Mathematical Models of Honey Bee Populations: Rapid Population Decline

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This thesis by **Kelly M. Brown** is accepted in its present form as satisfying the thesis requirement for Honors in Mathematics.

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Abstract

Recent reports of honey bee colony deaths worldwide [4] have prompted interest in mathematical models to study the decrease of bees within a colony. To study colony population decline, Khoury, Myerscough and Barron [1] derived a single-colony model with two differential equations describing how the hive bee and forager bee populations interact. The hive bee population $H$ changes at a rate dependent on their emergence rate from pupae and the transition rate to foraging. The forager bee population $F$ changes at a rate dependent on the transition rate from hive bee status and their death rate. Khoury et al [1] consider the death rate of the hive bees to be negligible. We have extended this model to include a more realistic queen laying rate $L$ and to include a hive bee per capita death rate $\mu$. Using a linear approximation of the model, we find three criteria that indicate the occurrence of a globally stable positive equilibrium. The model predicts the existence of a stable positive equilibrium in which both hive bees and forager bees persist when forager death rates are low. Past a threshold level when hive bee or forager death rates are high, colony failure is inevitable as the hive bee and forager bee numbers are driven to zero. Inclusion of more realistic values for the queen’s egg-laying rate and hive bee per capita death rate require brood survivability to increase to compensate. In addition, we modified the code for a Mathematica Demonstration to allow us to easily manipulate the hive bee and forager per capita death rates as well as a reflection of brood mortality to create Phase Plane Diagrams for our model on a custom scale.

1 Introduction

Labor tasks among honey bees differ by age: the younger hive bees $H$ perform maintenance tasks within the hive and the older forager bees $F$ perform more hazardous tasks outside the hive, such as collecting nectar, pollen, or water. Some factors contributing to the honey bee colony losses include Varroa mites, viruses, brood diseases, pesticides, inadequate nutrition, climate and seasonal changes, and the stresses of moving colonies for crop pollination. A new condition, Colony Collapse Disorder (CCD), describes mass colony deaths with no clear cause, and CCD features empty hives with dead brood and very few adult bees, yet adequate food stores, all signs of rapid depopulation. No one agent is thought to cause CCD [5], and lacking specific evidence, CCD is blamed on a combination of the multiple stressors listed above. Factors such as pesticide-contaminated pollen in food stores or Varroa mites would adversely affect hive bee mortality; thus it is important to take a hive bee death rate into consideration when creating a model.

2 Preliminaries

2.1 Bee Biology

Recent reports of globally declining bee populations have prompted interest in mathematical models to study decreasing bee populations within a colony. To represent declining honey bee populations with a mathematical model, it is important to understand some basic bee biology that will help create an accurate model. First, the three castes of bees are worker, queen, and drone. The worker and queen bees are both females and come from fertilized eggs. The queen bee is differentiated from a worker bee as a young larva when she is fed royal jelly. (See Figure 1.) Each colony typically has one queen. The drone bees are males and come from unfertilized eggs. Their only purpose is to mate with the queen, after which they die. A typical colony has between 40,000 to 60,000 bees.
The three castes of bees all go through the same four major stages of development - egg, larva, pupa, and adult; however, the average development time varies by caste. All three castes hatch from the egg after three days, but then the queen develops faster than the worker and drone bees, with an average total time from egg to adult emergence of 16 days compared to 21 days for worker bees and 24 days for drones [6]. (See Figures 2 and 3.)
The lifespan of a honeybee varies by the season, with worker bees surviving the longest in the winter, followed by the spring and fall, and having the shortest lifespan in the summer. On average, a worker bee lives around 140 days in the winter, 30 to 60 days in the spring and fall, and between 15 and 38 days in the summer. Drone bees have a life span between 21 and 32 days in spring and early summer, and about 90 days from mid-summer to fall. In the winter, the drone bees are expelled from the hive, so they typically do not survive. The lifespan for a typical queen bee is between 1 and 3 years [6]. Many factors affect worker bee lifespan. Worker bees live the longest in the winter because they are relatively inactive and have slower metabolic rates in comparison to the summer. Besides the season, viruses and brood diseases, such as nosema, are also a factor in determining lifespan, as is the availability of food with proper nutrition. Certain activities that put bees at risk for predation, such as foraging, as well as nest defense from humans or other animals, swarming, and differences between subspecies, decrease a bee’s overall lifespan [6].

The two types of worker bees are hive bees and forager bees. Hive bees are typically the younger bees, while the older bees begin foraging around 18 days of age. Around 25 percent of a colony’s bees work as foragers on any given day [3]. It is common to see overlap in duties performed between ages, however, as bees can perform multiple tasks. Within the hive, the youngest hive bees are responsible for tasks such as cleaning cells and tending to the brood and queen. When they are around 8 days old, they begin receiving nectar, handling pollen, building comb, and cleaning debris from the hive. As they get older and approach the transition from a hive bee into a forager, the younger bees begin doing tasks outside of the hive such as ventilating, patrolling, guard duty, and going on orientation flights so that they know the hive location once they start foraging. The older bees then begin foraging for nectar, pollen, water, and propolis, which is used as a sealant for the hive [6].

Social inhibition plays a role in the transition to foraging, as older forager bees transfer ethyl oleate to younger hive bees by mouth-to-mouth feeding, or trophallaxis, to delay their conversion to foragers [2]. In fact, an absence of hive bees will prompt foragers to revert to being a hive bee. Huang and Robinson [7] found that reverted nurse bees can regain the ability to feed brood even in colonies with no brood, due to hypopharyngeal gland regeneration. Alternatively, a decrease in forager bees will prompt younger hive bees to become foragers earlier, known as precocious foraging. Precocious foragers are weaker and less effective than foragers who begin foraging at the normal age. Precocious foraging shortens a bee’s overall lifespan, as foragers typically only live from four to five days after the onset of foraging because foraging is more dangerous. Thus, forager death rates increase even more to accelerate population decline. As more and more hive bees convert from hive bees to foragers, fewer hive bees are left to care for the brood, which in turn also accelerates population decline [6].

Recently various factors have resulted in a trend of globally declining bee populations. Some of the major factors include parasitic mites, such as Varroa destructor, viruses and brood diseases, such as nosema, the Small Hive Beetle (although this is more of a regional factor), pesticides, inadequate nutrition, climate and seasonal changes, and changes in bee management. Deformed wing virus, transferred by the Varroa mite’s bite and characterized by underdeveloped wings, is also a mortality factor as it causes premature death. In addition, Colony Collapse Disorder has emerged with no single known cause, but it is instead thought to be multi-causal. (See Figure 4.) Colony Collapse Disorder is characterized by vacant hives with dead brood and adequate food stores, but no adult bees to take care of the brood and keep them warm [4].
2.2 Definitions

Before describing a model that uses differential equations to model honeybee populations, it is important to understand some basic terminology. A system of differential equations

\[
\begin{align*}
\frac{dx}{dt} &= f(x, y) \\
\frac{dy}{dt} &= g(x, y)
\end{align*}
\]

is considered to be **autonomous** when \( f \) and \( g \) do not depend explicitly on the independent variable, time \( t \). That is, for an autonomous system we have \( f(x, y) \) and \( g(x, y) \), not \( f(t, x, y) \) and \( g(t, x, y) \). A system of differential equations is said to be **nonlinear** when \( f(x, y) \neq ax + by + h_1 \) and \( g(x, y) \neq cx + dy + h_2 \) for constants \( a, b, c, d, h_1, \) and \( h_2 \). A **solution** of a system is two differentiable functions, \( x \) and \( y \), that satisfy both the system’s equations. The **orbit** of a solution pair \((x, y)\) on an interval \( a < t < b \) is the set of points \((x, y)\) for \( a < t < b \) as graphed in the **Phase Plane**, or \( xy\)-plane. The **Phase Plane Diagram** is the graphical representation of solutions in the Phase Plane. An **equilibrium** of a system of differential equations is a constant pair \((x_e, y_e)\) that occurs when both \( f(x, y) = 0 \) and \( g(x, y) = 0 \). Note that an equilibrium \((x_e, y_e)\) is a solution of the system.

An equilibrium is said to be **hyperbolic** when its eigenvalues, \( \lambda \), have nonzero real parts. (See below.) If an equilibrium is **unstable**, then some solutions move away from the equilibrium as time approaches infinity. An equilibrium is **stable** if all nearby solutions approach the equilibrium as time approaches infinity. According to the **Linearization Principle**, the hyperbolic equilibrium of an autonomous equation, \( \frac{dx}{dt} = f(x) \), has the same stability as the linearization of the equation at the equilibrium. For a one-dimensional nonlinear differential equation, \( \frac{dx}{dt} = f(x) \), we use the tangent line at \( x_e \) to approximate \( f(x) \). Thus, the linearization of \( \frac{dx}{dt} = f(x) \) is \( \frac{du}{dt} = \frac{df}{dx}(x_e) \cdot u \) where \( u = x - x_e \). The Linearization Principle can be extended to systems of differential equations, using a tangent plane to a surface \( z = f(x, y) \). Here the approximations for the system become

\[
\begin{align*}
f(x, y) &\approx f(x_e, y_e) + a(x - x_e) + b(y - y_e) \\
g(x, y) &\approx g(x_e, y_e) + c(x - x_e) + d(y - y_e)
\end{align*}
\]
Since $\frac{dx}{dt} = 0$ and $\frac{dy}{dt} = 0$ at the equilibrium $(x_e, y_e)$, $f(x_e, y_e) = 0$ and $g(x_e, y_e) = 0$. Here the coefficients $a, b, c$, and $d$ are determined by the Jacobian Matrix, $J(x_e, y_e)$, evaluated at the equilibrium $(x_e, y_e)$. We define the Jacobian Matrix as follows

$$J(x_e, y_e) = A = \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix} \bigg|_{(x_e, y_e)}$$

Let $u = x - x_e$ and $v = y - y_e$. Then this implies that $\frac{du}{dt} = \frac{dx}{dt}$ and $\frac{dv}{dt} = \frac{dy}{dt}$ so the linearization of the nonlinear system is

$$\begin{cases} \frac{du}{dt} = au + bv \\ \frac{dv}{dt} = cu + dv \end{cases}$$

and the linearization approximates the above nonlinear system near the equilibrium $(x_e, y_e)$.

We determine the eigenvalues $\lambda_1$ and $\lambda_2$ of the system by finding the roots of the characteristic equation obtained by taking the determinant of the Coefficient Matrix (or in the case of a linearized system, the Jacobian Matrix) minus $\lambda \cdot I$

$$|A - \lambda \cdot I| = \left| \begin{pmatrix} a - \lambda & b \\ c & d - \lambda \end{pmatrix} \right| = \lambda^2 - (a + d)\lambda + (ad - bc) = 0$$

where $I$ refers to the 2x2 identity matrix $\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$.

An equilibrium is locally neutrally stable if all orbits starting close to $t = t_0$ will stay close to the equilibrium for all $t > t_0$. It is locally asymptotically stable, or simply stable, if all orbits starting close to the equilibrium approach the equilibrium as $t$ approaches infinity. In addition to stability, we can classify an equilibrium by type - either a node, saddle point, spiral point, or center. A stable node occurs when the eigenvalues are real, distinct and negative. If the eigenvalues are real, distinct, and positive, then the equilibrium is an unstable node. An equilibrium is a saddle point when the eigenvalues are real, distinct and have opposite signs. When the eigenvalues are real and the same, the equilibrium is considered to be an improper node. When the eigenvalues are complex numbers with a non-zero real part, the equilibrium is considered a stable spiral point if the real part is negative. If the real part is positive, then an unstable spiral point occurs. Lastly, a neutrally stable center occurs when the eigenvalues are pure imaginary numbers. Using the Interactive Differential Equations program, we obtain Phase Plane Diagrams for these types of equilibria in Figures 5, 6, and 7 below.

![Phase Plane Diagrams](image)

Figure 5: Phase Plane Diagrams of a stable node [left] and an unstable node [right]
Theorem 2.1. The equilibrium \((x_e, y_e)\) of the nonlinear system has the same general type (node, saddle point, or spiral point) and stability (stable or unstable) as the equilibrium of the linearized system with two exceptions. First, if the eigenvalues of the Jacobian Matrix \(A\) are equal, the equilibrium may be a node or a spiral point for the nonlinear system. Second, if the eigenvalues of \(A\) are pure imaginary, the equilibrium may be a center or a spiral point.

Theorem 2.2. Let \(\lambda_1\) and \(\lambda_2\) be the eigenvalues of the Jacobian Matrix \(A\) for an equilibrium \((x_e, y_e)\). If \(\lambda_1\) and \(\lambda_2\) are negative real numbers or are complex with negative real parts, then the equilibrium is stable. If \(\lambda_1\) and \(\lambda_2\) are pure imaginary numbers, then the equilibrium is neutrally stable. The equilibrium is unstable if \(\lambda_1\) and \(\lambda_2\) have at least one positive real part, i.e. if they are both positive real numbers, are both real numbers with opposite signs, or they are complex numbers with positive real parts.

It is also possible, and simpler in many cases, to determine the phase plane portrait of a system without finding the eigenvalues and instead looking at the signs of the trace and determinant of the coefficient matrix, given by the Jacobian Matrix for a linearized system. The trace of a matrix is denoted \(trA\) and is equal to \(a + d\). The determinant of a matrix is denoted \(detA\) and is equal to \(ad - bc\). Then, the characteristic equation can be represented as \(\lambda^2 - (trA)\lambda + (detA) = 0\). Using the quadratic formula, we find the eigenvalues

\[
\lambda = \frac{trA \pm \sqrt{(trA)^2 - 4detA}}{2}
\]

Representing \(a, b, c,\) and \(d\) from the Jacobian Matrix \(A\) as \(A, B, C,\) and \(D\), \(trA\) as \(p\), \(detA\) as \(q\) and \(\Delta\) as \((trA)^2 - 4detA\), Figure 8 shows how the signs of these numbers determine the type and stability with Phase Plane Diagrams.

Theorem 2.3. An equilibrium point \((x_e, y_e)\) is stable if both \(trA < 0\) and \(detA > 0\) hold at the point \((x, y) = (x_e, y_e)\).
Differential equations can be used to model the effect of different factors on colony failure. Specifically, a single-colony model derived by Khoury, Myerscough, and Barron [1], that uses two differential equations to describe the interaction between hive bee and forager bee populations, models the effects of forager death rate on colony decline. Let $H$ be the number of hive bees and $F$ be the number of forager bees. The time, $t$, will be measured in days. $L$ will represent the maximum laying rate of the queen, $w$ will be a reflection of brood mortality, $\alpha$ will represent the maximum rate at which hive bees will become foragers, and $\sigma$ will represent social inhibition. The rate of change of hive bee populations is then modeled by the equation

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

(1)

where the first term represents the emergence of hive bees from brood and the second term subtracts the hive bee population that transitions to foraging.

In the first term of (1), $\frac{L(H + F)}{(w + H + F)}$, it is assumed that the maximum rate of emergence is equivalent to the queen’s laying rate, and as the total number of worker bees, $H + F$, increases, the brood mortality factor, $w$, represents the rate at that which emergence approaches the total laying rate. Larger $w$ values reflect lower emergence rates from brood to adult. In the second term of (1), the rate that hive bees transition to foragers is proportional to the number of hive bees in the colony. The rate itself is represented by the maximum rate at which hive bees will become foragers, $\alpha H$, subtracting the factor of social inhibition, $\sigma \left( \frac{F}{H + F} \right)$, which inhibits hive bees from transitioning to foragers. The social inhibition term, $\sigma \left( \frac{F}{H + F} \right)$, is directly proportional to the number of foragers in the colony.

In addition, the differential equation

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

(2)

models the rate of change of the forager bee population. Here, the first term is identical to the second term in (1) $\frac{dH}{dt}$ as we are now adding the number of bees transitioning from hive bees into
the forager bee population. The second term of (2) is a subtraction of the term \( mF \) to represent forager death rate per day. Here \( m \) is the per capita death rate of foragers, which represents forager death rate as proportional to the forager population. We were able to replicate the results of Khoury et al and find an equilibrium \((H_e, F_e)\), where

\[
F_e = \frac{L}{m} - \frac{J}{J+1}, \quad H_e = \frac{1}{J} F_e
\]

\[
J = \frac{1}{2m} \left( \alpha - \sigma - m + \sqrt{(m + \sigma - \alpha)^2 + 4\alpha m} \right)
\]

Note that \( J > 0 \) so that \( H_e > 0 \) for \( F_e > 0 \). When

\[
m < \frac{L}{2w} \left( \frac{\alpha + \sigma + \sqrt{(\alpha - \sigma)^2 + 4L\sigma w}}{\alpha - \frac{L}{w}} \right) \quad \text{and} \quad \alpha - \frac{L}{w} > 0,
\]

a globally stable equilibrium occurs. This result means that when the conditions in (2a) are met, for any positive initial condition \((H_0, F_0)\) the orbit of (1) and (2) approaches the equilibrium \((H_e, F_e)\) as time \( t \) increases to infinity.

4 Our Model

While Khoury, Myerscough, and Barron considered the death rate of hive bees to be negligible, we have extended their model to consider hive bee death rate with the addition of the parameter \( \mu \). Assuming the per capita death rate of hive bees, \( \mu \), is proportional to the number of hive bees, we will now let

\[
\frac{dH}{dt} = \frac{L(H + F)}{(w + H + F)} - H \left( \alpha - \sigma \left( \frac{F}{H + F} \right) \right) - \mu H
\]

The equation for (2), \( \frac{dF}{dt} \), is not affected by this new parameter, \( \mu \). We will assume that \( \mu \) is proportional to \( m \), so that \( \mu = k \cdot m \) for some positive constant \( k \) where \( 0 < k < 1 \), because bees typically work as hive bees longer than they are foragers. Thus our model is represented by the system

\[
\begin{align*}
\frac{dH}{dt} &= \frac{L(H + F)}{(w + H + F)} - H \left( \alpha - \sigma \left( \frac{F}{H + F} \right) \right) - kmH \\
\frac{dF}{dt} &= H \left( \alpha - \sigma \left( \frac{F}{H + F} \right) \right) - mF
\end{align*}
\]

4.1 Equilibrium

To find the equilibrium \((H_e, F_e)\) of this system, we will set both equations equal to zero.

\[
\frac{dH}{dt} = \frac{L(H + F)}{(w + H + F)} - H \left( \alpha - \sigma \left( \frac{F}{H + F} \right) \right) - kmH = 0 \quad (4)
\]

\[
\frac{dF}{dt} = H \left( \alpha - \sigma \left( \frac{F}{H + F} \right) \right) - mF = 0 \quad (5)
\]
From (5),

\[ H \left( \alpha - \sigma \left( \frac{F}{H+F} \right) \right) = mF \]

So (4) becomes

\[ \frac{L(H+F)}{(w+H+F)} - mF - kmH = 0 \] (6)

Following the procedure of Khoury et al, we let \( H = \frac{1}{J} F \Rightarrow F = JH \). Then, (6) becomes

\[ \frac{L(H + JH)}{w + H + JH} - mJH - kmH = 0 \]
\[ \Rightarrow \frac{LH(1 + J)}{w + H(1 + J)} - mH(J + k) = 0 \]
\[ \Rightarrow LH(1 + J) = mH(J + k)(w + H(1 + J)) \]

Dividing by \( H \neq 0 \) and expanding the product on the right hand side leads to

\[ \Rightarrow L(1 + J) = mJw + mJH(1 + J) + mkw + mkH(1 + J) \]
\[ \Rightarrow L = \frac{mJw + mkw}{1 + J} + mJH + mkH \]
\[ \Rightarrow L - \frac{mJw + mkw}{1 + J} = H(mJ + mk) \]
\[ \Rightarrow H = \frac{L}{m(J + k)} - \frac{mJw + mkw}{(1 + J)(mJ + mk)} \]
\[ \Rightarrow H_e = \frac{L}{m(J + k)} - \frac{w}{1 + J} \]

From \( F = JH \),

\[ F_e = J \left[ \frac{L}{m(J + k)} - \frac{w}{1 + J} \right] \]

To solve for \( J \), we substitute \( F = JH \) into (5) to obtain

\[ H \left( \alpha - \sigma \left( \frac{JH}{H+JH} \right) \right) - mJH = 0 \]
\[ \Rightarrow H \left( \alpha - \sigma \left( \frac{J}{1 + J} \right) - mJ \right) = 0 \]

Assuming \( H \neq 0 \),

\[ \alpha - \sigma \left( \frac{J}{1 + J} \right) - mJ = 0 \]
\[ \Rightarrow \alpha - mJ = \sigma \left( \frac{J}{1 + J} \right) \]
\[ \Rightarrow J^2 + \left( -\frac{\alpha}{m} + \frac{\sigma}{m} + 1 \right) J - \frac{\alpha}{m} = 0 \]
We pick $J$ to be the positive solution of the quadratic so that $F_e > 0$

$$\Rightarrow J = \frac{1}{2} \left[ \left( \frac{\alpha}{m} - \frac{\sigma}{m} - 1 \right) + \sqrt{\left( \frac{\alpha}{m} - \frac{\sigma}{m} - 1 \right)^2 + 4 \frac{\alpha}{m}} \right]$$

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

as in the model of Khoury et al. Thus, we find an equilibrium $(H_e, F_e)$ where

$$F_e = \frac{L}{m(J + k) - \frac{w}{1 + J}} \quad \text{and} \quad H_e = \frac{1}{J} F_e$$

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

### 4.2 Global Stability of Equilibrium

To determine when there is global stability at the equilibrium $(H_e, F_e)$, we first find the Jacobian Matrix as follows:

$$A = J(H_e, F_e) = \left( \begin{array}{cc} -km + \frac{Lw}{(F+H+w)^2} - \alpha + \frac{F^2\sigma}{(F+H)^2} & \frac{Lw}{(F+H+w)^2} + \frac{H^2\sigma}{(F+H)^2} \\ \frac{F^2\sigma}{(F+H)^2} & -m - \frac{H^2\sigma}{(F+H)^2} \end{array} \right)_{(H_e, F_e)}$$

Calculating the trace of the Jacobian Matrix $A$, we obtain

$$trA = \left( -km + \frac{Lw}{(F+H+w)^2} - \alpha + \frac{F^2\sigma}{(F+H)^2} \right) + \left( -m - \frac{H^2\sigma}{(F+H)^2} \right)$$

$$= -m - km + \frac{Lw}{(F+H+w)^2} - \alpha + \frac{(F-H)\sigma}{F+H}$$

Evaluated at the equilibrium $(H_e, F_e)$, the trace becomes

$$trA_e = \frac{(J+k)^2m^2w - (1+J)L((1+J)(1+k)m + \alpha + J\alpha + \sigma - J\sigma)}{(1+J)^2L}$$

Next we calculate the determinant of $A$ as follows

$$detA = \left( -km + \frac{Lw}{(F+H+w)^2} - \alpha + \frac{F^2\sigma}{(F+H)^2} \right) \cdot \left( -m - \frac{H^2\sigma}{(F+H)^2} \right)$$

$$- \left( \frac{Lw}{(F+H+w)^2} + \frac{H^2\sigma}{(F+H)^2} \right) \cdot \left( \alpha - \frac{F^2\sigma}{(F+H)^2} \right)$$

$$= m \left( \alpha - \frac{F^2\sigma}{(F+H)^2} \right) + km \left( m + \frac{H^2\sigma}{(F+H)^2} \right) - \frac{Lw(F(m+\alpha - \sigma) + H(m+\alpha + \sigma))}{(F+H)(F+H+w)^2}$$

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At \((H_e, F_e)\), we have

\[
\det A_e = -\frac{1}{(1+J)^3L} \left[ -L\alpha - 3JL\alpha + k^2 mw(m + Jm + \alpha + J\alpha + \sigma - J\alpha) \\
+ J^2 (m^2 w + mw(\alpha - \sigma) + L(-\alpha + \sigma)) + J^2 (m^2 w + L(-3\alpha + \sigma) + mw(\alpha + \sigma)) \\
- k ((1+J)L ((1+J)^2m + \sigma) - 2Jmw(m + Jm + \alpha + J\alpha + \sigma - J\sigma)) \right]
\]

Since we are modeling a population, the equilibrium should also be positive. Assuming \(F_e > 0\),

\[
J \left[ \frac{L}{m(J+k)} - \frac{w}{1+J} \right] > 0
\]

\[\Rightarrow \frac{L}{w} > m \left( \frac{J+k}{J+1} \right)\]

Plugging (7) into \(\frac{J+k}{J+1}\), we obtain

\[
\frac{J+k}{J+1} = \frac{\frac{1}{2m} \left( \alpha - \sigma - m + \sqrt{(m+\sigma - \alpha)^2 + 4\alpha m} \right) + k}{\frac{1}{2m} \left( \alpha - \sigma - m + \sqrt{(m+\sigma - \alpha)^2 + 4\alpha m} \right) + 1}
\]

\[= \frac{\frac{1}{2m} \left( \alpha - \sigma - m + \sqrt{(m+\sigma - \alpha)^2 + 4\alpha m} + 2mk \right)}{\frac{1}{2m} \left( \alpha - \sigma - m + \sqrt{(m+\sigma - \alpha)^2 + 4\alpha m} + 2m \right)}
\]

\[= \frac{\alpha - \sigma - m + \sqrt{(m+\sigma - \alpha)^2 + 4\alpha m} + 2mk}{\alpha - \sigma - m + \sqrt{(m+\sigma - \alpha)^2 + 4\alpha m} + 2m}
\]

\[= \frac{(\alpha - \sigma) + m + 2mk + \sqrt{(m+\sigma - \alpha)^2 + 4\alpha m}}{(\alpha - \sigma) + m + \sqrt{(m+\sigma - \alpha)^2 + 4\alpha m}} \cdot \frac{(\alpha - \sigma) + m - \sqrt{(m+\sigma - \alpha)^2 + 4\alpha m}}{(\alpha - \sigma) + m - \sqrt{(m+\sigma - \alpha)^2 + 4\alpha m}}
\]

\[= \left( \frac{m^2 - m^2 k - mk\alpha + mk\sigma - \alpha m + \alpha m + m - (m - mk)\sqrt{(m+\sigma - \alpha)^2 + 4\alpha m}}{2\sigma m} \right)
\]

Hence

\[
m \left( \frac{m^2 - m^2 k - mk\alpha + mk\sigma - \alpha m + \alpha m - (m - mk)\sqrt{(m+\sigma - \alpha)^2 + 4\alpha m}}{2\alpha m} \right) < \frac{L}{w}
\]

\[\Rightarrow w \left( m^2 - m^2 k - mk\alpha + mk\sigma - \alpha m + \alpha m - (m - mk)\sqrt{(m+\sigma - \alpha)^2 + 4\alpha m} \right) < 2L\sigma
\]

\[\Rightarrow m^2 w - m^2 kw - mk\alpha w + mk\sigma w - \alpha mw + \sigma mw - 2L\sigma < mw(1-k)\sqrt{(m+\sigma - \alpha)^2 + 4\alpha m}
\]

\[\Rightarrow m^2 w(1-k) + mk\sigma w(\alpha - \alpha) + mw(\sigma - \alpha) - 2L\sigma < mw(1-k)\sqrt{(m+\sigma - \alpha)^2 + 4\alpha m}
\]

Checking our inequality with reasonable values of our parameters, both sides of the inequality are much larger than 1, so we find the inequality holds when both sides are squared. Note \(0 < k < 1\) and later we will see that in practice \(\sigma > \alpha\) and \(w > L\).
For stability, we need five days so switch from foraging back to hive bee tasks. For a healthy colony, foragers live between four and 

\[ \text{H} \approx 0.75 \because \text{Khoury et al cite a daily laying rate of a queen as 2000 eggs per day, a somewhat higher value than is truly realistic. Winston cites the daily laying rate of a queen as around 1500 eggs a day, so we will let } L = 1500 [6]. If there are no foragers in a hive, new workers will become foragers a minimum of 4 days after emergence; thus, let } \alpha = 0.25. The transition from hive bees to foragers is modeled by the function, \( T(H,F) = \alpha - \sigma \left( \frac{F}{H+F} \right) \), and since foragers switch back to hive bees if more than \( \frac{1}{3} \) of the colony are foragers, we set \( \sigma = 0.75 \) because \( \alpha - \sigma \left( \frac{F}{H+F} \right) = 0.25 - 0.75 \left( \frac{\alpha}{H+F} \right) = 0. \) If \( T \) is positive, this term means that less than \( \frac{1}{3} \) of the colony are foragers so bees are being recruited to be foragers, as we are subtracting the \( H \cdot T(H,F) \) term from (3) for \( \frac{dH}{dt} \). If \( T \) is negative, then more than \( \frac{1}{3} \) of the hive is foraging, and so the term is being added to (3) for \( \frac{dH}{dt} \) to model the switch from foraging back to hive bee tasks. For a healthy colony, foragers live between four and five days so \( m \approx \frac{1}{4} \) or \( \frac{1}{5} = 0.25 \) to 0.20. We will use \( m = 0.24 \) as a typical value for \( m \). In a healthy colony, hive bees live 18 days before foraging, so we will use \( \mu = \frac{1}{18} = 0.05 \approx 0.06 \) as a typical value for \( \mu \). We will let \( w = 10,000 \) to model a high emergence rate from brood to adult. At this low forager death rate, there is a positive equilibrium, as apparent in Figure 9, the Phase Plane Diagram for these parameters.
In fact, the persistence equilibrium occurs at \((H_e, F_e) = (3566, 1096)\). These parameters also satisfy the three conditions for stability, so we know that \((3566, 1096)\) is a stable node. These numbers are low for a normal-sized hive, but large for a mating nuc, or nucleus, hive. Increasing the forager bee death rate to \(m = 0.5\), yields a positive equilibrium at \((537, 120)\) as shown in Figure 10. Although the equilibrium values have decreased, these parameters still meet the three conditions for stability. This equilibrium would represent a fairly small mating nuc.

Increasing the forager death rate \(m\) to 0.6, we no longer obtain a positive equilibrium. Figure 11, the Phase Plane Diagram, shows that for a death rate this high, both the hive bee and forager bee populations approach zero. At this death rate, we find that the conditions for stability at a positive equilibrium are no longer met. Solving \(H_e = 0\) and \(F_e = 0\) for \(m\), we find solutions at \(m = 0.5837569\) and \(m = 0.132493\). While \(m = 0.132493\) is an extraneous solution, we find that when \(m = 0.5837569\), the system has a stable equilibrium at \((0,0)\). Increasing \(m\) past \(0.5837570\) no longer meets the conditions for stability. Thus, when \(\mu = 0.06\), for \(m < 0.5837570\), we have a stable positive equilibrium.
Using the parameter $m = .24$, we can also solve $H_e = 0$ and $F_e = 0$ to find the value of the hive bee death rate $\mu$ when there is a stable equilibrium at (0,0). We find this to occur at $\mu = 0.12234969$, as shown in Figure 12. For $\mu > 0.12234969$ the conditions of stability are no longer met.

To obtain larger populations, we must increase brood survivability as well as decrease the hive and forager bee death rates. For instance, decreasing $w$ to 9,000, $\mu$ to 0.0001 and $m$ to 0.175, we obtain a stable equilibrium $(H_e, F_e)$ at (18428,6271). (See Figure 13.)
6 Discussion of Results

Based on these results we can conclude that past a threshold level when forager and hive bee death rates are high, colony failure is inevitable as the hive bee and forager bee numbers are driven to zero. Assuming the hive bees live the normal 18 days before foraging, we find the populations of both hive and forager bees are driven to zero when the forager death is increased to $m = 0.5837569$, which represents a forager’s life span of 1.7 days compared to the typical four to five days. If we assume the foragers are living the typical four to five days, increasing the hive bee death rate to $\mu = 0.12234969$, representing a hive bee duration of 8.2 days, also drives both hive and forager bee numbers to zero. In the original model, Khoury, Myerscough, and Barron [1] used the parameter values $w = 27,000$ and $L = 2000$. For our model, we decreased $L$ to represent a more realistic queen laying rate, in addition to adding a term to represent hive bee death rate. Thus, as there are more factors decreasing adult bee population, brood survivability must increase to compensate, reflected in our model by an initial decrease in $w$ to $w = 10,000$. Realistically, however, it is hard to increase brood survivability as the colony needs enough hive bees to feed the brood and keep the brood warm. Furthermore, maintaining an egg-laying rate of 1500 could be difficult as the very young hive bees clean out the brood cells for the eggs. Moreover, an increased hive bee death rate would shut down the queen’s egg-laying if there were fewer hive bees to maintain the cells. To counteract these deleterious effects and achieve the desired larger colony population numbers, in addition to reducing both the hive and forager bee death rates, brood survivability must increase even more. Based on these results, we can conclude that smaller colony sizes occur, decreasing the colony’s fitness, which is its ability to carry its genes to the next generation.

7 Mathematica Model

![Mathematica Demonstration](image)

Figure 14: Screen Capture of Mathematica Demonstration
With such high population values, the Differential Systems program did not provide a window large enough to create the phase plane diagrams for our model without rescaling the model. After an extensive web search, we were unable to find a free, alternative software that would allow us to input our own system of differential equations to create a phase plane diagram. A Tour of Second-Order Ordinary Differential Equations contributed by Brian Vick to the Wolfram Demonstrations Project, allows a user to select a pre-defined system and change the values of one parameter to create a Phase Plane Diagram. For this project, we were able to change the original Mathematica code, to allow us to graph our model, change the window size, and change the values for multiple parameters. The resulting program graphs the phase portrait of \( H \) versus \( F \) and allows the parameter values to be changed using a slider or by manual input. The code is included in Appendix A.

To change the original demonstration to fit our needs, we must edit the existing code within the Initialization Code and Manipulate sections of the file. First, within the Initialization Code section, the (* systems *) section provides a list of preloaded functions for which the demonstration will graph solutions. To add our system of equations, we will add the line

\[
\text{bees}[x, y, \mu, m, w] := \{1500 \ast (x + y)/(w + x + y) - x \ast (0.25 - 0.75 \ast y/(y + x)) - \mu \ast x, \\
x \ast (0.25 - 0.75 \ast y/(y + x)) - m \ast y\}
\]

where ‘bees’ refers to the name of our function. Within the braces following bees, after \( x \) and \( y \), for each parameter we want to be able to manipulate, we list the parameter name followed by an underscore. For our model, since \( L, \alpha, \) and \( \sigma \) are constant, we will only include \( w, m, \) and \( \mu \). Here we will also delete the extra equations listed in the original demonstration.

The next modification occurs within the (* fixed points *) section. Within the braces of the fixedPoints function call, after \( f \), we must again add each parameter we want to manipulate followed by an underscore and within NSolve on the right hand side of the equation; after \( x \) and \( y \), we will list each parameter in the same order as in the function call, but without underscores. Under (* stability of the fixed points *) section, we must add the parameters with underscores to the stableQ parameter list. Within the stableQ function, we must add just the parameters within Eigenvalues\([D[f[x, y, \mu, m, w], \{x, y\}]])/.\text{fixedPoints}[f, \mu, m, w].\) Similarly, within the (* plot of fixed points *) section, we will add the parameters and underscores to the fixedPointsPlot, phasePortrait, and paraPlot function calls. We will add just the parameters to the stableQ, fixedPoints, and streamPlot function calls. Within the phasePortrait function, it is currently set to graph on the \( x \) and \( y \) axes from -1 to 1. We will change this setting to graph the desired range for our phase plane portrait. In the code included, this range is from 0 to 10,000 on the \( x \)-axis and 0 to 5,000 on the \( y \)-axis. Lastly, we need to add the list of parameters in the paraPlot function following \( y[t] \) in the lines \( x'[t] \) and \( y'[t] \).

Within the Manipulate section, first on the second and third lines in the phasePortrait and paraPlot function calls, we must list our added parameters directly following the ‘system’ and parameter. Then we must specify the range of \( x \) and \( y \) values to be included in the phase plane portrait. The original setting of \( \text{PlotRange} \rightarrow 1 \) means that it will plot points from -1 to 1 on both axes. For models of population, we need a larger range that does not need to include negative numbers. For our model, we will change the command to \( \text{PlotRange} \rightarrow \{(0,10000),(0,5000)\} \) to graph from 0 to 10,000 on the \( x \)-axis and 0 to 5,000 on the \( y \)-axis. These numbers should match the numbers used above in the phasePortrait function. Within the FrameLabel \rightarrow boxes, we can change the labels for the \( x \) and \( y \) axes. Within FrameTicks, we will also specify specific points to
label instead of having a range. Next, within the fixedPointsPlot function call, we must again add the parameters we want to manipulate after ‘system.’

If there is more than one system defined in the initialization code, the next line allows us to specify which system will be the default that is shown when the demonstration is initially run by listing the system name identical to how it was defined as the second parameter. For our model, we will change this code to \{\{system, bees, Our Model: \}, \}, where the third parameter is the text that will be displayed on the top left of the demonstration. Since we only have one system, we will delete the list of systems and the PopupMenu option and replace it with the name of our system, the text we want to be displayed on the demonstration, and the Appearance \rightarrow Labeled selection. Finally we will add a line for each parameter we will be manipulating in the following format

\{\{variable name, default value, text to be displayed to the left of the slider},
minimum value, maximum value, Appearance \rightarrow Labeled\},

to create the sliding bar for each parameter.

8 Future Plans

In the future, we plan to compare the predicted average lifespan with experimental data. We would also like to create a new model with different functions for the emergence rate from pupae and the transition rate to foraging.
A Mathematica Demonstration

(* conversion of cylindrical to rectangular systems *)
Cyl2Rect[fcyl_] :=
  FullSimplify[
    {fcyl[[1]]*Cos[θ] - r*Sin[θ]*fcyl[[2]], fcyl[[1]]*Sin[θ] + r*Cos[θ]*fcyl[[2]]}
    //. {r -> Sqrt[x^2 + y^2], Cos[θ] -> x.Sqrt[x^2 + y^2], Sin[θ] -> y.Sqrt[x^2 + y^2]}
]

(* systems *)
bees[x_, y_, µ_, m_, w_] :=
  {1500*(x + y)/(w + x + y) - x*(.25 - .75*y/(y + x)) - µ*x, 
    x*(.25 - .75*y/(y + x)) - m*y}

(* fixed points *)
fixedPoints[f_, µ_, m_, w_] := Chop[N Solve[f[x, y, µ, m, w] == 0, {x, y}]]

(* stability of the fixed points *)
stableQ[f_, µ_, m_, w_] :=
  Table[
    If[Re[eig[[1]]] < 0 && Re[eig[[2]]] < 0, True, False],
    {eig, Eigenvalues[D[f[x, y, µ, m, w], {{x, y}}]]/.fixedPoints[f, µ, m, w]}
    ]

(* plot of fixed points *)
fixedPointsPlot[f_, µ_, m_, w_] :=
  Join[{AbsoluteThickness[1]}, MapThread[If[Element[#2, Reals], If[#1, Disk[#2, .02], Unevaluated[Sequence[]]]]&,
    {stableQ[f, µ, m, w], {x, y} /. fixedPoints[f, µ, m, w]}]]

phasePortrait[f_, µ_, m_, w_, streamPts_] :=
  First[StreamPlot[f[x, y, µ, m, w], {x, 0, 10000}, {y, 0, 5000}, StreamPoints -> streamPts]]
paraPlot[f_, µ_, m_, w_, xy0_, tmax_] :=
  Module[{sol, tp},
    sol = Quiet@NDSolve[
      {x'[t] == f[x[t], y[t], µ, m, w][[1]],
        y'[t] == f[x[t], y[t], µ, m, w][[2]],
        x[0] == xy0[[1]],
        y[0] == xy0[[2]]},
      {x, y},
      {t, 0, tmax}];
\[ tp = 0.99 \times \text{Min}[t_{\text{max}}, \text{sol}[[1, 1, 2, 1, 2]]]; \]

\[
\text{First}\@\text{ParametricPlot[}
\quad \text{Evaluate[}\{x[t], y[t]\}/.\text{sol}],
\quad \{t, 0, tp\},
\quad \text{PlotStyle} \to \{\{\text{Thickness[0.005], Blue}\}\}
\]
\]

\[ \text{Manipulate[}
\quad \text{Graphics[}\{\text{Dynamic[phasePortrait[system, }\mu, m, w, \text{streamPts]}],}
\quad \quad \text{Dynamic[paraPlot[system, }\mu, m, w, xy0, t_{\text{max}}]]},
\quad \quad \text{PlotRange} \to \{\{0, 10000\}, \{0, 5000\}\}, \text{Frame} \to \text{True}, \text{FrameLabel} \to \{\text{Style[Hive Bees H, 12]},
\quad \quad \text{Style[Forager Bees F, 12]}\}, \text{PlotRangeClipping} \to \text{True},
\quad \quad \text{FrameTicks} \to \{\{0, 500, 1500, 2500, 3000, 3500, 4000, 4500, 5000\}, \text{None}\},
\quad \quad \{0, 1000, 2000, 3000, 4000, 5000, 6000, 7000, 8000, 9000\}, \text{None}\}\},
\quad \text{Epilog} \to \text{Dynamic[fixedPointsPlot[system, }\mu, m, w]]},
\quad \{\{\text{system, bees, Our Model;}\},
\quad \{\text{bees} \to 1500(H+F)/(w+H+F)-H(.25-.75F/(H+F))-\mu H, H(.25-.75F/(H+F))-mF\},
\quad \quad \text{Appearance} \to \text{Labeled}\},
\quad \{\{\mu, 0.06, \text{parameter } \mu\}, 0, 1, \text{Appearance} \to \text{Labeled}\},
\quad \{\{m, 0.24, \text{parameter } m\}, 0, 1, \text{Appearance} \to \text{Labeled}\},
\quad \{\{w, 10000, \text{parameter } w\}, 5000, 50000, \text{Appearance} \to \text{Labeled}\},
\quad \{\{xy0, \{0.5, 0.5\}\}, \{-1, -1\}, \{1, 1\}, \text{Locator}\}, \{\{t_{\text{max}}, 10, t_{\text{max}}\}, 0.01, 15, \text{Appearance} \to \text{Labeled}\},
\quad \{\{\text{streamPts, Coarse, stream points}\}, \{\text{None, Automatic, Coarse, Medium, Fine}\}\},
\quad \text{SaveDefinitions} \to \text{True, SynchronousUpdating} \to \text{False},
\quad \text{AutorunSequencing} \to \{\{1, 15\}, 2, 3, 4\}\]
\]
References


