Influence of brood deaths on Honey Bee population dynamics and the potential impact of insecticides

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Abstract—Honey bees (Apis mellifera) are responsible for pollinating nearly 80% of all food-producing plants, therefore, the success or failure of a colony is vital to global food production. However, not all insects are beneficial to humankind and sometimes it is necessary to reduce the population of disease-carrying mosquitoes by using insecticides. These chemical products not only affect mosquitoes but other insects such as Honey bees, causing imbalances across most ecosystems around the world. Our goal is to describe the influence of brood deaths on Honey Bee population dynamics and the potential impact of insecticides on these natural changes. We constructed a compartmental model using ordinary differential equations to describe brood birth, mortality, maturation and how the newly emerged adults live and die. To obtain our parameters we used data from 1975-76 to estimate the parameters in order to see how well our model fits the data. Finally, we implemented seasonality in our simulations to describe how the queen’s egg-laying rate changes in time. Finally we can conclude that approximately the half of the brood bees must die daily for the extinction of the population. However for the seasonality model we find that changing the brood death rate certainly changes the population dynamics but have no long time effect on the honey bee population dynamics.

I. INTRODUCTION

Western honey bees (Apis Mellifera) are a type of eusocial insect (an insect that has an advanced level of social organization, in which a single female produces the offspring and non-reproductive individuals cooperate in caring for the young ones) that forms complex colonies [22]. In these colonies every members’ livelihood depends on the other members’ well-being for the sake of colony survival [10]. A honeybee colony can be classified into several castes: brood (eggs, larvae), sealed brood (pupae), queens, male drones, and infertile female workers. The drones sole purpose in life is to mate with a queen during seasonal nuptial flights and die soon after. The queen's purpose is to lay eggs. When a virgin queen emerges from her cell, she quickly searches for other virgin queens and kills them. She then searches for a mate and begins to produce eggs. It takes about 21 days for a bee to go from an egg to an adult. When they emerge, they are adult workers. As an adult worker ages, their tasks move form within the hive to outside the hive. Tasks adults perform include brood care, hive maintenance, and foraging [13]. Honey bees produce food for themselves, the queen, and their brood (eggs and larvae). Besides producing honey for human consumption, they also actively pollinate many types of plants.

The general dynamics of the honey bees population follows a seasonal pattern that depends on resource availability. During Spring months (April, May and June), due to an increase in the day length and pollen availability, the birth rate exceeds the death rate leading the bee population to grow. The peak of the population is achieved around late June and remains high until the middle of summer when it begins to decline. The drop in the population continues through the fall and winter and reaches its seasonal low during February. Regarding the brood, the queen's egg-laying rate is very low during the late winter and starts increasing rapidly during the spring to take advantage of the blooming period. During the summer this rate stays high but lower than Spring levels and through the fall it may be a second peek in the egg-laying rate due to the blooming of certain species such as iron weed. After this brief recovery the rate drops to reach zero by December [10].

However, in the Winter of 2006-2007 and subsequently 2007-2008, beekeepers noticed a strange phenomena. They found hives abandoned by their inhabitants, only to find scarce amounts of honey and little to no brood and worker bees. This phenomena is known as Colony Collapse Disorder [5] and has lead to a decrease of 40 to 50% of the total honey bees colonies in the US and a decrease of 5 to 10% of the total colonies in the rest of the world [16]. Nevertheless, this is not the only situation that has been reported about Honey Bees population decreasing. During
the past few years different organizations have alarmed society about the decrease of honey bee populations and how this could have a substantial impact on food production and biodiversity.

Many studies have been conducted to explore what type of stressors lead to colonies collapse in general [5]. There are many suspected causes that lead to the failure of honey bee colonies. Such causes include parasites, pathogens, agricultural pesticides, beekeeper applied chemicals, genetically modified crops, insecticides, and changed cultural practices [14], [17]. Between all these causes the ones that are thought to have a greater impact are the use of chemicals such as pesticides and insecticides due to numerous surveys that have revealed high levels of both type of chemicals residue contamination in honey bee combs [23].

Vector-borne diseases are among the major causes of illness and death, particularly in tropical and subtropical countries [19]. Vector control, through the use of insecticides, plays a key role in the prevention and control of infectious diseases such as malaria, dengue, and filariasis [15]. This implies a frequent use of these chemicals and therefore a larger risk in Honey bee population. In table 1 are shown some of the most commonly used insecticides, to threat infectious diseases, that also represent a high risk for bees.

<table>
<thead>
<tr>
<th>Chemical</th>
<th>Bees risk</th>
<th>Mosquito affected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorpyrifos</td>
<td>High</td>
<td>Ae. aegypti, Ae. albopictus, Cx. molestus, Cx. pipiens, Cx. tarsalis.</td>
</tr>
<tr>
<td>Permethrin</td>
<td>High</td>
<td>Ae. aegypti, Ae. albopictus.</td>
</tr>
<tr>
<td>Fenthion</td>
<td>High</td>
<td>Ae. aegypti, Ae. albopictus.</td>
</tr>
<tr>
<td>Malathion</td>
<td>High</td>
<td>Ae. aegypti, Ae. albopictus, Cx. molestus, Cx. pipiens, Cx. tarsalis.</td>
</tr>
<tr>
<td>Naled</td>
<td>High</td>
<td>Ae. aegypti, Ae. albopictus, Cx. molestus, Cx. pipiens, Cx. tarsalis.</td>
</tr>
</tbody>
</table>

Table 1
ACTIVE CHEMICALS USED IN INSECTICIDES FOR INSECT VECTORS CONTROL, WHICH ALSO REPRESENT A HIGH RISK FOR HONEY BEE POPULATION.

There are multiple ways these chemicals affect Honey bee population dynamics. With respect to the queen, pesticides lead to the decrease of fecundity. With respect to the workers, the increase of pesticide leads to higher death rates and a reducton in their longevity. And as for the brood, an increase in pesticide leads to an increase in their death rates (due to the decrease of workers and therefore the lack of the care they need to receive in order to survive), and a delay in the maturation of the brood by an increase of a day or two [23]. A growing body of evidence shows that sub-lethal doses of other pesticides, such as Neonicotinoid, have the potential to induce a variety of behavioural difficulties in foraging honeybees, such as memory and learning dysfunctions and impairment of navigational skills by Thiamethoxam [7].

In order to approach to the problem, and considering the difficulty of observing Honey Bee population dynamics directly, it becomes necessary to develop a mathematical model to understand what factors have a larger influence in bees population. Several mathematical models have been developed to describe the dynamics of honey bee populations and the impact of anthropogenic stressors, particularly pathogens, parasites, and nutritional stressors, on the long-term viability of a colony [1–4], [6–11], [17], [20].

Of these previous studies, the most relevant are those of Khoury et al.(2011) in which a model was established to study different death rates of foragers and their impact on colony growth and development [9], [10]. Russell et al.(2013) examined the sensitivity of a colony by looking into seasonal variations, rates of forager mortality, food availability and factors that influence the transition age of worker to forager through discrete data [20]. Perry et al.(2015) conducted a case study and collected data to examine food shortage and the impact of rapid maturation on the success of a honeybee colony [17]. Finally, Henry et al.(2012) conducted experiments on foragers to see upper and lower bounds for forager death rates that included homing failure [7].

However, all of these models neglect the death rates of the brood (instead focusing on foraging bee death rates). Thus none of these models directly explore the potential of brood death that may lead to colony collapse. Our model is novel in that we propose a mathematical model that will explore the influence of brood death rate (as an effect of insecticides exposition) has on the dynamics of honeybee populations, while implementing the effects of seasonality in the egg laying rate. To our knowledge, our approach is the first to affirm mathematically that brood death rates may have an insignificant effect on honeybee colony and it is also the first to implement seasonality (which no other model has done before). The objective of our paper is three-fold:

1) Use differential equations to provide a tool to analyze mechanism underlying colony level patterns of population dynamics.
2) To understand the role of brood mortality in honey bee population dynamics.
3) This model will give us realistic predictions for honeybee population levels, and allows us to identify critical periods in growth that we can then perform other experiments to see how sensitive the honey bee colony may be at those points to population changes.

In order to achieve these goals, the model parameters where estimated based from the data found in Harrison's 1980 data. We used least squares likelihood fit on the differences in populations and Negative Binomial distribution on the
count data in order to estimate brood death rate, worker
death rate, and the number of adults needed to have
half the maximum egg laying rate (and their confidence
intervals) [6], [12].

II. Real Data

We use the data of Harrison (1980) which was collected
from a 0.9 kg of worker bees and was recorded for two
years [6]. Colonies were hived from packages containing
0.9 kg of worker bees (approximately 7000 worker bees),
and a mated queen of a yellow strain on April 24th, 1975
and April 22nd, 1976. During both years, the colonies were
located in commercial apiaries. Every 12 days, Harrison et.
al (1980) would hand count the number of sealed brood,
and using his algorithm in his thesis, estimate the number
of eggs, larvae, pupae, and adult bees in a single hive
weekly, from May 5th 1975, to October 22, 1975 and once
again from May 3rd 1976, to December 5th 1976. They
then provide a list of the time series data. For our model,
We take the sum of eggs, larvae, and pupae to be the
number of brood. We take the sum of adult bees younger
than 19 days and adult bees older than 19 days to be the
total amount of adults(see Figure 1).

To verify his estimation method, Harrison hand counts
the total population of each colony (20 colonies) and
used his estimation method to obtained the predicted
total population. Most differences were under 4000 bees,
in colonies where there can be over 80,000 bees(14/20
colonies had deviations under 4000 bees), with the greatest
deviation being 8427 bees from the actual data.

Also, it is important to mention that this data was taken
from colonies who were in no danger of contamination of
pesticides, therefore it shows a behaviour of bees under
neutral conditions.

III. Standard Model: Holling Type III Birth

Here we present our findings for our model with
the Holling Type 3 functional response using ordinary
differential equations (ODEs).

Let $B(t)$ be the number of brood (eggs, larvae, pupae) in a
given hive at time $t$ and let $H(t)$ be the number of adult
bees in a given hive at time $t$. The time $t$ will be in units of
every 12 days (as the data we used was collected every 12
days). We aim for developing a mechanistic model based
on nonlinear social interactions to explore how life history
parameters shape the population dynamics of a honeybee
colony. Ecological assumptions of the population dynamics
of A. mellifera are as follows:

A1: The brood are born into the brood compartment at an
egg laying rate $r$ by the queen. We assume that the
queen is fertile and is always well-fed.

A2: The brood are taken care of by the adult bees propor-
tional to the Holling Type 3 functional response. We
assume the Holling Type 3 functional response because
there is a minimum amount of adults needed to take
care of the brood, $K$. If there are not enough honey
bees, the colony will head towards extinction, but if
there is enough then they will grow. This is captured
in the sigmoidal shape of the Holling Type 3 functional
response.

A3: We assume that brood mortality is exponential and is
proportional to the amount of brood present at time
$t$. We also assume that adult mortality is exponential
and is proportional to the amount of adults present at
time $t$.

A4: Brood transition into adults at a rate $\phi$. We refer at this
as the eclosion rate and this will be constant.

A5: We assume that there are no drones in our system, as
their purpose is to reproduce with other queens.

These assumptions lead to the following system of non-
linear ordinary differential equations modeling the popula-
tion dynamics of A. Mellifera:

$$B' = \frac{rH^2}{K^2 + H^2} - \mu_b B - \phi B$$

$$H' = \phi B - \mu_h H$$

(1)

(2)
A. Mathematical Analysis

Basic properties of our system: Before analysing equilibrium points and stability of these we are interested in proving that our solutions \((B(t), H(t))\) will be bounded.

**Theorem III.1.** The system [1] - [2] is bounded, positive invariant, and has no limit cycles in \(\mathbb{R}^2\).

**Proof.** We prove boundedness by using differential inequalities:

For \(B'(t)\):

\[
B' = \frac{rH^2}{K^2+H^2} - \mu_B B - \phi B \leq r - \mu_B B - \phi B
\]

(3)

This implies that

\[
\limsup_{t \to \infty} B(t) \leq \frac{r}{\mu_B + \phi}
\]

Similarly for \(H'(t)\):

\[
H' = \frac{\phi B - r}{r^2} \leq \frac{\mu_h(\mu_B + \phi)}{\mu_h(\mu_B + \phi)}
\]

(5)

This implies that,

\[
\limsup_{t \to \infty} H(t) \leq \frac{r^2}{\mu_h(\mu_B + \phi)}.
\]

Thus \(H(t)\) and \(B(t)\) are bounded, as well as the total population \(N(t) = H(t) + B(t)\).

Naturally, as we are dealing with a ecological problem our solutions must be positive. Thus, we prove positive invariance by using Proposition B.7 by Smith [21]:

If \(B(t) = 0\):

\[
B' = \frac{rH^2}{K^2+H^2} \geq 0 \quad \forall \quad H \geq 0
\]

If \(H(t) = 0\):

\[
H' = \phi B \geq 0 \quad \forall \quad B \geq 0.
\]

So we can guarantee that our solutions will be positive and bounded.

Finally, we use the Bendixson criterion to show there are no limit cycles. Let \(f = B'(B, H)\) and let \(g = H'(B, H)\). First we know \(\frac{\partial f}{\partial B} = -\mu_B - \phi\) and \(\frac{\partial g}{\partial H} = -\mu_H\) are continuous. Then we have,

\[
\frac{\partial f}{\partial B} + \frac{\partial g}{\partial H} = -\mu_B - \mu_H - \phi < 0
\]

(8)

Thus there are no limit cycles in our system.

\(\square\)

**Biological significance:** Theorem [II.1] suggests that our system is well-defined biologically. This is because we will always have population that will not grow unbounded over time.

The maximum value of each compartment is actually the maximum population of brood and adults that can exist.

For the brood population the bound will be, as expected, proportional to the egg-laying rate \((r)\) so in the scenario in which the \(r\) is low the bound will be small and similarly if the sum of the brood death rate and the maturation rate \((\mu_B + \phi)\) is too high the bound will also be small. On the other hand, for the adult population the bound will be greater than the one for brood population as the relation with the brood death rate is a square relation, of course the term that corresponds to the adult death rate \((\mu_h)\) is added so if this rate is too high the bound will be lessen.

The first step to study the system [1] - [2] is to solve its steady states, i.e., equilibria. Upon inspection, we can conclude that \(B^* = H^* = 0\) is always an equilibrium of the system [1] - [2]. Let us look at the interior equilibrium, \((B^*, H^*)\).

Solving system [3], we see that:

**Trivial Equilibrium:**

\[
B^* = 0 \quad H^* = 0
\]

**Second Equilibrium:**

\[
B^* = \frac{r\phi + \zeta}{2\phi(\mu_B + \phi)} \quad H^* = \frac{r\phi + \zeta}{2\mu_h(\mu_B + \phi)}
\]

**Third Equilibrium**

\[
B^* = \frac{r\phi - \zeta}{2\phi(\mu_B + \phi)} \quad H^* = \frac{r\phi - \zeta}{2\mu_h(\mu_B + \phi)}
\]

Where \(\zeta = \sqrt{r^2\phi^2 - 4K^2\mu_h^2(\mu_B + \phi)^2}\).

We linearize the system [1] - [2] by taking the Jacobian of the system.

\[
\mathcal{J}(B, H) = \begin{vmatrix}
-\mu_B - \phi & \frac{rH^2}{(H+K)^2} \\
\phi & -\mu_h \\
\end{vmatrix}
\]

In the trivial equilibrium:

\[
\mathcal{J}(0, 0) = \begin{vmatrix}
-(\mu_B + \phi) & 0 \\
\phi & -\mu_h \\
\end{vmatrix}
\]

\[
det(\mathcal{J}) = \mu_h(\mu_B + \phi) \\
tr(\mathcal{J}) = -(\mu_B + \mu_h + \phi)
\]

(10)

In the second equilibrium:

\[
\mathcal{J}(B^*, H^*) = \begin{vmatrix}
-(\mu_B + \phi) & \frac{\mu_B(\mu_B + \phi)(r\phi - \zeta)}{r^2} \\
\phi & -\mu_h \\
\end{vmatrix}
\]

\[
det(\mathcal{J}) = \frac{\mu_h(\mu_B + \phi)\zeta}{r\phi} \\
tr(\mathcal{J}) = -(\mu_B + \mu_h + \phi)
\]

(11)
In the third equilibrium:

\[ J(B^*, H^*) = \begin{vmatrix} -(\mu_b + \phi) & \mu_h(\mu_b + \phi)(r\phi + c) \\ \phi & -\mu_h \end{vmatrix} \]

\[ det(J) = -\frac{\mu_h(\mu_b + \phi)\phi}{r\phi} \]

\[ tr(J) = -(\mu_b + \mu_h + \phi) \]

(12)

As we can see from the Jacobian matrix, the trace will always be negative, independent of \( B^*, H^* \). So, if \( det(J(B^*, H^*)) > 0 \), the equilibrium point \((B^*, H^*)\) will be stable and if \( det(J(B^*, H^*)) < 0 \) the equilibrium point \((B^*, H^*)\) will be unstable (for non-zero positive parameters). We can observe that \( det(J(0, 0)) > 0 \), this leads to conclude that \((B^* = 0, H^* = 0)\) is always stable. However for the second and third equilibrium we must be sure that \( \zeta^2 > 0 \) so the equilibrium point exists in biological conditions, i.e \( B^*, H^* \in \mathbb{R^+} \).

We define a variable \( R_d \) as the basic coexistence number. If \( R_d < 1 \) the honey bee population will be extinct (trivial equilibrium will be the only stable equilibrium), otherwise \( (R_d > 1) \) there will coexist to stable equilibrium as for the second equilibrium \( det(J(B^*, H^*)) > 0 \) for positive non-zero parameters. The second and trivial equilibrium coexist as stable equilibrium. Furthermore, the third equilibrium will be always unstable as \( det(J(B^*, H^*)) < 0 \)

B. Elasticity

To solve for elasticity, we use the general formula:

\[ E(\theta_i) = \frac{\partial f}{\partial \theta_i} \cdot \frac{\theta_i}{f} \]

for some function \( f \) and parameter \( \theta \). We will use \( f = R_d \).

Here \( \frac{\partial f}{\partial \theta_i} \) represents the reciprocal of the decrease in \( \theta_i \) required to reduce \( R_d \) by one percent. Rather than comparing absolute changes, we convert sensitivities to elasticities \( E(\theta_i) \) in order to compare percentage changes of parameters and values. This is done by multiplying the sensitivity by \( \frac{\theta_i}{f} \) (scaling factor). Note: we do not use the absolute value since we want to see how it can influence \( R_d \).

Here we present the analytical form of the elasticities, followed by a graph showing the elasticities for our given parameters:

\[ E(\phi) = \frac{2\mu_b}{\mu_b + \phi} \] (14)

\[ E(r) = +2 \]

(15)

\[ E(K) = -2 \]

(16)

\[ E(\mu_b) = -E(\phi) \]

(17)

\[ E(\mu_H) = -2 \]

(18)

Biological significance:

Notice that the brood death rate is related to the maturation rate in that the sensitivity of the maturation is just the negative value of the sensitivity of the brood death rate. If the bee mortality were to continue to increase, the sensitivity of the maturation rate would increase to 2, while the sensitivity of the death rate would increase to -2. That is, \( \lim_{\mu_b \to \infty} E(\phi) = 2 \) and \( \lim_{\mu_b \to \infty} E(\mu_h) = -2 \). This means that when the brood are dying at a fast rate, an increase in the maturation rate would lead to the survival of the colony at that instant (but would lead to precocious foragers and high mortality of foragers later on, as its been investigated \cite{7, 10}.). At some point, increasing the mortality of the brood will just have a constant effect on the sensitivity of the mortality of the brood and will collapse.
### Table II

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Best-fit value</th>
<th>CI</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r$</td>
<td>Egg-laying rate</td>
<td>25061.572</td>
<td>[18620.79, 31502.35]</td>
<td>Estimated</td>
</tr>
<tr>
<td>$\mu_B$</td>
<td>Death rate of the brood</td>
<td>0.575</td>
<td>[0.308, 0.842]</td>
<td>Estimated</td>
</tr>
<tr>
<td>$\mu_H$</td>
<td>Death rate of the adult bees</td>
<td>0.302</td>
<td>[0.221, 0.383]</td>
<td>Estimated</td>
</tr>
<tr>
<td>$\phi$</td>
<td>Transition rate from brood to adult</td>
<td>0.571</td>
<td>NA</td>
<td>Khoury et al. (2013)</td>
</tr>
<tr>
<td>$K$</td>
<td>Adults for half of the maximum rate $r$</td>
<td>3805.467</td>
<td>[1673.943, 5936.991]</td>
<td>Estimated</td>
</tr>
</tbody>
</table>

**Figure 2.** 1975 Data. The blue bars correspond to the elasticities for best-fit estimated parameters. $r = 25061.572$, $\mu_B = 0.575$, $\mu_H = 0.302$, $\phi = 0.571$, $K = 3805.467$ and the yellow bars to the elasticities for the critical brood death rate ($\mu_b$), i.e $R_d|_{\mu_b=\mu_b} = 1$.

**C. Parameter Estimation**

In order to obtain the values for the parameters in our model we minimized the Negative log likelihood to fit our data in years 1975 and 1976 during spring and summer seasons (Table II and IV), and used the f-min plus one half method to calculate the 95% confidence intervals. The only parameter we got from literature was $\phi$ which, as mentioned before, is the time that takes the transition from brood to adult.

**IV. Seasonality Model**

Here we present our findings for our model with the Holling Type 3 functional response with seasonality using ordinary differential equations (ODEs).

**Assumptions:** We still maintain the same ecological assumptions of the population dynamics of *A. mellifera* as previously mentioned, but with one extra factor:

**A5:** The egg laying rate $r(t)$ is dependent on the time of the season, where

$$r(t) = r_0 \left(1 + \cos \left(\frac{2\pi(t-\psi)}{\gamma}\right)\right)$$  \hspace{1cm} (19)

These assumptions lead to the following system of non-linear ordinary differential equations modelling the population dynamics of *A. Mellifera* with seasonality:

$$B' = \frac{r(t)H^2}{K^2 + H^2} - \mu_B B - \phi B$$ \hspace{1cm} (20)

$$H' = \phi B - \mu_H H$$ \hspace{1cm} (21)

**A. Mathematical Analysis**

Here we prove positive invariance and boundedness once more, but for obvious reasons this model has limit cycles:

**Theorem IV.1.** The system $\text{[20] - [21]}$ is bounded and positive invariant in $\mathbb{R}^2$.

**Proof.** The proof is similar to Theorem III.1. We prove boundedness by using differential inequalities: ↑

For $B'(t)$:

$$B' \leq \frac{r(t)H^2}{K^2 + H^2} - \mu_B B - \phi B$$ \hspace{1cm} (22)

And as the egg-laying rate is bounded as $-1 \leq \cos(\theta) \leq 1$:

$$r(t) \equiv r_0 \left(1 + \cos \left(\frac{2\pi(t-\psi)}{\gamma}\right)\right)$$

$$r(t) \in [0, 2r_0]$$

This implies that

$$\limsup_{t \to \infty} B(t) \leq \frac{2r_0}{\mu_B + \phi}$$

Similarly for $H'(t)$:

$$H' = \phi B - \mu_H H$$ \hspace{1cm} (24)

$$\leq \frac{4r_0^2}{\mu_H (\mu_B + \phi)}$$ \hspace{1cm} (25)
Thus, we prove positive invariance by using Proposition B.7 by Smith [21]:

\[ B(t) = 0 \]

And as \( r(t) \in [0, 2r_0] \):

\[ B' = \frac{rH^2}{K^2 + H^2} \geq 0 \quad \forall \quad H \geq 0 \]

Similarly if \( H(t) = 0 \):

\[ H' = \phi B \geq 0 \quad \forall \quad B \geq 0 . \]

So we can guarantee that our solutions will be positive and bounded.

### B. Parameter Estimation I

As in the previous model we did parameter estimation for this model in order to see if the values where more accurate. Even though, \( r \) no longer needed to be estimated and neither \( r_0 \), because as the maximum value \( r \) can have is \( 2r_0 \) (Eqn [19]), we set \( r_0 \) as the half of the maximum value of eggs found in our data.

### C. Parameter Estimation II

There are obvious differences in the number of eggs laid by the queen in the different seasons, and all other parameters can also be different depending in the season. Therefore we decided to find a different \( r(t) \) to each season by adjusting a function to the data of eggs laid in spring, summer, and fall (Fig 3).

\[
\begin{align*}
    r(t)_{\text{Spring}} &= 735t^2 + 2709t + 13478 \quad t \in [1, 7] \\
    r(t)_{\text{Summer}} &= -599.36t + 5450.3 \quad t \in [1, 7] \\
    r(t)_{\text{Fall}} &= 27.714t^2 - 226.6429t + 460.8571 \quad t \in [1, 7]
\end{align*}
\]

With these equations we estimated the parameters \( \mu_b \), \( \mu_{by} \), and \( k \) for each season. In order to find intrinsic values for these variables for a specific season. This was done with the 1976 data.

![Graphs for different functions r(t)](image_url)
V. Results

Figure 4. 1975 Data. Basic coexistence number vs brood death rate. Here the red line is the correspondent value of $R_d$ for the confidence interval of $\mu_b$ [0.308, 0.842] calculated in Table II. The critical $\mu_b$ referred as the minimum brood death rate that will lead to the extinction of the colony. Critical $\mu_b = 5.6591$. Parameter values used to generate figure are $r = 25061.572$, $\mu_H = 0.302$, $\phi = 0.571$, $K = 3805.467$. Note: The time unit is every 12 days.

A. Simulations

We ran simulations of the model with the different parameters estimated for spring, summer and fall. There are three different situations, the first, simulates the possible effects of applying insecticides during spring by increasing the value of $\mu_b$ of spring. The second, corresponds to the situation of the insecticides being applied during the summer, by increasing the value of $\mu_b$ of summer. And the final one simulates the effect of applying insecticides during fall, increasing the $\mu_b$ value of fall. The simulations were done for a period of two years.

2) Simulation $\mu_b$ Summer:

Figure 5. Simulations increasing the value of $\mu_b$ for spring simulating the application of insecticides during this season. Black: Normal brood death rate, Blue: 30% increase, Red: 500% increase, Magenta: 1500% increase. Dotted lines correspond to adult population and continuous lines correspond to brood population.

3) Simulation $\mu_b$ Fall:

Figure 6. Simulations increasing the value of $\mu_b$ for summer simulating the application of insecticides during this season. Black: Normal brood death rate, Blue: 30% increase Red: 80% Magenta: 1000%. Dotted lines correspond to adult population and continuous lines correspond to brood population.
VI. DISCUSSION

As it can be seen, in every graph there is a dotted black line at a constant value. This is K, which as mentioned before is the minimum number of adults needed to take care of the brood in order to allow the population survival. Therefore, this is viewed as a threshold which if the number of adults goes below this number the population will be extinguished.

The three simulations where done in order to see if by inducing insecticides into the bees colonies and affecting $\mu_b$, the effect will be significant. The more sensitive season appears to be summer, even though no perturbation to $\mu_b$ will lead to the extinguish of the population. With respect to applying insecticides in spring, big increases apparently do not affect at all the total population. But an increase of 1000% will lead to the colony extinction. And this is the same case for fall.

VII. CONCLUSIONS

Respect to $\mu_b$ can be concluded that little perturbations on it wont affect the total dynamics of the population. Also, the season that represents a higher risk to bees in order to apply insecticides appear to be spring and fall.

According to the sensibility analysis apparently perturbations on $\mu_b$, lees than the 1000% are not significant for the population dynamics. The parameter that seems to affect the most is changes in $r$, and hopefully in $\mu_h$. Nevertheless, this perturbation is not far from the on the we found analytically in which for the colony to collapse it is necessary that half the brood dies during the its birth day.

REFERENCES


