Modeling the Interaction Dynamics between Honeybees and Food Availability

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Abstract

The success of honeybee (Apis mellifera) colonies is critical to the United States agriculture with 35% of American diets dependent on honeybee pollination. There are various complex factors that can contribute to a colonys failure, such as nutritional stress. Nutritional stressors primarily pertain to food scarcity, lack in diversity of food, and the availability of food with low nutritional value. Previous mathematical models have examined the impact of nutrition and the early recruitment on honeybee population dynamics. These models do not include the impact of a food supply with a limited storage space within a single hive. In this work, we use a mathematical model to investigate the impact of food scarcity and limited storage space on honeybee viability, early recruitment rates of workers into foragers, and the influence of these rates on the growth of a colony. A threshold, R_d, was found for conditions when a colony will persist or collapse. We found conditions for the stable coexistence of a honeybee population and food supply as well as conditions for periodic behavior. Through sensitivity analysis we find that a honeybee colony is most sensitive to changes in the rate at which a worker bee encounters food and the rate food is entering the food supply. There are no qualitative differences between using a Holling Type I or Holling Type II functional response in honeybee population persistence when modeling the interaction between a honeybee colony and the availability of food.

1 Introduction

Honeybee colonies are highly complex societies with each individual's survival dependent on one another and the honeybee's longevity influenced by their role in the colony [10]. In addition to their role in the colony, honeybees play a vital role in global food production in which honeybees are responsible for pollinating 80% of all pollinated plants. Pollination is crucial to food production and the economy; food coming from pollinated plants accounts for 35% of an American's diet, with $15 billion annually in the United States, and exceeds $200 billion globally [11, 12]. Honeybee health is therefore a topic that has over the past decade received considerable attention, especially given reports of an unexpected and undetermined cause of colony losses since October 2006. During the winter of 2006-2007 and subsequently 2007-2008, apiaries lost up to 90% of their colonies due to a condition referred to as Colony Collapse Disorder (CCD) [7]. Many studies are being conducted to explore what stressors may be causing honeybee colonies to collapse not only due to CCD, but in general [7]. It is suggested that a combination of one of the following anthropogenic stressors such as parasites, pathogens, certain agricultural pesticides, beekeeper applied chemicals, genetically modified crops, and changed cultural practices may be leading to the failure of honeybee colonies [13, 14].

Depressed honey prices have forced beekeepers to change their cultural practices by seeking alternative income through the leasing of colonies for pollination–typically almond pollination [13]. Resulting from the lack of diversity in plants and restricted floral resources due to crop monocultures, adequate nutrition may not be provided and is reducing the ability of colonies to endure stress. In addition to poor nutritional sources, transporting colonies in holding yards may also inflict stress on the honeybees. The honeybees eventually are trucked to a location with exceptional floral resources in order to feed on high quality pollen to restore their protein levels, which is not practiced by all beekeepers. Additional studies observed that even when presented with nutritionally diverse diets, the bees failed to adjust their intake to improve their survival when exposed to other stressors [1]. These studies draw attention to the impact of food scarcity, and how the sensitivity of changes to food storage, inflow of food, and consumption of food affect the division of labor of bees.

The complex social life of honeybees includes a division of labor among worker bees and forager bees. The primary form of division of labor is called "temporal polyethism", in which younger adult bees referred to as workers perform tasks within the colony such as nursing the brood, maintaining the nest, and storing food collected by forager bees. Approaching the end of the third week of the worker's life, assuming the hive is at homeostasis, worker bees will become forager bees and begin foraging for food and protecting the nest for the remainder of their life [16]. The division of labor among the workers and foragers is associated with differences in age, genotype, and morphology, all of which are based on the worker's behavioral development. This method of dividing labor is thought to contribute immensely to the overall growth and development of a honeybee colony.

There is great flexibility in this pattern of dividing labor amongst the adult bee population [16, 20]. For example, bees exhibit social inhibition in which the transition to foraging is socially regulated such that the existence of an established foraging population in the colony delays the recruitment of worker bees to the role of a forager. In response to multiple stressors, such as a loss in the forager population, low food storage, or diseases, worker bees expedite their behavioral development in order to fulfill the needs of the colony [9]. Precocious foragers may not be optimally adapted for the foraging tasks outside the colony. There is evidence that precocious foragers are heavier and less efficient fliers than adequate foragers and the efficiency of the foraging force is reduced, which may have serious consequences such as a food shortage [14].

Additionally, brood rearing is also sensitive to a shortage in food supply. For example, in a honeybee colony, most of the protein income comes from pollen which is utilized to feed the uncapped brood. Thus the colony's capability of raising brood successfully depends on keeping a sufficient supply of pollen. The brood's mean capping age highly correlates with the mean pollen income; the less pollen stored in the colony during the brood's development, the earlier the brood are capped. This leads to an accelerated reduction in the quantity of uncapped older brood in response to a shortage of available pollen. Older uncapped brood have the highest pollen demand, so worker bees will cannibalize younger uncapped brood to compensate for a shortage of pollen supply by reducing pollen demand. The protein gained from cannibalism enriches the royal jelly, and the early capping of older brood saves the oldest part of the brood, which represents the maximum brood care investment [18].

Several mathematical models have been developed to describe the dynamics of honeybee populations and the impact of anthropogenic stressors, particularly pathogens, parasites, and nutritional stressors, on the long-term viability of a colony [2, 3, 5, 6, 8–11, 14, 17]. Of these previous studies, the most relevant are those of Khoury et al. in which a model was established to study different death rates of foragers and the impact these had on colony growth and development [9,10]. Russell et al. examined the sensitivity of a colony by looking into seasonal variations, rates of forager mortality, food availability and factors that influence the transition age of worker to forager. [17]. Perry et al. studied a model and collected data to examine food shortage and the impact of rapid maturation on the success of a honeybee colony [14]. However, to our knowledge, our approach is the first to recognize a finite food storage, and the impact of the food storage on early and delayed recruitment within a honeybee colony.

In this study, we employ a mathematical model to simulate the potential influence of food shortage and storage space on honeybee population dynamics. We explore how a finite food supply or shortage in food supplies influence rapid maturation of worker bees, and overall growth or collapse of the colony. In the following sections we describe the stage-structured model employed, the sources of data used in this analysis, which is then followed by a presentation of results and a discussion.

2 Model

2.1 Model Framework

In order to study the impact of food supply on the dynamics of a honeybee colony, we have constructed a simple model consisting of three classes: a class for the brood, a class for the worker bees, and a class for the forager bees . The bee life cycle outlined in the model starts with the queen bee's production of brood, in which the birth rate of brood grows or decays with respect to the available food supply and worker bee population. A conversion factor is utilized to convert what food is available and how many workers there are into the amount of brood born. The brood leave the brood class through the process of eclosion, and become worker bees or they die a natural death or death induced by lack of food supply.

Brood enter the worker class through the process of eclosion and then are naturally recruited to foraging typically within three weeks . When the forager population is too low, more workers are recruited to become foragers. In the case of too many foragers, either there is a delay in recruitment, referred to as social inhibition, or a portion of foragers transition back to the role of a worker [**?**]. Aside from recruitment, workers may also leave the worker class through natural death or death induced by lack of food supply. Workers are entering the forager class via natural recruitment, or hastened recruitment, depending on the forager population. Foragers leave the forager class either through recruitment back to the worker class due to overpopulation of foragers, or through natural death or death induced by lack of food supply.

With the food supply, we assume the foragers are consuming their portion of food (in grams) and storing the remainder that is collected in the hive. The food supply is assumed to grow logistically. Note that with a lower forager population, the overall growth rate of the incoming food supply is lower. Food is then removed from the supply by the workers in order to feed and nurture themselves along with the existing brood; also this relationship between workers, supply, and workers encountering food per unit time is dictating how many brood are being born.

A compartmental diagram of the model can be seen in Figure 1. Empirical data supports that sex-allocation ratios of pupae or adults are typically female biased; therefore this model only considers the female population of the hive [15]. We do not distinguish between uncapped brood and capped brood, and assume them all to be a part of the brood class similarly. Although the food supply in a bee colony consists of mostly nectar (carbohydrates) and a small quantity of pollen (protein), we do not distinguish between the two.

2.2 Logistic Growth of Food with Holling Type II Functional Response for Consumption

In the absence of a bee population, the food supply (S) grows logistically at the rate, r, with a carrying capacity, K. We implement a Holling Type II functional response to examine the

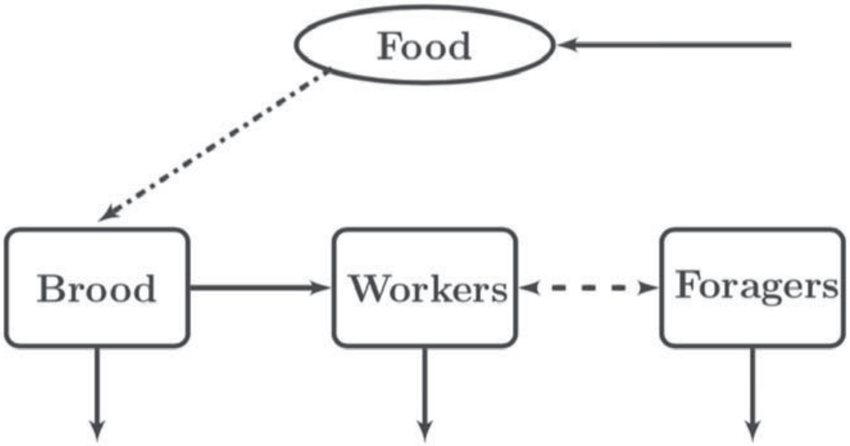

Figure 1: Schematic representation of the compartmental model. Brood eclose into workers, then mature to foragers. Food is collected by the foragers, while the workers and available food develop brood (dashed-dotted line). In the case of not enough foragers, workers precociously transition to the forager class; and if there is an abundance of foragers, the recruitment of workers to foragers is delayed or foragers revert back to workers (dashed line).

relationship between the food supply, workers (W), and brood (B) being born. Here a is the encounter rate of the workers with the food supply per unit time, c is the conversion of the food to brood, and b is the amount food required to reach half the maximum birth rate of brood. Brood eclose at a rate, γ, and the workers are naturally recruited to foraging at the rate, α_{min}. The ratio of foragers (F) to workers is represented by α, and when the populations are out of proportion the adult bees will transition either to or from each class at a rate of σ. We assume the death rates for each class (μ_B, μ_W, and μ_F) and growth rate of food supply to be constant.

These assumptions lead to the following system of non-linear ordinary differential equations:

$$\begin{aligned}
\frac{dB}{dt} &= \frac{caSW}{b+S} - \gamma B - \mu_B B,\\
\frac{dW}{dt} &= \gamma B - \alpha_{min} W - \sigma(\alpha W - F) - \mu_W W,\\
\frac{dF}{dt} &= \alpha_{min} W + \sigma(\alpha W - F) - \mu_F F,\\
\frac{dS}{dt} &= rS\left(1 - \frac{S}{K}\right) - \frac{aSW}{b+S}.
\end{aligned}$$

3 Analysis

We analyze the mathematical model by first rescaling it to reduce the number of parameters in order to simplify the analysis. We find the existence of three equilibria and linearize about each one to determine the stability. We use conditions on the stability of the nontrivial boundary equilibria to find a demographic reproductive number, R_d. We substitute in our original parameters and provide a biological interpretation for R_d. We explore the dynamics of this system numerically by varying parameters to simulate different existence and stability combinations and observe limit cycles formed from a Hopf bifurcation which implies that populations may never stabilize to fixed values.

3.1 Scaled Model

Our rescaled model is found by first letting, $x(\tau) = \frac{\gamma a B(t)}{r^2}, y(\tau) = \frac{aW(t)}{r}, z(\tau) = aF(t), u(\tau) = \frac{S(t)}{k}, \tau = rt$.

We substitute $x(\tau)$, $y(\tau)$, $z(\tau)$, and $u(\tau)$ to obtain the following rescaled form:

$$\begin{aligned}
\frac{dx}{d\tau} &= \frac{Huy}{J+u} - Vx, && (1)\\
\frac{dy}{d\tau} &= x - Ey + Gz, && (2)\\
\frac{dz}{d\tau} &= Ay - Dz, && (3)\\
\frac{du}{d\tau} &= u(1-u) - \frac{uy}{k(J+u)}, && (4)
\end{aligned}$$

where the new parameters (consisting of original parameters) are the following:

$H = \frac{\gamma c}{r^2}, J = \frac{b}{k}, V = \frac{1}{r}(\gamma + \mu_B), E = \frac{1}{r}\left(\alpha_{min} + \sigma\alpha + \mu_W\right), G = \frac{\sigma}{r^2}, A = \alpha_{min} + \alpha\sigma,$

$D = \frac{1}{r}(\sigma + \mu_F)$.

3.2 Equilibria and Stability

In order to determine the existence of equilibria we set the system equal to zero and solve for x^*, y^*, z^*, and u^*. We find the existence of three equilibria: $(0,0,0,0), (0,0,0,1)$, and an interior equilibrium, where $(0,0,0,0)$ is extinction with no food supply, $(0,0,0,1)$ is extinction with food supply, and the interior equilibrium is coexistence between food and the colony. We find the general Jacobian and evaluate the Jacobian at each equilibria and determine stability by finding the eigenvalues of the resulting matrix.
The general Jacobian matrix is as follows:

$$\mathscr{J}(x^*, y^*, z^*, u^*) = \begin{pmatrix} -V & \frac{Hu}{J+u} & 0 & \frac{HJy}{(J+u)^2} \\ 1 & -E & G & 0 \\ 0 & A & -D & 0 \\ 0 & \frac{-u}{ku+b} & 0 & 1 - 2u - \frac{by}{(b+ku)^2} \end{pmatrix}$$

3.2.1 Stability of the Trivial Equilibrium

We evaluate the Jacobian at the equilibrium point $(0,0,0,0)$ and find the eigenvalues of the resulting matrix:

$$\mathscr{J}(0,0,0,0) = \begin{pmatrix} -V & 0 & 0 & 0 \\ 1 & -E & G & 0 \\ 0 & A & -D & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}$$

With a positive 1 for an eigenvalue, the equilibrium $(0,0,0,0)$ is unstable. This implies that once a bee or food has entered the system, the trajectories never tend to the extinction point with no food. This is biologically valid because it is unnatural for all of the bees and food supply to disappear in a colony collapse.

We evaluate the Jacobian at the equilibrium $(0,0,0,1)$ and find the eigenvalues of the resulting matrix:

$$\mathscr{J}(0,0,0,1) = \begin{pmatrix} -V & \frac{H}{J+1} & 0 & 0 \\ 1 & -E & G & 0 \\ 0 & A & -D & 0 \\ 0 & \frac{-1}{b+k} & 0 & -1 \end{pmatrix}.$$

We can see that -1 is an eigenvalue. We can remove the last row and column of $\mathscr{J}(0,0,0,1)$ because it suffices to focus on the resulting 3 by 3 matrix, denoted as M. We then utilize the Routh-Hurwitz Criteria to determine the stability of the equilibrium point.

$$M = \begin{pmatrix} -V & \frac{H}{J+1} & 0 \\ 1 & -E & G \\ 0 & A & -D \end{pmatrix}.$$

The Routh-Hurwitz Criteria requires computing the negative determinant of matrix M, w_1, the negative trace of matrix M, w_2, and the sum of the minors of matrix M from the first row, w_3, resulting in the following:

$$\begin{aligned} w_1 &= -\det(M) = V(ED - AG) - \frac{HD}{J+1}, && (5) \\ w_2 &= -\operatorname{Tr}(M) = V + E + D, && (6) \\ w_3 &= \left(VE - \frac{H}{J+1}\right) + ED - AG + VD. && (7) \end{aligned}$$

The real parts of all eigenvalues of M are negative thus the equilibrium is stable if and only if $w_i > 0$, $i =$ 1,2,3 and $w_2 w_3 > w_1$. If these conditions are satisfied then we have stability. We now show that the equilibrium $(0,0,0,1)$ is locally asymptotically stable if $w_1 > 0$.

Lemma 1. *If $w_1 > 0$, then the Routh-Hurwitz Criteria is satisfied for the equilibrium (0,0,0,1) under Holling Type 2.*

Proof. Assume $w_1 > 0$, then from (5)

$$\begin{aligned} ED &> AG \qquad (8) \\ VE &> \frac{H}{J+1} \qquad (9) \end{aligned}$$

From (8) and (9), it follows that $w_3 > 0$. Since $D, E, V > 0$, it follows that $w_2 > 0$. To meet the second condition of the Routh-Hurwitz Criteria, we multiply w_2 and w_3:

$$\begin{aligned} w_2 w_3 &= (V+E+D)\left(VE - \frac{H}{J+1} + ED - AG\right) \\ &= V\left(VE - \frac{H}{J+1} + ED - AG\right) + E\left(VE - \frac{H}{J+1} + ED - AG\right) \\ &+ D\left(VE - \frac{H}{J+1} + ED - AG\right) \\ &= V(ED - AG) + V\left(VE - \frac{H}{J+1}\right) + Ew_3 - \frac{HD}{J+1} + D(VE + ED - AG) \end{aligned}$$

By (5), (8), and (9) we get, $w_2 w_3 = w_1 + V(VE - \frac{H}{J+1}) + Ew_3 + D(VE + ED - AG)$. Thus $w_2 w_3 > w_1$. Therefore by assuming $w_1 > 0$, we have shown the equilibrium point (0,0,0,1) is locally asymptotically stable. This completes the proof. □

3.2.2 Calculation of the Demographic Reproductive Number, R_d

Here we provide a condition for collapse of the honeybee colony by demographic factors. Recall that $w_1 = -\det(M) = V(ED - AG) - \frac{HD}{J+1}$. Assume that $w_1 > 0$, then we have, $V(ED - AG) - \frac{HD}{J+1} > 0$. Rearranging terms and simplifying we have $\frac{H}{(J+1)(VE)} + \frac{AG}{ED} < 1$.

We define our demographic reproduction number, $R_d = \frac{H}{(J+1)(VE)} + \frac{AG}{ED}$. If $w_1 > 0$ this implies $R_d < 1$, and under this condition the honeybee colony will collapse. Substituting the original parameter values from the parameters A, C, D, and E into R_d and simplifying, we have:

$$R_d = \frac{(\alpha\sigma + \alpha_{min})\sigma}{(\alpha\sigma + \alpha_{min} + \mu_W)(\sigma + \mu_F)} + \frac{\gamma c k}{(\gamma + \mu_B)(\alpha\sigma + \alpha_{min} + \mu_W)(b + k)}. \qquad (10)$$

Theorem 1. *If $R_d < 1$, then the equilibrium $(0,0,0,1)$ is locally asymptotically stable.*

Proof. Suppose $R_d < 1$. Then $\frac{H}{(J+1)(VE)} + \frac{AG}{ED} < 1$. Multiply by DVE and rearrange, then $V(ED - AG) - \frac{HD}{J+1} > 0$. By Lemma 1, since $w_1 > 0$, then $(0,0,0,1)$ is stable. □

This theorem implies that if $R_d < 1$ then the honeybee colony collapses. So, to keep the population from collapsing it is necessary to have $R_d > 1$.

To highlight the role of social inhibition (σ) on R_d, we rewrite (10):

$$R_d = \sigma\left(\frac{\alpha\sigma+\alpha_{min}}{\alpha\sigma+\alpha_{min}+\mu_W}\frac{1}{\sigma+\mu_F} - \frac{\gamma}{\gamma+\mu_B}\frac{kc}{b+k}\frac{\alpha}{\alpha\sigma+\alpha_{min}+\mu_W}\frac{1}{\alpha_{min}+\mu_W}\right) + \frac{\gamma}{\gamma+\mu_B}\frac{kc}{b+k}\frac{1}{\alpha_{min}+\mu_W}.$$

We can give a biological interpretation of the demographic reproduction number. The term $\frac{\alpha\sigma+\alpha_{min}}{\alpha\sigma+\mu_W}$, is the proportion of workers promoted to the role of foraging, $\frac{\sigma}{\sigma+\mu_F}$, is the proportion of foragers demoted to the role of a worker, $\frac{\gamma}{\gamma+\mu_B}$ is the proportion of brood that survive and become workers, $\frac{kc}{b+k}$ is the number of brood produced by a worker per unit time, $\frac{\alpha\sigma}{\alpha\sigma+\alpha_{min}+\mu_W}$ is the proportion of precocious workers becoming foragers, and $\frac{1}{\alpha_{min}+\mu_W}$ is the average time spent as a worker when the colony is in homeostasis.

To better understand the meaning of R_d we consider the simple case $\sigma = 0$ (without social inhibition), which we denote as r_d. Therefore the value for r_d is the following:

$$r_d = \left(\frac{\gamma}{\gamma+\mu_B}\right)\left(\frac{kc}{b+k}\right)\left(\frac{1}{\alpha_{min}+\mu_W}\right).$$

The first term in r_d is $\frac{\gamma}{\gamma+\mu_B}$ which is the number of brood produced by a worker per unit time. Next the term, $\frac{Kc}{b+K}$, is the the proportion of brood eclosing into workers. Finally the last term, $\frac{1}{\alpha_{min}+\mu_W}$, is the average time spent in the worker class during homeostasis. Therefore the demographic reproduction number during homeostasis represents the average number of worker bees produced per worker bee during the average lifespan of a worker bee.

3.2.3 Existence of the Interior Equilibrium

We take the rescaled form of the model and set the system equal to zero. Solving for y^* using Equation (4), $y^* = (1-u^*)(b+ku^*)$. Solving for z^* using Equation (3), $z^* = \frac{A}{D}y^*$. Solving for x^* using Equation (2), $x^* = (E-\frac{AG}{D})y^*$. Solving for u^* using Equation (1), $u^* = \frac{VJ(E-\frac{AG}{D})}{H-V(E-\frac{AG}{D})}$.

This results in the following interior equilibrium:$\left((E-\frac{AG}{D})y^*, (1-u^*)(b+ku^*), \frac{A}{D}y^*, u^*\right)$, if $H - V(E-\frac{AG}{D}) > 0$ and $\frac{VJ(E-\frac{AG}{D})}{H-V(E-\frac{AG}{D})} < 1$.

We can rearrange u^* to be in terms of R_d.

$$u^* = \frac{J}{(J+1)R_d - 1}$$

So if we suppose $R_d > 1$, then the interior equilibrium u^*, y^*, x^*, z^* exists.

$$\begin{aligned}
u^* &= \frac{J}{(J+1)R_d - 1} < \frac{J}{JR_d} = \frac{1}{R_d} < 1, \\
y^* &= (1-u^*)(b+ku^*), \\
x^* &= \frac{1}{D}(ED - GA)y^*, \\
z^* &= \frac{A}{D}y^*.
\end{aligned}$$

Table 1: Stability of Equilibria

Equilibrium	Component	Existence	Stability
Extinction without food supply - E_0	$(0,0,0,0)$	always	never
Extinction with food supply - E_1	$(0,0,0,1)$	always	$R_d < 1$
Coexistence of bees with food supply - E_2	(x^*, y^*, z^*, u^*)	$R_d > 1$	conditional

4 Hopf Bifurcation

The appearance or the disappearance of an orbit through a local change in the stability of an equilibrium point is known as a Hopf bifurcation. We will show the existence of a Hopf bifurcation using a numerical approach.

First, we found the interior equilibrium of the original model:

$B^* = \frac{1}{\gamma}\left(\alpha_{min} + \sigma\alpha - \frac{\sigma(\alpha_{min}+\sigma\alpha)}{\sigma+\mu_F} + \mu_W\right)W^*,$
$W^* = \frac{r}{a}\left(1 - \frac{S^*}{K}\right)(b + S^*),$
$F^* = \frac{\alpha_{min}+\sigma\alpha}{\sigma+\mu_F}W^*,$
where
$S^* = \frac{(\gamma+\mu_B)(\alpha_{min}+\sigma\alpha-\frac{\sigma(\alpha_{min}+\sigma\alpha)}{\sigma+\mu_F}+\mu_W)}{\gamma c-(\gamma+\mu_B)(\alpha_{min}+\sigma\alpha-\frac{\sigma(\alpha_{min}+\sigma\alpha)}{\sigma+\mu_F}+\mu_W)}$

We use b as our bifurcation parameter and then fix the other parameters such that the numerical simulations exhibit periodic solutions for the honeybee population and food supply. We then evaluated the Jacobian matrix at this point:

$$\mathscr{J}(B^*, W^*, F^*, S^*) =$$

$$\begin{pmatrix}
-0.048719 & \frac{0.184433}{b+0.461083} & 0 & \frac{0.004281b}{(b+0.461083)^2} \\
0.047619 & -.149647 & 0.092945 & 0 \\
0 & 0.094091 & -0.332945 & 0 \\
0 & \frac{-6.752379}{b+0.461083} & 0 & 0.156746 - \frac{0.156747b}{b+0.461083}
\end{pmatrix}.$$

We then found the coefficients of the characteristic polynomial $p(\lambda) = \lambda^4 + a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0$. The condition $a_3 - 4\left(a_2 - \frac{a_1}{a_3}\right) > 0$ guarantees that the purely imaginary roots are the only complex roots, while the condition $a_0 = \frac{a_2 a_1}{a_3} - \left(\frac{a_1}{a_3}\right)^2$ shows the existence of a purely imaginary number as a root of the characteristic polynomial.

To show that a Hopf bifurcation occurs, we need to show that the conditions:

$$\begin{aligned} F(b_c) &= 0 && (11) \\ \left.\frac{dF}{db}\right|_{b=b_c} &\neq 0 && (12) \end{aligned}$$

are satisfied where $F = a_0 - \frac{a_2 a_1}{a_3} - \left(\frac{a_1}{a_3}\right)^2$ and b_c is a particular numeric value of the parameter b. Using Maple we found that $b_c = 3.194001536$. Using this value, two eigenvalues of the Jacobian have negative real parts and the other two are purely imaginary, hence a Hopf bifurcation.

Additionally, for any b close to b_c, we have that the equilibrium (x^*, y^*, z^*, u^*) is asymptotically stable.

4.1 Parameter Estimation and Quantitative Analysis

Most model parameters were estimated from the literature. Khoury estimated the brood to eclose in about 3 weeks ($\frac{1}{\gamma}$), and Kribs estimated workers to be naturaly recruited to foraging in approximately 3 weeks also ($\frac{1}{\alpha_{min}}$) [9, 11]. Brown estimates worker bees to die naturally within 18 days ($\frac{1}{\mu_W}$), and foragers within approximately 4.17 days ($\frac{1}{\mu_F}$) [?]. Khoury et al. suggests there is on average a 1:2 ratio of foragers to workers ($\alpha W - F = 0$ when $\alpha = .5$). Like Khoury we assume that the effects of low food availability are not evident when there is a kilogram or more food within the colony, we can then estimate that b = 500. Schmickl estimates an average colony to contain 100,000 cells, so we calculate an average ratio of pollen to honey to find out how many cells contained each and then calculated the total milligrams kept in each cell and converted to grams for a total possible carrying capacity within an average colony [19]. The rate of growth of the colony food supply was estimated by evaluating the integral of the logistic equation from 0 to the carrying capacity and solving for the rate set equal to the average amount of foragers multiplied by the average food collected each day per forager. The Pearson Chi Square goodness-of-fit statistic was used to estimate the conversion factor of food to brood, the brood death rate, the transition rate to and from the adult classes, and the encounter rate of the workers with the food supply. To estimate the model parameters that optimally describe the honeybee population data, we randomly sample the parameters of the model from a uniform distribution and calculated the Pearson Chi Square goodness-of-fit statistic comparing the model prediction to the honeybee population data [4].

Table 2: Parameter definitions, units, and values in our model.

Parameter	Description	Units	Estimate	Reference
γ	Eclosion rate	time^{-1}	0.04761905	Kribs 2014
α_{min}	Natural recruitment rate	time^{-1}	0.04761905	Kribs 2014
α	Ratio of foragers to workers	—	0.5	Khoury 2011
μ_B	Natural death rate of brood	time^{-1}	0.00111	Estimated
μ_W	Natural death rate of workers	time^{-1}	0.05555556	Brown 2013
μ_F	Natural death rate of foragers	time^{-1}	0.24	Brown 2013
r	Growth rate of food supply	time^{-1}	0.1567	Estimated
a	Encounter rate	$\frac{grams}{worker \cdot time}$	14.6445884	Estimated
c	Conversion factor of food to brood	$\frac{brood}{grams}$	0.02731384	Estimated
K	Carrying capacity of food supply	grams	49310	Schmickl 2007
σ	Additional recruitment rate	time^{-1}	0.092945	Estimated
b	Amount of food when half of max collecting rate is reached	grams	500	Khoury 2013

5 Simulations

The following are four numerical simulations for each compartment in our model. These simulations show the population growth and decline of the brood, workers, foragers, and food supply over time. If we look at Figure 2, one can see that if there is an initial amount of food in the hive, then the brood, workers, foragers and food supply will all grow and decline periodically. In our simulations we have the period of each oscillation to be 500 days. Looking at these simulations one can see that the honeybees have a strong resilience, since when the population is near zero the bees are able to survive and prevent total collapse. If we consider a stochastic effect on the population near zero, then there is a probability that the bees can die out.

Figure 2 shows that when there is a low amount of food, there is a low population of the brood, workers, and foragers. We can infer that since the quantity of food is low, the mechanism of early recruitment is at play in helping the colony to persist and increase its numbers. However, as the population grows, the demand for food also increases, therefore the overall food supply decreases. This behavior becomes cyclic, creating periodic behavior as shown in the numerical simulations.

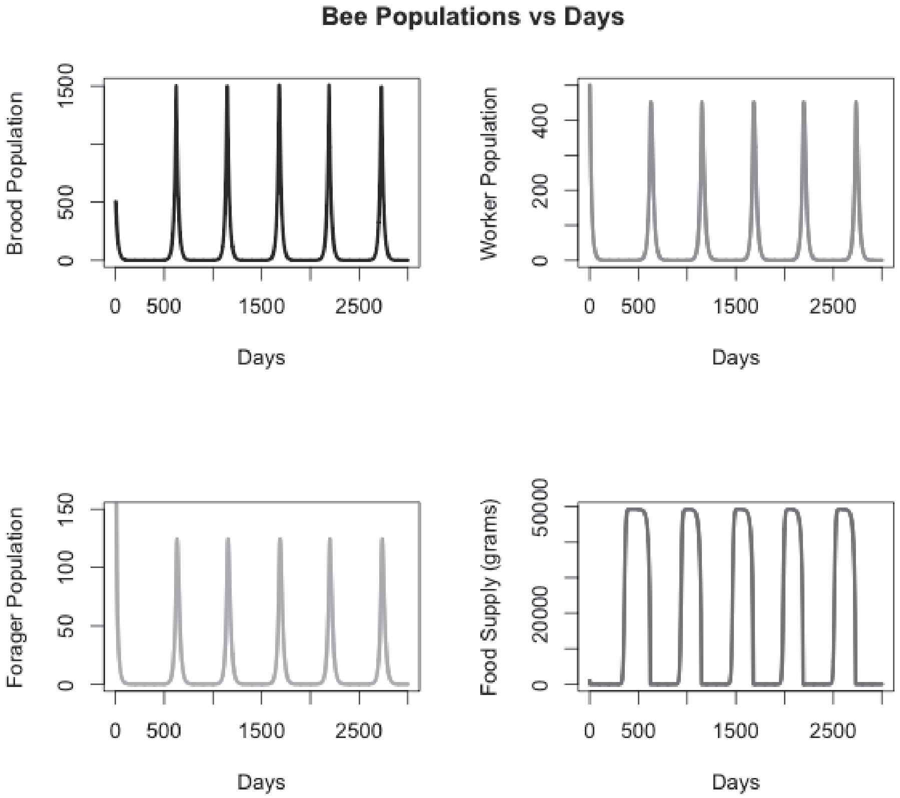

Figure 2: These numerical simulations illustrate oscillating behavior for all three honeybee classes, as well as in the food supply within the colony.

6 Sensitivity Analysis

Sensitivity analysis is used to determine which parameters are the most influential on the outcome of a model, whether we analyze equilibrium points, time, or basic reproductive number.

We are interested in what conditions affect honey bee colony viability. Thus we analyze the reproductive number R_d. If $R_d > 1$ then the colony will thrive. However if $R_d < 1$ the colony will surely collapse. All of our parameters influence the basic reproductive number and stability of equilibria. However we are most interested in σ, the social inhibition rate, and r, the gathering rate of food, since both play a key role in survivability. We determine the sensitivity of s_p of the quantity Q to the parameter p using the formula

$$s_p = \frac{\partial Q}{\partial p}$$

This represents the reciprocal of the decrease in p required to reduce Q by one percent. For example, a sensitivity of -10 indicates that p should be increase by $\frac{1}{10}$ to reduce Q by 1. Rather than comparing absolute changes, we convert sensitivities to sensitivity indices or elasticities e_p, which compare percentage changes of parameters and values:

$$e_p = \frac{p}{Q}\frac{\partial Q}{\partial p}$$

In our model all parameters are positive values. We do not use the absolute value of the scaling factor since our quantity of interest is R_d, which is also a positive value. Thus the scaling factor is always positive. The resulting elasticities are displayed in Figure 2, with their computed values provided in the Appendix.

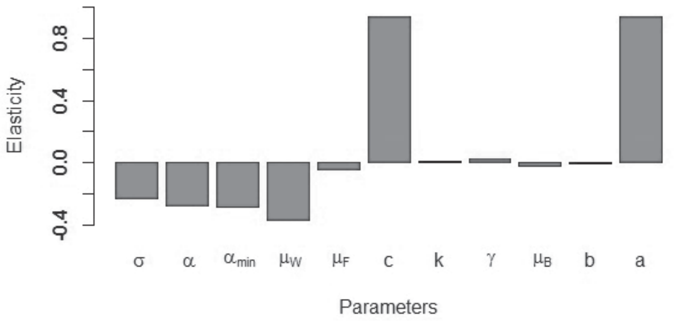

Figure 3: Elasticity of the parameters and their effect on scaled R_d

The parameters with the least amount of influence on R_d include the amount of food when half of the maximum birth rate is reached$b$, the carrying-capacity of the hive k, the eclosion rate γ, the death rate of foragers μ_F, and the death rate of brood μ_B.
Increasing the amount of food when half of the maximum birth rate is reached b can induce colony collapse because foragers need to gather more food to feed the growing brood population, thus the foragers will die out faster.
The brood population increases at an exponential rate significantly higher than the death rate, and as a result the death rate of brood μ_B is rendered insignificant to the vitality of the hive. Nevertheless, increasing the brood mortality can lead to colony collapse.
Increasing the amount of food that bees can store K can increase R_d since the more food the colony can store, the more capable it is of surviving. An interesting relationship to note is that the elasticity of the death of brood is of the opposite sign of the elasticity of eclosion rate γ. Increasing the eclosion rate can lead to colony survival, as the rate of brood becoming worker bees increases with no negative consequences (as the eclosion rate would be natural).
Surprisingly, the death of foragers μ_F has very little influence relative to other parameters, but realistically it could lead to colony collapse since the colony depends on foragers to collect food. This is not the case with our model since the growth rate of food supply is not a function of the amount of foragers.
An increase in social inhibition σ can lead to colony collapse, since social inhibition is caused by the pheromones from foragers signaling for the delay of worker to forager promotion (higher social inhibition rate means the delay of recruitment) . Thus increasing σ can potentially halt the flow from workers to foragers.

The parameter with the second most considerable influence on R_d is the conversion factor, c. An increase in the conversion factor can lead to survival. This is reasonable since the conversion factor is in terms of the amount of food given to the brood, as well the birthrate of the brood. Thus c is necessary to expand the brood class. Note that an increase of c does not imply a food shortage caused by the amount of brood, for the conversion factor considers an increase in nutrition that would maintain the population.
Finally, the elasticity analysis indicates that the encountering rate between workers and food a is consistently the most influential parameter among those we examined. Since the elasticity of a is .93, then an increase of a by 1 percent would lead to an increase in R_d by .93%. We hypothesized that increased contact between worker and food would lead to survival since the workers are responsible for nursing the brood. Based on this result, we conclude that encouraging more contact between workers and food can lead to colony survival, as well as reducing the death rate of workers.

7 Conclusion

Honey bees live in a very complex society, with three different classes, the brood, the workers, and the foragers. Honey bees are very important since 35% of our diet depends on their pollination of various plants [11, 12]. There are many reasons why a honey bee colony will collapse, some reasons include parasites, pesticides, and food stressors.

In this paper, we model the interaction dynamics between honey bees and the food available in a honey bee colony. Depending on parameter values, our model shows that the brood, workers, and foragers all die if there is no food. However if there is food inside the hive, our model shows that the brood, workers, foragers, and food supply can coexists. We then found a threshold value R_d, where if $R_d < 1$ the bees die out and if $R_d > 1$ the bees will live on.

Sensitivity analysis was done on our threshold R_d. Through finding the elasticity of each parameter on R_d, we found that the rate at which a worker bee encounters food, a, has the strongest positive effect on the threshold R_d. While the death rate of the worker bees, μ_W, has the strongest negative effect on our threshold R_d.

Under our parameters, simulations show the extinction of the population if no food is introduced in the system, even with an arbitrary amount of foragers. Extinction under these circumstances occurs because the hive cannot sustain itself; it sends workers to their early deaths, and the foragers die at a faster rate. Eventually the workers and foragers die out, and the brood closely follow their demise. As long as we have food in the system, the population will find a way to thrive, since the initial condition of food is data sensitive. If there is a lack of workers, the foragers will revert to workers at a fast rate. It also follows that if there is a lack of foragers, the influx of workers will be tremendous at first but then slow down.

Previous models have also included the food supply within a honey bee colony. For example in Khourys 2013 paper, *Modelling Food and Population Dynamics in Honey Bee Colonies*, which models the population of a honey bee colony with the supply of food within the hive. Our model is similar to Khourys model in the sense that we have a food supply compartment. Khourys model brings in food into the supply at a constant rate, while our model brings food into the supply as a logistic function. In Khourys model of the food supply, Khoury has the honey bees remove food from the food supply at a constant rate. Our model uses a Holling Type II function to remove food from the food supply.

We have different conditions for the stability of the equilibria, where Khoury does not mention stability or equilibria. The equilibria of (0,0,0,0) is never stable, the equilibria of (0,0,0,1) is stable if $R_d < 1$, and the the stability of the interior equilibria is conditional. Sensitivity analysis was also done on our model, which shows that the encounter rate has a positive effect on our demographic reproduction number R_d. Or sensitivity analysis also showed that the worker death rate had a large effect on R_d, thus worker deaths have an impact on the mode. While Khoury did not do any sensitivity analysis on their model and assumed worker deaths to be negligible.

Khourys simulations includes plots for the population of each honeybee class. Our model also has simulations for each individual honeybee class. The simulations in Khourys paper shows the growth of of honeybees varying the death rate of the foragers. While our simulations show that the honeybee populations can grow and decline periodically without dieing out.

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8 Appendix

8.1 Logistic Growth Holling Type I Model

Our original model became too intractable and difficult to carry out the analysis. To overcome this, we simplified the model by keeping the death rates for each class (μ_B, μ_W, and μ_F)

and growth rate of food supply (r) constant. We examine the relationship between the food supply, workers, and brood born via a Holling Type I functional response. Here a is the encounter rate of the workers with the food supply and c is the conversion of the food to brood.

These assumptions lead to the following system of ordinary differential equations:

$$\begin{aligned}
\frac{dB}{dt} &= cSW - \gamma B - \mu_B B,\\
\frac{dW}{dt} &= \gamma B - \alpha_{min} W - \sigma(\alpha W - F) - \mu_W W,\\
\frac{dF}{dt} &= \alpha_{min} W + \sigma(\alpha W - F) - \mu_F F,\\
\frac{dS}{dt} &= rS\left(1 - \frac{S}{k}\right) - aSW,
\end{aligned}$$

8.1.1 Scaled Model

To simplify the analysis, we re-scaled the model:

Let $x(\tau) = \frac{\gamma a B(t)}{r^2}, y(\tau) = \frac{aW(t)}{r}, z(\tau) = \frac{aF(t)}{\alpha_{min}+\alpha\sigma}, u(\tau) = \frac{S(t)}{k}, \tau = rt,$

We substitute $x(\tau)$, $y(\tau)$, $z(\tau)$, and $u(\tau)$ to receive the following scaled form:

$$\begin{aligned}
\frac{dx}{d\tau} &= Auy - Gx,\\
\frac{dy}{d\tau} &= x - Cy + Dz,\\
\frac{dz}{d\tau} &= y - Ez,\\
\frac{du}{d\tau} &= u(1-u) - uy,
\end{aligned}$$

where the new parameters (consisting of original parameters) are the following:

$A = \frac{ck\gamma}{r^2}, G = \frac{1}{r}(\gamma + \mu_B), C = \frac{1}{r}(\alpha_{min} + \sigma\alpha + \mu_W), D = \frac{\sigma(\alpha_{min}+\alpha\sigma)}{r^2}, E = \frac{1}{r}(\sigma + \mu_F).$

8.1.2 Equilibria and Stability

In order to determine the existence of equilibria we set the system equal to zero and solve for x^*,y^*,z^*, and u^*. We find the existence of three equilibria: $(0,0,0,0)$, $(0,0,0,1)$, and interior equilibrium, where $(0,0,0,0)$ is extinction with no food supply, $(0,0,0,1)$ is extinction with food supply, and the interior equilibrium is coexistence between food and the colony. We find the general Jacobian and evaluate the Jacobian at each equilibria and determine stability by finding the eigenvalues of the resulting matrix.

$$\mathscr{J}(x,y,z,u) = \begin{pmatrix} -G & Au & 0 & Ay \\ 1 & -C & D & 0 \\ 0 & 1 & -E & 0 \\ 0 & -u & 0 & -2u-y+1 \end{pmatrix}$$

We evaluate the Jacobian at the equilibrium point $(0,0,0,0)$ and find the eigenvalues of the resulting matrix:

$$\mathscr{J}(0,0,0,0) = \begin{pmatrix} -G & 0 & 0 & 0 \\ 1 & -C & D & 0 \\ 0 & 1 & -E & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}.$$

With a positive 1 for an eigenvalue, the equilibrium $(0,0,0,0)$ is unstable. This implies that once a bee or food has entered the system, the trajectories never tend to the extinction point with no food. This is biologically valid because it is unnatural for all of the bees and food supply to disappear in a colony collapse.
We evaluate the Jacobian at $(0,0,0,1)$ and find the eigenvalues of the resulting matrix:

$$\mathscr{J}(0,0,0,1) = \begin{pmatrix} -G & A & 0 & 0 \\ 1 & -C & D & 0 \\ 0 & 1 & -E & 0 \\ 0 & -1 & 0 & -1 \end{pmatrix}.$$

We can see that -1 is an eigenvalue. The other three eigenvalues are found by removing the last row and column of $\mathscr{J}(0,0,0,1)$ resulting in matrix M, and using the Routh-Hurwitz Criteria to determine the stability:

$$M = \begin{pmatrix} -G & A & 0 \\ 1 & -C & D \\ 0 & 1 & -E \end{pmatrix}.$$

The Routh-Hurwitz Criteria, requires computing the negative determinant of matrix M, w_1, the negative trace of matrix M, w_2, and the sum of the minors of matrix M, w_3, resulting in the following:

$$\begin{aligned} w_1 &= -det(M) = G(CE-D) - AE, && (13)\\ w_2 &= -trace(M) = G + C + E, && (14)\\ w_3 &= GC - A + GE + CE - D, && (15)\\ & && (16) \end{aligned}$$

The real parts of all eigenvalues of M are negative and the equilibrium is stable if and only if $w_i > 0$, $i = 1,2,3$ and $w_2 w_3 > w_1$. We can show that if $w_1 > 0$, then we have the equilibrium point $(0, 0, 0, 1)$ is stable.

Lemma 2. *If $w_1 > 0$, then the Routh-Hurwitz Criteria is satisfied for the equilibrium (0,0,0,1) under Holling Type I .*

Proof.
Assume $w_1 > 0$ then from (13)

$$\begin{aligned} CE - D &> 0\\ GCE - AE &> 0 \end{aligned}$$

By 13, it follows that $w_3 > 0$. Since $G, C, E > 0$, it follows that $w_2 > 0$. To meet the second condition of the Routh-Hurwitz Criteria, we multiply w_2 and w_3 to get the following product: We now show $w_3 w_2 > w_1$:

$$\begin{aligned} w_3 w_2 &= (GC - A + GE + CE - D)(G + C + E)\\ &= G(CE - D) - EA + G(GC - A + GE) + E(GC + GE + CE - D) + C(GC - A + GE + CE - D) \end{aligned}$$

By (14) and (15) we get, $w_2 w_3 = w_1 + G(GC - A + GE) + E(GC + GE + CE - D) + C(GC - A + GE + CE - D)$. Thus $w_2 w_3 > w_1$. Therefore by assuming $w_1 > 0$, we have shown the equilibrium point (0,0,0,1) is stable. This completes the proof. □

8.1.3 Calculation of the Demographic Reproductive Number

Here we provide a condition for collapse of the honeybee colony by demographic factors. Recall that $w_1 = -\det(M) = G(CE - D) - AE$. Assume that $w_1 > 0$, we have, $G(CE - D) - AE > 0$. Rearranging terms and simplifying we have $\frac{GD+AE}{GCE} < 1$.

We define our demographic reproduction number, $R_d = \frac{GD+AE}{GCE}$. If $w_1 > 0$ this implies $R_d < 1$, and under this condition the honeybee colony will collapse. Substituting the original parameter values from the parameters A,C,D,E,G into R_d and simplifying, we have:

$$R_d = \frac{\sigma(\alpha\sigma + \alpha_{min})}{(\alpha\sigma + \alpha_{min} + \mu_W)(\sigma + \mu_F)} + \frac{ck\gamma}{(\gamma + \mu_B)(\alpha\sigma + \alpha_{min} + \mu_W)} \qquad (17)$$

Theorem 2. *If $R_d < 1$, then the equilibrium $(0, 0, 0, 1)$ is locally asymptotically stable.*

Proof. Suppose $R_d < 1$. Then $\frac{GD+AE}{GCE} < 1$. Multiply by GCE and rearrange, then $G(CE - D) - AE > 0$. By Lemma 2, since $w_1 > 0$, then $(0, 0, 0, 1)$ is stable. □

To highlight the role of social inhibition (σ) on R_d, we rewrite (17):

$$R_d = \sigma\Big(\frac{1}{\sigma + \mu_F}\frac{\alpha\sigma + \alpha_{min}}{\alpha\sigma + \alpha_{min} + \mu_W} - ck\frac{\gamma}{\gamma + \mu_B}\frac{\alpha}{\alpha\sigma + \alpha_{min} + \mu_W}\frac{1}{\alpha_{min} + \mu_W}\Big) + ck\frac{\gamma}{\gamma + \mu_B}\frac{1}{\alpha_{min} + \mu_W}$$

8.1.4 Interpretation of R_d

In our R_d the ck represents the number of brood produced by a worker per unit time, while $\frac{\gamma}{\gamma+\mu_B}$ is the proportion of brood that eclose into workers, the term $\frac{1}{\alpha\sigma+\alpha_{min}\mu_W}$ is the average time spent in the worker class, the term $\frac{1}{\alpha_{min}+\mu_W}$ is the time spent as a worker when the colony is at homeostasis, and $\frac{\alpha\sigma+\alpha_{min}}{\alpha\sigma+\alpha_{min}+\mu_F}$ is the proportion of workers recruited into foragers. Finally the term $\frac{\sigma}{\sigma+\mu_F}$ is the proportion of foragers that transition back into workers.

To better understand the meaning of R_d we consider the simple case $\sigma = 0$ (without social inhibition), which we denote as r_d. Therefore the value for r_d is the following:

$$r_d = \left(\frac{\gamma}{\gamma+\mu_B}\right)(kc)\left(\frac{1}{\alpha_{min}+\mu_W}\right).$$

The first term in r_d is $\frac{\gamma}{\gamma+\mu_B}$, which is the proportion of brood eclosing to workers. Next the following term, kc, represent the birth rate of the brood per unit time. Finally the last term, $\frac{1}{\alpha_{min}+\mu_W}$, is the average lifetime of a worker during homeostasis. This demographic reproduction number represents the average number of worker bees produced per worker bee during the average lifespan of a worker bee.

8.1.5 Interior Equilibrium

Using the rescaled form of the model:

$$\begin{aligned} x' &= Auy - Gx, && (18)\\ y' &= x - Cy + Dz, && (19)\\ z' &= y - Ez, && (20)\\ u' &= u(1-u) - uy, && (21) \end{aligned}$$

we set the system equal to zero. Solving for y^* using Equation (21), $y^* = 1 - u^*$. Solving for z^* using Equation (20) , $z^* = \frac{1}{E}y^*$. Solving for x^* using Equation (19), $x^* = (C - \frac{D}{E})y^*$. Solving for u^* using Equation (18), $u^* = \frac{G}{AE}(EC - D)$.

This results in the following interior equilibrium: $\left((C - \frac{D}{E})y^*, 1 - u^*, \frac{1}{E}y^*, u^*\right)$, if $EC - D > 0$ and $GEC - GD - AE < 0$.

8.1.6 Sensitivity Analysis of R_d in Holling Type I

Using Mathematica, we computed the values for sensitivity indices. To ease the analysis, we change variables. Let $A = ack\gamma, B = \mu_f + \sigma, C = \alpha_{min} + \alpha\sigma, D = \gamma + \mu_B, E = C + \mu_W, G = \alpha_{min} + \mu_W, H = \mu_W\sigma, I = \alpha\sigma, J = \mu_F\sigma$.

Then we have the following index values:

$$\begin{aligned}
\frac{\partial R_d}{\partial \sigma}\frac{\sigma}{R_d} &= \tfrac{\mu_F}{B} + \tfrac{G}{E} - \tfrac{\alpha_{min}\sigma D + A(2\mu_F+\sigma)}{AB+D\sigma C} \\
\frac{\partial R_d}{\partial \alpha}\frac{\alpha}{R_d} &= \tfrac{I(HD-AB)}{E(AB+D\sigma c)} \\
\frac{\partial R_d}{\partial \mu_W}\frac{\mu_W}{R_d} &= -\tfrac{\mu_W}{E} \\
\frac{\partial R_d}{\partial \alpha_{min}}\frac{\alpha_{min}}{R_d} &= \tfrac{\alpha_{min}(HD-AB)}{E(AB+D\sigma c)} \\
\frac{\partial R_d}{\partial \mu_F}\frac{\mu_F}{R_d} &= \tfrac{JDC}{B(AB+D\sigma C)} \\
\frac{\partial R_d}{\partial c}\frac{c}{R_d} &= \tfrac{AB}{AB+D\sigma C} \\
\frac{\partial R_d}{\partial k}\frac{k}{R_d} &= \tfrac{\partial R_d}{\partial c}\tfrac{c}{R_d} \\
\frac{\partial R_d}{\partial \gamma}\frac{\gamma}{R_d} &= \tfrac{\mu_B AB}{D(AB+D\sigma C)} \\
\frac{\partial R_d}{\partial \mu_B}\frac{\mu_B}{R_d} &= -\tfrac{\partial R_d}{\partial \gamma}\tfrac{\gamma}{R_d} \\
\frac{\partial R_d}{\partial a}\frac{a}{R_d} &= \tfrac{\partial R_d}{\partial c}\tfrac{c}{R_d}
\end{aligned}$$

where $\left|\frac{\partial R_d}{\partial \mu_B}\frac{\mu_B}{R_d}\right| = \frac{\partial R_d}{\partial \gamma}\frac{\gamma}{R_d} < \frac{\partial R_d}{\partial k}\frac{k}{R_d} = \frac{\partial R_d}{\partial c}\frac{c}{R_d} = frac\partial R_d \partial a\frac{a}{R_d}$ and $\frac{\partial R_d}{\partial \alpha}\frac{\alpha}{R_d} < \frac{\partial R_d}{\partial \alpha_{min}}\frac{\alpha_{min}}{R_d}$ if $\alpha\sigma < \alpha_{min}$

We now use our parameters and substitute them back into the indices to obtain the following values:

Table 3: Elasticity of Parameters on R_d

Elasticity Indices	Numerical Value
$\frac{\partial R_d}{\partial \sigma}\frac{\sigma}{R_d}$	-0.3105
$\frac{\partial R_d}{\partial \alpha}\frac{\alpha}{R_d}$	-0.3105
$\frac{\partial R_d}{\partial \mu_W}\frac{\mu_W}{R_d}$	-0.3712
$\frac{\partial R_d}{\partial \alpha_{min}}\frac{\alpha_{min}}{R_d}$	-0.3182
$\frac{\partial R_d}{\partial \mu_F}\frac{\mu_F}{R_d}$	$-.0000009$
$\frac{\partial R_d}{\partial c}\frac{c}{R_d}$	1.000
$\frac{\partial R_d}{\partial k}\frac{k}{R_d}$	1.000
$\frac{\partial R_d}{\partial \gamma}\frac{\gamma}{R_d}$	0.0226
$\frac{\partial R_d}{\partial \mu_B}\frac{\mu_B}{R_d}$	-0.0226
$\frac{\partial R_d}{\partial a}\frac{a}{R_d}$	1.0000

8.2 Detailed Computations of the Logistic Growth Holling Type II Model

$$\begin{aligned}
\frac{dB}{dt} &= \frac{cSW}{b+S} - \gamma B - \mu_B B, \\
\frac{dW}{dt} &= \gamma B - \alpha_{min} W + \sigma(F - \alpha W) - \mu_W W, \\
\frac{dF}{dt} &= \alpha_{min} W - \sigma(F - \alpha W) - \mu_F F, \\
\frac{dS}{dt} &= rS\left(1 - \frac{S}{k}\right) - \frac{aSW}{b+S}.
\end{aligned}$$

8.2.1 Rescaled Form

To simplify the analysis, we rescale the model:

Let $x = \frac{B}{\phi_1}, y = \frac{W}{\phi_2}, z = \frac{F}{\phi_3}, u = \frac{S}{\phi_4}, \tau = \frac{t}{T}$

We then get the rescaledl form of our model to be the following:

$$\begin{aligned}
\frac{dx}{d\tau} &= \frac{Tcu\phi_4 y\phi_2}{\phi_1(b+u\phi_4)} - T\gamma x - \mu_B xT, \\
\frac{dy}{d\tau} &= \gamma T\frac{\phi_1}{\phi_2}x - T\alpha_{min}y + \sigma T\left(\frac{\phi_3}{\phi_2}z - \alpha y\right) - \mu_W Ty, \\
\frac{dz}{d\tau} &= T\alpha_{min}\frac{\phi_2}{\phi_3}y - T\sigma z + T\alpha\frac{\phi_2}{\phi_3}y\sigma - T\mu_F z, \\
\frac{du}{d\tau} &= Tru\left(1 - \frac{u\phi_4}{k}\right) - \frac{Ta\phi_2 uy}{b+u\phi_4}.
\end{aligned}$$

If we let $T = \frac{1}{r}, \phi_1 = \frac{r^2}{\gamma a}, \phi_2 = \frac{r}{a}, \phi_3 = \frac{1}{a}$, and $\phi_4 = k$, we then get the rescaled equations to simplify to:

$$\begin{aligned}
\frac{dx}{d\tau} &= \frac{Huy}{J+u} - Vx, \\
\frac{dy}{d\tau} &= x - Ey + Gz, \\
\frac{dz}{d\tau} &= Ay - Dz, \\
\frac{du}{d\tau} &= u(1-u) - \frac{uy}{k(J+u)},
\end{aligned}$$

where the new parameters (consisting of original parameters) are the following:

$H = \frac{\gamma c}{r^2}, V = \frac{1}{r}(\gamma + \mu_B), J = \frac{b}{k}, E = \frac{1}{r}\left(\alpha_{min} + \sigma\alpha + \mu_W\right), G = \frac{\sigma}{r^2}, D = \frac{1}{r}(\sigma + \mu_F)$,
$A = \alpha_{min} + \alpha\sigma$.

8.2.2 Equilibria and Stability

We first compute the equilibria, which turns out to be $(0,0,0,0), (0,0,0,1)$ and an interior equilibrium. We compute the general Jacobian, and found it to be:

$$\mathscr{J}(x,y,z,u) = \begin{pmatrix} -V & \frac{Hu}{J+u} & 0 & \frac{HyJ}{(J+u)^2} \\ 1 & -E & G & 0 \\ 0 & A & -D & 0 \\ 0 & \frac{-u}{ku+b} & 0 & 1 - 2u - \frac{by}{(b+ku)^2} \end{pmatrix}$$

We then compute the Jacobian of $(0,0,0,0)$:

$$\mathscr{J}(0,0,0,0) = \begin{pmatrix} -V & 0 & 0 & 0 \\ 1 & -E & G & 0 \\ 0 & A & -D & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}$$

and we found the equilibrium point $(0,0,0,0)$ to be unstable because one eigenvalue is positive. We then look at Jacobian matrix evaluated at the equilibrium point $(0,0,0,1)$:

$$\mathscr{J}(0,0,0,1) = \begin{pmatrix} -V & \frac{H}{J+1} & 0 & 0 \\ 1 & -E & G & 0 \\ 0 & A & -D & 0 \\ 0 & \frac{-1}{b+k} & 0 & -1 \end{pmatrix}$$

We remove the last row and column because the last eigenvalue is negative. Then we can analyze the resulting matrix for stability:

$$M = \begin{pmatrix} -V & \frac{H}{J+1} & 0 \\ 1 & -E & G \\ 0 & A & -D \end{pmatrix}$$

We look towards the Routh-Hurwitz Criteria, where

$$\begin{aligned} w_1 &= -det(M) = V(ED - AG) - \frac{HD}{J+1}, \\ w_2 &= -trace(M) = D + E + V, \\ w_3 &= \left(VE - \frac{H}{J+1}\right) + ED - AG + VD, \end{aligned}$$

with w_1 is the negative determinant of M, w_2 is the negative trace of M, and w_3 is the minors of the matrix M. If $w_1, w_2, w_3 > 0$ and $w_2 w_3 > w_1$, then the system is stable. We now show that the equilibrium $(0,0,0,0)$ is asymptotically stable if $w_1 > 0$.

Proof.
Assume $w_1 > 0$, then

$$\begin{aligned} ED &> AG && (22)\\ VED &> \frac{DH}{J+1} && (23)\\ VE &> \frac{H}{J+1} && (24) \end{aligned}$$

By (22) and (24), it follows that $w_3 > 0$. Thus if $w_1 > 0$ then $w_3 > 0$.
$w_2 > 0$ since $D, E, V > 0$.
We multiply w_2 with w_3 to get the following product:

$$\begin{aligned} w_2 w_3 &= (V+E+D)\left(VE - \frac{H}{J+1} + ED - AG\right) + VD \\ &= V(ED - AG) + V\left(VE - \frac{H}{J+1}\right) + Ew_3 - \frac{DH}{J+1} + D(VE + ED - AG) \end{aligned}$$

By (22) and (24) we get, $w_2 w_3 = V(ED - AG) - \frac{HD}{J+1} +$ positive terms, which is just $w_1 +$ positive terms $> w_1$. Thus $w_2 w_3 > w_1$.
If we assume (22) and (23) then $w_1, w_2, w_3 > 0$ and $w_2 w_3 > w_1$ the equilibrium point (0,0,0,1) is stable. □

8.2.3 Calculation of Demographic Reproductive Number R_d for equilibrium (0,0,0,1)

Now we examine w_1. Recall that $w_1 = -det(M) = V(ED - AG) - \frac{HD}{J+1}$, let's assume that $w_1 > 0$, then we get,

$V(ED - AG) - \frac{HD}{J+1} > 0$ is equivalent to $1 > \frac{H}{(J+1)(VE)} + \frac{AG}{ED}$.

We define $R_d = \frac{H}{(J+1)(VE)} + \frac{AG}{ED}$. Now we have the following: If $w_1 > 0 \Rightarrow R_d < 1$, then honey bee colony collapses.

Substituting the values of C, E, D, A back into R_d and simplifying the equation, we have:

$$\begin{aligned} R_d &= \frac{(\gamma + \mu_B)(\alpha\sigma + \alpha_{min})\sigma}{(\gamma + \mu_B)(\alpha\sigma + \alpha_{min} + \mu_W)(\sigma + \mu_F)} + \frac{\gamma c k(\sigma + \mu_F)}{(\gamma + \mu_B)(\alpha\sigma + \alpha_{min} + \mu_W)(\sigma + \mu_F)(b + k)} \\ &= \frac{\alpha\sigma + \alpha_{min}}{\alpha\sigma + \alpha_{min} + \mu_W}\frac{\sigma}{\sigma + \mu_F} - \frac{\gamma}{\gamma + \mu_B}\frac{kc}{b+k}\frac{\alpha\sigma}{\alpha\sigma + \alpha_{min} + \mu_W} + \frac{\gamma}{\gamma + \mu_B}\frac{kc}{b+k}\frac{1}{\alpha_{min} + \mu_W} \end{aligned}$$

We have successfully separated away all the σ terms. That way, we can determine whether σ plays a role in R_d becoming greater or less than 1. R_d is the demographic reproductive number for foragers.

8.2.4 Interpretation of R_D

Now we interpret R_d, where the $\frac{\alpha\sigma+\alpha_{min}}{\alpha\sigma+\mu_W}$ term is the proportion of workers promoted to foragers, the $\frac{\sigma}{\sigma+\mu_F}$ term is the proportion of foragers becoming workers. Then the $\frac{\gamma}{\gamma+\mu_B}$ term is the proportion of brood that become workers, then the $\frac{kc}{b+k}$ term is the proportion of food converting to brood, then the $\frac{\alpha\sigma}{\alpha\sigma+\alpha_{min}+\mu_W}$ term is the proportion of premature workers becoming foragers, and finally the term $\frac{1}{\alpha_{min}+\mu_W}$ is the time spent as a worker during homeostasis.

Consider $R_D(\sigma)$. For the case when $\sigma = 0$, then we have the value for $R_d(0)$: $R_d(0) = \frac{\gamma}{\gamma+\mu_B}\frac{kc}{b+k}\frac{1}{\alpha_{min}+\mu_W}$, where $\frac{kc}{b+k}$ is the proportion of food capacity, while $\frac{\gamma}{\gamma+\mu_B}$ is the proportion of brood eclosing into workers, and $\frac{1}{\alpha_{min}+\mu_W}$ is the average time spent in the worker class during homeostasis.

8.2.5 Interior Equilibrium

$$\frac{dx}{d\tau} = \frac{Huy}{J+u} - Vx, \tag{25}$$
$$\frac{dy}{d\tau} = x - Ey + Gz, \tag{26}$$
$$\frac{dz}{d\tau} = Ay - Dz, \tag{27}$$
$$\frac{dz}{d\tau} = u(1-u) - \frac{uy}{b+ku}. \tag{28}$$

To solve for equilibria , we set the system equal to 0.
Solving for y using equation (28), $u(1-u) - \frac{uy}{b+ku} = 0$ and $(1-u)(b+ku) - y = 0$. Solving for y in the previous expression, $y = (1-u)(b+ku)$. Solving for z using equation (27), $Ay - Dz = 0$. We can simplify the expression to be $z = \frac{A}{D}y$.Solving for x using equation (26), $x - Ey + Gz = 0$, which we can simplfy to $x = (E - \frac{GA}{D})y$. Solving for u using equation (25), $\frac{Huy}{J+u} - Vx = 0$. Since $y = (1-u)(b+ku)$, if $y = 0$ then either $u = 1$ or $b + ku = 0$ (which is not biologically relevant since we cannot have a negative value for u). Suppose $y \neq 0$, then $\frac{Hu}{J+u} - V(E - \frac{GA}{D}) = 0$. Solving for u, $u^* = \frac{VJ(E-\frac{GA}{D})}{H-V(E-\frac{GA}{D})}$
Suppose $u^* = 0$. Then $x^* = 0$ and $Ay^* - Dz^* = 0 \Rightarrow y^* = z^* = 0$. Suppose $u^* = 1$. Then $y^* = 0 \Rightarrow x^* = z^* = 0$. Suppose $u^* = \frac{VJ(E-\frac{GA}{D})}{H-V(E-\frac{GA}{D})}$, $0 < u^* < 1$ and $y^* = (1-u^*)(b+ku^*)$, $z^* = \frac{A}{D}y^*$, and $x^* = (E - \frac{GA}{D})y^*$

Conditions on positive equilibrium interior are $H - V(E - \frac{GA}{D}) > 0$ and $\frac{VJ(E-\frac{GA}{D})}{H-V(E-\frac{GA}{D})} < 1$.

Recall that

$$\begin{aligned} R_d &= \frac{HD}{V(J+1)(DE-GA)} \\ u^* &= \frac{JV(E-\frac{GA}{D})}{H-V(E-\frac{GA}{D})} \\ &= \frac{J}{(J+1)R_d-1} \end{aligned}$$

Suppose $R_d > 1$:
$u^* = \frac{J}{(J+1)R_d-1}$,
$= \frac{J}{JR_d+R_d-1} < \frac{J}{JR_d} = \frac{1}{R_d} < 1$,
$y^* = (1-u^*)(b+ku^*)$,
$x^* = (E-\frac{GA}{D})y^* = \frac{1}{D}(ED-GA)y^*$,
$z^* = \frac{A}{D}y^*$.

8.2.6 Sensitivity Analysis of R_d in Holling Type II

Using Mathematica, we computed the values for sensitivity indices. To ease the analysis, we change variables. Let $A = ack\gamma, B = \mu_f + \sigma, C = \alpha_{min} + \alpha\sigma, D = \gamma + \mu_B, E = C + \mu_W, F = b + k, G = \alpha_{min} + \mu_W, H = \mu_W\sigma, I = \alpha\sigma, J = \mu_F\sigma$.

Then we have the following index values:

$$\begin{aligned}
\frac{\partial R_d}{\partial \sigma}\frac{\sigma}{R_d} &= \frac{\sigma(-\frac{A\alpha}{FD}+\alpha_{min}\mu_F G+2\alpha\mu_F G\sigma+I^2\mu_F+IH)}{E(\frac{A}{FD}+\frac{\sigma C}{B})}\\
\frac{\partial R_d}{\partial \alpha}\frac{\alpha}{R_d} &= \frac{I(FDH-AB)}{E(AB+FD\sigma C)}\\
\frac{\partial R_d}{\partial \mu_W}\frac{\mu_W}{R_d} &= -\frac{\mu_W}{E}\\
\frac{\partial R_d}{\partial \alpha_{min}}\frac{\alpha_{min}}{R_d} &= \frac{\alpha_{min}(FDH-AB)}{E(AB+FD\sigma C)}\\
\frac{\partial R_d}{\partial \mu_F}\frac{\mu_F}{R_d} &= \frac{FDJC}{B(AB+FD\sigma C)}\\
\frac{\partial R_d}{\partial c}\frac{c}{R_d} &= \frac{AB}{AB+FD\sigma C}\\
\frac{\partial R_d}{\partial k}\frac{k}{R_d} &= \frac{bAB}{F(AB+FD\sigma C)}\\
\frac{\partial R_d}{\partial \gamma}\frac{\gamma}{R_d} &= \frac{\mu_B AB}{D(AB+FD\sigma C)}\\
\frac{\partial R_d}{\partial \mu_B}\frac{\mu_B}{R_d} &= -\frac{\partial R_d}{\partial \gamma}\frac{\gamma}{R_d}\\
\frac{\partial R_d}{\partial b}\frac{b}{R_d} &= \frac{\partial R_d}{\partial k}\frac{k}{R_d}\\
\frac{\partial R_d}{\partial a}\frac{a}{R_d} &= \frac{\partial R_d}{\partial c}\frac{c}{R_d}
\end{aligned}$$

where $\left|\frac{\partial R_d}{\partial \mu_B}\frac{\mu_B}{R_d}\right| = \frac{\partial R_d}{\partial \gamma}\frac{\gamma}{R_d} < \frac{\partial R_d}{\partial k}\frac{k}{R_d} = \frac{\partial R_d}{\partial b}\frac{b}{R_d} < \frac{\partial R_d}{\partial c}\frac{c}{R_d}$

and $\frac{\partial R_d}{\partial \alpha}\frac{\alpha}{R_d} < \frac{\partial R_d}{\partial \alpha_{min}}\frac{\alpha_{min}}{R_d}$ if $\alpha\sigma < \alpha_{min}$

We now use our parameters and substitute them back into the indices to obtain the following values:

$$
\begin{aligned}
\frac{\partial R_d}{\partial \sigma}\frac{\sigma}{R_d} &= \quad -.2333 \\
\frac{\partial R_d}{\partial \alpha}\frac{\alpha}{R_d} &= \quad -.0.2792 \\
\frac{\partial R_d}{\partial \mu_W}\frac{\mu_W}{R_d} &= \quad -0.3712 \\
\frac{\partial R_d}{\partial \alpha_{min}}\frac{\alpha_{min}}{R_d} &= \quad -0.2860 \\
\frac{\partial R_d}{\partial \mu_F}\frac{\mu_F}{R_d} &= \quad -0.0458 \\
\frac{\partial R_d}{\partial c}\frac{c}{R_d} &= \quad 0.9364 \\
\frac{\partial R_d}{\partial k}\frac{k}{R_d} &= \quad 0.0094 \\
\frac{\partial R_d}{\partial \gamma}\frac{\gamma}{R_d} &= \quad 0.0211 \\
\frac{\partial R_d}{\partial \mu_B}\frac{\mu_B}{R_d} &= \quad -0.0211 \\
\frac{\partial R_d}{\partial b}\frac{b}{R_d} &= \quad -0.0094 \\
\frac{\partial R_d}{\partial a}\frac{a}{R_d} &= \quad 0.9364
\end{aligned}
$$

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