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Honey Bee and Varroa Destructor Population Dynamics

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HONEY BEE AND *VARROA DESTRUCTOR* POPULATION
DYNAMICS

by

Karissa Palmer

A thesis submitted in partial fulfillment
of the requirements for the
University Honors Program

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Abstract

Honey Bee and *Varroa destructor* Population Dynamics

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Director: Dan Van Peurseem, Ph.D.

Over a decade ago, Colony Collapse Disorder (CCD) began to plague honey bee colonies in the United States. An identified contributor has been the *Varroa destructor* parasitic mite that infests honeybee cells in the early stages of development. Bees with this mite as a parasite are weakened and their lifespan decreases. A system of differential equations with a control on the mites was created to model the populations of the hive bee, forager bee, and mites. The different equilibrium points that result from the varying levels of the mites' death rate is investigated. A bifurcation point at approximately 0.0165 was found. With a mite death rate less 0.0165, the hive and foragers bees, and mites coexist in a hive over the course of a year with an initial low mite population. These values are based on other set parameters: the daily laying rate of eggs by the queen, brood mortality, the transition rate from hive bee to forager bee, social inhibition, the death rate of foragers, the death rate of hive and forager bees due to mites, growth rate of the mite population, and the carrying capacity of the hive, all parameters which are found in literature.

KEYWORDS: Honey bees, differential equations, population modeling.

1 Introduction

In recent years, a new phenomena called Colony Collapse Disorder (CCD) has begun to surface in honey bee colonies. The disorder is characterized by the disappearance of a colony's worker bees, leaving behind the queen and hive bees and sufficient food stores, signaling rapid depopulation. Honey bees are critical to food production because of the pollination they perform, and consequently integral to the economy and health of the world. Researchers have been unable to pinpoint a specific cause, instead attributing CCD to a variety of causes, such as new or emerging diseases, inadequate forage, and pesticides. One of the identified causes is the *Varroa destructor* mite. Since the impact of the mites has been classified as a contributor to CCD, it is therefore important to include the mite's impact when modeling hive populations.

Bee Biology

The *Varroa destructor* mite has played a significant role in the collapse of honey bee colonies. To understand the impact of the mite, background on the biology of the three different castes of bees will be useful. There are three basic castes of honey bees: queen, drone, and worker. Prior to birth, a queen bee is fed royal jelly, which separates her from the rest of the bees. Each hive only has one queen bee. The drone bees are all male and their main purpose is to mate with the queen bee. After they mate with the queen bee, those particular drone bees die. The rest of the drone bees are removed from the hive to die in the fall. Worker bees are split between the hive and the forager bees. The hive bees are the younger worker bees and work to maintain the hive by cleaning cells and caring for the brood. When the hive bees are approximately eight days old, their responsibilities change as they begin to receive nectar, handle pollen, build comb, and clean the hive. As the hive bees get closer to a foraging age, they begin to work outside the hive by ventilating, patrolling, guard duty, and going on orientation flights so they are familiar with their surroundings once they begin foraging [11]. The hive bees overall have a low mortality rate, with the majority of hive bees living to forager age [5].

At about 18 days of age, the hive bees turn to foraging [10]. Their responsibilities consist of foraging for nectar, pollen, water, and propolis, a sealant for the hive. However, this behavioral development process is dependent on social feedback. If there is a decline in the number of forager bees, the hive bees will accelerate their behavioral development and begin foraging at an earlier age to compensate for the lower forager numbers [5]. Hive bees switching to foraging earlier, known as precocious foraging, is associated with overall shorter lifespans because they are weaker and less effective [5]. Foragers have lifespans of less than seven days, approximately four to five, as foraging is more dangerous, and precocious foraging results in even shorter lifespans [5]. Colonies maintain a forager population of approximately 25 percent and will compensate to preserve that ratio [10]. The reverse change can occur as well, with foragers reverting to hive bees if there is a deficit in the number of hive bees. This reverse process is known as ‘social inhibition’ and is accomplished through the process of old forager bees delivering ethyl oleate to young hive bees by way of trophallaxis, or mouth-to-mouth feeding [5].

The lifespan of the honey bee changes depending on the season, and is also dependent on the caste into which a bee falls. In the summer season, honey bees have the shortest lifespan, with the longest lifespans occurring during the winter months. Lifespans in the fall and spring are in between the length of the summer and winter lifespans. During the winter, on average, a worker bee will live around 140 days. In the spring and fall, this average drops to 30 to 60, and in the summer decreases to 15 to 38. However, the queen bee’s lifespan is typically between 1 and 3 years [11]. The differences in a worker bee’s lifespans, depending on the season, can be attributed to their activity level in each season [11]. In the winter, worker bees are less active and have slower metabolic rates, in comparison to the summer. Other outside factors, such as the aforementioned precocious foraging or social inhibition, viruses and brood diseases, and food availability all affect the lifespan of the honey bee too.

***Varroa destructor* Mite**

The *Varroa destructor* mite's natural host is the *Apis cerana*, the Asiatic honey bee. Its host began to shift in the late 1950's and 1960's to the *Apis mellifera*, the Western honey bee. Since then the *Varroa destructor* population has grown quickly. The *Varroa destructor* female utilizes a sealed honey bee brood cell to reproduce [8]. To complete this, the female enters the brood cell prior to capping. Once the cell is capped, the *Varroa destructor* feeds on the developing bee and begins to lay eggs. First, one male egg is laid along with several female eggs in 30-hour intervals [8]. During this time, the mother mite prepares a place on the host bee for her offspring to feed, mature, and mate within the cell. The male mites take approximately 5 to 6 days to develop, and the females about 7 to 8 [1]. The immature female mites die off as the host bee leaves the cell because they are unable to survive outside the sealed cell. Similarly, the male mites die inside the cell, after mating occurs [1]. Once the host bee is ready to leave the cell, the adult female mite becomes attached to the bee [8]. Mature female mites become attached to the bee during a process known as the phoretic phase where the mite pierces the inter segmental membrane of the bees to feed on the bee's haemolymph [8]. After two weeks, the mites will lay eggs in other brood cells, beginning the cycle again [1].

In development, the *Varroa destructor* displays a preference for drone brood cells to worker brood cells. The drone brood cells are capped for longer than worker brood cells, so there is a greater period of time for the female mite to reproduce within the cell [1]. For a female mite that entered a drone brood cell it will, on average, produce 2.6 adult female mites, versus 1.6 for eggs laid on worker bee brood [1]. It follows that the average reproductive rate within the drone brood is greater than the reproductive rate in the worker brood. However, in the absence of any brood, the mite population begins to decline. Estimates give that *Varroa destructor* populations will decline by approximately 10% every month that brood is absent [1].

Typically, the *Varroa destructor* has a lifespan of 2 to 3 months during the summer months, and are able to complete 3 to 4 reproductive cycles [1]. Since they are parasitic

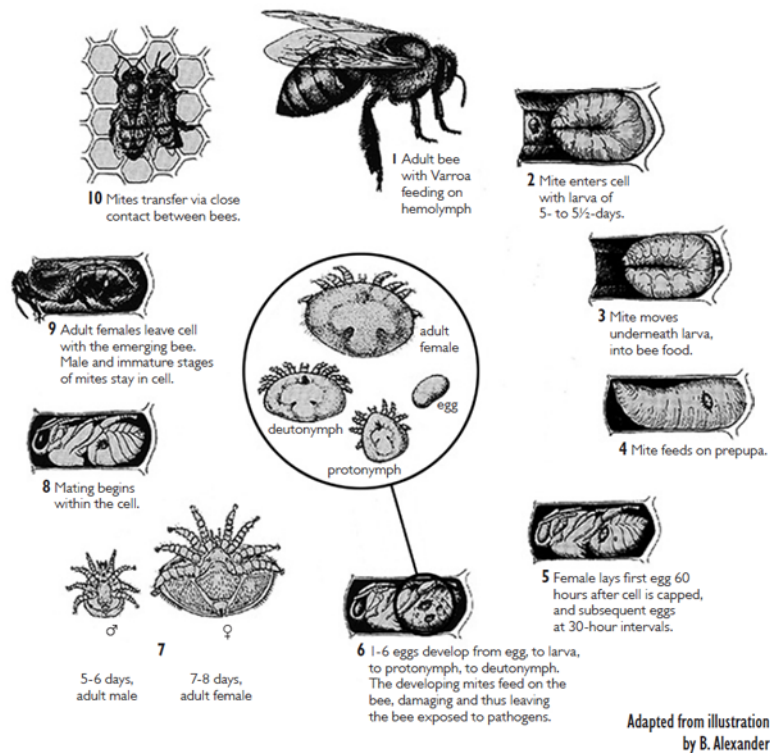


Figure 1: Life Cycle of the *Varroa destructor* Mite [1]

animals, the lifespan and ability to reproduce is dependent on the presence of female mites in the colony. It is estimated, that on average, the mite population is able to increase 12-fold in colonies that have brood available for half the year, and 800-fold in colonies that have brood year-round. The population growth of the mite is also dependent on the number that initially invade the colony. Exponential growth does occur in either scenario of a low number of initial mites versus high but will be aided if the initial number of mites is higher.

Individually, the *Varroa destructor* affects the honey bee through physical debilitation. Honey bees that have been infested with the mite will generally survive into adulthood but may show signs of physical or physiological weakness as an adult [1]. As stated earlier, the *Varroa destructor* feeding on the bee results in the loss of haemolymph during the brood development, which decreases the bee's hatching weight. This loss of weight can lead to lower flight performance. Furthermore, the bee's ability to feed developing brood is affected because the loss of haemolymph reduced hypopharyngeal glands, which secrete the royal jelly. The worker bees infested with *Varroa destructor* also have a

reduced lifespan. These worker bees have a lower rate of return to the colony, a decreased capability of non-associated learning, and prolonged absences from the colony [1]. Mites also affect the honey bees indirectly, through the transfer of viruses [8]. Through the parasitic nature of the mite, it acts as a vector for viral diseases, such as the Acute Bee Paralysis Virus (ABPV), or nosema. Thus, the bees that are infested with the *Varroa destructor* also commonly have physical deformities [8]. Severe *Varroa destructor* infestation can result in the entire colony collapsing. Although mite infestation symptoms may take 2 to 3 years to appear throughout the entire colony, the effects are detrimental [1].

There are a number of ways that both bees and beekeepers work toward reducing the mite populations in hives. One way that mites are naturally regulated in a hive is through the grooming behavior of bees. Honey bee workers groom themselves and other bees [9]. When *Varroa jacobsoni*, a species of the *Varroa* genus, were introduced into a hive with *Apis cerana*, the Asian honey bee, 98% of the mites were removed from the bees' bodies through grooming within a matter of minutes [7]. Furthermore, it is thought that environmental factors, such as temperature, have an indirect effect on the mite via the host [9]. Another way that mite populations are regulated by bees is through the removal of dead, diseased, or parasitized brood cells. Removal of these cells interrupts the reproductive cycle of the mites, which can result in the death of the mites. Additionally, controlling the mite reproduction is considered to be one of the most effective ways to limit the reproductive success of the mites in a hive [9]. This can be done through numerous ways, including: low attractivity of the brood based on race of the honey bees; the availability of bee brood, especially drone brood; the duration of the post-capping stage, and the cell size of some honey bee subspecies [9]. The most common long-term solution for beekeepers themselves to control the mite population is the selective breeding of *Varroa* tolerant bees. Researchers have conducted a variety of studies that are aimed at determining which honey bee populations are resistant (i.e. are more prone to the hygienic practices that control the mite population of a hive) to

the *Varroa* mites.

2 The Khoury, Myerscough, and Barron Model

Khoury, Myerscough, and Barron utilized a system of two differential equations, (2.1) and (2.2), to demonstrate interaction between hive and forager bee populations in a hive. They used this system to obtain analytical steady state results. Their model is represented by

$$\frac{dH}{dt} = L \left(\frac{H + F}{\omega + H + F} \right) - H \left(\alpha - \sigma \left(\frac{F}{H + F} \right) \right) \quad (2.1)$$

$$\frac{dF}{dt} = H \left(\alpha - \sigma \left(\frac{F}{H + F} \right) \right) - mF \quad (2.2)$$

In this model, H and F represent the number of hive and forager bees, respectively. The independent variable, t , measures the time in days. The parameter L corresponds to the maximum egg laying rate of the queen, ω is a reflection of brood mortality, α is the maximum rate that hive bees will become foragers, σ represents social inhibition, and m is the per capita death rate of foragers.

In (2.1) the first term represents hive bees emerging from brood whereas the second term subtracts the population of hive bees that are transitioning to foraging. Thus, the total change in population of hive bees are represented by the first equation. The first term, $L \left(\frac{H+F}{\omega+H+F} \right)$ assumes that the maximum rate of emergence is equal to the queen's laying rate, so all laid eggs emerge from the brood cell. This is the case when the brood mortality $\omega = 0$. As the total number of worker bees, $H + F$, increases, the brood mortality begins to increase. A higher brood mortality reflects a lower emergence from brood as a proportion of L .

The first term of (2.1) is highly dependent on the choice of ω . As aforementioned, when $\omega = 0$, each of the laid eggs survives. When ω begins to increase, the proportion of laid eggs surviving begins to decrease. If ω increases to infinity, the number of eggs surviving decreases to zero. The number of eggs surviving impacts the number of hive

bees, as well as the number of forager bees, and has implications for the health of the hive. The importance of ω on the overall health of a hive is demonstrated in Figure (2), where $N = H + F$.

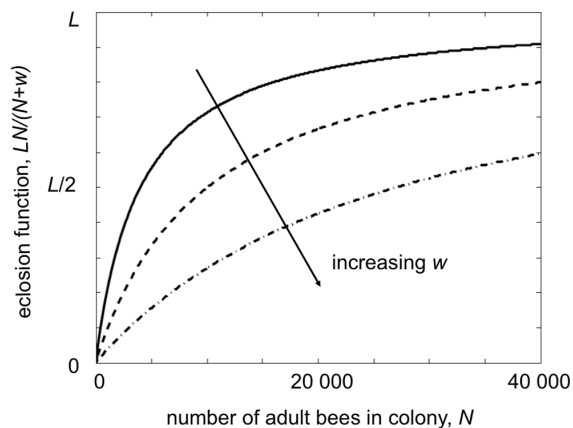


Figure 2: Plot of $L \left(\frac{H+F}{\omega+H+F} \right)$ for different values of ω [5].

The second term of the first equation can be broken into two parts by distributing H so it becomes $-H\alpha$ and $\frac{\sigma HF}{H+F}$. The first part, $-H\alpha$, represents the rate at which hive bees are transitioning to foragers, and is directly proportional to the number of hive bees. This decreases the total hive bee population. The term $\frac{\sigma HF}{H+F}$ accounts for the social inhibition of the transition from hive to forager bees. Specifically, the term $\frac{F}{H+F}$ represents the proportion of forager bees. If this proportion increases more than the hive can sustain, then forager bees begin to revert back to hive bees. Furthermore, if $\frac{\sigma F}{H+F} > \alpha$, $\frac{dH}{dt} > 0$ for this term implying an increase in hive bees since the rate at which forager bees are reverting to hive bees is greater than the rate that hive bees are becoming foragers, which would eventually drive the forager population to zero. However, if $\frac{\sigma F}{H+F} < \alpha$, $\frac{dH}{dt} < 0$ for the second term implying a decrease in hive bees since the rate at which hive bees are becoming forager bees outstrips the rate of forager bees reverting back to hive bees. This inequality aids in determining the real value of σ . Overall, the second term represents the rate at which hive bees that are transitioning to foraging, while simultaneously controlling for social inhibition which positively contributes to the number of hive bees. In this manner, (2.1) displays the rate of change of hive bee population for a colony.

The equation (2.2) likewise represents the rate of change of the forager bee popu-

lation. The first term, $H \left(\alpha - \sigma \left(\frac{F}{H+F} \right) \right)$ is from the second term of (2.1) since it now portrays the number of hive bees transitioning to foragers in the colony. The second term in (2.2), mF , is subtracted to account for the number of forager bees dying per day. As m is the forager per capita death rate, it represents the forager death rate in proportion to the forager population.

Khoury, Myerscough, and Barron utilized analysis of these differential equations to find the steady state of the system. They were able to find an equilibrium point, (H_e, F_e) by setting both (2.1) and (2.2) equal to zero, which yielded the solutions

$$F_e = \frac{L}{m} - \omega \frac{J}{J+1}, \quad (2.3)$$

and

$$H_e = \frac{1}{J} F_e \quad (2.4)$$

where

$$J = \frac{1}{2m} \left(\alpha - \sigma - m + \sqrt{(m + \sigma - \alpha)^2 + 4\alpha m} \right). \quad (2.5)$$

Khoury *et al* report conditions for $H_e > 0$ and $F_e > 0$ include

$$m < \frac{L}{2\omega} \left(\frac{\alpha + \sigma + \sqrt{(\alpha - \sigma)^2 + 4\frac{L\sigma}{\omega}}}{\alpha - \frac{L}{\omega}} \right), \quad (2.6)$$

and

$$\alpha - \frac{L}{\omega} > 0. \quad (2.7)$$

See Appendix A for an explanation of these conditions. To investigate stability dependent upon m , Khoury *et al* used constant values for L , ω , α , and σ that were consistent with the literature. The daily laying rate of the queen was chosen as $L = 2000$, and brood mortality as $\omega = 27,000$. Concerning the choice of α as the uninhibited transition to foraging, based on previous research, it was determined that $\alpha = 0.25$ was appropriate [4]. With $\alpha = 0.25$, this implies that the hive bees will transition to foraging after four days. This is because the term $-H\alpha$ represents the hive bees transitioning to foraging, so after four days the entire hive bee population will have transitioned to

foraging. The quotient between σ and α should be the reciprocal of the desired ratio between the number of forager bees to hive bees. They chose $\sigma = 0.75$ because $\frac{0.75}{0.25} = 3$, with its reciprocal consequently being $\frac{1}{3}$. This implies that foragers would only revert to hive bees if more than one third of the total hive are foragers, based on the quotient between σ and α . Utilizing equilibrium values they found for (H_e, F_e) , Khoury *et al* found that for $m > 0.355$, the steady state equilibrium point is $(0, 0)$, shown in Figure 3.

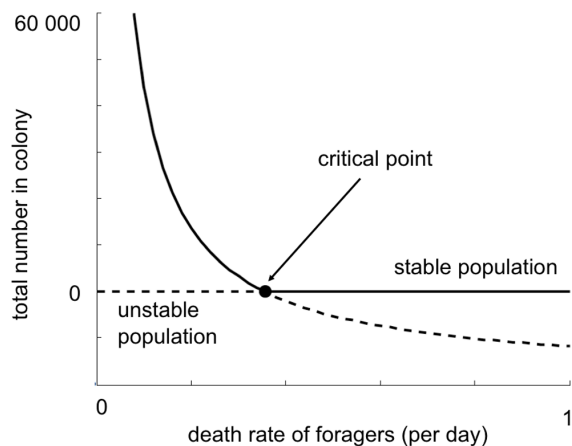


Figure 3: Colony Population at Equilibrium Contingent on Death Rate of Foragers [5]

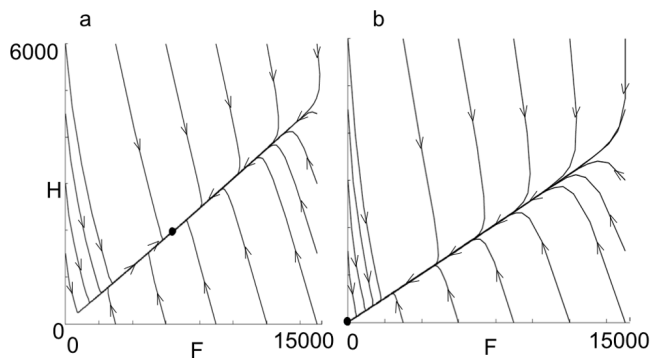


Figure 4: Plot of $(H_e, F_e) > 0$ for $m = 0.24$ and $(H_e, F_e) = (0, 0)$ for $m = 0.40$ [5]

The stability for $m > 0.355$ and $m \leq 0.355$ is illustrated in Figure 4. In (a), m is chosen to be 0.24 and the population tends toward a stable equilibrium point, which is marked by a dot. In (b) m is chosen as 0.40 and is therefore greater than 0.355 and the hive populations begin to declines to $(0, 0)$.

3 Our Model

While Khoury, Myerscough, and Barron investigated the population of both the hive and forager bees, we have expanded their model to include a third equation in the system that accounts for the population of the *Varroa destructor* mite on the overall hive. Our model accounts for the death of hive and forager bees due to the *Varroa destructor* by adding an extra term to the Khoury equations, as well as an extra equation for the mite population. The altered model is represented by the following equations.

$$\frac{dH}{dt} = \frac{L(H+F)}{(\omega+H+F)} - H \left(\alpha - \sigma \left(\frac{F}{H+F} \right) \right) - \rho MH \quad (3.1)$$

$$\frac{dF}{dt} = H \left(\alpha - \sigma \left(\frac{F}{H+F} \right) \right) - mF - \rho MF \quad (3.2)$$

$$\frac{dM}{dt} = rM \left(1 - \frac{M}{\alpha_2 H} \right) - \rho_2 M \quad (3.3)$$

The additional third equation models the population of the *Varroa destructor* mite as logistic growth, with ρ_2 accounting for the per capita death rate of the mites, M . Similarly, the additional ρMH and ρMF terms in the first and second equations, respectively, represent the per capita deaths of the hive and forager bees due to the mite. The first term of $\frac{dM}{dt}$ is a logistic growth rate of the mite population with r representing the growth rate of the mites. In this equation, the term $\alpha_2 H$ is the carrying capacity of mites in a hive.

The model we created has three physical equilibrium points: (H_e, F_e, M_e) , $(H_e, F_e, 0)$ and $(0, 0, 0)$. Note that when $M = 0$, the model reduces to the Khoury *et al* model. The first point (H_e, F_e, M_e) will be the focus of this thesis, with the other two equilibrium points being a result of Khoury *et al*. If either the population of hive or forager bees is driven to zero, the other two populations are driven to zero in the steady state as demonstrated below. First, we have that from Equation 3.3, that there are two steady states for the mite population, when $M = 0$ and when $M = \alpha_2 H \left(\frac{r - \rho_2}{r} \right)$. It follows that if $H = 0$, Equation 3.1 will force $F = 0$ and $M = 0$ in either case of M . Similarly, if $F = 0$, Equation 3.2 will force $H = 0$ and $M = 0$ in either case again. Since the *Varroa*

destructor is parasitic in nature, it is unable to survive without the hive or forager bees present. This provides further validation to the governing equations.

The equilibrium point (H_e, F_e, M_e) represents a steady state where hive and forager bees, and mites are able to coexist. In consideration of the number of parameters that our model contained, we were unable to analytically find a steady state, as Khoury *et al* were able to accomplish in their model. Instead, the equilibrium point was found partially analytically, resorting to numerical results for the final piece, using parameters for each of the variables in the model.

Although some of the parameters such as L or α are the same as Khoury's model, their values are altered slightly to better replicate what is observed in spring populations. The process of choosing the values for each of the parameters is inherently based in creating a population of approximately 60,000 bees within a 3-month span in the absence of mites. This population and lifespan of the colony are commonly seen in beekeeping, so the replication of this was a goal in choosing the values. Part of creating our model included choosing initial values for the hive and forager bees. These were chosen as $H_0 = 14000$ and $F_0 = 7000$. In terms of values of parameters, L was chosen to be 1780. Khoury *et al* had chosen $L = 2000$, which is a high estimate for the queen's daily laying rate. Winston cites the daily laying rate as 1500, which is a commonly accepted laying rate. However, the actual laying rate can differ depending on season, the number of adult worker bees, disease or pest prevalence, or the number of available cells. In consideration of this, $L = 1780$ is chosen as an appropriate laying rate. The representation of brood mortality, ω , is maintained at 27000. With these values, the first term, $L \left(\frac{H+F}{\omega+H+F} \right)$ becomes $1780 \left(\frac{14000+7000}{27000+14000+7000} \right) = 778.75$ and represents the initial number of eggs resulting in live hive bees.

The parameter α is altered slightly as well and is selected as $\alpha = 0.15$ rather than the $\alpha = 0.25$ in the Khoury *et al* model. This value of α implies that hive bees are not transferring to foraging until they are seven days old, whereas in the Khoury *et al* model, hive bees transitioned at four days old. An α value of 0.15 is more realistic for

a colony, as foraging is generally not reported for workers less than seven days old, even after colony demographics are manipulated [6], [2]. In the Khoury *et al* model the daily death rate of foragers, m , was determined to be less than 0.355 for the population to stay at a globally steady state. Khoury *et al* asserts that the purpose of their model was to explore why the forager death rate has such a significant effect on the colony population size, rather than simulate the growth observed in real colonies. In our model, m is chosen to be $m = 0.12$ which implies a longer forager lifespan and overall healthier colony [5]. Furthermore, this death rate of foragers is the value that is present in creating the ideal population and hive lifespan in the absence of mites.

The term representing social inhibition, σ , is maintained at 0.75. Maintaining $\sigma = 0.75$ indicates that foragers make up approximately one fifth of the total hive population, using the quotient between the values of σ and α , as illustrated in the discussion of the Khoury *et al* model. In the Khoury *et al* model, the parameter would have the composition of the number of forager bees being one third of the number of hive bees. With the chosen values for parameters and initial values $H = 14000$ and $F = 7000$, our model is displayed in Figure 5. The red line displays the hive bee population while the green represents the forager.

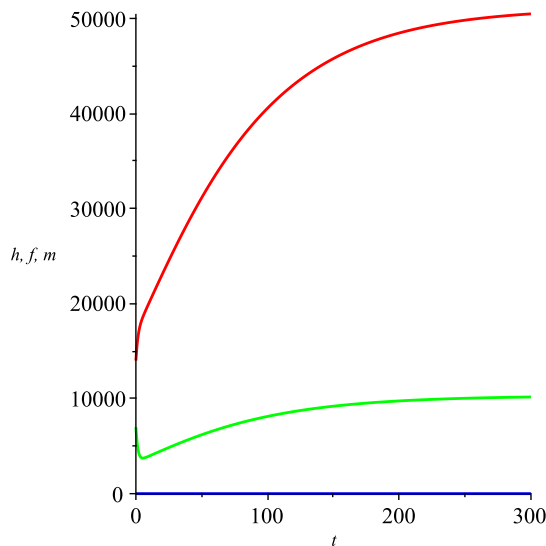


Figure 5: Our Population Model showing overall hive population tending to 60000 with $L = 1780$, $\omega = 27000$, $\alpha = 0.15$, $\sigma = 0.75$, and $m = 0.12$.

The parameters that are introduced in our model include ρ , r , α_2 , and ρ_2 . In our model, when the mite population was introduced, the values of the parameters were again chosen to create the desired 3-month growth to 60,000 total hive population. The death per capita due to the mites for both hive and foragers bees was chosen as $\rho = 5.0 \times 10^{-6}$. The difference between how the mites affect the hive versus forager bees is negligible, so the death rate is appropriately chosen as the same. This chosen value of ρ also yields the desired growth rate for low mite populations. The growth rate of the mites, r , was chosen to be equal to 0.0165 [3]. A study found that for mites present in brood cells, a growth rate of 0.0165 was present [3]. In studying the carrying capacity of mites in a hive, it was determined that bees have a carrying capacity of approximately 0.3, so α_2 was chosen as 0.3 [8].

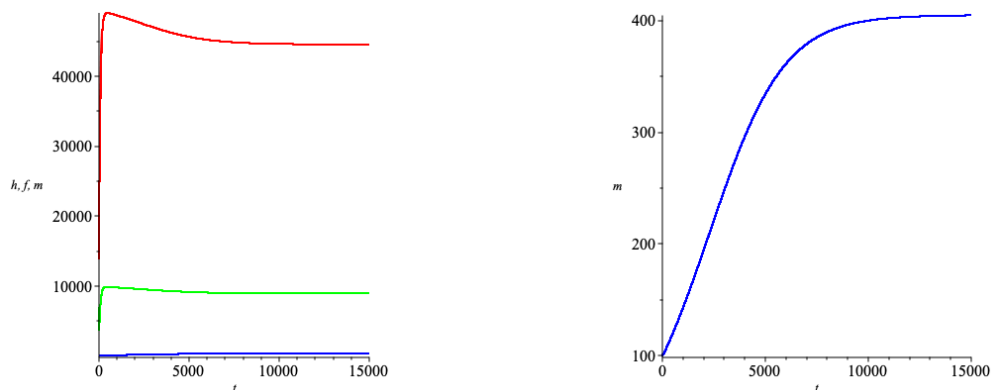
Our Model at Equilibrium

The value of ρ_2 , our control parameter, was altered to determine at which level of mite death rate per capita the equilibrium point (H_e, F_e, M_e) would be obtained and at which point the equilibrium point $(H_e, F_e, 0)$ would be reached. Initially, it was attempted to solve the system analytically in a similar manner to Khoury *et al.* As shown earlier, the steady state of Equation (3.3) is $M = \alpha_2 H \left(\frac{r - \rho_2}{r} \right)$. Here we note that for $\rho_2 = r$, we have $M = 0$. We let $K = \alpha_2 \left(\frac{r - \rho_2}{r} \right)$ and substituted $M = KH$ into Equation (3.2). Finding the steady state of Equation (3.2) resulted in the following, with details provided by Equations 3.5-3.14.

$$F = \frac{-H(\sigma + m + \rho KH - \alpha) \pm \sqrt{[H(\sigma + m + \rho KH - \alpha)]^2 + 4(m + \rho KH)(\alpha H^2)}}{2(m + \rho KH)} \quad (3.4)$$

The process of finding the steady state of Equation (3.2) is expanded upon in the section Stability at Equilibrium. When it was attempted to substitute (3.4) and $M = KH$ into Equation (3.1), it resulted in a fifth degree polynomial and the computer was unable to solve for H . This prompted a numerical approach to be taken for finding the equilibrium points of the system.

A bifurcation point on the parameter ρ_2 was found at $\rho_2 = r$, as noted above. For $\rho_2 \geq 0.0165$, the mite population is driven to zero, and for $\rho_2 < 0.0165$, the population of mites grows to a stable population. To analyze stability at either equilibrium point, values of $\rho_2 = 0.016$ and $\rho_2 = 0.017$ were chosen. Given $\rho_2 = 0.016$, the steady state equilibrium point is $(44575, 8956, 405)$. This low growth rate of the mites allows for the hive and forager bees to grow unimpeded by the mites and each population is able to coexist in a steady state. This dynamic is displayed in Figure 6. In each of the plots, the red line corresponds to the hive bee population, the green line to the forager, and the blue line to the mite population. Similar to Figure 5, the initial values are $H_0 = 14000$ and $F_0 = 7000$, and $M_0 = 100$ [3].



(a) Full plot with $\rho_2 = 0.016$

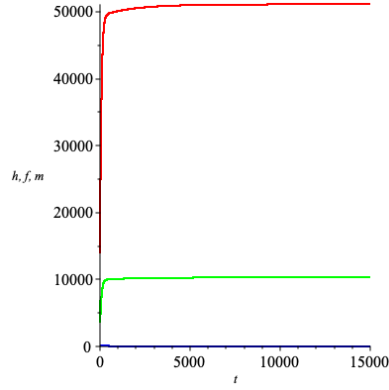
(b) Plot focused on mite population

Figure 6: Our Population Model with $L = 1780$, $\omega = 27000$, $\alpha = 0.15$, $\sigma = 0.75$, $m = 0.12$, $\rho = 5.0 \times 10^{-6}$, $r = 0.0165$, $\alpha_2 = 0.3$, and $\rho_2 = 0.016$.

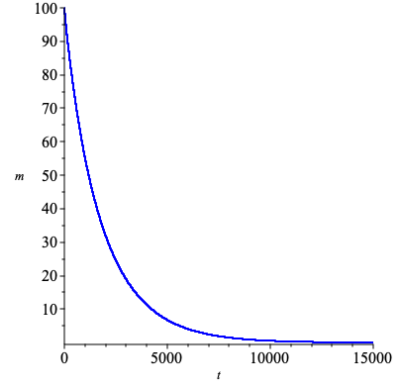
When the death rate per capita of the mites is increased to $\rho_2 = 0.017$, the equilibrium point (H_e, F_e, M_e) is $(62818, 12719, 0)$. This dynamic is displayed in Figure 7. When $\rho_2 = 0.017$ the mite population begins to decrease, and at any point when $\rho_2 \geq 0.0165$, the mite population dies off.

Stability at Equilibrium

After finding the equilibrium points of the system of differential equations, stability is evaluated. In the case of Khoury *et al*, they were able to determine stability through



(a) Full plot with $\rho_2 = 0.017$



(b) Plot focused on mite population

Figure 7: Our Population Model with $L = 1780$, $\omega = 27000$, $\alpha = 0.15$, $\sigma = 0.75$, $m = 0.12$, $\rho = 5.0 \times 10^{-6}$, $r = 0.0165$, $\alpha_2 = 0.3$, and $\rho_2 = 0.017$.

analyzing the trace and determinant of the Jacobian matrix. With parameters ensuring that for the Jacobian, J , $tr(J) < 0$ and $det(J) > 0$ then the equilibrium points they found would be stable. This is the traditional analyzation through eigenvalues and eigenvectors.

Here the eigenvalues and eigenvectors are used, based on Theorem 3.1 and Theorem 3.2.

Theorem 3.1. *An equilibrium point (x_e, y_e, z_e) of a system of differential equations is stable if all the eigenvalues of J_e , the Jacobian matrix evaluated at (x_e, y_e, z_e) , are negative real numbers or are complex numbers with negative real parts.*

Theorem 3.2. *An equilibrium point (x_e, y_e, z_e) of a system of differential equations is unstable if at least one eigenvalue of J_e , the Jacobian matrix evaluated at (x_e, y_e, z_e) , is a positive real number or is a complex number with positive real parts.*

To calculate the eigenvectors of the Jacobian matrix, the values of (H_e, F_e, M_e) are first calculated using the parameters' values. Initially, the equations are solved in terms of H and evaluated at both values of ρ_2 , $\rho_2 = 0.016$ and $\rho_2 = 0.017$. First, $\frac{dM}{dt}$ is set

equal to zero and solved for M in terms of H .

$$0 = rM \left(1 - \frac{M}{\alpha_2 H} \right) - \rho_2 M \quad (3.5)$$

$$M = \frac{\alpha_2 H (r - \rho_2)}{r} \quad (3.6)$$

The same process is repeated for $\frac{dF}{dt}$, using the calculated value of M .

$$0 = H \left(\alpha - \sigma \left(\frac{F}{H + F} \right) \right) - mF - \rho \left(\frac{\alpha_2 H (r - \rho_2)}{r} \right) F \quad (3.7)$$

$$0 = H\alpha - \frac{F\sigma H}{H + F} - mF - \frac{\rho\alpha_2 H F (r - \rho_2)}{r} \quad (3.8)$$

$$H\alpha = \frac{F\sigma Hr + mF(H + F)r + (H + F)\rho\alpha_2 H(r - \rho_2)F}{r(H + F)} \quad (3.9)$$

$$\begin{aligned} \alpha r H^2 + r F H \alpha &= F H r \sigma + F H m r + F^2 m r + F H^2 r \rho \alpha_2 - F H^2 \rho \rho_2 \alpha_2 \\ &\quad + F^2 H r \rho \alpha_2 - F^2 H \rho \rho_2 \alpha_2 \end{aligned} \quad (3.10)$$

$$\begin{aligned} 0 &= F^2 H r \rho \alpha_2 - F^2 H \rho \rho_2 \alpha_2 + F^2 m r + F H^2 r \rho \alpha_2 - F H^2 \rho \rho_2 \alpha_2 \\ &\quad + F H r \sigma + F H m r - r F H \alpha - \alpha r H^2 \end{aligned} \quad (3.11)$$

From here, the quadratic formula may be used to solve for F in terms of H , with the coefficients of each term being

$$F^2 : H r \rho \alpha_2 + r m - H \rho \rho_2 \alpha_2 \quad (3.12)$$

$$F : H r (-\alpha + \sigma + m + H \rho \alpha_2) - H^2 \rho \rho_2 \alpha_2 \quad (3.13)$$

$$F^0 : -H^2 r \alpha. \quad (3.14)$$

F and M in terms of H were then substituted in $\frac{dH}{dt}$ to numerically solve for H . Since a bifurcation point of the mite population was found at $\rho_2 \approx 0.0165$, behavior of our model is investigated at $\rho_2 = 0.016$ and $\rho_2 0.017$.

Stability With $\rho_2 = 0.016$

The real valued solutions of H , F , and M with $L = 1780$, $\omega = 27000$, $\alpha = 0.15$, $\sigma = 0.75$, $m = 0.12$, $\rho = 5.0 \times 10^{-6}$, $r = 0.0165$, $\alpha_2 = 0.3$, and $\rho_2 = 0.016$ are

$$H \approx 44574.97673, F \approx 8956.26184, \text{ and } M \approx 405.22706.$$

The Jacobian matrix of the system of equations is calculated and is displayed in (3.15).

$$\begin{bmatrix} \frac{L\omega}{(\omega + H + F)^2} + \frac{F^2\sigma}{(H + F)^2} - \alpha - M\rho & \frac{L\omega}{(\omega + H + F)^2} + \frac{H^2\sigma}{(H + F)^2} & -H\rho \\ \alpha - \frac{F^2\sigma}{(H + F)^2} & \frac{-H^2\sigma}{(H + F)^2} - m - M\rho & -F\rho \\ \frac{M^2r}{H^2\alpha_2} & 0 & r \left(1 - \frac{2M}{H\alpha_2}\right) - \rho_2 \end{bmatrix} \quad (3.15)$$

Substituting the values of each parameter into the Jacobian results in (3.16)

$$J_{\rho_2=0.016} \begin{bmatrix} -0.1236211244 & 0.5274464864 & -0.222875 \\ 0.1290067963 & -0.642068146 & -0.044780 \\ 4.540357317 \times 10^{-6} & 0 & -0.00049943915 \end{bmatrix} \quad (3.16)$$

Calculating $\det(J_{\rho_2=0.016} - \lambda I)$ where I is the identity matrix and solving for λ gives the eigenvalues for the given parameters. The resulting eigenvalues are

$$-0.750589669127497, -0.0150228311333072, \text{ and } -0.000568877889196346$$

Each eigenvalue is negative, so by Theorem 3.1, the equilibrium point with $\rho_2 = 0.016$ is stable.

Stability With $\rho_2 = 0.017$

Using the same parameters as defined earlier, $L = 1780$, $\omega = 27000$, $\alpha = 0.15$, $\sigma = 0.75$, $m = 0.12$, $\rho = 5.0 \times 10^{-6}$, $r = 0.0165$, and $\alpha_2 = 0.3$ with $\rho_2 = 0.017$, the real valued solutions for H , F , and M are

$$H \approx 62817.90986, F \approx 12718.53561, \text{ and } M = 0.$$

Utilizing Matrix (3.15), the Jacobian matrix with the defined parameters and $\rho_2 = 0.017$ is (3.17).

$$J_{\rho_2=0.017} \begin{bmatrix} -0.1241659362 & 0.5232698439 & -0.3140895493 \\ 0.1287371050 & -0.6386986752 & -0.06359267805 \\ 0 & 0 & 0.0005 \end{bmatrix} \quad (3.17)$$

Similar to determining stability with $\rho_2 = 0.016$, calculating $\det(J_{\rho_2=0.017} - \lambda I)$ where I is the identity matrix and solving for λ gives the eigenvalues of (3.17). For $\rho_2 = 0.017$, the resulting eigenvalues are

$$-0.0159870571152106, \quad -0.746877554284789, \quad \text{and} \quad 0.00050$$

We have that one of the eigenvalues is positive, so by Theorem 3.2 the equilibrium point with $\rho_2 = 0.017$ is unstable. Our graphs show that the populations tends to the point $(H_e, F_e, 0)$ for this case. Instability indicates that if there are perturbations to the system, the equilibrium point $(H_e, F_e, 0)$ would tend to the point (H_e, F_e, M_e) rather than toward $(H_e, F_e, 0)$. This is confirmed by Figure 7 because the equilibrium point displayed in the Figure is not the same equilibrium we found above. Further investigation of stability is required at this equilibrium point.

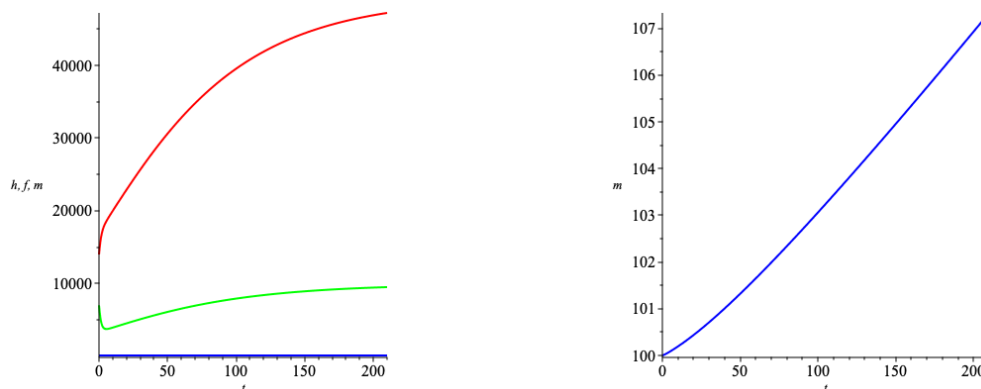
4 Results

Analyzing the equilibrium points (H_e, F_e, M_e) and $(H_e, F_e, 0)$ is imperative because it allows beekeepers to understand what continual death rate on the mites they must achieve in order to eliminate mites. Knowing the percent of mites that must continually die or be removed in a hive for the mite population to go to zero will aid in controlling the mite population and the longevity of the hive. Maintaining a continual death rate of $\rho_2 \geq 0.0165$ allows for the mites to go to extinction. When the death rate of the mites, ρ_2 decreases below 0.0165, the mites and bees will coexist. We note that for the equilibrium point $(0, 0, 0)$, where the entire hive goes extinct, the death rate of the forager bees would need to increase, as shown by Khoury *et al.* For the chosen value of the forager death

rate, we have from Equation 3.6 that the mite population is proportional to the number of hive bees.

Discussion

The model we created was extended to 15000 days to reach the equilibrium points. To investigate the population dynamics of the hive with regard to its biological processes, the populations are explored at 210 days. In the model we created, the set populations are based on the population of a hive in the spring [5]. Reaching 210 days indicates the beginning of winter for the hive, where the population dynamics change drastically. The lifespans of the bees increase and there is much less overall movement. Considering this, the hive and forager bee, and mite populations over the course of 210 days are displayed below.



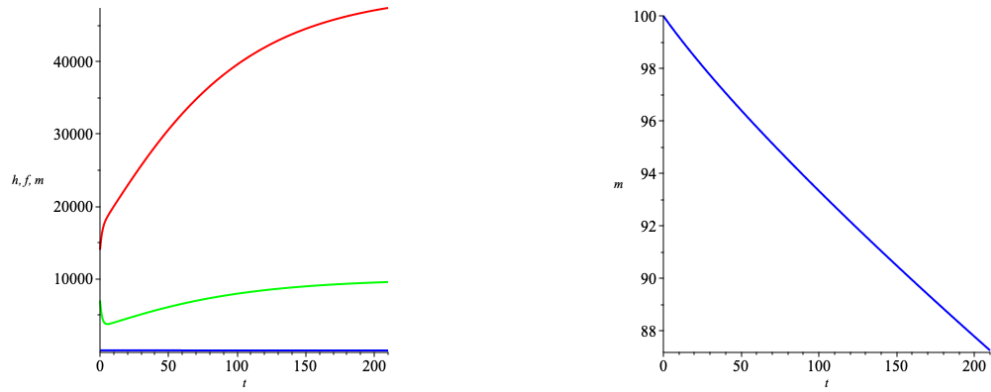
(a) Full plot with $\rho_2 = 0.016$ to 210 days

(b) Plot focused on mite population

Figure 8: Our Population Model with $L = 1780$, $\omega = 27000$, $\alpha = 0.15$, $\sigma = 0.75$, $m = 0.12$, $\rho = 5.0 \times 10^{-6}$, $r = 0.0165$, $\alpha_2 = 0.3$, and $\rho_2 = 0.016$ up to 210 days.

This shows that for $\rho_2 = 0.016$, at 210 days, the hive bee population is approximately 47219, the forager population is approximately 9500, and there are 107 mites. When ρ_2 is increased to 0.017, the hive and forager bee, and mite populations are in displayed in Figure 9.

With $\rho_2 = 0.017$, the hive and forager bee populations approach 47440 and 9545, respectively, at 210 days. The mites population decreases to 87 over the same time

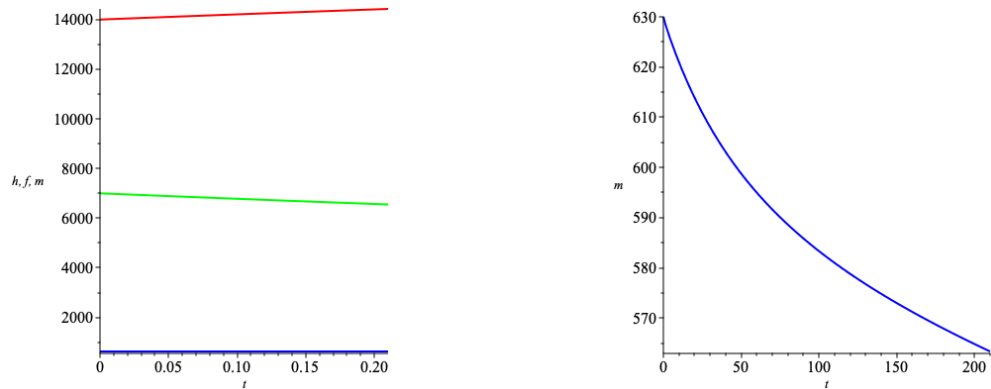


(a) Full plot with $\rho_2 = 0.017$ to 210 days (b) Plot focused on mite population

Figure 9: Our Population Model with $L = 1780$, $\omega = 27000$, $\alpha = 0.15$, $\sigma = 0.75$, $m = 0.12$, $\rho = 5.0 \times 10^{-6}$, $r = 0.0165$, $\alpha_2 = 0.3$, and $\rho_2 = 0.017$ up to 210 days

period.

With the low initial value of the mites, $M_0 = 100$, the hive was still able to sustain itself over the course of a season. If the initial value of the mites increases, the effect that they have on the hive will be more pronounced. This is demonstrated below, in Figure 10, with the initial value of the mites being increased to $M_0 = 630$, so they make up 3% of the hive, with $\rho_2 = 0.016$.



(a) Full plot with $M_0 = 630$ to 210 days (b) Plot focused on mite population

Figure 10: Our Population Model with $M_0 = 630$

Future Plans

The model created currently does not account for the continuous arrival of *Varroa destructor* mites into the colony due to mites attaching to forager bees during foraging. The model could be altered to include the influx of mites that arrive on forager bees as they return to the hive. This would likely require a higher value of ρ_2 to keep the mite population under control.

5 Acknowledgements

I would like to express sincere gratitude to Dr. Dan Van Peurseem for his invaluable assistance, insight, and guidance throughout this process. I would like to also thank Drs. Catalin Georgescu and José Flores for their willingness to propogate student research. Additionally, I am grateful to Dr. Dan Kemp for helping to spark an interest in research. Finally, thank you to my family for their unwavering support.

Appendix A Mathematics of Khoury *et al* Model

F_e is defined as $\frac{L}{m} - \omega \frac{J}{J+1}$ for $J = \frac{1}{2m} \left(\alpha - \sigma - m + \sqrt{(m + \sigma - \alpha)^2 + 4\alpha m} \right)$ To find

$$m < \frac{L}{2\omega} \left(\frac{\alpha + \sigma + \sqrt{(\alpha - \sigma)^2 + 4\frac{L\sigma}{\omega}}}{\alpha - \frac{L}{\omega}} \right) \text{ and } \alpha - \frac{L}{\omega} > 0$$

begin by setting $F_e > 0$. Then

$$L > m\omega \left(\frac{J}{J+1} \right)$$

$$LJ + L > m\omega J$$

$$L > m\omega J - LJ$$

$$L > J(m\omega - L)$$

Let $A = \frac{\alpha}{m} - \frac{\sigma}{m} - 1$ and $B = \frac{4\alpha}{m}$. It follows that, from definition of J ,

$$L > (m\omega - L) \left(\frac{A}{2} + \frac{1}{2} \sqrt{A^2 + B} \right)$$

$$L > (m\omega - L) \left(\frac{A}{2} \right) + (m\omega - L) \left(\frac{1}{2} \sqrt{A^2 + B} \right)$$

$$L - (m\omega - L) \left(\frac{A}{2} \right) > (m\omega - L) \left(\frac{1}{2} \sqrt{A^2 + B} \right)$$

$$L^2 - LA(m\omega - L) + \frac{A^2}{4} (m\omega - L)^2 > (m\omega - L)^2 \left(\frac{1}{4} (A^2 + B) \right)$$

$$L^2 - LA m\omega + L^2 A + \frac{A^2 m^2 \omega^2}{4} - \frac{A^2 m\omega L}{2} + \frac{A^2 L^2}{4} > \frac{A^2 m^2 \omega^2}{4} - \frac{A^2 m\omega L}{2} + \frac{A^2 L^2}{4} + \frac{B m^2 \omega^2}{4} - \frac{B m\omega L}{2} + \frac{L^2 B}{4}$$

$$4L^2 - 4LA m\omega + 4L^2 A > B m^2 \omega^2 - 2B m\omega L + L^2 B$$

$$4L^2 - 4LA m\omega + 4L^2 A - B m^2 \omega^2 + 2B m\omega L - L^2 B > 0$$

Substitution for A and B yields

$$\begin{aligned}
4L^2 - 4L \left(\frac{\alpha}{m} - \frac{\sigma}{m} - 1 \right) m\omega + 4L^2 \left(\frac{\alpha}{m} - \frac{\sigma}{m} - 1 \right) - \frac{4\alpha}{m} m^2 \omega^2 + 2 \frac{4\alpha}{m} m\omega L - L^2 \frac{4\alpha}{m} &> 0 \\
4L\alpha\omega + 4L\sigma\omega + 4Lm\omega - \frac{4L^2\sigma}{m} - 4\alpha m\omega^2 &> 0 \\
Lm\alpha\omega + Lm\sigma\omega + Lm^2\omega - L^2\sigma - \alpha\omega^2 m^2 &> 0 \\
m^2 (L\omega - \alpha\omega^2) + m(L\alpha\omega + L\sigma\omega) - L^2\sigma &> 0
\end{aligned}$$

Khoury *et al* stipulated that $\alpha - \frac{L}{\omega} > 0$ so it follows that $(L\omega - \alpha\omega^2) < 0$ and the parabola created by the above equation opens downward. Utilizing the quadratic formula in solving for m , the inequality that follows gives m is bounded by a quantity, rather than equal to since the original inequality stipulated that it was greater than zero.

$$\begin{aligned}
&\frac{-(L\alpha\omega + L\sigma\omega) \pm \sqrt{(L\alpha\omega + L\sigma\omega)^2 + 4(L\omega - \alpha\omega^2)(L^2\sigma)}}{2(L\omega - \alpha\omega^2)} \\
&\frac{-(\alpha\omega + \sigma\omega) \pm \sqrt{(\alpha\omega + \sigma\omega)^2 + 4\sigma(L\omega - \alpha\omega^2)}}{2\left(\omega - \frac{\alpha\omega^2}{L}\right)} \\
&\frac{-(\alpha + \sigma) \pm \sqrt{(\alpha + \sigma)^2 + 4\sigma\left(\frac{L}{\omega} - \alpha\right)}}{2\left(1 - \frac{\alpha\omega}{L}\right)} \\
&\frac{-(\alpha + \sigma) \pm \sqrt{(\alpha - \sigma)^2 + \frac{4L\sigma}{\omega}}}{2\left(1 - \frac{\alpha\omega}{L}\right)} \\
&-\frac{L}{2\omega} \left(\frac{(\alpha + \sigma) \pm \sqrt{(\alpha - \sigma)^2 + \frac{4L\sigma}{\omega}}}{\frac{L}{\omega} - \alpha} \right) \\
&\frac{L}{2\omega} \left(\frac{(\alpha + \sigma) \pm \sqrt{(\alpha - \sigma)^2 + \frac{4L\sigma}{\omega}}}{\alpha - \frac{L}{\omega}} \right)
\end{aligned}$$

Since the value of m must be greater than zero since it is in regard to a population, it follows that m is bounded between

$$\frac{L}{2\omega} \left(\frac{(\alpha + \sigma) - \sqrt{(\alpha - \sigma)^2 + \frac{4L\sigma}{\omega}}}{\alpha - \frac{L}{\omega}} \right) < m < \frac{L}{2\omega} \left(\frac{(\alpha + \sigma) + \sqrt{(\alpha - \sigma)^2 + \frac{4L\sigma}{\omega}}}{\alpha - \frac{L}{\omega}} \right).$$

Khoury *et al* bounded m strictly as $m < \frac{L}{2\omega} \left(\frac{(\alpha + \sigma) + \sqrt{(\alpha - \sigma)^2 + \frac{4L\sigma}{\omega}}}{\alpha - \frac{L}{\omega}} \right)$.

Appendix B Maple Code

Graph Code

with(plots):

$$\text{sys} := \left\{ \begin{array}{l} \frac{d}{dt}h(t) = L \cdot \left(\frac{h(t) + f(t)}{\text{omega} + h(t) + f(t)} \right) - h(t) \cdot \left(\alpha - \text{sigma} \cdot \left(\frac{f(t)}{h(t) + f(t)} \right) \right) \\ -\rho \cdot m(t) \cdot h(t), \frac{d}{dt}f(t) = h(t) \cdot \left(\alpha_1 - \text{sigma} \cdot \left(\frac{f(t)}{h(t) + f(t)} \right) \right) - m \cdot f(t) - \rho \cdot m(t) \cdot f(t), \\ \frac{d}{dt}m(t) = r \cdot m(t) \cdot \left(1 - \frac{m(t)}{\alpha_2 \cdot h(t)} \right) - \rho_2 \cdot m(t), h(0) = 14000, f(0) = 7000, m(0) = 100 \end{array} \right\}$$

p := dsolve(sys, numeric, method = rkf45, maxfun = 10000000, parameters

= [L, sigma, alpha_1, omega, rho, rho, m, r, alpha_2, rho_2])

p(parameters)

p(parameters = [1780, 0.75, 0.15, 27000, 0.000005, 0.000005, 0.12, 0.0165, 0.3, 0.016])

odeplot(p, [[t, h(t), color=red, thickness=2], [t, f(t), color=green, thickness=2], [t, m(t), color=blue, thickness=2]], 0...15000, numpoints=1050000)

odeplot(p, [[t, h(t), color=red, thickness=2]], 0...15000, numpoints=1050000)

odeplot(p, [[t, f(t), color=green, thickness=2]], 0...15000, numpoints=1050000)

odeplot(p, [[t, m(t), color=blue, thickness=2]], 0...15000, numpoints=1050000)

$\rho_2 = 0.016$ Numerical Solve Code

assign(L, 1780)

assign(omega, 27000)

assign(alpha, 0.15)

assign(sigma, 0.75)

assign(rho, 0.000005)

assign(m, 0.12)

assign(r, 0.0165)

assign(alpha_2, 0.3)

assign(ρ_2 , 0.016)

with(*VectorCalculus*):

with(*LinearAlgebra*):

solve $\left(r \cdot M \cdot \left(1 - \frac{M}{\alpha_2 \cdot H} \right) - \rho_2 \cdot M, M \right)$

assign(K , 0.00909090909092 · H)

solve $\left(H \cdot \left(\alpha - \text{sigma} \cdot \left(\frac{F}{H + F} \right) \right) - m \cdot F - \rho \cdot K \cdot F, F \right)$

assign $\left(J_1, - \frac{1}{2.272727273 \cdot 10^9 \cdot H + 6.00 \cdot 10^{15}} \cdot (.50000 \cdot (2.272727273 \cdot 10^9 \cdot H + 3.60000 \cdot 10^{16} - 1.0 \cdot \text{sqrt}(5.165289257 \cdot 10^{18} \cdot H^2 + 2.318181818 \cdot 10^{26} \cdot H + 1.476000 \cdot 10^{33})) \cdot H) \right)$

solve $\left(\frac{L \cdot (H + J_1)}{\text{omega} + H + J_1} - H \cdot \left(\alpha - \text{sigma} \cdot \left(\frac{J_1}{H + J_1} \right) \right) - \rho \cdot K \cdot H, H \right)$

assign $\left(J_2, - \frac{1}{2.272727273 \cdot 10^9 \cdot H + 6.00 \cdot 10^{15}} \cdot (.50000 \cdot (2.272727273 \cdot 10^9 \cdot H + 3.60000 \cdot 10^{16} + 1.0 \cdot \text{sqrt}(5.165289257 \cdot 10^{18} \cdot H^2 + 2.318181818 \cdot 10^{26} \cdot H + 1.476000 \cdot 10^{33})) \cdot H) \right)$

solve $\left(\frac{L \cdot (H + J_2)}{\text{omega} + H + J_2} - H \cdot \left(\alpha - \text{sigma} \cdot \left(\frac{J_2}{H + J_2} \right) \right) - \rho \cdot K \cdot H, H \right)$

assign(H , 44574.97673)

solve $\left(H \cdot \left(\alpha - \text{sigma} \cdot \left(\frac{F}{H + F} \right) \right) - m \cdot F - \rho \cdot K \cdot F, F \right)$

solve $\left(r \cdot M \cdot \left(1 - \frac{M}{\alpha_2 \cdot H} \right) - \rho_2 \cdot M, M \right)$

$\rho_2 = 0.017$ **Numerical Solve Code**

assign(L , 1780)

assign(omega , 27000)

assign(α , 0.15)

assign(sigma , 0.75)

assign(ρ , 0.000005)

assign(m , 0.12)

assign(r , 0.0165)

assign(α_2 , 0.3)

assign(ρ_2 , 0.017)

with(*VectorCalculus*):

with(*LinearAlgebra*):

solve $\left(r \cdot M \cdot \left(1 - \frac{M}{\alpha_2 \cdot H} \right) - \rho_2 \cdot M, M \right)$

assign(K , $-0.00909090909092 \cdot H$)

solve $\left(H \cdot \left(\alpha - \text{sigma} \cdot \left(\frac{F}{H + F} \right) \right) - m \cdot F - \rho \cdot K \cdot F, F \right)$

assign $\left(J_1, -\frac{1}{2.272727273 \cdot 10^9 \cdot H + 6.00 \cdot 10^{15}} \cdot (.50000 \cdot (2.272727273 \cdot 10^9 \cdot H - 3.60000 \cdot 10^{16} - 1.0 \cdot \text{sqrt}(5.165289257 \cdot 10^{18} \cdot H - 2.318181818 \cdot 10^{26} \cdot H + 1.476000 \cdot 10^{33})) \cdot H) \right)$

solve $\left(\frac{L \cdot (H + J_1)}{\text{omega} + H + J_1} - H \cdot \left(\alpha - \text{sigma} \cdot \left(\frac{J_1}{H + J_1} \right) \right) - \rho \cdot K \cdot H, H \right)$

assign $\left(J_2, -\frac{1}{2.272727273 \cdot 10^9 \cdot H + 6.00 \cdot 10^{15}} \cdot (.50000 \cdot (2.272727273 \cdot 10^9 \cdot H - 3.60000 \cdot 10^{16} + 1.0 \cdot \text{sqrt}(5.165289257 \cdot 10^{18} \cdot H - 2.318181818 \cdot 10^{26} \cdot H + 1.476000 \cdot 10^{33})) \cdot H) \right)$

solve $\left(\frac{L \cdot (H + J_2)}{\text{omega} + H + J_2} - H \cdot \left(\alpha - \text{sigma} \cdot \left(\frac{J_2}{H + J_2} \right) \right) - \rho \cdot K \cdot H, H \right)$

assign(H , 62817.90986)

solve $\left(H \cdot \left(\alpha - \text{sigma} \cdot \left(\frac{F}{H + F} \right) \right) - m \cdot F - \rho \cdot K \cdot F, F \right)$

solve $\left(r \cdot M \cdot \left(1 - \frac{M}{\alpha_2 \cdot H} \right) - \rho_2 \cdot M, M \right)$

$\rho_2 = 0.016$ Eigenvalues Code

assign(*L*, 1780)

assign(*omega*, 27000)

assign(α , 0.15)

assign(*sigma*, 0.75)

assign(ρ , 0.000005)

assign(*m*, 0.12)

assign(*r*, 0.0165)

assign(α_2 , 0.3)

assign(ρ_2 , 0.016)

assign(*H*, 44575)

assign(*F*, 8956)

assign(*M*, 405)

with(*VectorCalculus*):

with(*LinearAlgebra*):

$$A := \text{Matrix} \left(\left[\left[\frac{(L \cdot \text{omega})}{(\text{omega} + H + F)^2} + \frac{(\text{sigma} \cdot F^2)}{(H + F)^2} - \alpha - \rho \cdot M, \frac{(L \cdot \text{omega})}{(\text{omega} + H + F)^2} + \frac{(\text{sigma} \cdot H^2)}{(H + F)^2}, -\rho \cdot H \right], \left[\alpha - \frac{(\text{sigma} \cdot F^2)}{(H + F)^2}, -\frac{(\text{sigma} \cdot H^2)}{(H + F)^2} - m - \rho \cdot M, -\rho \cdot F \right], \left[\frac{r \cdot M^2}{\alpha_2 \cdot H^2}, 0, r \cdot \left(1 - \frac{2 \cdot M}{\alpha_2 \cdot H} \right) - \rho_2 \right] \right] \right)$$

Eigenvalues(*A*)

$\rho_2 = 0.017$ Eigenvalues Code

assign(*L*, 1780)

assign(*omega*, 27000)

assign(α , 0.15)

assign(*sigma*, 0.75)

assign(ρ , 0.000005)

assign(*m*, 0.12)

assign(*r*, 0.0165)

assign(α_2 , 0.3)

assign(ρ_2 , 0.017)

assign(*H*, 62817.91)

assign(*F*, 12718.54)

assign(*M*, 0)

with(*VectorCalculus*):

with(*LinearAlgebra*):

$$B := \text{Matrix} \left(\left[\left[\left[\frac{(L \cdot \text{omega})}{(\text{omega} + H + F)^2} + \frac{(\text{sigma} \cdot F^2)}{(H + F)^2} - \alpha - \rho \cdot M, \frac{(L \cdot \text{omega})}{(\text{omega} + H + F)^2} + \frac{(\text{sigma} \cdot H^2)}{(H + F)^2}, -\rho \cdot H \right], \left[\alpha - \frac{(\text{sigma} \cdot F^2)}{(H + F)^2}, -\frac{(\text{sigma} \cdot H^2)}{(H + F)^2} - m - \rho \cdot M, -\rho \cdot F \right], \left[\frac{r \cdot M^2}{\alpha_2 \cdot H^2}, 0, r \cdot \left(1 - \frac{2 \cdot M}{\alpha_2 \cdot H} \right) - \rho_2 \right] \right] \right]$$

Eigenvalues(*B*)

References

- [1] Plant Health Australia. Bee Aware: Varroa Mites, <http://beeaware.org.au/archive-pest/varroa-mites/>
- [2] Calderone, N.M. “Proximate mechanisms of age polyethism in the honey bee *Apis mellifera*.” *Apidologie*. 1998; 29:127-158.
- [3] DeGrandi-Hoffman, G., Ahumada, F., Zazueta, V., Chambers, M., Hidalgo, G., & Watkins deJong, E. “Population growth of *Varroa destructor* (Acari: Varroidae) in honey bee colonies is affected by the number of foragers with mites” *Experimental and Applied Acarology*. 2016; 69.1:21-34.
- [4] Fahrbach, S.E., & Robinson, G.E. “Juvenile hormone, behavioral maturation and brain structure in the honey bee.” *Developmental Neuroscience*. 1996; 18:102-114.
- [5] Khoury, D. S., Myerscough, M. R., & Barron, A. B. “A quantitative model of honey bee colony population dynamics” *PloS ONE* 6(4): e18491. doi: 10.1371/journal.pone.0018491.
- [6] Page, R.E., Robinson, G.E., Britton, D.S., & Fondrk, M.K. “Genotypic variability for rates of behavioral development in worker honeybees (*Apis mellifera*).” *Behavioral Ecology*. 1992; 3:173-180.
- [7] Peng, Y.S., Fang, Y., Xu, S., & Ge, L. “The resistance mechanism of the Asian honey bee, *Apis cerana* Fabr., to an ectoparasitic mite *Varroa jacobsoni* Oudemans.” *Journal of Invertebrate Pathology*. 1987; 46:54-60.
- [8] Ratti, V., Kevan, P., & Hermann, E. “A mathematical model for population dynamics in honeybee colonies infested with *Varroa destructor* and the Acute Bee Paralysis Virus.” *Can. Appl. Math. Q.*. 2013; 21.1:63-93.
- [9] Rosenkranz, P., Aumeier, P., & Ziegelmann, B. “Biology and control of *Varroa destructor*.” *Journal of Invertebrate Pathology*. 2010; 103.S:96-119.

- [10] Seeley, T.D. (1995). *The wisdom of the hive*. Cambridge, MA: Harvard University Press.
- [11] Winston, M.L. (1987). *The biology of the honey bee*. Cambridge, MA: Harvard University Press.