per minute} = 200$$

$$\text{flowers per hour (one tree): } 200 \text{ flowers per minute} * 60 \text{ minutes} = 12000$$

$$\text{flowers per day (one tree): } 12000 \text{ flowers per hour} * 4 \text{ hours} = 48000$$

$$\text{total flowers per day: } 48000 \text{ flowers per tree} * 100 \text{ trees} = 4800000$$

$$\textbf{flowers visited in first 2 days: 4800000 flowers per day} * \textbf{2 days} = \textbf{9600000}$$

$$\text{average number of visits for each unique flower per day: } \frac{4800000 \text{ flowers per day}}{2000000 \text{ unique flowers}} = 2.4$$

$$\textbf{pollen gathered per bee in 1 day: } \frac{4.8 \text{ kg in 2 days}}{2 \text{ days}} =$$

$$\frac{2.4 \text{ kg}}{4000 \text{ forager bees}} = 0.0006$$

$$0.0006 \text{ kg} =$$

$$\mathbf{0}.6 \textbf{ grams per bee per day}$$

This value is represented by $c = 0.7$ in our model, along with the fluctuations in available pollen represented by the $\mu_p(t)$ activation function.

The optimal amount of beehives is between 1 and 2 colonies, with 1 hive insuring the survival of the bees in the long run and 2 hives insuring maximum pollination.

6 Conclusion

The use of differential equations and activation functions to model a bee colony over time allows for an in depth solution to many of the problems plaguing bees today. Our model shows the detrimental effects food shortages, competition between colonies, and mites/viruses can have on a seemingly healthy colony. Additionally, our model provides conclusive results on how to maintain a 20 acre parcel of land with bee-reliant plants. Adding more layers of depth to the model, such as accounting for drones, diseases, nutrients, plant variations, and other aspects of bee colonies, could improve accuracy, but our model still manages to illustrate, to a high degree of precision, a bee hive over time.

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Modeling a Honey Bee Population

Goal

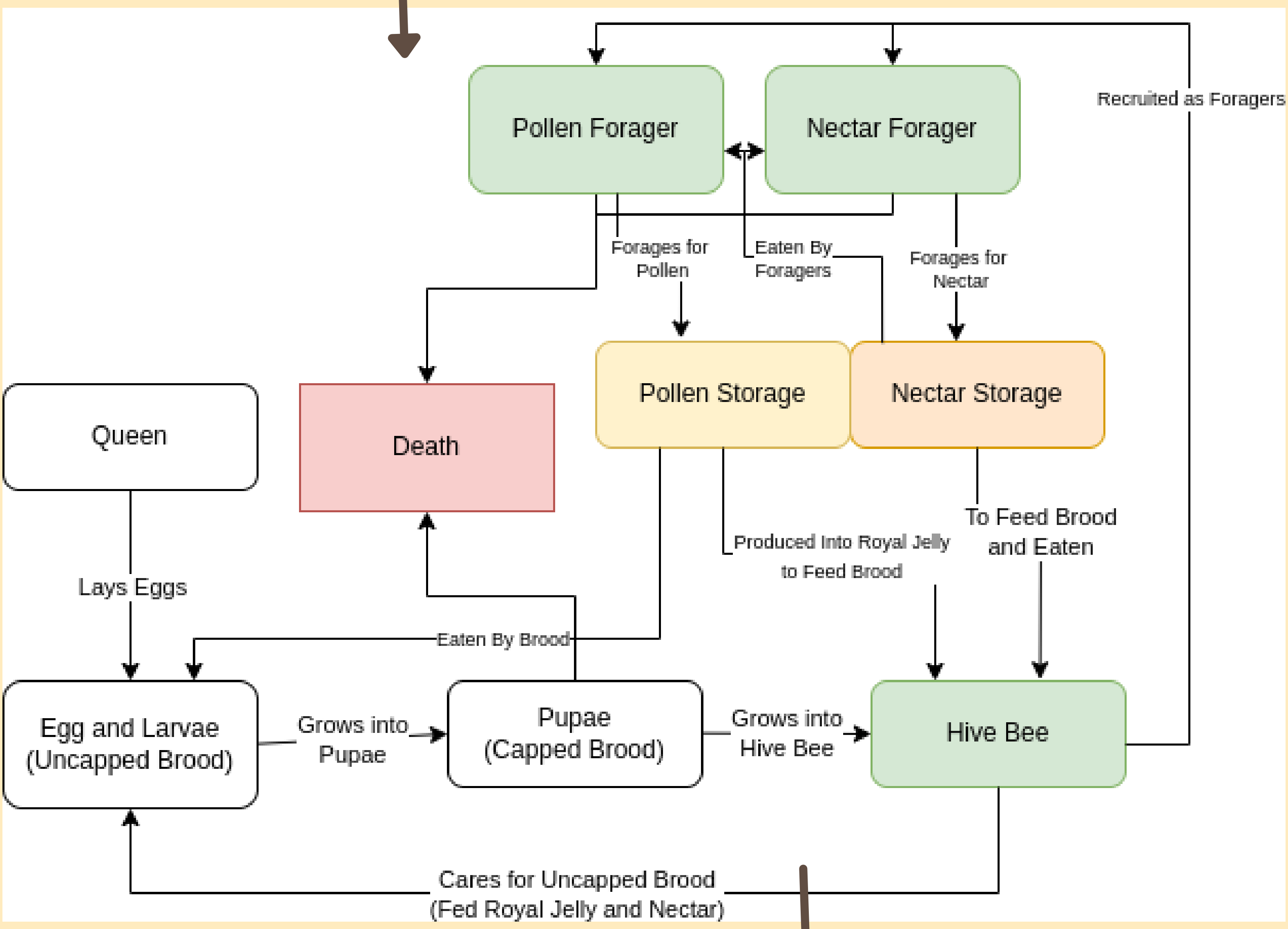
Determine optimal beehive deployment that meets agricultural pollination needs while ensuring long-term survival of bee colonies.

Background Information

Concerns regarding the endangerment of honeybee colonies due to Colony Collapse Disorder add urgency to understanding the effects of different factors on colony survival.

Our Approach to the Problem

Modeling each stage of bee lifecycle and connecting stages together to calculate the effect of each factor on colony evolution.



Conclusions

Our model shows the large effects that factors such as pollen collection, mortality rates, and specialization of workers have on the survival of a honeybee colony. This evidence allows us to conclude that the optimal range for the number of honey bee colonies per acre of farmland is...

insures hive survival

1-2 Hives

insures maximum pollination