

Threshold Conditions for West Nile Virus Outbreaks

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Abstract In this paper, we study the stability and saddle-node bifurcation of a model for the West Nile virus transmission dynamics. The existence and classification of the equilibria are presented. By the theory of K-competitive dynamical systems and index theory of dynamical systems on a surface, sufficient and necessary conditions for local stability of equilibria are obtained. We also study the saddle-node bifurcation of the system. Explicit subthreshold conditions in terms of parameters are obtained beyond the basic reproduction number which provides further guidelines for accessing control of the spread of the West Nile virus. Our results suggest that the basic reproductive number itself is not enough to describe whether West Nile virus will prevail or not and suggest that we should pay more attention to the initial state of West Nile virus. The results also partially explained the mechanism of the recurrence of the small scale endemic of the virus in North America.

Keywords West Nile virus · Differential equations · Multiple equilibria and stability · Backward bifurcation · Threshold conditions · Dynamics

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1. Introduction

Since the first outbreak in New York in the late summer of 1999, West Nile virus (WNV) has been spreading through the continent of North America for the last several years (Centers for Disease Control and Prevention, 2003). It was believed that WNV is maintained in nature in a mosquito-bird-mosquito transmission cycle (Campbell et al., 2002; Hayes, 2001; Komar et al., 2003; Lanciotti et al., 2003). Many areas in North America, such as Southern Ontario, Canada (West Nile Virus Monitor—West Nile Virus Surveillance Information. West Nile Virus—Public Health Agency of Canada. <http://www.phac-aspc.gc.ca/wn-no/index-e.html>), have been experiencing for the last several years small scale outbreaks of the virus. It is imperative to gain some insights into the transmission dynamics of WNV in the mosquito-bird population.

Compartmental epidemiological models have played a significant role in understanding the mechanism of dynamical transmission of various virus. Since the pioneering work of Kermack–Mckendrick, SIR/SEIR epidemiological models have received much attention from scientists (see Brauer and Castillo-Chavez, 2000; Hethcote, 2002; Diekmann and Heesterbeek, 2000 and references therein). However, to our knowledge, the literature on the mathematical modeling studies of the transmission of WNV is rather scant. Lord and Day (2001) carried out simulation studies of St. Louis encephalitis and West Nile virus using the models of differential equations. Thomas and Urena (2001) formulated a difference equation model for WNV targeting its effects on New York City. Wonham et al. (2004) presented a single-season ordinary differential equations model for WNV transmission in the mosquito-bird population. Kenkre et al. (2005) provided a theoretical framework for the analysis of the West Nile virus epidemic and for dealing with mosquito diffusion and birds migration. Bowman et al. (2005) proposed a model system incorporating mosquito-bird-human population for assessing control strategies against West Nile virus. Cruz-Pacheco et al. (2005) formulated a model for the transmission of WNV and by using experimental and field data as well as the numerical simulations, they found the phenomena of damped oscillations of the infected birds population. By using a reaction-diffusion model, Lewis et al. (2006a) studied the spatial spread of the virus, established the existence of traveling waves computed the spatial spread speed of infection. Liu et al. (2006) studied the impact of directional dispersal of birds on the spatial spreading of West Nile virus. In a more recent work by Lewis et al. (2006b), they made a comparative study of the discrete-time model (Thomas and Urena, 2001) and the continuous-time model (Wonham et al., 2004). This interesting study suggests that a slightly different but seemingly reasonable assumptions for the modeling of WNV can yield very different biological conclusions on the basis of analysis of the basic reproduction number.

To our knowledge, the aforementioned modeling studies on West Nile virus are the only mathematical models available in the literature. In all of these models, the threshold conditions, the basic reproduction numbers were calculated or estimated which serves as crucial control threshold for the eradication of the West Nile virus. In particular, these studies suggested that when the basic reproduction number, $\mathbb{R}_0 < 1$, the disease free equilibrium would be globally asymptotically stable and the infections eventually die out. In this paper, we are going to analytically study the model proposed by Bowman et al. (2005). The model undergoes a saddle-node bifurcation when the basic reproduction number is smaller than one. The saddle-node bifurcation suggests that more attention should

be paid to the initial number of the infected mosquitoes and birds, which may also partially explain the mechanism of the recurrence of the small scale endemic of the virus in North America.

The model in Bowman et al. (2005) consists of nine differential equations and describes the transmission of the WNV among the mosquito-bird-human populations. Though humans, horses, and other large domestic mammals can be infected by an infectious mosquito, they do not transmit the disease, therefore, the dynamics of the whole model are indeed determined by the four dimensional system involving only the mosquitoes and birds. Hence, the model for the transmission of the virus in the primary mosquito-bird cycle reads

$$\begin{cases} \frac{dM_u}{dt} = \Pi_M - \frac{b_1\beta_1 M_u B_i}{B_i + B_u} - \mu_M M_u, \\ \frac{dM_i}{dt} = \frac{b_1\beta_1 M_u B_i}{B_i + B_u} - \mu_M M_i, \\ \frac{dB_u}{dt} = \Pi_B - \frac{b_1\beta_2 M_i B_u}{B_i + B_u} - \mu_B B_u, \\ \frac{dB_i}{dt} = \frac{b_1\beta_2 M_i B_u}{B_i + B_u} - \mu_B B_i - d_B B_i, \end{cases} \tag{1}$$

where following the symbols and notations in Bowman et al. (2005), $M_u(t)$ and $M_i(t)$ are the populations of uninfected and infected female mosquitoes, respectively; $B_u(t)$ and $B_i(t)$ represent the population of susceptible and infected birds, respectively, and Π_M and Π_B are the recruitment rates of the uninfected birds (either by birth or immigration) of susceptible mosquitoes and birds, respectively; b_1 is the per capita biting rate of mosquitoes on the primary host (bird); β_1 and β_2 are the West Nile virus transmission probabilities from infected birds to uninfected mosquitoes and from mosquitoes to birds, respectively; μ_M and μ_B are the natural death rates of mosquitos and birds, respectively; d_B denotes the WNV-induced death rate of infected birds. The parameters in this model are all positive constants.

Here, we remark that for the model proposed in Bowman et al. (2005), the basic reproduction number was calculated, and sufficient conditions for the local and global stability of the associated equilibria were obtained and detail explanations were also given for their theoretic results. However, one important phenomena was ignored: the existence of multiple equilibria when the control parameter, the basic reproduction number, is smaller than one. As have been seen, system (1) may undergo a backward bifurcation.

Let

$$M(t) = M_u(t) + M_i(t). \tag{2}$$

It follows from system (1) that $M(t)$ satisfies the following differential equation:

$$\frac{dM}{dt} = \Pi_M - \mu_M M. \tag{3}$$

This leads to $M(t) \rightarrow \frac{\Pi_M}{\mu_M}$ as $t \rightarrow +\infty$. Thus, system (1) is reduced to the following three dimensional system:

$$\begin{cases} \frac{dM_i}{dt} = \frac{b_1\beta_1(\frac{\Pi_M}{\mu_M} - M_i)B_i}{B_i + B_u} - \mu_M M_i, \\ \frac{dB_u}{dt} = \Pi_B - \frac{b_1\beta_2 M_i B_u}{B_i + B_u} - \mu_B B_u, \\ \frac{dB_i}{dt} = \frac{b_1\beta_2 M_i B_u}{B_i + B_u} - \mu_B B_i - d_B B_i. \end{cases} \tag{4}$$

One of the important subjects in epidemiological modeling studies is to obtain a threshold condition for accessing control of the disease or virus. In most cases, it is the so-called basic reproduction number \mathbb{R}_0 that may determine the persistence and eradication of the disease (Anderson and May, 1991; Brauer and Castillo-Chavez, 2000; Hethcote, 2002). The spread of the disease can be controlled or the virus can be eradicated if the basic reproduction number $\mathbb{R}_0 < 1$, and otherwise the disease will be endemic. However, our study of system (4) indicates that the basic reproductive number cannot simply determine whether West Nile virus will prevail or not and suggests that one needs to pay more attention to the initial number of the infected mosquitoes and birds.

This paper is organized as follows: in Section 2, we will examine the existence of multiple equilibria and provide a detailed classification of the equilibria of system (1). We will discuss the local stability of all the disease free equilibrium (DFE) and endemic equilibria in Section 3. In Section 4, we will develop and present explicitly the threshold conditions for the saddle-node bifurcation of the model; we will also describe the bifurcation diagram by using the recruitment rate of susceptible mosquitoes Π_M and the natural death rate of mosquitos μ_M as parameters. In the last section, we conclude with some numerical simulations and discussions.

2. Existence and classification of equilibria

As in Bowman et al. (2005), we let

$$\mathbb{D} = \left\{ (M_i, B_u, B_i) \mid 0 \leq M_i \leq \frac{\Pi_M}{\mu_M}, \frac{\Pi_B}{\mu_B + d_B} \leq B_u + B_i \leq \frac{\Pi_B}{\mu_B} \right\}.$$

Then we have

Proposition 2.1. *All solutions of the system (4) remain nonnegative. Moreover, \mathbb{D} is a global attractor in \mathbb{R}_+^3 and positively invariant for (4).*

Proof: The first statement is trivial. It easily follows from the argument for reduction in the last section that $0 \leq M_i(t) \leq \frac{\Pi_M}{\mu_M}$. It follows from system (4) that we have

$$\Pi_B - (\mu_B + d_B)(B_i + B_u) \leq \frac{d(B_i + B_u)}{dt} \leq \Pi_B - \mu_B(B_i + B_u)$$

for all $t \geq 0$, then the second statement follows immediately. □

Thus, we always assume that the initial points $(M_i(0), B_u(0), B_i(0))$ lie in \mathbb{D} . The following basic reproduction number was calculated in Bowman et al. (2005):

$$\mathbb{R}_0 = \sqrt{\frac{b_1^2 \beta_1 \beta_2 \mu_B \Pi_M}{\mu_M^2 (\mu_B + d_B) \Pi_B}}. \tag{5}$$

To examine the existence of equilibrium, we set

$$f(B_i) = a_2 B_i^2 + a_1 B_i + a_0, \tag{6}$$

where

$$\begin{aligned} a_2 &= \frac{d_B(\mu_M d_B - b_1 \beta_1 \mu_B)}{b_1 \beta_2 \mu_B}, \\ a_1 &= \frac{b_1 \beta_1 \Pi_M}{\mu_M} - \frac{(2\mu_M d_B - b_1 \beta_1 \mu_B) \Pi_B}{b_1 \beta_2 \mu_B}, \\ a_0 &= \frac{\mu_M \Pi_B^2 (1 - \mathbb{R}_0^2)}{b_1 \beta_2 \mu_B}. \end{aligned} \tag{7}$$

We use the notations in Bowman et al. (2005) and denote

$$\begin{aligned} \Delta &= a_1^2 - 4a_0 a_2, \\ B_{i1}^* &= \frac{\mu_M \Pi_B}{\mu_M d_B - b_1 \beta_1 \mu_B}, \quad B_{i2}^* = \frac{\Pi_B}{\mu_B + d_B}. \end{aligned}$$

Now we are able to state the principal results in this section.

Theorem 2.2. *The system (4) can have up to three equilibria. More precisely, we have*

- (i) *The boundary equilibrium, the disease free equilibrium (DFE) $E_0(0, \frac{\Pi_B}{\mu_B}, 0)$, always exists.*
- (ii) *If $\mathbb{R}_0 > 1$, there exists a unique positive equilibrium $E^*(M^*, B_u^*, B_i^*)$. Moreover, if $a_2 \neq 0$, we have*

$$B_i^* = \frac{-a_1 + \sqrt{\Delta}}{2a_2}, \quad M_i^* = \frac{(\Pi_B - d_B B_i^*) B_i^*}{b_1 \beta_2 (B_{i2}^* - B_i^*)}, \quad B_u^* = \frac{\mu_B + d_B}{\mu_B} (B_{i2}^* - B_i^*);$$

if $a_2 = 0$, which is equivalent to $d_B = 0$ or $\mu_M d_B - b_1 \beta_1 \mu_B = 0$, then

$$B_i^* = \frac{-a_0}{a_1}, \quad M_i^* = \frac{(\Pi_B - d_B B_i^*) B_i^*}{b_1 \beta_2 (B_{i2}^* - B_i^*)}, \quad B_u^* = \frac{\mu_B + d_B}{\mu_B} (B_{i2}^* - B_i^*).$$

- (iii) *If $\mathbb{R}_0 < 1$, then*
 - (a) *if $a_2 \leq 0$, there is no positive equilibrium;*

(b) if $a_2 > 0$, system (4) has two positive equilibria if and only if

$$\Delta > 0, \quad \text{and} \quad 0 < \frac{-a_1}{2a_2} < B_{i2}^*. \tag{8}$$

These two equilibria $E^1(M_i^1, B_u^1, B_i^1)$ and $E^2(M_i^2, B_u^2, B_i^2)$ are

$$B_i^1 = \frac{-a_1 - \sqrt{\Delta}}{2a_2}, \quad M_i^1 = \frac{(\Pi_B - d_B B_i^1) B_i^1}{b_1 \beta_2 (B_{i2}^* - B_i^1)},$$

$$B_u^1 = \frac{\mu_B + d_B}{\mu_B} (B_{i2}^* - B_i^1),$$

$$B_i^2 = \frac{-a_1 + \sqrt{\Delta}}{2a_2}, \quad M_i^2 = \frac{(\Pi_B - d_B B_i^2) B_i^2}{b_1 \beta_2 (B_{i2}^* - B_i^2)},$$

$$B_u^2 = \frac{\mu_B + d_B}{\mu_B} (B_{i2}^* - B_i^2).$$

These two equilibria coalesce if and only if $0 < \frac{-a_1}{2a_2} < B_{i2}^*$ and $\Delta = 0$; otherwise, there is no positive equilibrium.

Proof: It is obvious that the boundary equilibrium $E_0(0, \frac{\Pi_B}{\mu_B}, 0)$ always exists and is unique.

Now we prove the other two cases. It is easy to see that a positive equilibrium of (4) must satisfy the following equations:

$$\begin{cases} \frac{b_1 \beta_1 (\frac{\Pi_M}{\mu_M} - M_i) B_i}{B_i + B_u} - \mu_M M_i = 0, \\ \Pi_B - \frac{b_1 \beta_2 M_i B_u}{B_i + B_u} - \mu_B B_u = 0, \\ \frac{b_1 \beta_2 M_i B_u}{B_i + B_u} - \mu_B B_i - d_B B_i = 0. \end{cases} \tag{9}$$

Adding the second and third equations leads to

$$B_u = \frac{\Pi_B}{\mu_B} - \left(1 + \frac{d_B}{\mu_B}\right) B_i. \tag{10}$$

Putting (10) into (9), as in Bowman et al. (2005), the positive equilibrium, if exists, is the intersection of the two curves:

$$M_i = \frac{\frac{b_1 \beta_1 \Pi_M}{\mu_M} B_i}{\frac{\Pi_B}{\mu_B} \mu_M + (b_1 \beta_1 - \mu_M \frac{d_B}{\mu_B}) B_i} = \Gamma_1(B_i), \tag{11}$$

and

$$M_i = \frac{(\Pi_B - d_B B_i) B_i}{b_1 \beta_2 (B_{i2}^* - B_i)} = \Gamma_2(B_i). \tag{12}$$

It is clear that if (M_i, B_i, B_u) is a positive solution for (9), then $B_i \leq B_{i2}^*$, and satisfies

$$\Gamma_1(B_i) = \Gamma_2(B_i). \quad (13)$$

A straightforward calculation yields that if the positive equilibrium exists, its B_i coordinate is the root of the quadratic equation

$$f(B_i) = a_2(B_i)^2 + a_1 B_i + a_0 = 0 \quad (14)$$

in the interval $[0, B_{i2}^*]$.

Consider the parabola $f(B_i)$ on the interval $[0, B_{i2}^*]$. Substituting $B_i = B_{i2}^* = \frac{\Pi_B}{\mu_B + d_B}$ into $f(B_i)$ gives

$$\begin{aligned} f(B_{i2}^*) &= a_2 \left(\frac{\Pi_B}{\mu_B + d_B} \right)^2 + a_1 \frac{\Pi_B}{\mu_B + d_B} + a_0 \\ &= \frac{1}{(\mu_B + d_B)^2} \left[\frac{d_B(\mu_M d_B - b_1 \beta_1 \mu_B)}{b_1 \beta_2 \mu_B} \Pi_B^2 + \frac{b_1 \beta_1 \Pi_M}{\mu_M} (\mu_B + d_B) \Pi_B \right. \\ &\quad \left. - \frac{2\mu_M d_B - b_1 \beta_1 \mu_B}{b_1 \beta_2 \mu_B} (\mu_B + d_B) \Pi_B^2 + \frac{\mu_M \Pi_B^2 (1 - \mathbb{R}_0^2)}{b_1 \beta_2 \mu_B} (\mu_B + d_B)^2 \right] \\ &= \frac{\Pi_B}{(\mu_B + d_B)^2} \left[\frac{-\mu_M d_B}{b_1 \beta_2 \mu_B} \Pi_B d_B + \frac{b_1 \beta_1 \Pi_M}{\mu_M} (\mu_B + d_B) \right. \\ &\quad \left. - \frac{2\mu_M d_B - b_1 \beta_1 \mu_B}{b_1 \beta_2 \mu_B} \Pi_B \mu_B + \frac{\mu_M \Pi_B (1 - \mathbb{R}_0^2)}{b_1 \beta_2 \mu_B} (\mu_B + d_B)^2 \right] \\ &= \frac{\Pi_B}{(\mu_B + d_B)^2} \left[\frac{-\mu_M d_B}{b_1 \beta_2 \mu_B} \Pi_B d_B + \frac{b_1 \beta_1 \Pi_M}{\mu_M} (\mu_B + d_B) \right. \\ &\quad \left. - \frac{2\mu_M d_B - b_1 \beta_1 \mu_B}{b_1 \beta_2 \mu_B} \Pi_B \mu_B \right. \\ &\quad \left. + \frac{\mu_M^2 \Pi_B (\mu_B + d_B) - b_1^2 \beta_1 \beta_2 \mu_B \Pi_M}{b_1 \beta_2 \mu_B \mu_M} (\mu_B + d_B) \right] \\ &= \frac{\mu_B \Pi_B^2 (\mu_M + b_1 \beta_1)}{(\mu_B + d_B)^2 b_1 \beta_2} > 0. \end{aligned}$$

Case $\mathbb{R}_0 > 1$. It is obvious that $a_0 < 0$. Hence, $f(0) = a_0 < 0$. Since $f(B_i)$ is a quadratic function (or a linear function), it follows that $f(B_i) = 0$ has a unique positive root in the interval $[0, B_{i2}^*]$. Therefore, it follows that system (4) has a unique positive equilibrium $E^*(M_i^*, B_u^*, B_i^*)$.

If $a_2 = 0$, then either $d_B = 0$ or $\mu_M d_B - b_1 \beta_1 \mu_B = 0$, the result is straightforward.

Assume that $a_2 \neq 0$. Then the positive root for (13) is to the right of the line $B_i = -\frac{a_1}{2a_2}$ in the case when $a_2 > 0$, while it lies on the left of the line $B_i = -\frac{a_1}{2a_2}$ if $a_2 < 0$. This shows that the positive root has the expression $B_i^* = \frac{-a_1 + \sqrt{\Delta}}{2a_2}$. It follows from (10) and (12) that the other coordinates of the unique equilibrium must be as given in the theorem. Figures 1(a) and (b) show the two cases of the unique equilibrium with the two different positions of the asymptote of Γ_1 .

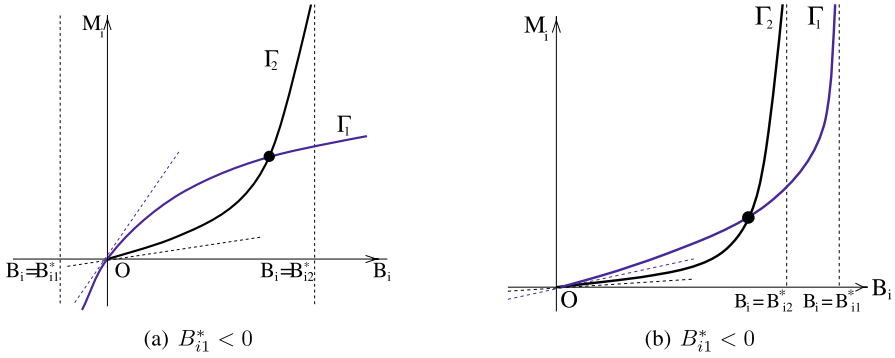


Fig. 1 Case $\mathbb{R}_0 > 1$: the unique positive equilibrium.

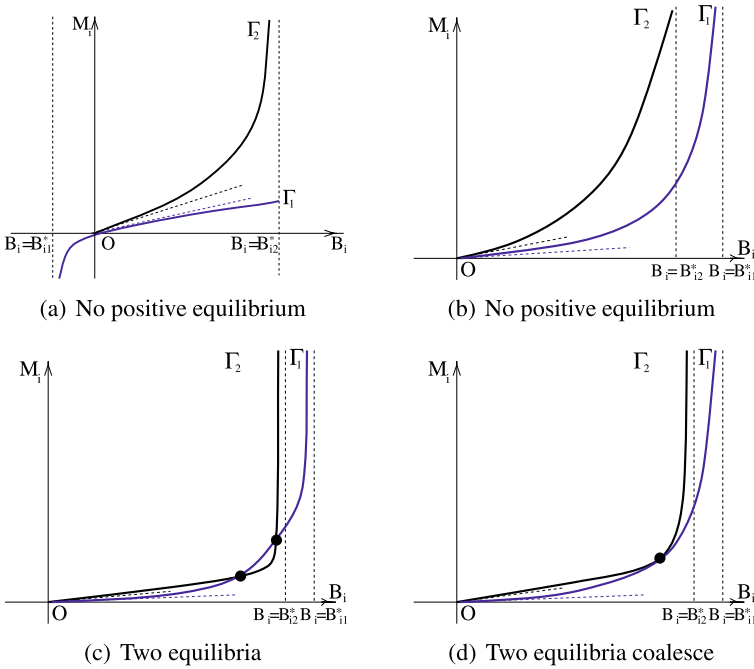


Fig. 2 Case $\mathbb{R}_0 < 1$: system (4) can have zero, one, and two positive equilibria.

Case $\mathbb{R}_0 < 1$. Obviously we have $a_0 > 0$. It follows that $f(0) = a_0 > 0$. Since $f(B_i)$ is either quadratic or linear in B_i , we can prove that (14) has no positive root in the interval $[0, B_{i2}^*]$ in the case $a_2 \leq 0$. It remains to consider the case $a_2 > 0$.

It is clear that Eq. (14) has two real roots in the interval $[0, B_{i2}^*]$ if and only if $0 < \frac{-a_1}{2a_2} < B_{i2}^*$ and $f(\frac{-a_1}{2a_2}) < 0$ ($\Delta > 0$); see Fig. 2(c). Solving (14) gives the two equilibria as given in the theorem. The system (4) has a unique positive equilibrium (multiplicity

two) if and only if $0 < \frac{-a_1}{2a_2} < B_{i2}^*$ and $f(\frac{-a_1}{2a_2}) = 0$ ($\Delta = 0$). This is the case when the two positive equilibria coalesce; see Fig. 2(d). One can solve (14) to get $B_i^1 = -\frac{a_1}{2a_2}$. The other cases correspond to the situation where there is no positive equilibrium. \square

3. The local stability analysis

In this section, we shall study the local stability of all the equilibria of system (4). In what follows, we first state some results for three dimensional K -competitive dynamical systems, which will prove to be useful in the discussion of the stability of the positive equilibrium.

Consider the differential equations:

$$\dot{x} = f(x), \tag{15}$$

where $x \in \mathbb{R}_+^3$. A matrix A is called *type K -competitive* and *irreducible* (Smith, 1995) if A has the following form

$$\begin{pmatrix} * & - & + \\ - & * & + \\ + & + & * \end{pmatrix}.$$

The system (15) is called *type K -competitive* and *irreducible* if the Jacobian $Df(x)$ of f is type K -competitive and irreducible for each $x \in \mathbb{R}_+^3$. Now we set

$$K = \{(x, y, z) \mid x \geq 0, y \geq 0, z \leq 0\}.$$

It follows from Perron–Frobenius theorem that A has a real eigenvalue, which has a unique unit eigenvector in $\text{Int } K$, and the real part of the other two eigenvalues is strictly greater than this real eigenvalue if A is type K -competitive and irreducible.

A vector x is called *K -positive* if $x \in K$, *strictly K -positive* if $x \in \text{Int } K$. Two distinct points $u, v \in \mathbb{R}^3$ are *K -related* if either $u - v$ or $v - u$ is strictly K -positive. A set S is called *K -balanced* if no two distinct points of S are related.

It is obvious that the Jacobian of system (4) is

$$\begin{pmatrix} -(\mu_M + \frac{b_1\beta_1 B_i}{B_i+B_u}) & -\frac{b_1\beta_1(\frac{\mu_M}{\mu_M}-M_i)B_i}{(B_i+B_u)^2} & \frac{b_1\beta_1(\frac{\mu_M}{\mu_M}-M_i)B_u}{(B_i+B_u)^2} \\ -\frac{b_1\beta_2 B_u}{B_i+B_u} & -(\frac{b_1\beta_2 M_i B_i}{(B_i+B_u)^2} + \mu_B) & \frac{b_1\beta_2 M_i B_u}{(B_i+B_u)^2} \\ \frac{b_1\beta_2 B_u}{B_i+B_u} & \frac{b_1\beta_2 M_i B_i}{(B_i+B_u)^2} & -(\mu_B + d_B + \frac{b_1\beta_2 M_i B_u}{(B_i+B_u)^2}) \end{pmatrix}.$$

Therefore, system (4) is K -competitive in \mathbb{D} . From the expressions of $M_i^1, B_u^1, B_i^1, M_i^2, B_u^2, B_i^2, M_i^*, B_u^*, B_i^*$, it is not difficult to see that the equilibria E^1, E^2, E_0 or E_0 and E^* are unordered in the K -order. It follows from Proposition 3.2 in Wang and Jiang (2001) and Proposition 1.3 in Takac (1992) that there exists a two-dimensional compact Lipschitz submanifold Σ such that $E^1, E^2 \in \text{Int } \Sigma$ or $E^* \in \text{Int } \Sigma, E_0 \in \partial \Sigma$. Moreover, Σ is K -balanced. Since Σ is a two-dimensional compact Lipschitz submanifold and homeomorphic to a compact domain in the plane, it is obvious that Poincaré–Bendixson theorem holds for the dynamics of (4) on Σ .

Let $E^\#(M_i^\#, B_u^\#, B_i^\#)$ be an arbitrary equilibrium of (4). Then the variational system associated with (4) about $E^\#(M_i^\#, B_u^\#, B_i^\#)$ is

$$\begin{cases} \frac{dM_i}{dt} = - \left(\mu_M + \frac{b_1\beta_1 B_i^\#}{B_i^\# + B_u^\#} \right) M_i - \frac{b_1\beta_1 \left(\frac{\Pi_M}{\mu_M} - M_i^\# \right) B_i^\#}{(B_i^\# + B_u^\#)^2} B_u \\ \quad + \frac{b_1\beta_1 \left(\frac{\Pi_M}{\mu_M} - M_i^\# \right) B_u^\#}{(B_i^\# + B_u^\#)^2} B_i, \\ \frac{dB_u}{dt} = - \frac{b_1\beta_2 B_u^\#}{B_i^\# + B_u^\#} M_i - \left(\frac{b_1\beta_2 M_i^\# B_i^\#}{(B_i^\# + B_u^\#)^2} + \mu_B \right) B_u + \frac{b_1\beta_2 M_i^\# B_u^\#}{(B_i^\# + B_u^\#)^2} B_i, \\ \frac{dB_i}{dt} = \frac{b_1\beta_2 B_u^\#}{B_i^\# + B_u^\#} M_i + \frac{b_1\beta_2 M_i^\# B_i^\#}{(B_i^\# + B_u^\#)^2} B_u - \left(\mu_B + d_B + \frac{b_1\beta_2 M_i^\# B_u^\#}{(B_i^\# + B_u^\#)^2} \right) B_i. \end{cases} \tag{16}$$

The corresponding characteristic equation reads

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0, \tag{17}$$

where

$$\begin{aligned} A_1 &= \mu_M + 2\mu_B + d_B + \frac{b_1\beta_1 B_i^\# + b_1\beta_2 M_i^\#}{B_i^\# + B_u^\#}; \\ A_2 &= \frac{1}{(B_i^\# + B_u^\#)^2} \left[(2\mu_M\mu_B + 2b_1\beta_1\mu_B + (\mu_B + d_B)\mu_B + \mu_M d_B + b_1\beta_1 d_B)(B_i^\#)^2 \right. \\ &\quad + (4\mu_M\mu_B + 2b_1\beta_1\mu_B + 2\mu_B^2 + 2d_B\mu_B + 2\mu_M d_B + b_1\beta_1 d_B)(B_i^\# B_u^\#) \\ &\quad + (2\mu_M\mu_B + (\mu_B + d_B)\mu_B + \mu_M d_B)(B_u^\#)^2 \\ &\quad + \left(\mu_M b_1\beta_2 M_i^\# + \mu_B b_1\beta_2 M_i^\# - b_1\beta_2 b_1\beta_1 \left(\frac{\Pi_M}{\mu_M} - M_i^\# \right) \right) B_u^\# \\ &\quad \left. + b_1\beta_2(\mu_M + \mu_B + d_B + b_1\beta_1) M_i^\# B_i^\# \right]; \\ A_3 &= \frac{1}{(B_i^\# + B_u^\#)^3} \left\{ \mu_M\mu_B(\mu_B + d_B)(B_i^\# + B_u^\#)^3 \right. \\ &\quad + b_1[\beta_2 M_i^\# B_i^\# \mu_M(\mu_B + d_B)(B_i^\# + B_u^\#) + \beta_1 B_i^\# \mu_B(\mu_B + d_B)(B_i^\# + B_u^\#)^2 \\ &\quad + \beta_2 M_i^\# B_u^\# \mu_M\mu_B(B_i^\# + B_u^\#)] \\ &\quad + b_1^2\beta_1\beta_2[B_i^\# \mu_B M_i^\# B_u^\# + B_i^\# M_i^\# B_i^\#(\mu_B + d_B)] \\ &\quad \left. - B_u^\# \left(\frac{\Pi_M}{\mu_M} - M_i^\# \right) (B_i^\# + B_u^\#)\mu_B - B_u^\# \left(\frac{\Pi_M}{\mu_M} - M_i^\# \right) d_B B_i^\# \right\}. \end{aligned}$$

For any equilibrium $E^\#(M_i^\#, B_u^\#, B_i^\#)$ of the system (4), to determine the sign of the eigenvalues, the roots for the characteristic Eq. (17), we need the following proposition.

Proposition 3.1. *For any equilibrium $E^\#(M_i^\#, B_u^\#, B_i^\#)$ of the system with characteristic Eq. (17), we always have*

$$A_1 A_2 - A_3 > 0. \tag{18}$$

Proof: For the equilibrium $E^\#(M_i^\#, B_u^\#, B_i^\#)$, note that

$$M_i^\# = \frac{(\Pi_B - d_B B_i^\#) B_i^\#}{b_1 \beta_2 (B_{i2}^* - B_i^\#)},$$

$$B_u^\# = \frac{\mu_B + d_B}{\mu_B} (B_{i2}^* - B_i^\#),$$

$$M_i^\# = \frac{b_1 \beta_1 \mu_B \Pi_M B_i^\#}{\mu_M [\Pi_B \mu_M + (b_1 \beta_1 \mu_B - \mu_M d_B) B_i^\#]}.$$

Substituting the above into the expressions for A_1 , A_2 , and A_3 . With extensive algebraic manipulations, we get

$$A_1 = \frac{1}{(\Pi_B - d_B B_i^\#)(B_{i2}^* - B_i^\#)} [b_1 \beta_1 \mu_B B_i^\# (B_{i2}^* - B_i^\#) + (\Pi_B - d_B B_i^\#) [(\mu_M + 2\mu_B + d_B)(B_{i2}^* - B_i^\#) + \mu_B B_i^\#]];$$

$$A_2 = \frac{\mu_M \mu_B \Pi_B}{(\Pi_B - (\mu_B + d_B) B_i^\#)} + \frac{\mu_B [(\Pi_B - d_B B_i^\#)^2 + d_B \mu_B B_i^\# B_i^\#]}{(\Pi_B - d_B B_i^\#)(B_{i2}^* - B_i^\#)} + \frac{\Pi_B \mu_B^2 b_1 \beta_1 B_i^\#}{(\Pi_B - d_B B_i^\#)(\Pi_B - (\mu_B + d_B) B_i^\#)} + \frac{b_1 \beta_1 \mu_B (\mu_B + d_B) B_i^\#}{\Pi_B - d_B B_i^\#};$$

$$A_3 = \frac{(\mu_B + d_B) \mu_B B_i^\#}{(\Pi_B - d_B B_i^\#)^2 (\Pi_B - (\mu_B + d_B) B_i^\#)} [d_B (\mu_B + d_B) (b_1 \beta_1 \mu_B - d_B \mu_M) (B_i^\#)^2 + 2 \Pi_B d_B (d_B \mu_M - b_1 \beta_1 \mu_B) B_i^\# + \Pi_B^2 (b_1 \beta_1 \mu_B + \mu_M \mu_B - d_B \mu_M)].$$

Expressing $A_1 A_2 - A_3$ in terms of b_1 , we have

$$A_1 A_2 - A_3 = D_2 b_1^2 + D_1 b_1 + D_0, \tag{19}$$

where

$$D_2 = \frac{[(\mu_B + d_B)^2 (B_{i2}^* - B_i^\#) + \Pi_B \mu_B] (\beta_1 \mu_B B_i^\#)^2}{(\mu_B + d_B) (\Pi_B - d_B B_i^\#)^2 (B_{i2}^* - B_i^\#)};$$

$$D_1 = \frac{\mu_B \beta_1 B_i^\# \mu_M ((d_B + \mu_B)^2 (B_{i2}^* - B_i^\#) + 2 \Pi_B \mu_B)}{(\Pi_B - d_B B_i^\#) (\Pi_B - (\mu_B + d_B) B_i^\#)} + \frac{\mu_B \beta_1 B_i^\# ((d_B + \mu_B) (\Pi_B - (d_B + \mu_B) B_i^\#) + \Pi_B \mu_B)^2}{(\Pi_B - d_B B_i^\#) (\Pi_B - (\mu_B + d_B) B_i^\#)^2};$$

$$D_0 = \frac{\Pi_B \mu_B \mu_M^2}{(\mu_B + d_B) (B_{i2}^* - B_i^\#)} + \frac{1}{(\Pi_B - d_B B_i^\#) (\Pi_B - (\mu_B + d_B) B_i^\#)^2}$$

$$\begin{aligned} & \times [\Pi_B \mu_B \mu_M (\mu_B + d_B) ((\mu_B + d_B)^2 (B_{i2}^* - B_i^\#)^2 \\ & + (2\mu_B + d_B)(\mu_B + d_B)(B_{i2}^* - B_i^\#)(\Pi_B - d_B B_i^\#) + \mu_B B_i^\# (\Pi_B - d_B B_i^\#)) \\ & + \mu_B (\mu_B + d_B) [(d_B + \mu_B)^2 (B_{i2}^* - B_i^\#) \\ & + \Pi_B \mu_B] ((\Pi_B - d_B B_i^\#)^2 + \mu_B d_B (B_i^\#)^2)]. \end{aligned}$$

Then it becomes obvious from (19) and the expressions for D_0 , D_1 , and D_2 that (18) is true since $0 < B_i^\# < B_{i2}^* = \frac{\Pi_B}{\mu_B + d_B} < \frac{\Pi_B}{d_B}$. □

To discuss the local stability of the positive endemic equilibrium (if exists), we need the sign of A_3 in the characteristic Eq. (17). It is not an easy task to write A_3 in detail, but for the technique, we shall use for the stability of the positive equilibrium; we only need to know when it vanishes. Hence, we introduce an auxiliary function

$$g(B_i) = (b_1 \beta_1 \mu_B - d_B \mu_M) [d_B (\mu_B + d_B) B_i^2 - 2 \Pi_B d_B B_i + \Pi_B^2] + \Pi_B^2 \mu_M \mu_B.$$

A straightforward lengthy calculation shows that for any equilibrium $E^\#(M_i^\#, B_u^\#, B_i^\#)$, $A_3 = 0$ if and only if $g(B_i^\#) = 0$.

Proposition 3.2. *For any equilibrium $E^\#(M_i^\#, B_u^\#, B_i^\#)$ of the system with characteristic equation (17), $g(B_i^\#) = 0$ is equivalent to $\Delta = 0$. Also, $g(B_i^\#) = 0$ if and only if the parameters satisfy*

$$\Pi_M^2 - \frac{2 \Pi_B (2 d_B \mu_M - b_1 \beta_1 (\mu_B - d_B)) \mu_M}{b_1^2 \beta_1 \beta_2 (\mu_B + d_B)} \Pi_M + \frac{\Pi_B^2}{b_1^2 \beta_2^2} \mu_M^2 = 0. \tag{20}$$

Now we present the results on the local stability of the equilibria. The following theorem about the stability of the disease free equilibrium for (4) is from Bowman et al. (2005).

Theorem 3.3. *If $\mathbb{R}_0 < 1$, then the boundary equilibrium (DFE) E_0 is locally asymptotically stable; if $\mathbb{R}_0 > 1$, then E_0 is unstable.*

The following theorem regarding the local stability for the unique endemic equilibrium when $\mathbb{R}_0 > 1$ was proved in Bowman et al. (2005). Here, we give a different proof using the index theory for planar systems.

Theorem 3.4. *If $\mathbb{R}_0 > 1$, then the unique positive equilibrium $E^*(M_i^*, B_u^*, B_i^*)$ is locally asymptotically stable.*

Proof: First note that if $\mathbb{R}_0 > 1$, then the positive endemic equilibrium is unique. It follows from Proposition 3.2 that we have $g(B_i^*) \neq 0$.

By (17), we know that the characteristic equation of system (4) about $E^*(M_i^*, B_u^*, B_i^*)$ reads

$$\lambda^3 + A_1(B_i^*) \lambda^2 + A_2(B_i^*) \lambda + A_3(B_i^*) = 0. \tag{21}$$

Let $\lambda_1(B_i^*), \lambda_2(B_i^*), \lambda_3(B_i^*)$ be the roots of (21) and assume $\text{Re } \lambda_1(B_i^*) \leq \text{Re } \lambda_2(B_i^*) \leq \text{Re } \lambda_3(B_i^*)$. It follows from the relations between the roots and the polynomial coefficients and the assumption $g(B_i^*) \neq 0$ that

$$\lambda_1(B_i^*) + \lambda_2(B_i^*) + \lambda_3(B_i^*) = -A_1(B_i^*) < 0, \tag{22}$$

$$\lambda_1(B_i^*)\lambda_2(B_i^*)\lambda_3(B_i^*) = -A_3(B_i^*) \neq 0. \tag{23}$$

These together with Perron–Frobenius theorem, imply that $\lambda_1(B_i^*) < 0$ and $\lambda_2(B_i^*) \neq 0, \lambda_3(B_i^*) \neq 0$.

It is easy to prove system (4) is uniformly persistent if $\mathbb{R}_0 > 1$. Now suppose the positive equilibrium $E^*(M_i^*, B_u^*, B_i^*)$ is unstable. Then there must hold $\text{Re } \lambda_3(B_i^*) \geq 0$. It follows from Theorem 3.4.2 of Smith (1995) that there exists a stable closed orbit $\gamma \subset \Sigma$. Thus, from the index theory for planar systems, we have

$$\text{Re } \lambda_2(B_i^*) \geq 0, \quad \text{Re } \lambda_3(B_i^*) \geq 0. \tag{24}$$

Inequalities (23) and (24) imply that $A_3(B_i^*) = -\lambda_1(B_i^*)\lambda_2(B_i^*)\lambda_3(B_i^*) > 0$, which together with $A_1(B_i^*) > 0, A_1(B_i^*)A_2(B_i^*) - A_3(B_i^*) > 0$ and Routh–Hurwitz criterion implies that

$$\text{Re } \lambda_2(B_i^*) < 0, \quad \text{Re } \lambda_3(B_i^*) < 0,$$

contradicting (24). Therefore, $\text{Re } \lambda_3(B_i^*) < 0$. Thus, the positive equilibrium $E^*(M_i^*, B_u^*, B_i^*)$ is locally asymptotically stable. \square

The next theorem is about the stability of the multiple equilibria when they exist.

Theorem 3.5. *Consider the case when $\mathbb{R}_0 < 1$. If $a_2 > 0, 0 < \frac{-a_1}{2a_2} < B_{i2}^* = \frac{\mu_B}{\mu_B + d_B}$ and $\Delta > 0$, then the positive equilibrium E^1 is a saddle point and there exists an orbit connecting E^1 and E_0 , and the positive equilibrium E^2 is locally asymptotically stable; the E_0 is globally asymptotically stable for the other parameter cases.*

Proof: It follows from Theorem 2.2 that system (4) has two positive equilibria under our assumptions. Also, it follows from $\Delta > 0$ and Proposition 3.2 that we have $g(B_i^1) \neq 0, g(B_i^2) \neq 0$. By $a_2 > 0$, we have $\mu_M d_B > b_1 \beta_1 \mu_B$, hence the auxiliary function $g(B_i)$ is strictly increasing on $[0, B_{i2}^*]$. Note that $B_i^2 > B_i^1$, we have $g(B_i^2) > g(B_i^1)$.

For convenience, let $\lambda_1(B_i^1), \lambda_2(B_i^1), \lambda_3(B_i^1)$ and $\lambda_1(B_i^2), \lambda_2(B_i^2), \lambda_3(B_i^2)$ be the eigenvalues associated to E^1 and E^2 , respectively. We can also assume that $\text{Re } \lambda_1(B_i^1) \leq \text{Re } \lambda_2(B_i^1) \leq \text{Re } \lambda_3(B_i^1)$ and $\text{Re } \lambda_1(B_i^2) \leq \text{Re } \lambda_2(B_i^2) \leq \text{Re } \lambda_3(B_i^2)$. It follows from the relations between the roots and the polynomial coefficients that we have

$$\lambda_1(B_i^1) + \lambda_2(B_i^1) + \lambda_3(B_i^1) = -A_1(B_i^1) < 0,$$

$$\lambda_1(B_i^2) + \lambda_2(B_i^2) + \lambda_3(B_i^2) = -A_1(B_i^2) < 0.$$

Since $g(B_i^1) \neq 0$ and $g(B_i^2) \neq 0$, it follows from Perron–Frobenius theorem that we have $\lambda_1(B_i^2) < 0, \lambda_1(B_i^1) < 0$ and $\lambda_2(B_i^1), \lambda_3(B_i^1), \lambda_2(B_i^2), \lambda_3(B_i^2) \neq 0$.

To show that the positive equilibrium E^2 is locally asymptotically stable, it suffices to prove that $\text{Re } \lambda_3(B_i^2) < 0$. Since $g(B_i^2) \neq 0$, hence we finish the proof by the two cases: $\lambda_2(B_i^2)\lambda_3(B_i^2) > 0$ and $\lambda_2(B_i^2)\lambda_3(B_i^2) < 0$.

Consider the first case $\lambda_2(B_i^2)\lambda_3(B_i^2) > 0$. Then

$$A_3(B_i^2) = -\lambda_1(B_i^2)\lambda_2(B_i^2)\lambda_3(B_i^2) > 0.$$

Just as in the proof of Theorem 3.4, one can conclude that $\text{Re } \lambda_3(B_i^2) < 0$. Therefore, E^2 is locally asymptotically stable.

Now consider the second case $\lambda_2(B_i^2)\lambda_3(B_i^2) < 0$. Then we have $\lambda_2(B_i^2) < 0$ and $\lambda_3(B_i^2) > 0$. Therefore, E^2 is a saddle. In the following, we will rule out this case. By contrary, if $\lambda_2(B_i^2) < 0$ and $\lambda_3(B_i^2) > 0$, it is easy to see that $A_3(B_i^2) < 0$, i.e., $g(B_i^2) < 0$. Thus, we have $g(B_i^1) < 0$, i.e., $A_3(B_i^1) < 0$. Since

$$\lambda_1(B_i^1)\lambda_2(B_i^1)\lambda_3(B_i^1) = -A_3(B_i^1) > 0, \quad \lambda_1(B_i^1) < 0,$$

we have $\lambda_2(B_i^1) < 0$ and $\lambda_3(B_i^1) > 0$. This implies that the other positive equilibrium E^1 is also a saddle point. Let Σ be a K -balanced and invariant compact Lipschitz submanifold such that E_0, E^1 and $E^2 \in \Sigma$. The existence of Σ is due to the result in Wang and Jiang (2001). It is easy to see that $E_0 \in \partial \Sigma$. Also, note that E^1 and E^2 are both saddle points on Σ . It then follows from the property of the planar system that system (4) has no periodic and homoclinic orbits on Σ . Therefore, the ω -limit set of the unstable manifold of E^k are either E_0 or E^l for $k, l = 1, 2$. Therefore, either there exists a heteroclinic cycle connecting both E^1 and E^2 , or nonconstant solutions on the unstable manifolds of E^1 (E^2) tend to E_0 . Since E_0 is asymptotically stable and $E_0 \in \partial \Sigma$, it follows from the properties of the planar system that there must exist another equilibrium, which is different from the existing equilibria E_0, E^1 and E^2 . This contradicts to the fact about the number of the equilibria in Theorem 2.2. Thus, equilibrium E^2 must be locally asymptotically stable.

In the following, we prove that the equilibrium $E^1(M_i^1, B_i^1, B_i^1)$ is a saddle point. Let U be the basin of attraction for of E_0 on Σ and ∂U be the boundary of U . It is obvious that ∂U is positively invariant, and every positive trajectory on ∂U is convergent. Because E^2 is asymptotically stable, the ω -limit set on ∂U must be the positive equilibrium E^1 , thus E^1 is unstable. Then we have $\text{Re } \lambda_3(B_i^1) \geq 0$. If $\lambda_2(B_i^2)\lambda_3(B_i^2) > 0$, the same proof as in the last paragraph leads to $\text{Re } \lambda_3(B_i^1) < 0$, a contradiction. Therefore, there must hold $\lambda_2(B_i^2) > 0$ and $\lambda_3(B_i^2) < 0$, that is, the equilibrium E^1 is a saddle point.

The stable manifold of E^1 on Σ separates Σ into two parts, one contains E^2 and one branch $W_1^u(E^1)$ of the unstable manifold of E^1 , the other contains E_0 and the other branch $W_2^u(E^1)$ of the unstable manifold of E^1 , the positive trajectory on the latter branch tends to E_0 , which implies that there exists an orbit connecting E_0 and E^1 .

Assume that $\mathbb{R}_0 < 1$ and the system (16) has the unique equilibrium E_0 . Then we can easily rule out the existence of periodic orbit by the theory of competitive system, hence E_0 is globally attractive. □

4. Backward bifurcation and subthreshold outbreak conditions

Usually one would expect that the endemic can be controlled if the basic reproduction number is smaller than one. In some cases, the system would undergo a backward

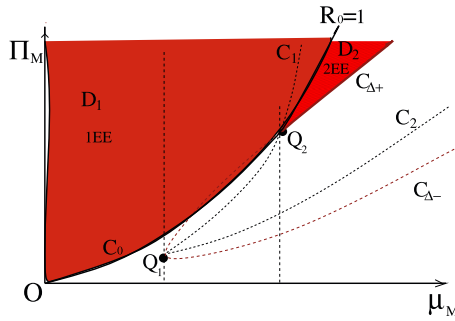


Fig. 3 A saddle-node bifurcation occurs on $C_{\Delta+}$. In D_1 , $\mathbb{R}_0 > 1$ and system (4) has a unique endemic equilibrium. In D_2 , system (4) has two endemic equilibria.

transcritical bifurcation which generates multiple endemic equilibria, and it becomes impossible to control the endemic by just reducing the basic reproduction number. In the aforementioned 6 models proposed for the West Nile virus transmission dynamics (Cruz-Pacheco et al., 2005; Kenkre et al., 2005; Liu et al., 2006; Lord and Day, 2001; Thomas and Urena, 2001; Wonham et al., 2004), the basic reproduction number serves as the essential controlling threshold condition. In the model proposed in Bowman et al. (2005), a backward bifurcation may occur which produces multiple endemic equilibria. Therefore, a further threshold condition beyond the basic reproduction is essential for the control of the spread of the virus.

It follows from Theorem 2.2 and Theorem 3.5 that there exist multiple endemic equilibria if and only if

$$\mathbb{R}_0 < 1, \quad a_2 > 0, \quad 0 < -\frac{a_1}{2a_2} < B_{i2}^* \quad \text{and} \quad \Delta > 0. \tag{25}$$

To describe the backward bifurcation, we choose the recruitment rate of susceptible mosquitoes Π_M and the natural death rate of mosquitos μ_M as parameters. We will present the bifurcation diagram in the first quadrant in the (μ_M, Π_M) plane.

The basic reproduction number $\mathbb{R}_0 = 1$ defines a parabola shown in Fig. 3; we denote this part of the parabola by C_0 :

$$C_0 : \Pi_{M_{C_0}} = \frac{(\mu_B + d_B)\Pi_B}{b_1^2\beta_1\beta_2\mu_B}\mu_M^2, \quad \mu_M > 0. \tag{26}$$

The condition $a_2 = 0$ corresponds to the curve Γ_1 has a vertical asymptote to the right of $B_i = B_{i2}^*$, as shown in Fig. 1(b) and Fig. 2(b)–(d). For $a_2 > 0$, we need $\mu_M > \frac{b_1\beta_1\mu_B}{d_B}$. As shown in Fig. 3, the vertical line $\mu_M = \frac{b_1\beta_1\mu_B}{d_B}$ corresponds to $a_2 = 0$, and to the right of the line we have $a_2 > 0$.

Let the parabola defined by $a_1 = 0$ be C_1 , Fig. 3. Solving $a_1 = 0$ in terms of μ_M gives

$$C_1 : \Pi_{M_{C_1}} = \frac{d_B\Pi_B}{b_1^2\beta_1\beta_2\mu_B} \left(2\mu_M^2 - \frac{b_1\beta_1\mu_B}{d_B}\mu_M \right), \quad \mu_M \geq \frac{b_1\beta_1\mu_B}{d_B}. \tag{27}$$

Let C_2 be the parabola defined by $B_{i_2}^* + \frac{a_1}{2a_2} = 0$, Fig. 3. Then we have

$$C_2 : \Pi_{M_{C_2}} = \frac{d_B \Pi_B}{b_1^2 \beta_1 \beta_2 (\mu_B + d_B)} \left(2\mu_M^2 - \frac{b_1 \beta_1 (\mu_B - d_B)}{d_B} \mu_M \right), \quad \mu_M \geq \frac{b_1 \beta_1 \mu_B}{d_B}. \tag{28}$$

A straightforward calculation yields

$$\Pi_{M_{C_1}} - \Pi_{M_{C_2}} = \frac{2d_B^2 \Pi_B}{b_1^2 \beta_1 \beta_2 \mu_B (\mu_B + d_B)} \mu_M \left(\mu_M - \frac{b_1 \beta_1 \mu_B}{d_B} \right). \tag{29}$$

Hence, $\Pi_{M_{C_1}} > \Pi_{M_{C_2}}$ for $\mu_M > \frac{b_1 \beta_1 \mu_B}{d_B}$. It is shown in Fig. 3 that C_1 is always above C_2 .

Now let us consider the curve defined by $\Delta = 0$. It defines a curve with two branches, denoted by $C_{\Delta\pm}$, Fig. 3. It follows from $\Delta = 0$, or equivalently from (20), that

$$C_{\Delta\pm} : \Pi_{\Delta\pm} = \frac{2 d_B \Pi_B}{b_1^2 \beta_1 \beta_2 (\mu_B + d_B)} \mu_M \times \left[\mu_M - \frac{b_1 \beta_1 (\mu_B - d_B)}{2d_B} \pm \sqrt{(\mu_M + b_1 \beta_1) \left(\mu_M - \frac{b_1 \beta_1 \mu_B}{d_B} \right)} \right], \tag{30}$$

$$\mu_M \geq \frac{b_1 \beta_1 \mu_B}{d_B}.$$

One can verify that all the four curves C_1 , C_2 , and $C_{\Delta\pm}$ pass through the same point $Q_1(\frac{b_1 \beta_1 \mu_B}{d_B}, \frac{\beta_1 \mu_B \Pi_B}{d_B \beta_2})$ on the vertical line $\mu_M = \frac{\beta_1 \mu_B \Pi_B}{d_B}$, Fig. 3.

One needs to compare the relative positions of the three curves C_0 , C_1 , and $C_{\Delta+}$. A straightforward calculation yields

$$\Pi_{M_{C_1}} - \Pi_{M_{C_0}} = \frac{\mu_M \Pi_B}{b_1 \beta_2} \left(1 - \frac{(d_B - \mu_B) \mu_M}{b_1 \beta_1 \mu_B} \right).$$

Hence, if $d_B > \mu_B$ and $\mu_M > \frac{b_1 \beta_1 \mu_B}{d_B - \mu_B}$, the curves C_1 and C_0 have an intersection at the point $Q_2(\frac{b_1 \beta_1 \mu_B}{d_B - \mu_B}, \frac{(\mu_B + d_B) \Pi_B \beta_1}{\beta_2 (d_B - \mu_B)^2})$, and C_1 is above the curve C_0 for $\mu_M > \frac{b_1 \beta_1 \mu_B}{d_B}$. Furthermore, it follows from (26) and (30) that

$$\begin{aligned} & \Pi_{M_{C_0}} - \Pi_{\Delta+} \\ &= \frac{\Pi_B \mu_M}{b_1^2 \beta_1 \beta_2 \mu_B (\mu_B + d_B)} (\mu_B \sqrt{b_1 \beta_1 + \mu_M} - \sqrt{d_B (d_B \mu_M - b_1 \beta_1 \mu_B)})^2 \\ &\geq 0. \end{aligned} \tag{31}$$

Hence, for $\mu_M > \frac{b_1 \beta_1 \mu_B}{d_B}$, C_0 is always above $C_{\Delta+}$. Note that the curves C_0 and $C_{\Delta+}$ intersect at the point Q_2 , therefore, they form a region D_2 ; see Fig. 3, where system (4) has two positive equilibria.

We summarize the above analysis in the following theorem regarding the backward bifurcation and the subthreshold condition for the endemic of the virus.

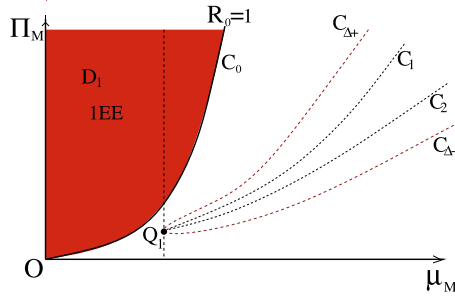


Fig. 4 Bifurcation diagram when $d_B < \mu_B$. In D_1 where $\mathbb{R}_0 > 1$, system (4) has a unique endemic equilibrium; outside the region D_1 , system does not have endemic equilibrium.

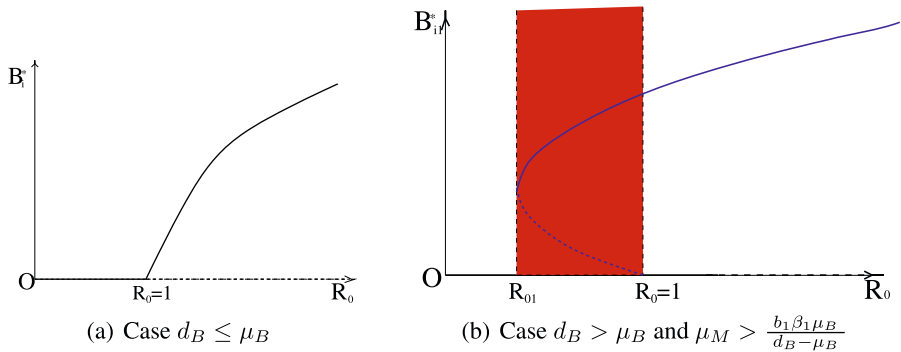


Fig. 5 Bifurcation diagram using the basic reproduction number \mathbb{R}_0 as parameter.

Theorem 4.1. *The system (4) undergoes a saddle-node bifurcation if and only if*

$$d_B > \mu_B, \quad \text{and} \quad \frac{d_B}{\mu_B} > 1 + \frac{b_1\beta_1}{\mu_M}. \tag{32}$$

Furthermore, in the region D_2 where

$$D_2 = \left\{ (\mu_M, \Pi_M) \mid \mu_M > \frac{b_1\beta_1\mu_B}{d_B - \mu_B}, \Pi_{\Delta+} < \Pi_M < \Pi_{M_{C_0}} \right\}$$

system (4) has two endemic equilibria.

From the above description and analysis for the backward bifurcation curves, one can see that if $d_B < \mu_B$, the backward bifurcation does not occur and the corresponding bifurcation diagram is given in Fig. 4.

In this model, it follows from Theorem 3.5 that if $d_B \leq \mu_B$ and $\mathbb{R}_0 < 1$, the disease free equilibrium is locally asymptotically stable, Fig. 5(a). If $d_B > \mu_B$, a backward bifurcation will occur if (32) is satisfied. Two positive endemic equilibria will appear, one is a stable node and the other is a saddle point, Fig. 5(b).

As shown in Fig. 3, when $d_B > \mu_B$, for any $\mu_M > \frac{b_1\beta_1\mu_B}{d_B - \mu_B}$ and Π_M between C_0 and $C_{\Delta+}$, system has two endemic equilibria even though we have $\mathbb{R}_0 < 1$.

Let $\mathbb{R}_{01} = \mathbb{R}_0|_{\Pi_M = \Pi_{\Delta+}}$. Then it follows from (30) that

$$\mathbb{R}_{01} = \frac{1}{\mu_B + d_B} \sqrt{2d_B\mu_B \left[1 + \frac{b_1\beta_1(d_B - \mu_B)}{2d_B\mu_M} + \sqrt{\left(1 + \frac{b_1\beta_1}{\mu_M}\right)\left(1 - \frac{b_1\beta_1\mu_B}{d_B\mu_M}\right)} \right]}. \tag{33}$$

One can verify that when $d_B > \mu_B$ and $\mu_M > \frac{b_1\beta_1\mu_B}{d_B - \mu_B}$, we have $0 < \mathbb{R}_{01} < 1$.

We summarize the condition for the saddle-node bifurcation in terms of the basic reproduction in the following theorem.

Theorem 4.2. *The system (4) undergoes a saddle-node bifurcation if and only if*

$$d_B > \mu_B, \quad \mu_M > \frac{b_1\beta_1\mu_B}{d_B - \mu_B} \quad \text{and} \quad \mathbb{R}_{01} < \mathbb{R}_0 < 1. \tag{34}$$

And the bifurcation diagram using the basic reproduction number \mathbb{R}_0 as parameter is given in Fig. 5.

5. Simulations and discussions

For the full model in Bowman et al. (2005), numerical simulations were carried out for both the cases of $\mathbb{R}_0 < 1$ and $\mathbb{R}_0 > 1$. In this paper, we focus only on the case when $\mathbb{R}_0 < 1$ and $d_B > \mu_B$ and system (4) has multiple equilibria.

It follows from the discussion in Bowman et al. (2005) that the most effective and realistic strategy to prevent the spread of the West Nile virus is to control the mosquitoes. Mosquito reduction strategies like the elimination of mosquito breeding sites (through improved drainage and prevention of standing water), larvaciding (killing mosquito larvae before they become adults), and adulticiding (killing adult mosquitoes *via* fogging) using appropriate biological agents (Nosal and Pellizzari, 2003). In order to investigate the controlling strategy for the West Nile virus related to mosquito control, we therefore use the recruitment rate of susceptible mosquitoes Π_M and the natural death rate of mosquitos μ_M as parameters.

For our simulations, except for Π_M and μ_M which are taken as bifurcation parameters, parameters are taken from Bowman et al. (2005) and listed in Table 1. It should be mentioned that compare to the parameters in Bowman et al. (2005), we increase b_1 to 0.2 while we increase the West Nile virus induced death rate d_B to 0.005 due to the fact that the infected crow family of birds have higher death rate when they are infected with the virus (Centers for Disease Control and Prevention, 2003; West Nile Virus Monitor—West Nile Virus Surveillance Information. West Nile Virus—Public Health Agency of Canada. <http://www.phac-aspc.gc.ca/wn-no/index-e.html>). It is assumed here that the maximum lifespan of a mosquito is 2 to 3 weeks, and we take as 21 days (that is, $1/\mu_M \leq 21$ days) and the maximum number of recruited mosquitoes is 2×10^5 .

Table 1 Model parameters and their interpretations

| Parameter | Description | Estimated value |
|-----------|--|-----------------|
| Π_M | Recruitment rate of uninfected mosquitoes (<i>per day</i>) | Parameter |
| Π_B | Recruitment rate of susceptible birds (<i>per day</i>) | 1000 |
| $1/\mu_M$ | Average lifespan of a mosquito (days) | Parameter |
| $1/\mu_B$ | Average lifespan of a bird (days) | 1000 |
| b_1 | Biting rate of mosquitoes on birds | 0.02 |
| β_1 | Transmission probability from bird to mosquito | 0.16 |
| β_2 | Transmission probability from mosquito to bird | 0.88 |
| d_B | WNV-induced death rate of birds (fraction <i>per day</i>) | 0.005 |

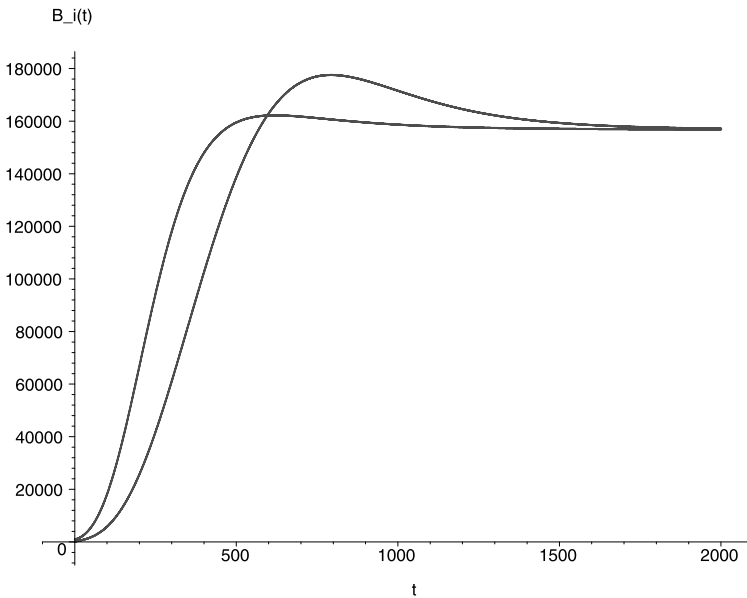


Fig. 6 For the parameters taken as in Table 1 and $\mu_M = \frac{1}{21}$, $\Pi_M = 200000$, we have the basic reproduction number $\mathbb{R}_0 = 0.9099$, while $\mathbb{R}_{01} = 0.7552$, system (4) has two positive endemic equilibria $E^1(16088, 44491, 733048)$ and $E^2(195514, 59026, 156828)$.

The numerically simulated results are depicted in Fig. 6. For the purpose of displaying the asymptotic behavior, in the simulations the time interval was taken as $t \in [0, 2000]$, an interval of about 6 years. For different initial sizes of the infected mosquitoes and birds, the corresponding population size of the infected birds saturates at the equilibrium state $B_i^2 = 156828$. Note that for the cases in North America, like the spreading of the virus in the southern Ontario, Canada (West Nile Virus Monitor—West Nile Virus Surveillance Information. West Nile Virus—Public Health Agency of Canada. <http://www.phac-aspc.gc.ca/wn-no/index-e.html>), the mosquito season ends in late October due to the cold weather. Hence, if we consider the model and combine the cases in Southern Ontario, we can see that even though the basic reproduction number is smaller than one, we can observe the growth of the number of infected birds. This might explain why the

small scale outbreaks of the virus keep occurring in the region where there was an outbreak in the previous year(s). The analytical and numerical analysis both suggest that the basic reproductive number alone cannot simply determine whether West Nile virus will prevail or not, and that one needs to pay more attention to the initial sizes of the infected mosquito and bird population.

If $\mathbb{R}_0 > 1$, system has a unique positive equilibrium. The global stability of the endemic equilibrium was proved in Bowman et al. (2005) with the assumption that $d_B > 0$ and sufficiently small. Numerical simulations suggest that the unique endemic equilibrium remains to be globally asymptotically stable even for large values of d_B , but a rigorous proof of the global stability of the endemic equilibrium remains an open problem.

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