

Eighth Mississippi State - UAB Conference on Differential Equations and Computational Simulations. *Electronic Journal of Differential Equations*, Conf. 19 (2010), pp. 85–98.  
ISSN: 1072-6691. URL: <http://ejde.math.txstate.edu> or <http://ejde.math.unt.edu>  
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## IMPORTANCE OF BROOD MAINTENANCE TERMS IN SIMPLE MODELS OF THE HONEYBEE - VARROA DESTRUCTOR - ACUTE BEE PARALYSIS VIRUS COMPLEX

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**ABSTRACT.** We present a simple mathematical model of the infestation of a honeybee colony by the Acute Paralysis Virus, which is carried by parasitic varroa mites (*Varroa destructor*). This is a system of nonlinear ordinary differential equations for the dependent variables: number of mites that carry the virus, number of healthy bees and number of sick bees. We study this model with a mix of analytical and computational techniques. Our results indicate that, depending on model parameters and initial data, bee colonies in which the virus is present can, over years, function seemingly like healthy colonies before they decline and disappear rapidly (e.g. Colony Collapse Disorder, wintering losses). This is a consequence of the fact that a certain number of worker bees is required in a colony to maintain and care for the brood, in order to ensure continued production of new bees.

### 1. INTRODUCTION

A famous folklore quote says that four years after honeybees vanish from the Earth, mankind will vanish too. Commonly attributed to Albert Einstein, there seems to be little evidence that it is authentic [9]. Nevertheless, the message is clear: No bees, no pollination, no crops, no people.

Besides cows, pigs, and poultry, western honeybees (*Apis mellifera*) are among the economically most important domestic livestock in Europe and Northern America, not to mention their ecological importance [11]. Due to the demand of honey and other hive products, but in particular because of the demand for pollination services, apiculture has developed to become a profitable business. Honeybees (*Apis* spp.: *Hymenoptera*: *Apidea*) live in highly integrated and complex social colonies to the extent that a single colony can be thought of as a super organism [11]. Like all animals, honeybees are hosts to parasites and pathogens. For the temperate zone biotypes of western honeybees, the devastating attacks of parasitic mites, especially *Varroa destructor*, have created major problems for beekeepers around the world. The damage caused by the mites has been exacerbated by mite-borne infections of viruses [3], notably the Acute Paralytic Bee Virus (APV, ABPV). In recent years,

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2000 *Mathematics Subject Classification.* 92D25, 92D30.

*Key words and phrases.* Honeybees; varroa destructor; acute bee paralysis virus; colony collapse disorder; wintering losses; mathematical model.

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Published September 25, 2010.

beekeepers in the USA, and now other parts of the world, have reported huge losses of colonies to the extent that there is national, continental and international alarm over their demise, e.g. [7]. The combination of parasitic mites and virus infections have been indicated as a major cause of Colony Collapse Disorder (CCD) as the syndrome is diagnosed in USA. Elsewhere, symptoms are not exactly the same as in CCD, but huge and worrisome losses, in particular wintering losses, are also recorded with the same parasite/virus complex suggested as a major cause. It has been suggested that various other stresses, such as hard management, pesticides, weather, and poor diet may also be involved to make matters worse [4].

The Acute Bee Paralysis virus kills larvae, pupae, and adults only in association with varroa mites [3, 6]. In contrast to other viruses, such as the *Deformed Wing Virus*, larvae and pupae that are affected by the virus die before they develop into bees [6, 10]; i.e., all bees that are infected with the APV virus must have acquired it as adults.

In this small study we present and analyze a simple model of three ordinary differential equations for the disease dynamics of the bee-mite-APV complex, that follows the classical SIR-like approach of mathematical epidemiology. It will be formulated for the dependent variables: (i) number of mites that carry the virus, (ii) number of healthy bees and (iii) number of infected bees. Our work builds firmly on the previous study [10], but introduces a simple but important extension: In their original model [10], the authors assumed that the birth rate of bees might be affected by the presence of the virus in the colony, but it is not directly linked to the size of the worker bee population. In other words, even if all healthy bees are gone, the pupae in the brood will develop into adults. Moreover, since it is assumed that the queen bee is not affected by the virus, this would allow a constant birth of new bees during spring, summer, and autumn. However, carrying for and maintaining the brood is an important task in bee hives, in which many workers are involved [5, 11, 13]. If the bee population becomes too small, larvae and pupae cannot be reared and die in the brood cells before they can develop into adult bees. To reflect this in the model, we introduce an additional brood maintenance term in the birth rate which depends on the current size of the worker population. From a mathematical point of view, including such a maintenance term affects the structure of the omega limit set of the system, because it allows for additional equilibria. Moreover, it can change the stability of the existing equilibria. Like [10], we will study our model separately for the four seasons. Additionally we will use computer simulations to investigate the fate of the bee colony through the years according to our model.

## 2. MATHEMATICAL MODEL

The mathematical model is formulated in terms of the dependent variables

$m$ : number of mites that carry the virus,

$x$ : number of honeybees that are virus free,

$y$ : number of honeybees that are infected with the virus.

It reads

$$\frac{dm}{dt} = \beta_1(M - m)\frac{y}{x + y} - \beta_2m\frac{x}{x + y} \quad (2.1)$$

$$\frac{dx}{dt} = \mu g(x)h(m) - \beta_3m\frac{x}{x + y} - d_1x \quad (2.2)$$

$$\frac{dy}{dt} = \beta_3 m \frac{x}{x+y} - d_2 y \quad (2.3)$$

In equation (2.1), the parameter  $M$  denotes the number of mites in the bee colony. With the same arguments as in [10], we will treat  $M$  as a parameter rather than a dependent variable; in particular,  $M$  is independent of  $m$ . By treating  $M$  as a parameter we implicitly assume that the mite population reaches its carrying capacity very rapidly; i.e., we make a quasi-steady state argument.

The parameter  $\mu$  in (2.2) is the maximum birth rate, specified as the number of worker bees born per day.

The parameter  $\beta_1$  in (2.1) is the rate at which mites that do not carry the virus acquire it. The rate at which infected mites lose their virus to an uninfected host is  $\beta_2$ . The rate at which uninfected bees become infected is  $\beta_3$ , in bees per virus carrying mite and time.

Finally,  $d_1$  and  $d_2$  are the death rates for uninfected and infected honeybees. We can assume that infected bees live shorter than healthy bees, thus  $d_2 > d_1$ .

The function  $g(x)$  expresses that a sufficiently large number of healthy worker bees is required to care for the brood. The inclusion of this term is the only difference between the model studied here and the model in [10], on which this study is based. We think of  $g(x)$  as a switch function. If  $x$  falls below a critical value, which may seasonally depend on time, essential work in the maintenance of the brood cannot be carried out anymore and no new bees are born. If  $x$  is above this value, the birth of bees is not hampered. Thus  $g(0, \cdot) = 0$ ,  $\frac{dg(0)}{dx} \geq 0$ ,  $\lim_{x \rightarrow \infty} g(x) = 1$ . A convenient formulation of such switch like behavior is given by the sigmoidal Hill function

$$g(x) = \frac{x^n}{K^n + x^n} \quad (2.4)$$

where the new parameter  $K$  is the size of the bee colony at which the birth rate is half of the maximum possible rate and the exponent  $n > 1$ , see also Figure 1. If  $K = 0$  is chosen, then the original model of [10] is obtained. In this case the brood is always reared at maximum capacity, independent of the actual bee population size, since  $g(x) \equiv 1$ .

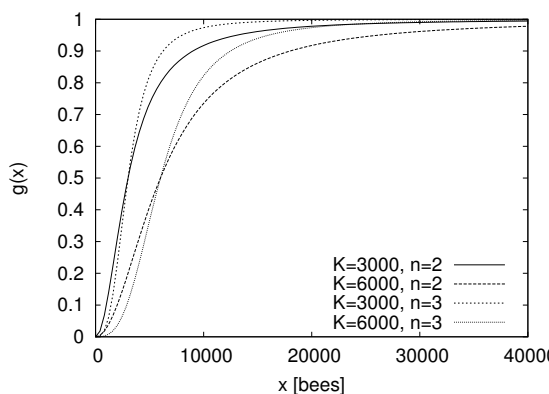


FIGURE 1. Brood maintenance coefficient  $g(x) = \frac{x^n}{K^n + x^n}$  as a function of bee population size for various choices of  $K$  and  $n$

TABLE 1. Seasonal averages of model parameters, derived from the data presented in [10].

Parameter	Spring	Summer	Autumn	Winter
$\beta_1$	0.1593	0.1460	0.1489	0.04226
$\beta_2$	0.04959	0.03721	0.04750	0.008460
$\beta_3$	0.1984	0.1460	0.1900	0.03384
$d_1$	0.02272	0.04	0.02272	0.005263
$d_2$	0.2	0.2	0.2	0.005300
$\mu$	500	1500	500	0

The function  $h(m)$  in (2.2) indicates that the birth rate is affected by the presence of mites that carry the virus. This is in particular important for viruses like APV that kill infected pupae before they develop into bees. The function  $h(m)$  is assumed to decrease as  $m$  increases,  $h(0) = 1$ ,  $\frac{dh}{dm}(m) < 0$  and  $\lim_{m \rightarrow \infty} h(m) = 0$ ; [10] suggests that this is an exponential function  $h(m) \approx e^{-mk}$ , where  $k$  is a non-negative function. We will use this in the computer simulations later on.

The parameters  $M, \mu, \beta_i, d_i, g(x), h(m)$  are assumed to be non-negative. They can change with time. In particular major differences may be observed between seasons. For example, the life span of a worker bee in summer is much shorter than in winter [1, 8]; the birth rate for bees is higher in summer than in spring and autumn, and it drops down to 0 in winter [11]. Seasonal averages for the model parameters  $\beta_{1,2,3}, \mu, d_{1,2}$  can be derived from the data in [10]. These are summarized in Table 1. We will treat the remaining parameters  $M$  and  $K$  as unknown in the next section of this study. We will investigate the long term behavior and fate of the colony in dependence of these two parameters. The size of the mite population  $M$  is an obvious parameter to choose for such a study. This will give us insight in how strong an infestation can be fought off by a bee colony. The brood maintenance coefficient  $K$  is chosen as a free parameter, because we do not have a good estimate. We will assume it to be in the order of several thousands; in [10] it is mentioned that at least 3000 worker bees are required in the beginning of spring to maintain the brood. In particular, we are interested how the maximum mite population size  $M$  that can be tolerated by the bee colony depends on  $K$ .

For the discussion of the model in the subsequent sections, the following result will be helpful.

**Lemma 2.1.** *There exists a  $\tilde{R} > 0$  such that the set*

$$\mathcal{K}_R := \{(m, x, y) \in \mathbb{R}^3 : 0 < m < M_\infty, x > 0, y > 0, x + y < R\}$$

*is positively invariant under (2.1)-(2.3) for all  $R > \tilde{R}$ , where by  $M_\infty$  we denote  $M_\infty := \max_t M(t)$ .*

*Proof.* We apply the usual tangent criterion [12]. At  $m = 0$  we have  $\frac{dm}{dt} = \beta_1 M \frac{y}{x+y} > 0$  and at  $m = M$  we have  $\frac{dm}{dt} = -\beta_2 M \frac{x}{x+y} < 0$  for  $x > 0, y > 0$ . Thus solutions with  $0 < m(0) < M$  will satisfy  $0 < m(t) < M$  for all  $t > 0$ . Similarly, for  $y = 0$  we have  $\frac{dy}{dt} = \beta_3 m \frac{x}{x+y} > 0$  and for  $x = 0$  we have  $\frac{dx}{dt} = 0$ . Thus our system (2.1)-(2.3) is positivity preserving.

The remaining boundary of the set  $\mathcal{K}_R$  is the plane  $R - x - y = 0$ , which has the outer normal vector  $n = (0, 1, 1)^T$ . To apply the tangent criterion we have to

show that along  $R - x - y = 0$  the inequality

$$\left(\frac{dx}{dt} + \frac{dy}{dt}\right)_{R-x-y=0} = \mu g(x)h(m) - d_1x - d_2y \leq 0$$

holds for all large enough  $R$ ; i.e., that

$$\mu g(x)h(m) + (d_2 - d_1)x - d_2R \leq 0, \quad \text{for all } x \leq R. \tag{2.5}$$

As noted above, we can assume  $d_2 > d_1$ . Thus we obtain with  $x < R$  and  $0 \leq g(x) \leq 1, 0 \leq h(m) \leq 1$  from (2.5) the inequality

$$\mu g(x)h(m) + (d_2 - d_1)x - d_2R < \mu - d_1R.$$

Hence the assertion (2.5) holds certainly for  $R > \tilde{R} = \mu/d_1$ . □

Note, however, that this inequality is not sharp; i.e., one can even find a smaller  $\tilde{R}$  with the same property.

Thus, all solutions of (2.1)-(2.3) that start in  $\mathcal{K}_R, R > \tilde{R}$ , remain there. In particular they are positive and bounded from above by constants. Moreover, even if initially  $m(0) > M$ , the solution will be attracted by  $\mathcal{K}_R$ .

### 3. THE AUTONOMOUS CASE

We start our investigation of the disease dynamics model (2.1)-(2.3) with the simple case of constant coefficients as in [10], pointing out that these results only have quantitative meaning if the characteristic time scale of the dynamics is shorter than the period over which the parameters can be assumed to be constant. However, in many cases, e.g. Table 1, parameter values are only available in form of seasonal averages, and this is the situation that we have in mind. We have to distinguish between three types of equilibria of (2.1)-(2.3).

**3.1. Equilibrium points. Disease free equilibrium.** This is the equilibrium that is attained by an entirely healthy population,

$$m = 0, \quad x = x^*, \quad y = 0 \tag{3.1}$$

where  $x^*$  is a root of the function

$$F(x) = \mu g(x) - d_1x. \tag{3.2}$$

For maintenance functions of the form  $g(x) = \frac{x^n}{K^n + x^n}$  this reduces to finding the positive roots of the polynomial of degree  $n, G(x) = x^n - \frac{\mu}{d_1}x^{n-1} + K^n$ . According to Descartes's rule of signs, there are at most two such roots. In the case  $n = 2$  these are easily calculated as

$$x_{1,2}^* = \frac{1}{2} \left( \frac{\mu}{d_1} \pm \sqrt{\frac{\mu^2}{d_1^2} - 4K^2} \right). \tag{3.3}$$

They exist if  $\mu/d_1 > 2K$ . The Jacobian of the system (2.1)-(2.3) in general form reads

$$J(m, x, y) = \begin{bmatrix} -\frac{\beta_1 y + \beta_2 x}{x+y} & -\frac{y(\beta_1(M-m) + \beta_2 m)}{(x+y)^2} & \frac{x(\beta_1(M-m) + \beta_2 m)}{(x+y)^2} \\ \mu g(x)h'(m) - \frac{\beta_3 x}{x+y} & \mu g'(x)h(m) - \frac{\beta_3 m y}{(x+y)^2} - d_1 & \frac{\beta_3 m x}{(x+y)^2} \\ \frac{\beta_3 x}{x+y} & \frac{\beta_3 m y}{(x+y)^2} & -\frac{\beta_3 m x}{(x+y)^2} - d_2 \end{bmatrix}. \tag{3.4}$$

In the case of the disease free equilibrium this reduces to

$$J(0, x^*, 0) = \begin{bmatrix} -\beta_2 & 0 & \frac{\beta_1 M}{x^*} \\ d_1 x^* h'(0) - \beta_3 & \mu g'(x^*) - d_1 & 0 \\ \beta_3 & 0 & -d_2 \end{bmatrix}. \quad (3.5)$$

Its eigenvalues are

$$\lambda_1 = \mu g'(x^*) - d_1, \quad \lambda_{2,3} = -\frac{1}{2} \left( \beta_2 + d_2 \mp \sqrt{(\beta_2 - d_2)^2 + 4 \frac{\beta_1 \beta_3 M}{x^*}} \right). \quad (3.6)$$

We note that the eigenvalues depend on the specific form of the brood maintenance term  $g(x)$  via  $x^*$  and (3.2). For the special case  $g(x) = \frac{x^2}{K^2 + x^2}$ , the eigenvalue  $\lambda_1$  takes the simpler form

$$\lambda_1 = \mp d_1 \sqrt{1 - 4K^2 \left( \frac{d_1}{\mu} \right)^2}. \quad (3.7)$$

Particularly it is real. The disease free equilibrium with  $x = x_2^*$  is always unstable, because  $\lambda_1 > 0$ . On the other hand, for  $x_1^*$ , the associated eigenvalue  $\lambda_1$  is negative. The eigenvalues  $\lambda_{2,3}$  are always real,  $\lambda_3$  is always negative. Therefore, it is the eigenvalue  $\lambda_2$  that decides the stability of the disease free equilibrium with  $x = x_1^*$ . Stability is achieved if it is negative, i.e. if

$$M < \frac{\beta_2 d_2 x_1^*}{\beta_1 \beta_3} =: M_{\text{crit}}, \quad (3.8)$$

where  $x_1^*$  depends on birth and death rate of the bee population as well as on  $K$ . We plot  $M_{\text{crit}}$  as a function of  $K$  in Figure 2 for the parameters in Table 1. We note that the critical value for the model [10] is obtained for the special case  $K = 0$ . Thus, if one includes the consideration that in order to rear the brood, a critical bee population size is needed, a drastic reduction in the maximum number of mites that can be fought off by the colony is observed.

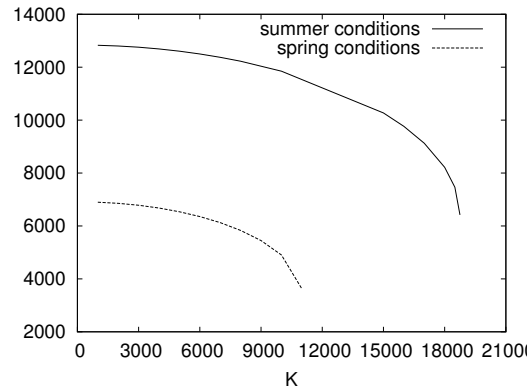


FIGURE 2. Critical mite population  $M_{\text{crit}}$  as a function of the half maintenance population size  $K$ .

**Collapse equilibrium.** This equilibrium describes the vanishing of the bee population. These are the points

$$m = m^*, \quad x = 0, \quad y = 0 \quad (3.9)$$

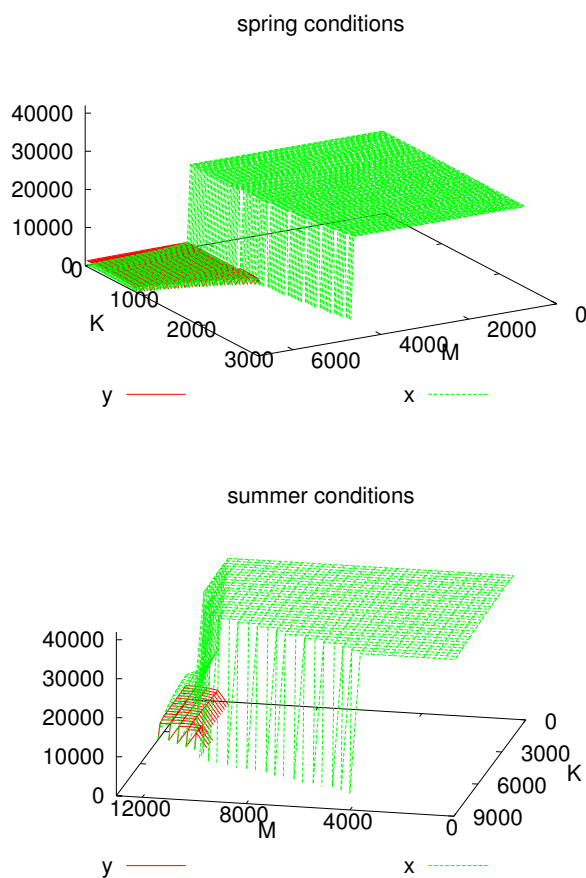


FIGURE 3. Long-term behavior of model (2.1)-(2.3) in dependence of number of mites  $M$  and maintenance size of the population  $K$ . Plotted are healthy bees  $x$  (green) and infected bees  $y$  (red) at steady state.

where  $m^* > 0$  can be any positive number. Moreover, since for  $m(0) < M$  we will always have  $m(t) \leq M$ . Therefore, we are only interested in  $0 < m^* < M$ . Of course, from a practical point of view, the absence of bees will imply the absence of mites, and thus  $m = 0$  as a consequence.

The right hand side of (2.1)-(2.3) does not satisfy a Lipschitz condition for  $x = y = 0$ , and some of the coefficients of the Jacobian (3.4) blow up. Using the same Lyapunov argument as in Lemma 2.1, we note that inequality (2.5) is also satisfied for all sufficiently small  $r > 0$  and all  $x < r$ . To show this, we need to show again for sufficiently small  $r$  that

$$\mu g(x)h(m) + (d_2 - d_1)x - d_2r \leq 0, \quad \text{for all } x \leq r. \quad (3.10)$$

By continuity and monotonicity of  $g(x)$ , and because of  $h(m) \leq 1$ , we obtain that this is satisfied if

$$\mu g(r) - d_1 r \leq 0.$$

The last inequality is certainly satisfied for all  $r$  with  $0 < r \leq x_2^*$  from (3.3)<sup>1</sup>. Thus,  $\mathcal{K}_r$  is positively invariant for  $0 < r \leq x_2^*$ . Therefore, after small perturbations, the solutions remain close to the collapse equilibrium, which is therefore stable. We point out that the unconditional stability of the collapse equilibrium stems from the fact that a large enough bee population is required to care for the brood in our model. In models that do not make this assumption this is not the case. The model of [10] is the special case  $K = 0$  in (2.2), in which  $x_2^*$  vanishes.

If (3.8) is satisfied, we have several stable equilibria with  $y^* = 0$  (as well as the always unstable steady state  $(0, x_2^*, 0)$  above). Whether one of these equilibria is attained, and if so, which one, therefore, depends on the initial strength of the colony. If the initial bee population lies within  $\mathcal{K}_{\bar{r}}$ , which depends on the parameters, then a collapse equilibrium is attained. Otherwise the disease can be fought off.

**Endemic equilibrium.** In this state, the colony contains healthy and sick bees. The equilibrium generally takes the form

$$m = m^*, \quad x = x^{**}, \quad y = y^{**}. \quad (3.11)$$

The algebraic treatment of this steady state leads to involved expressions that do not lend themselves to an insightful analysis. While the eigenvalues of a three-dimensional system can be explicitly calculated, this involves look-up tables to distinguish between a multitude of possible cases. Instead of presenting these calculations here, which can be performed by computer algebra software, we demonstrate the long-term behavior of the system in computational simulations, where we use for  $\beta_{1,2,3}, d_{1,2}, \mu$  the parameters in Table 1, for spring and summer conditions.

**3.2. Computer simulations.** In Figure 3, we plot the populations size of healthy and infected bees,  $x$  and  $y$ , at steady state (all solutions do converge to a steady state), in dependence of the number of mites  $M$  and the population size that is required to maintain the population,  $K$ , for the maintenance function  $g(x) = \frac{x^2}{K^2 + x^2}$ . This is for the initial conditions  $m(0) = 0.2M$ ,  $x(0) = 3000$ ,  $y(0) = 0$ . We show the results for spring and summer conditions. As can be seen from Table 1, the fall parameter values are very similar to those in spring and one obtains very similar results.

In both cases, spring and summer, we observe that for small values of  $K$  (i.e. higher birth rates of healthy bees) and  $M$  (i.e. less risk to catch the disease) the disease free equilibrium is attained, as expected from criterion (3.8). Equilibria of the type  $x = x^{**} > 0$ ,  $y = y^{**} > 0$  are found for small values  $K$  and large values  $M$ . However, in this case, the bee population  $x + y$  is small compared to the size of an entirely healthy population. Thus, we conclude that such endemic colonies, while in a stable equilibrium, are not functioning like healthy populations. For large values of  $K$  (i.e. a strong colony is required to maintain the brood) and  $M$  (i.e. high risk to be infected), the population dies out and attains the collapse equilibrium. Moreover, the unconditional stability of the collapse equilibrium also

<sup>1</sup>Note: with the same argument, a better estimate for  $\tilde{R}$  in Lemma 2.1 than  $\tilde{R} = d_1/\mu$  is obtained as  $\tilde{R} := x_1^*$



implies that colonies which are initially very small will never develop into healthy colonies, because they will never reach the required population strength for brood maintenance (not shown in our simulations). This is in particular important for the spring season, because in winter no bees are born but the colony naturally declines due to bee death. If at the end of the winter the colony is not strong enough to rear the brood, it will die out.

We note that under winter conditions, the only and asymptotically stable equilibrium is the trivial equilibrium  $x^* = y^* = 0$ . However, winter worker bees live much longer than spring, summer or fall bees, namely several months compared to several weeks, cf also [1]. Hence the winter bee death rate is small, therefore, decline in the population is slow, compared to the duration of the season. Therefore, long term analysis of the model for winter conditions, as we conducted here for the case of constant parameters, does not lead to any useful insight. A bee colony that is large enough at the beginning of winter that, by the end of winter it is big enough to recover, will survive. A healthy population will decline exponentially according to

$$\frac{dx}{dt} = -d_1x.$$

If infected bees are present at the beginning of the winter, this, however, gives only an upper estimate. A lower estimate is obtained from

$$\frac{dx}{dt} + \frac{dy}{dt} = -d_1x - d_2y > -d_2(x + y).$$

#### 4. BEE COLONIES THROUGH THE SEASONS: THE NON-AUTONOMOUS CASE

A rigorous qualitative analysis of the model for time varying parameters is essentially more complicated than the autonomous case, even if we assume that the parameters are time periodic with a period of one year. The quantitative data that are available to us are seasonal averages. In principle we can construct an infinite number of non-negative periodic functions with the same seasonal averages. However, on an objective basis, it is not possible to decide which of these interpolated functions is more realistic or better than other ones. Therefore, we simply assume the model parameters to be constant across four seasons of 91 days each, at their average values, but varying between seasons, cf Table 1. The model parameters are repeated in every year. In order to explore the dynamics of (2.1)-(2.3) through the seasons we conduct computer simulations. The inclusion of the colony maintenance term  $g(x, t)$  can cause the model to become stiff for small bee colony sizes. In order to deal with this situation we implemented a simple first order Rosenbrock-Wanner method for the integration of our governing equations.

We assume all parameters but  $K$  and  $M$  to be given and we investigate the effect of these two parameters on the disease dynamics. Moreover, the analysis above has shown several stable steady states can be found for the autonomous system. Therefore, it can be expected that the initial data might play a role for the fate of the bee colony in the simulations.

A numerical exploration cannot give a complete picture of the dynamics of the model. Instead we aim at illustrating the possible outcomes for the model solutions in examples.

**4.1. Simulation I: effect of size of mite population  $M$ .** In a first simulation experiment we investigate the effect of the number of mites,  $M$ , on the fate of the

bee colony. The analysis of the autonomous case has shown that there is a critical number of mites,  $M_{\text{crit}}$  [cf. (3.8) above]. For mite populations smaller than  $M_{\text{crit}}$  the virus can be fought off, while for values greater than  $M_{\text{crit}}$  the disease will take its toll and the bee population will die out.

In this simulation we test for mite populations  $M$  somewhat smaller than this critical value,  $0.8M_{\text{crit}} \leq M \leq M_{\text{crit}}$ . More specifically, we conduct the following 4 simulations

- $K := 0.4\mu/d_1$  (recall:  $K < 0.5\mu/d_1$  is required for  $x_1^*$  to be stable),
- $M = \delta M_{\text{crit}}$  where  $\delta = 0.8, 0.85, 0.9, 0.95$ .

Note that thus defined  $K$  and  $M$  are piecewise constant periodic functions of time, since they are defined relative to the other model parameters.

We assume that initially only a small number of mites carry the virus. Moreover we assume that initially no sick bees are in the colony. The number of healthy bees is chosen large enough to exceed  $K$  and  $x_1^*$  above.

- $m(0) = 0.01M$  (1% of all mites carry virus),
- $x(0) = x_0$  (10% larger than  $K$  and  $x_1^*$  of the autonomous case),
- $y(0) = 0$  (no bees initially sick).

The simulations were run over a period of 6000 days or until the colony dies out, whichever came first. The results are plotted in Figure 4.

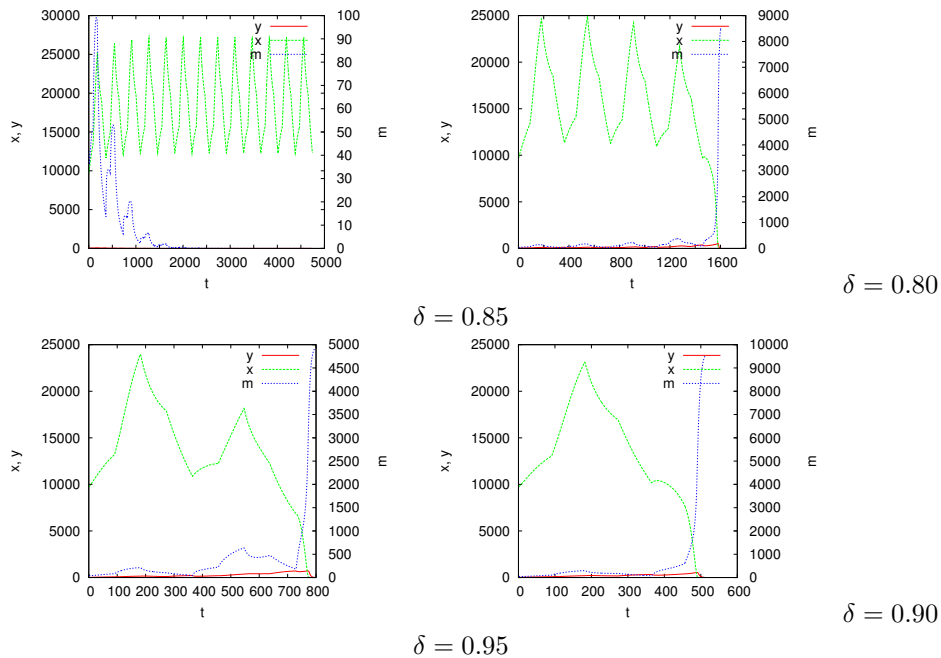


FIGURE 4. Simulation of bee-mite-virus dynamics for varying mite population size  $M = \delta M_{\text{crit}}$

We observe that for the smallest value for  $M$  in our survey,  $M = 0.8M_{\text{crit}}$ , the virus infestation is fought off. While for the first few years virus carrying mites can be found in the colony, their number decreases over the years. Like the bee

population itself, the number of virus carrying mites is highest in summer and decreases in fall. The maximum number of  $m$  decreases over the first 4 years, after which the virus has virtually disappeared from the colony. The number of healthy bees is periodic and seems to be little affected by the presence of the virus.

As the number of mites  $M$  in the population is increased to 85% of the critical mite load, the qualitative picture changes. While the number of virus carrying mites still follows the seasonal fluctuations, with highest numbers in summer, the maximum number of virus carrying mites increases from year to year. Over the first four years the healthy bee population appears to follow a pattern similar to the previous case, although we do notice that the maximum population size becomes slightly smaller each year. After the fourth year of the infestation, the colony vanishes rapidly, during the spring season. Over the whole period of four years, the number of virus carrying bees is small compared to the number of healthy bees. The colony dies because the number of healthy bees drops below the levels required to maintain the brood.

Increasing the number of mites  $M$  further to 90% and 95% of the critical value, we observe qualitatively the same picture, but the decline of the bee population to levels that cannot sustain the brood happens earlier, after two years and one year, respectively.

The sudden decline of the bee population after several years is a consequence of gradual changes. Eventually the population size falls below the critical threshold that is required for it to recover, and then the colony dies rapidly.

**4.2. Simulation II: effect of brood maintenance parameter  $K$ .** In the second simulation experiment we fix the number of mites  $M$  at 85% of the critical value  $M_{\text{crit}}$  and vary the brood maintenance coefficient  $K$  between 40% and 80% of the value that is necessary to allow for a nontrivial disease free equilibrium. More specifically

- $K := \kappa * 0.5\mu/d_1$ , where  $\kappa = 0.4, 0.6, 0.7, 0.8$ ,
- $M = 0.85M_{\text{crit}}$ .

Note that the case  $\kappa = 0.8$  is identical to  $\delta = 0.85$  in the previous simulation experiment. The initial data are chosen as in the previous simulation experiment:

- $m(0) = 0.01M$  (1% of all mites carry virus),
- $x(0) = x_0$  (10% larger than  $K$  and  $x_1^*$ ),
- $y(0) = 0$  (no bees initially sick)

As before, the simulations were run over a period of 6000 days or until the colony dies out, whichever came first. The results are plotted in Figure 5.

The simulation results are easily summarized: if the number of bees that is required to maintain the brood is small compared to the birth/death rate ratio, i.e. if relatively few worker bees are required for this task, an initially healthy population can fight off a virus epidemic. Virus carrying mites can be found initially but, after adjusting for seasonal fluctuations, their numbers decline. Eventually the colony is disease free. The larger  $K$  is, the longer it will take to rid the colony from the virus. As the parameter  $K$  increases; i.e., if the number of worker bees that is required to care for the brood becomes large enough, the colony cannot fight off the disease and eventually dies out, – 4 years in our simulations. Again, the number of sick bees  $y$  is always small compared to the overall colony size.

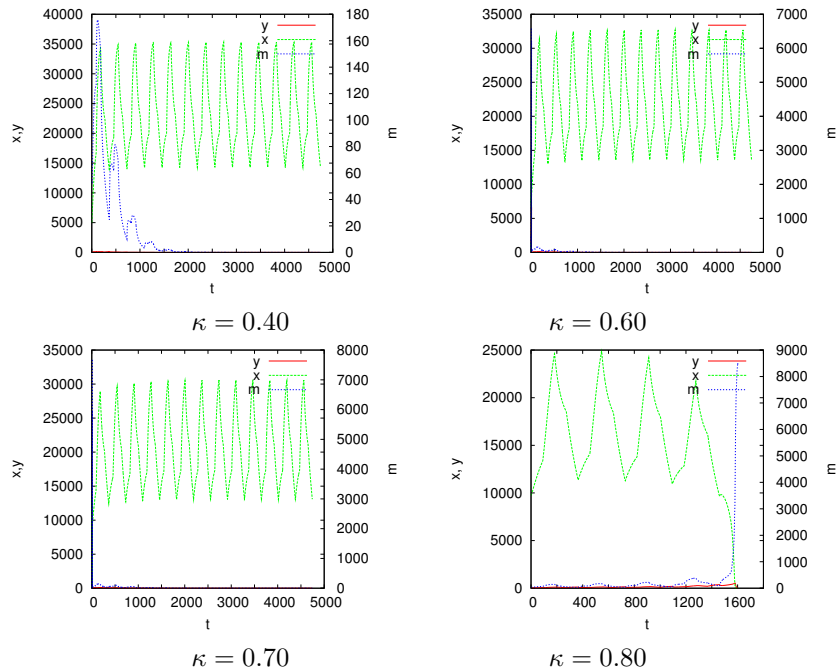


FIGURE 5. Simulation of bee-mite-virus dynamics for varying  $K = 0.5\mu/d_1\kappa$

#### 4.3. Simulation III: effect of initial number of virus carrying mites $m(0)$ .

In a third simulation experiment we fix the number of mites  $M$  to be 80% of the critical mite load, and the brood maintenance parameter  $K$  to be at 60% of the value that is needed to establish a stable bee population.

- $K := 0.3\mu/d_1$ ,
- $M = 0.80M_{\text{crit}}$ .

In the previous simulations, where the number of mites carrying the virus initially was small, at  $m(0)$  being 1% of all the mites, it was found that these parameters are small enough for the colony to fight of the diseases. In this simulation experiment, we investigate whether this also holds true if at the starting point of our simulation more mites carry the virus. We test the initial data

- $m(0) = \nu M$  where  $\nu = 0.1, 0.11, 0.12$ ,
- $x(0) = x_0$  (10% larger than  $K$  and  $x_1^*$ ),
- $y(0) = 0$  (no bees initially sick).

The results are plotted in Figure 6.

For the smallest value  $m(0)$  of initially virus carrying mites tested, the colony can fight off the disease. The temporal patterns of the healthy population  $x(t)$  and for the number of mites that carry the virus  $m(t)$  are qualitatively similar to the ones observed before for small enough mite numbers  $M$  and brood maintenance coefficients  $K$ :  $m(t)$  oscillates over the years, but the peak value in summer decreases until  $m$  virtually disappears;  $x(t)$  oscillates over the years as well, with increasing maximum population sizes as the number of virus carrying mites decreases.

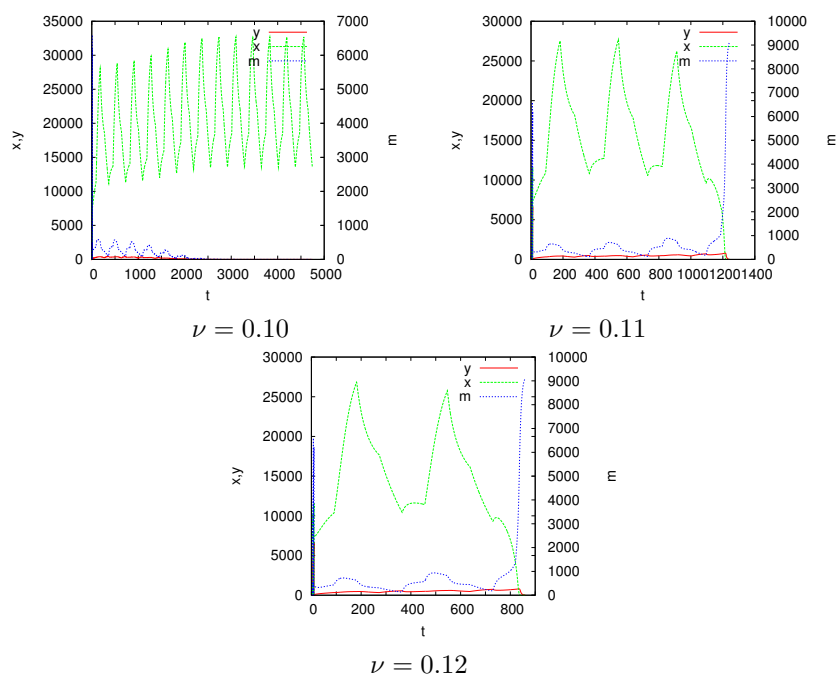


FIGURE 6. Simulation of bee-mite-virus dynamics for varying number of initially virus carrying mites  $m_0$

As  $m(0)$  is slightly changed from  $m(0) = 0.10M$  to  $m(0) = 0.11M$ , the long term behavior changes drastically. The number of virus carrying mites, after adjusting for seasonal fluctuations, increases slightly and the number of healthy bees, again after adjusting for seasonal fluctuations, slightly decreases. After the third cycle, the healthy bee population enters the spring too small to be able to fight off the virus, and dies out. When increasing  $m(0)$  further to 12% of the total number of mites, this is accelerated and the colony disappears after only two years. As before, the number of sick bees is small compared to the overall colony size.

**4.4. Conclusion.** The mathematical model presented here is simple, yet it is too complex for a complete rigorous analytical treatment. Therefore, we studied it with a combination of analytical and computational arguments. It is a straightforward extension of a model that was previously formulated and analyzed in [10]. We (i) focus on the role of a brood maintenance term and how it affects the disease dynamics of the Acute Paralysis Virus in a bee colony qualitatively, and (ii) investigate how this affects the bee colony long-term, over several years.

Our results indicate that models that do not account for the fact that a certain colony strength is required to maintain the brood and thus to sustain the colony development might underestimate the maximum number of mites that a bee population can tolerate. Our mix of mathematical analysis and computer simulation indicates that the long term behavior of a bee population can depend on a variety of parameters, including the initial data. Our computer simulations have shown that an infested colony might be able to function seemingly like a healthy colony

for years and then suddenly can collapse and disappear. In all our simulations, if this occurs it happens in the spring season because the bee population is too small to rear the brood. These preliminary simulation results are in accordance with the recent study [2] on wintering losses in Canada.

Many important processes that can affect the long term fate of a colony over the years are not yet included in this model. Examples are gradual changes of the environment; the size of the mite population as a dynamically varying variable; the possible loss of the queen and its replacement by an emergency queen; or swarming when a new queen emerges. Some such processes can be included in this model in a rather straightforward manner, however, always at the expense of introducing new unknown model parameters. Thus, increasing biological complexity of the model is at the expense of increasing also the mathematical complexity. Therefore we decided to keep the model simple in our first study of the topic.

*Acknowledgements.* This study was supported in part by the Canadian Pollination Initiative (CANPOLIN), a NSERC Strategic Network (PI: PGK). M. R. Frederick acknowledges the support received through a NSERC Postgraduate Scholarship. H. J. Eberl acknowledges the support received from the Canada Research Chairs program.

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