



A Mathematical Model and Simulation of Virus Epidemics in Varroa-infested Honey Bee Colonies

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ABSTRACT

We present a simple mathematical model describing the infection of a honeybee colony by the Acute Paralysis Virus (APV), which is carried by parasitic varroa mites. We make reasonable assumptions about the model and conduct a linear stability analysis. We provide the analytical solution via homotopy perturbation method (HPM) and the results are presented graphically. Our results show that epidemic occurs and that M and m_0 play a crucial role in the growth and decline of the populations size of healthy and infected bees. This is an indication that the healthy bee colonies can be maintained if the population size of virus carrying mites can be controlled.

Keywords : honey bee, *Varroa destructor*, hemolymph, animal pollinators, phoretic phase, virus-free equilibrium.

1. INTRODUCTION

Fifteen to 30% of the human food supply depends on animal pollinators, especially bees. Many farmers rely on managed colonies of the honey bee (*Apis mellifera*) to provide pollination during bloom but honey bees are not always the most effective pollinators of a given crop. For example, Honey bees provide essential pollination services to US fruit and vegetable growers, adding \$8-10 billion annually to farm income. Recent studies show that native, unmanaged bee populations also provide significant pollination services to various crops, particularly on farms near to natural habitat. In addition, the numbers of honey bee colonies, both domesticated and feral, has declined precipitously since the 1950s around the world due to the spread of the mite, *Varroa destructor*, leading to shortages.

The varroa mite is an external parasite that attacks both adult bees and the developing honey bee larvae. The adult mites have a flattened oval shape, are reddish-brown in color, and are about 0.06 inches wide, about the size of the head of a pin. An adult female *Varroa* mite lives either attached to an adult honey bee, known as the phoretic phase, or within a sealed brood cell where it reproduces. During the phoretic phase, mites remain attached to adult bees, occasionally moving between adult bees. To reproduce, a female mite enters a brood cell just prior to it being sealed, lays up to six eggs of which only the first develops into a male and the rest develop into females. Mating, typically between brother and sisters, occurs within the sealed cell [1]. Adult female mites are then released into the colony, either when the developed bee emerges from the cell or adult bees remove the dead brood [2]. Most of the female mites move to a new adult worker bee soon after being released from the cell [3]. All mite stages feed on bee haemolymph, which is obtained by piercing the bee cuticle of the developing or adult

bee using specialized mouth-parts [4]. Mites only carry viruses so long as they are attached to an overtly infected bee. When a virus-free phoretic mite moves from an uninfected to an infected adult bee, it will begin carrying the virus [5].

Mathematical modeling offers a powerful tool to investigate complicated systems, among them, biological events. However, very few attempts have been made, to compile current knowledge of *Varroa* mite interaction with the honey bee into a useful mathematical model of the parasite's population dynamics. Recently, Sumpter and Martin [6] used a mathematical model parameterized by recently collected data on bee viruses, to investigate the relationship between the mite load in a colony and the possibility of a virus epidemic occurring within a bee colony. Eberl et al. [7] presented a simple mathematical model of the infestation of a honeybee colony by the Acute Paralysis Virus. They extended the model in [6] by introducing an additional brood maintenance term in the birth rate which depends on the current size of the worker population. They studied this model with a mix of analytical and computational techniques.

Our work builds firmly on the previous study [7], but with little modification. In our model we assume the rate at which mites acquire the virus from infected bees to be the same as the rate at which virus-carrying mites transmit the virus to their new host. We conduct a linear stability analysis for the model and provide an analytical solution via homotopy perturbation method.

2. MODEL FORMULATION

Based on our assumption and following [7], the mathematical model is formulated in terms of the dependent variables (where details of derivation can be found in [6]):



m : number of mites that carry the virus,
 x : number of honey bees that are virus free,
 y : number of honey bees that are infected with the virus.

It reads:

$$\left. \begin{aligned} \frac{dm}{dt} &= \beta_1(M - m)\frac{y}{x + y} - \beta m\frac{x}{x + y} \\ \frac{dx}{dt} &= \mu g(x)h(m) - \beta m\frac{x}{x + y} - d_1x \\ \frac{dy}{dt} &= \beta m\frac{x}{x + y} - d_2y \end{aligned} \right\} \quad (1)$$

with initial conditions:

$$m(0) = m_0, \quad x(0) = x_0, \quad y(0) = y_0, \quad (2)$$

In these equations, the parameter M denotes the number of mites in the bee colony. Here, we will treat M as a parameter (i.e., we assume that the mite population reaches its carrying capacity very rapidly). The parameter μ is the maximum birth rate, specified as the number of worker bees born per day. The parameter β_1 is the rate at which mites that do not carry the virus acquire it. The parameter β is the rate at which infected mites lose their virus to an uninfected host. d_1 is the death rate for uninfected honeybees and d_2 is the death rate for infected honeybees. We can assume that infected bees live shorter than healthy bees, thus $d_2 > d_1$.

According to [7], the function $g(x)$ expresses that a sufficiently large number of healthy worker bees is required to care for the brood. [7] suggests that this is a switch function and is given by the sigmoidal Hill function

$$g(x) = \frac{x^n}{K^n + x^n} \quad (3)$$

where K is the size of the bee colony at which the birth rate is half of the maximum possible rate and the exponent $n > 1$.

The function $h(m)$ indicates that the birth rate is affected by the presence of mites that carry the virus. The function $h(m)$ is

assumed to decrease as m increases. [6] suggests that this is an exponential function.

$$h(m) \approx e^{-km} \quad (4)$$

Where k is a non-negative function.

By definition, all the parameters are non-negative. Then using (3) and (4) in equation (1), we obtain:

$$\left. \begin{aligned} \frac{dm}{dt} &= \beta_1(M - m)\frac{y}{x + y} - \beta m\frac{x}{x + y} \\ \frac{dx}{dt} &= \frac{\mu x^n e^{-km}}{K^n + x^n} - \beta m\frac{x}{x + y} - d_1x \\ \frac{dy}{dt} &= \beta m\frac{x}{x + y} - d_2y \end{aligned} \right\} \quad (5)$$

3. METHOD OF SOLUTION

3.1 Equilibrium Solutions

Here, we obtain the equilibrium solution by setting each of three differential equations (5) equal to zero, and solve for m, x and y . This gives the equilibrium solutions, i.e., it gives values of m, x and y for which the system will no longer change (since all of the derivatives, or rates of change, will be zero).

We first consider the equilibrium solution(s) for which $m = 0$. In this case, Equation (5), when $n = 2$, implies that $y = 0$

and $x = 0$ or $x = \frac{\mu \pm \sqrt{\mu^2 - 4d_1^2 K^2}}{2d_1} = x_{1,2}^*$ and this

implies that there are three equilibria for which $m = 0$. We let $p_1 = (0, x^*, 0)$ represent the disease free equilibrium. This is the equilibrium that is attained by an entirely healthy population.

Next, we consider the equilibrium solution(s) for which $x = 0$. In this case, Equation (5) implies that $y = 0$ and $m = M$, and there are no other equilibrium for which $x = 0$. We let $p_2 = (M, 0, 0)$ represent the collapse equilibrium. This is the equilibrium that describes the vanishing of the bee population. But, from a practical point of view, the absence of bees will imply the absence of mites, and thus $m = 0$ as a consequence.



For the endemic equilibrium, the colony contains healthy and sick bees. The equilibrium generally takes the form $p_3 = (m^*, x^{**}, y^*)$. Here, m^* , x^{**} and y^* are the equilibrium values obtained by solving equations (5).

3.2 Stability Analysis of the Disease-free State

To determine the behavior of m , x and y near each of the equilibrium solutions, we need to compute the linearization of the system, which is obtained from the Jacobian matrix of the system. For the system of equations (5) the Jacobian is:

$$Df(m,x,y) = \begin{pmatrix} -\frac{1}{x+y}(\beta_1 y + \beta x) & -\frac{y}{x+y}(\beta_1(M-m) + \beta m) & \frac{x}{x+y}(\beta_1(M-m) + \beta m) \\ -\left(\frac{\mu k x^2 e^{-km}}{K^2 + x^2} + \frac{\beta x}{x+y}\right) & \frac{n\mu K^2 x^2 e^{-km}}{x(K^2 + x^2)^2} - \left(\frac{\beta m y}{(x+y)^2} + d_1\right) & \frac{\beta m x}{(x+y)^2} \\ \frac{\beta x}{x+y} & \frac{\beta m y}{(x+y)^2} & -\left(\frac{\beta m x}{(x+y)^2} + d_2\right) \end{pmatrix} \quad (6)$$

The linearization of (5) at p_1 is:

$$Df(0, x^*, 0) = \begin{pmatrix} -\beta & 0 & \beta_1 M \\ -\alpha & \sigma & 0 \\ \beta & 0 & -d_2 \end{pmatrix} \quad (7)$$

with eigenvalues $\lambda_1 = \sigma$,

$$\lambda_{2,3} = \frac{-(\beta + d_2) \pm \sqrt{(\beta + d_2)^2 - 4\beta(d_2 - \beta_1 M)}}{2},$$

where

$$\alpha = \left(\frac{\mu k x^{*2}}{K^2 + x^{*2}} + \beta \right) \quad \sigma = \frac{n\mu K^2 x^*}{(K^2 + x^{*2})^2} - d_1$$

Here, we have three eigenvalues λ_i , $i = 1, 2, 3$, with distinct, non-zero roots. One of these eigenvalues is greater than zero. Then the disease free equilibrium is unstable and mathematically speaking, this implies that an epidemic occurs.

3.3 Analytical Solution

Homotopy perturbation method (HPM) was first proposed by He and was successfully applied to various engineering problems [8].

We apply Homotopy-perturbation to equations (2.5), where details can be found in He [8]. We construct a homotopy in the form:

$$(1-p)(x+y) \frac{dm}{dt} + p \left((x+y) \frac{dm}{dt} - \beta_1(M-m)y + \beta mx \right) = 0 \quad (8)$$

$$(1-p)(x+y) \frac{dx}{dt} + p \left((x+y) \frac{dx}{dt} - \frac{\mu x^n (x+y) e^{-km}}{K^n + x^n} + \beta mx + d_1 x(x+y) \right) = 0 \quad (9)$$

$$(1-p)(x+y) \frac{dy}{dt} + p \left((x+y) \frac{dy}{dt} - \beta mx + d_2 y(x+y) \right) = 0 \quad (10)$$

Using $e^m = 1 + m + \frac{m^2}{2!} + \dots$ and

$$(1+x)^{-1} = 1 - x + x^2 - \dots$$

Let

$$\left. \begin{aligned} m &= m_0 + pm_1 + p^2 m_2 + \dots \\ x &= x_0 + px_1 + p^2 x_2 + \dots \\ y &= y_0 + py_1 + p^2 y_2 + \dots \end{aligned} \right\} \quad (11)$$

Then

$$\left. \begin{aligned} m' &= m'_0 + pm'_1 + p^2 m'_2 + \dots \\ x' &= x'_0 + px'_1 + p^2 x'_2 + \dots \\ y' &= y'_0 + py'_1 + p^2 y'_2 + \dots \end{aligned} \right\} \quad (12)$$

Substituting (11) and (12) into equations (8) – (10) and collecting the coefficient of power of p , we have:

$$p^0 : (x_0 + y_0) m'_0 = 0 \quad (13)$$



$$(x_0 + y_0)x'_0 = 0 \tag{14}$$

$$(x_0 + y_0)y'_0 = 0 \tag{15}$$

$$p^1 : \\ (x_0 + y_0)m'_1 + (x_1 + y_1)m'_0 - \beta_1 M y_0 + \beta_1 m_0 y_0 + \beta m_0 x_0 = 0 \tag{16}$$

$$(x_0 + y_0)x'_1 + (x_1 + y_1)x'_0 - \frac{\mu}{K^n} (x_0 + y_0)x_0^n \left(1 - \frac{x_0^n}{K^n}\right) (1 - km_0) + \beta m_0 x_0 + d_1 x_0 (x_0 + y_0) = 0 \tag{17}$$

$$(x_0 + y_0)y'_1 + (x_1 + y_1)y'_0 - \beta m_0 x_0 + d_2 y_0 (x_0 + y_0) = 0 \tag{18}$$

$$p^2 : \\ (x_0 + y_0)m'_2 + (x_1 + y_1)m'_1 + (x_2 + y_2)m'_0 - \beta_1 M y_1 + \beta_1 m_1 y_0 + \beta_1 m_0 y_1 + \beta m_0 x_1 + \beta m_1 x_0 = 0 \\ (x_0 + y_0)x'_2 + (x_1 + y_1)x'_1 + (x_2 + y_2)x'_0 - \frac{\mu x_0^n}{K^n} (x_1 + y_1) \left(1 - \frac{x_0^n}{K^n}\right) (1 - km_0) - \frac{\mu n x_1}{K^n} (x_0 + y_0) \left(1 - \frac{x_0^n}{K^n}\right) (1 - km_0) + \frac{\mu x_0^n n x_1}{K^{2n}} (x_0 + y_0) (1 - km_0) + \frac{\mu x_0^n k m_1}{K^n} (x_0 + y_0) \left(1 - \frac{x_0^n}{K^n}\right) + \beta m_1 x_0 + \beta m_0 x_1 + d_1 x_0 (x_1 + y_1) + d_1 x_1 (x_0 + y_0) = 0 \tag{19}$$

$$\frac{\mu x_0^n n x_1}{K^{2n}} (x_0 + y_0) (1 - km_0) + \frac{\mu x_0^n k m_1}{K^n} (x_0 + y_0) \left(1 - \frac{x_0^n}{K^n}\right) + \beta m_1 x_0 + \beta m_0 x_1 + d_1 x_0 (x_1 + y_1) + d_1 x_1 (x_0 + y_0) = 0 \tag{20}$$

$$(x_0 + y_0)y'_2 + (x_1 + y_1)y'_1 + (x_2 + y_2)y'_0 - \beta m_0 x_1 - \beta m_1 x_0 + d_2 y_0 (x_1 + y_1) + d_2 y_1 (x_0 + y_0) = 0 \tag{21}$$

$$m_0(t) = m_0 \tag{22}$$

$$x_0(t) = x_0 \tag{23}$$

$$y_0(t) = y_0 \tag{24}$$

$$m_1(t) = \frac{1}{x_0 + y_0} (\beta_1 (M - m_0) y_0 - \beta m_0 x_0) t \tag{25}$$

$$x_1(t) = \frac{1}{x_0 + y_0} \left[\begin{aligned} & \left(\frac{\mu x_0^n}{K^n} (x_0 + y_0) \left(1 - \frac{x_0^n}{K^n}\right) \right) \\ & (1 - km_0) - \beta m_0 x_0 - \\ & d_1 x_0 (x_0 + y_0) \end{aligned} \right] t \tag{26}$$

$$y_1(t) = \frac{1}{x_0 + y_0} (\beta m_0 x_0 - d_2 y_0 (x_0 + y_0)) t \tag{27}$$

$$m_2(t) = \frac{1}{2(x_0 + y_0)^2} \left[\begin{aligned} & \left(\beta_1 (M - m_0) \left(\frac{\beta m_0 x_0}{d_2 y_0 (x_0 + y_0)} \right) - \right. \\ & \left. \beta_1 y_0 \left(\frac{\beta_1 (M - m_0) y_0}{\beta m_0 x_0} \right) - \right. \\ & \left. \left(\frac{\mu x_0^n}{K^n} (x_0 + y_0) \right) \right. \\ & \left. \beta m_0 \left(\left(1 - \frac{x_0^n}{K^n}\right) (1 - km_0) - \right. \right. \\ & \left. \left. \beta m_0 x_0 - d_1 x_0 (x_0 + y_0) \right) \right. \\ & \left. \beta x_0 (\beta_1 (M - m_0) y_0 - \beta m_0 x_0) - \right. \\ & \left. \frac{1}{x_0 + y_0} \left(\frac{\beta_1 (M - m_0) y_0}{\beta m_0 x_0} \right) \right. \\ & \left. \left(\left(\frac{\mu x_0^n}{K^n} (x_0 + y_0) \left(1 - \frac{x_0^n}{K^n}\right) \right) \right. \right. \\ & \left. \left. (1 - km_0) - \right. \right. \\ & \left. \left. \beta m_0 x_0 - d_1 x_0 (x_0 + y_0) \right) \right. \\ & \left. \left((\beta m_0 x_0 - d_2 y_0 (x_0 + y_0)) \right) \right] t^2 \tag{28}$$

Solving equation (13) – (21), we obtain



$$y_2(t) = \frac{1}{2(x_0 + y_0)^2} \left[\begin{aligned} & \left(-\frac{1}{x_0 + y_0} \left(\beta m_0 x_0 - d_2 y_0 (x_0 + y_0) \right) \right. \\ & \left. \left(\frac{\mu x_0^n}{K^n} (x_0 + y_0) \right) \right. \\ & \left. \left(\left(1 - \frac{x_0^n}{K^n} \right) (1 - km_0) - \beta m_0 x_0 - d_1 x_0 (x_0 + y_0) \right) \right. \\ & \left. \left(\beta m_0 x_0 - d_2 y_0 (x_0 + y_0) \right) \right) \right] + \\ & \left[\begin{aligned} & \left(\frac{\mu x_0^n}{K^n} (x_0 + y_0) \right) \right. \\ & \left(\left(1 - \frac{x_0^n}{K^n} \right) (1 - km_0) - \beta m_0 x_0 - d_1 x_0 (x_0 + y_0) \right) \right] + \\ & \beta x_0 (\beta_1 (M - m_0) y_0 - \beta m_0 x_0) - \\ & \left[\begin{aligned} & \left(\frac{\mu x_0^n}{K^n} (x_0 + y_0) \right) \right. \\ & \left(\left(1 - \frac{x_0^n}{K^n} \right) (1 - km_0) - \beta m_0 x_0 - d_1 x_0 (x_0 + y_0) \right) \right] + \\ & \left(\beta m_0 x_0 - d_2 y_0 (x_0 + y_0) \right) \right] - \\ & \left(d_2 (x_0 + y_0) (\beta m_0 x_0 - d_2 y_0 (x_0 + y_0)) \right) \end{aligned} \right] t^2 \tag{30}$$

According to the homotopy perturbation method, the approximation solution of equations (2.5) can be expressed as a series of the power of p , i.e.

$$m(t) = \lim_{p \rightarrow 1} m_0(t) + pm_1(t) + p^2m_2(t) + \dots \tag{31}$$

$$x(t) = \lim_{p \rightarrow 1} x_0(t) + px_1(t) + p^2x_2(t) + \dots \tag{32}$$

$$y(t) = \lim_{p \rightarrow 1} y_0(t) + py_1(t) + p^2y_2(t) + \dots \tag{33}$$

The computations were done using computer symbolic algebraic package MAPLE.

4. RESULTS AND DISCUSSION

We have obtained the equilibrium solution of a mathematical model describing the infection of a honeybee colony by the Acute Paralysis Virus and conducted a linear stability analysis of the disease-free state.

The graphs of populations' size of virus carrying mites, healthy and infected bees are presented in Figures 1 – 12. Figure 1 displays the graph of $x(t)$ against t for different values of M .

It is seen that population size of healthy bees decreases as size of mite population increases. Figure 2 displays the graph of $y(t)$ against t for different values of M . It is seen that population size of infected bees increases as size of mite population increases.

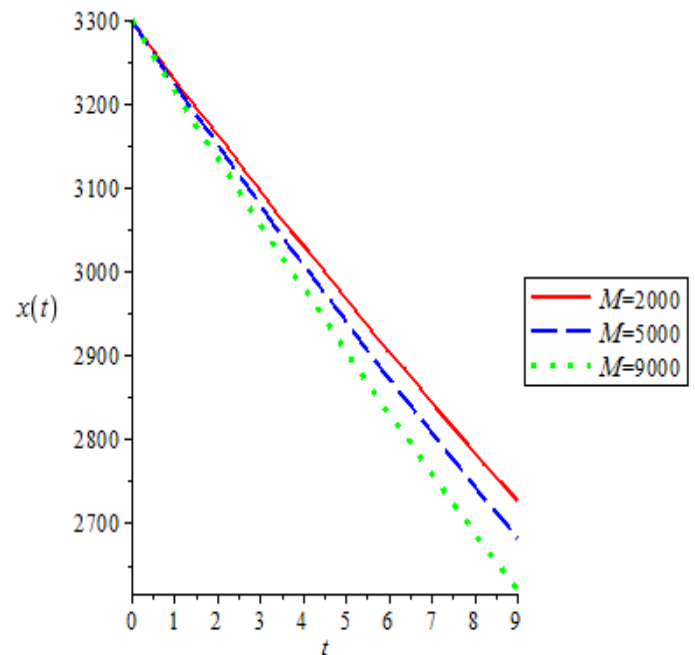


Figure 1: Plots of $x(t)$ against time t for different values of M and $K = 3000, \beta_1 = 0.04, \beta = 0.02, \mu = 500, d_1 = 0.02, d_2 = 0.2, n = 2, k = 1$

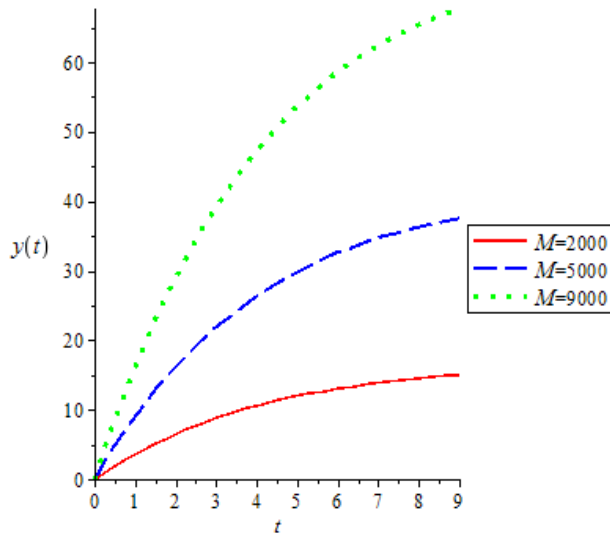


Figure 2: Plots of $y(t)$ against time t for different values of M and $K = 3000, \beta_1 = 0.04, \beta = 0.02, \mu = 500, d_1 = 0.02, d_2 = 0.2, n = 2, k = 1$

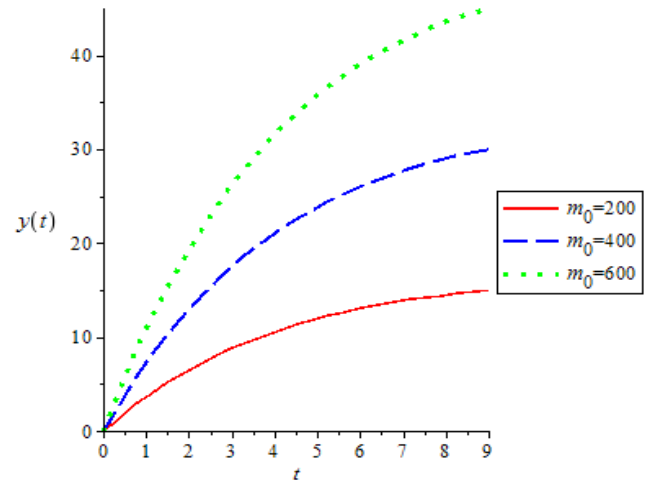


Figure 4: Plots of $y(t)$ against time t for different values of m_0 and $M = 2000, K = 3000, \beta_1 = 0.04, \beta = 0.02, \mu = 500, d_1 = 0.02, d_2 = 0.2, n = 2, k = 1$

Figure 3 displays the graph of $x(t)$ against t for different values of m_0 . It is seen that population size of healthy bees decreases as initial number of virus carrying mites increases. Figure 4 displays the graph of $y(t)$ against t for different values of m_0 . It is seen that population size of infected bees increases as initial number of virus carrying mites increases.

Figure 5 displays the graph of $m(t)$ against t for different values of β_1 . It is seen that population size of virus carrying mites increases as the rate at which mites that do not carry the virus acquire it increases. Figure 6 displays the graph of $y(t)$ against t for different values of β_1 . It is seen that population size of infected bees increases as the rate at which mites that do not carry the virus acquire it increases.

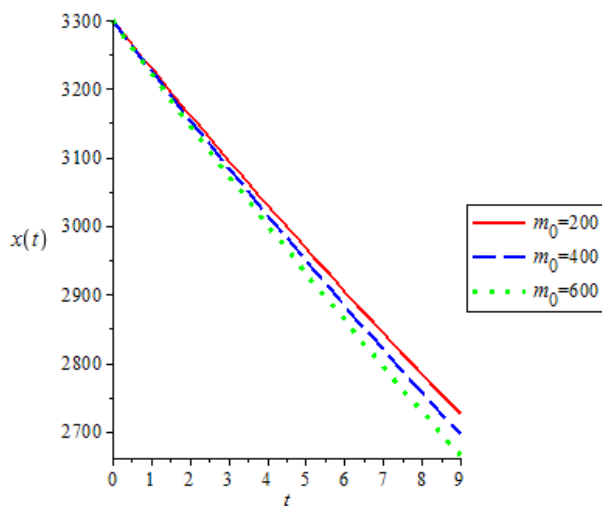


Figure 3: Plots of $x(t)$ against time t for different values of m_0 and $M = 2000, K = 3000, \beta_1 = 0.04, \beta = 0.02, \mu = 500, d_1 = 0.02, d_2 = 0.2, n = 2, k = 1$

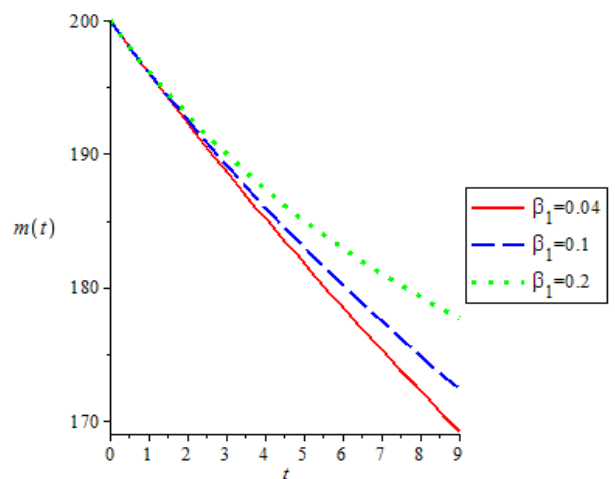


Figure 5: Plots of $m(t)$ against time t for different values of β_1 and $M = 2000, K = 3000, \beta = 0.02, \mu = 500, d_1 = 0.02, d_2 = 0.2, n = 2, k = 1$

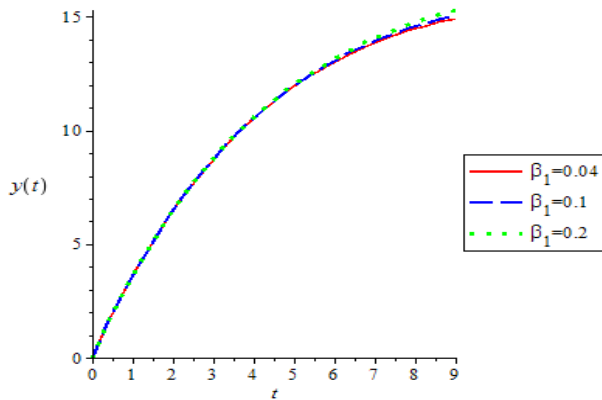


Figure 6: Plots of $y(t)$ against time t for different values of β_1 and $M = 2000, K = 3000, \beta = 0.02, \mu = 500, d_1 = 0.02, d_2 = 0.2, n = 2, k = 1$

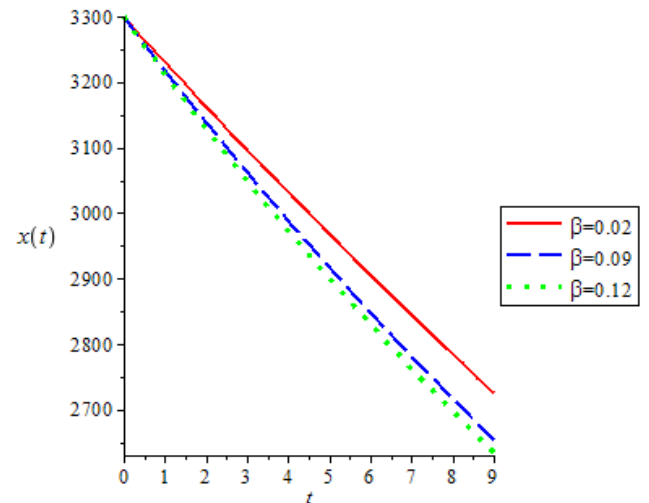


Figure 8: Plots of $x(t)$ against time t for different values of β and $M = 2000, K = 3000, \beta_1 = 0.04, \mu = 500, d_1 = 0.02, d_2 = 0.2, n = 2, k = 1$

Figure 7 displays the graph of $m(t)$ against t for different values of β . It is seen that population size of virus carrying mites decreases as the virus transmission rate increases. Figure 8 displays the graph of $x(t)$ against t for different values of β . It is seen that population size of healthy bees decreases as the virus transmission rate increases. Figure 9 displays the graph of $y(t)$ against t for different values of β . It is seen that population size of infected bees increases as the virus transmission rate increases.

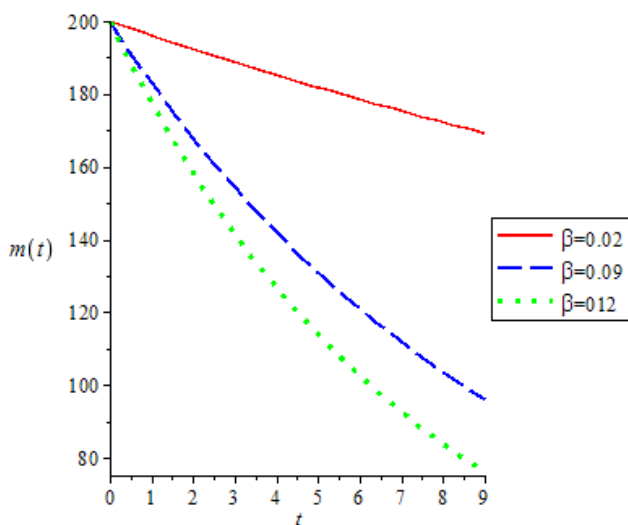


Figure 7: Plots of $m(t)$ against time t for different values of β and $M = 2000, K = 3000, \beta_1 = 0.04, \mu = 500, d_1 = 0.02, d_2 = 0.2, n = 2, k = 1$

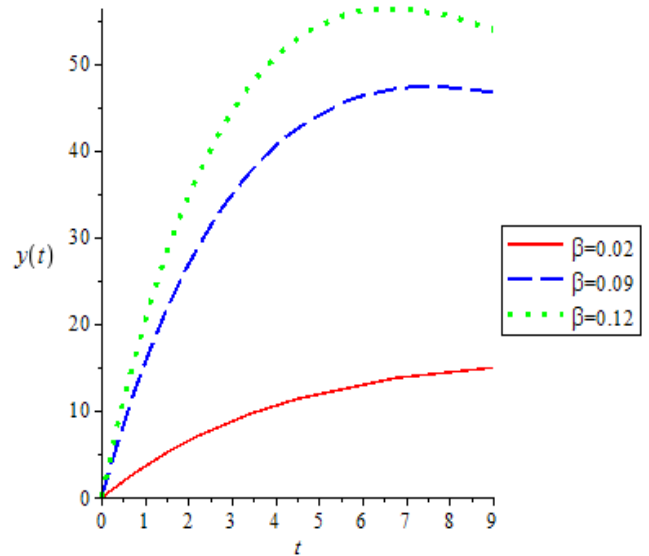


Figure 9: Plots of $y(t)$ against time t for different values of β and $M = 2000, K = 3000, \beta_1 = 0.04, \mu = 500, d_1 = 0.02, d_2 = 0.2, n = 2, k = 1$

Figure 10 displays the graph of $x(t)$ against t for different values of d_1 . It is seen that population size of healthy bees decreases as the death rate for uninfected honeybees increases.

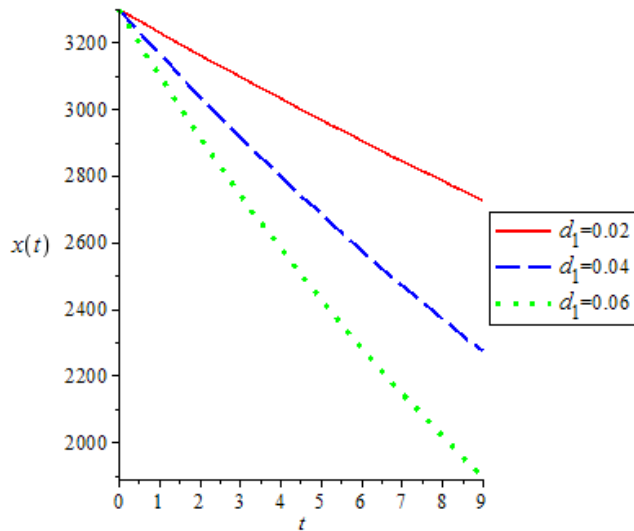


Figure 10: Plots of $x(t)$ against time t for different values of d_1 and $M = 2000, K = 3000, \beta_1 = 0.04, \beta = 0.02, \mu = 500, d_2 = 0.2, n = 2, k = 1$

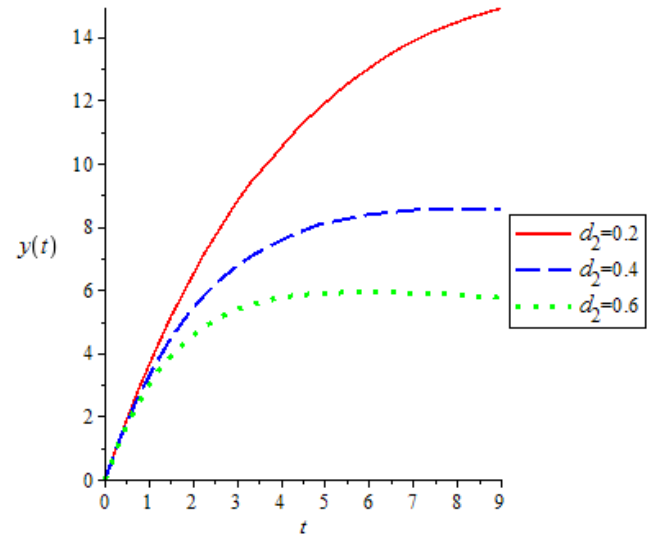


Figure 12: Plots of $y(t)$ against time t for different values of d_2 and $M = 2000, K = 3000, \beta_1 = 0.04, \beta = 0.02, \mu = 500, d_1 = 0.02, n = 2, k = 1$

Figure 11 displays the graph of $m(t)$ against t for different values of d_2 . It is seen that population size of virus carrying mites decreases as the death rate for infected honeybees increases. Figure 12 displays the graph of $y(t)$ against t for different values of d_2 . It is seen that population size of infected bees decreases as the death rate for infected honeybees increases.

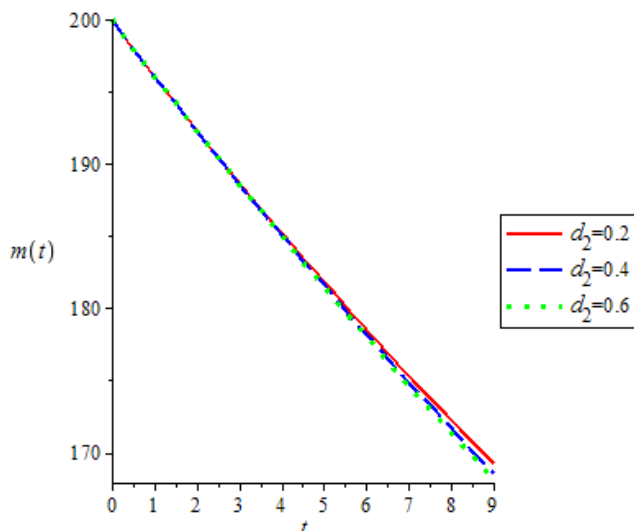


Figure 11: Plots of $m(t)$ against time t for different values of d_2 and $M = 2000, K = 3000, \beta_1 = 0.04, \beta = 0.02, \mu = 500, d_1 = 0.02, n = 2, k = 1$

5. CONCLUSION

In this paper, we established the equilibrium states of a mathematical model describing the infection of a honeybee colony by the Acute Paralysis Virus. We conducted a linear stability analysis. The results show that the disease free equilibrium is unstable. This implies that an epidemic occurs. For the simulation, an analytical method via Homotopy perturbation method was used. The results obtained showed that M and m_0 play a crucial role in the growth and decline of the populations' size of healthy and infected bees. This is an indication that the healthy bee colonies can be maintained if the population size of virus carrying mites can be controlled.

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