

## Research Article

# Modeling *Wolbachia* Diffusion in Mosquito Populations by Discrete Competition Model

Yijie Li, Zhiming Guo , and Yanyuan Xing

School of Mathematics and Information Sciences, Guangzhou University, Guangzhou 510006, China

Correspondence should be addressed to Zhiming Guo; guozm@gzhu.edu.cn

Received 11 November 2019; Accepted 20 January 2020; Published 27 February 2020

Academic Editor: Guang Zhang

Copyright © 2020 Yijie Li et al. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Dengue fever is caused by dengue virus and transmitted by *Aedes* mosquitoes. A promising avenue to control this disease is to infect the wild *Aedes* population with the bacterium *Wolbachia* driven by cytoplasmic incompatibility (CI). To study the invasion of *Wolbachia* into wild mosquito population, we formulate a discrete competition model and analyze the competition between released mosquitoes and wild mosquitoes. We show the global asymptotic properties of the trivial equilibrium, boundary equilibrium, and positive equilibrium and give the conditions for the successful invasion of *Wolbachia*. Finally, we verify our findings by numerical simulations.

## 1. Introduction

Dengue fever is a mosquito-borne infectious disease caused by dengue virus, mainly transmitted by *Aedes aegypti* [1]. More than 2.5 billion people in more than 100 countries are currently at risk from this disease, making mosquito control a major public health priority. Conventional measures, such as mass spraying of insecticides, are limited and unsafe, and worse, no effective vaccine that against dengue has yet been developed [2].

An innovative and effective method of mosquito control is using specific endosymbiotic bacterium *Wolbachia* to block the transmission of dengue fever. With infection, *Wolbachia* can reduce the mosquito's dengue transmission potential. Besides, *Wolbachia* often induces cytoplasmic incompatibility (CI) which leads to early embryonic death when *Wolbachia*-infected males mate with uninfected females, so the release of infected males helps to reduce mosquito populations [3]. This bacterium infects many arthropods, including some mosquito species in nature, which was first identified in 1924 [4]. However, *Wolbachia* is not present in some important mosquito vectors. In 2005, Xi et al. established stable mosquito strains carrying *Wolbachia* for the first time by injecting *Wolbachia* into *Aedes aegypti* [5, 6], which is the basis of using *Wolbachia* to control mosquito-borne diseases. The strategies of using *Wolbachia* for mosquito vector control mainly include population

suppression and population replacement. The former only releases infected males, and produces CI effect after mating with female mosquitoes in the field to suppress the number of mosquito vectors in the field [7, 8]; the latter releases both male and female mosquitoes infected with *Wolbachia* using vertical maternal transmission of *Wolbachia* and certain advantages to let *Wolbachia* spread in the mosquito population to stop spreading disease [9].

In recent years, the spreading dynamics of *Wolbachia* has become a hot research topic in academia. In 2014, Zheng et al. have established a delay differential equation model to study *Wolbachia* infection dynamics [10]. They gave a precise threshold for the infection frequency, and their numerical simulation is well fitting with the experimental data; then, Huang et al. proposed the corresponding reaction diffusion equations with homogeneous Neumann boundary condition and obtained similar results [11, 12]. In 2019, Zheng et al. have carried out a mathematical model to study combining incompatible and sterile insect techniques (IIT-SIT) to eliminate the population of *Aedes* mosquitoes in the wild, and they proved the feasibility of regional control of mosquito vector population by combining IIT-SIT through field experiments [13]. Besides, some interesting mathematical models have also been developed, such as the time-delay continuous model [8, 14–16], the discrete model [17, 18], and the stochastic systems of differential equations [19].

Motivated by those valuable research studies and since the experimental data of the detection of mosquito population in the field are discrete, we managed to establish a discrete model and make it as reasonable as possible. In this paper, a discrete model was established to study the spread of *Wolbachia* in mosquito populations from the perspective of competition, which is rarely mentioned in the existing literature.

The most frequently used equation for studying the discrete model is the Beverton-Holt equation:

$$x_{t+1} = b \frac{1}{1 + c_{11}x_t} x_t, \quad (1)$$

where  $b > 0$  denotes the birth rate and  $c_{11} > 0$  denotes the intraspecific competition coefficient. If  $b > 1$ , then all solutions of the equation with  $x_0 > 0$  tend monotonically to the equilibrium  $x = (b - 1)/c_{11}$ . If  $x_t$  is considered as the number of a species at time  $t$ , it is a discrete model similar to the classical logistic continuous model [20]. If we consider the discrete model of competition between two species, the Beverton-Holt equation needs to be modified, which leads to the Leslie-Gower discrete competition model:

$$\begin{cases} x_{t+1} = b_1 \frac{1}{1 + c_{11}x_t + c_{12}y_t} x_t, \\ y_{t+1} = b_2 \frac{1}{1 + c_{21}x_t + c_{22}y_t} y_t, \end{cases} \quad (2)$$

where  $b_1, b_2 > 0$  denote the birth rate of  $x_t, y_t$ , respectively.  $c_{11}, c_{22} > 0$  denote the intraspecific competition coefficient and  $c_{12}, c_{21} > 0$  denote the interspecific competition coefficient, respectively. Model (2) has rich dynamic properties and satisfies the competitive exclusion principle [21, 22]. Based on (2), we establish a discrete competition model describing *Wolbachia* spread in mosquito population. We assume that  $x_t$  represents the number of mosquito population infected with *Wolbachia* at  $t$  and  $y_t$  represents the number of uninfected mosquito population at  $t$ , and their birth rates are  $b_1$  and  $b_2$ , respectively. Since the mosquitoes are overlapping generation populations, we introduce  $d_1, d_2$  as the mortality rates of  $x_t$  and  $y_t$ , respectively. Then, their survival rates are, respectively,  $1 - d_1$  and  $1 - d_2$ . Because *Wolbachia* often induces fitness cost [10], and it is reasonable to assume that  $0 < d_2 < d_1 < 1$ . Furthermore, considering that both  $x_t$  and  $y_t$  denote the numbers of *Aedes aegypti*, for simplicity, we ignore the difference between intraspecific competition and interspecific competition and focus on the effect of competitions on their birth rates, so we assume  $c_{11} = c_{12} = \alpha$  and  $c_{21} = c_{22} = \beta$  denote the competition coefficient within (or between) species, respectively. Finally, considering the infection *Wolbachia* CI mechanism of mosquito population and vertical maternal transmission of *Wolbachia* [23], the birth rate of  $y_t$  is replaced by  $b_2 y_t / (x_t + y_t)$ ; hence, the discrete model of competition between two species is as follows:

$$\begin{cases} x_{t+1} = \frac{b_1 x_t}{1 + \alpha(x_t + y_t)} + (1 - d_1)x_t, \\ y_{t+1} = \frac{b_2 y_t}{1 + \beta(x_t + y_t)} \frac{y_t}{x_t + y_t} + (1 - d_2)y_t, \end{cases} \quad (3)$$

where all the coefficients are positive, and we mainly discuss this model.

The structure of this paper is arranged as follows. In Section 2, firstly, we prove the nonnegativity and boundedness of the solution of model (3) and obtain the positive invariant set. Secondly, we give four equilibrium points, including the trivial equilibrium  $E_0$ , boundary equilibrium  $E_1, E_2$ , and positive equilibrium  $E_3$  as well as their existence conditions, and we also introduce the global attraction conditions for each equilibrium by stability analysis. In Section 3, some numerical simulations are presented to illustrate the behavior of the model and we interpret our main results biologically. Finally, the conclusion and discussion will be given in Section 4.

## 2. Model Analysis

We first consider the positivity and boundedness of the solution of model (3), positivity is clear, and the boundedness can be obtained as follows. From the first equation of model (3), we find

$$x_{t+1} \leq \frac{b_1}{\alpha} + (1 - d_1)x_t. \quad (4)$$

Let  $\sigma = 1 - d_1$ , then we have  $x_{t+1} - \sigma x_t \leq (b_1/\alpha)$ . Furthermore, we can obtain a series of inequalities

$$\begin{cases} x_t - \sigma x_{t-1} \leq \frac{b_1}{\alpha}, \\ \sigma x_{t-1} - \sigma^2 x_{t-2} \leq \sigma \frac{b_1}{\alpha}, \\ \sigma^2 x_{t-2} - \sigma^3 x_{t-3} \leq \sigma^2 \frac{b_1}{\alpha}, \\ \dots \\ \sigma^{t-1} x_1 - \sigma^t x_0 \leq \sigma^{t-1} \frac{b_1}{\alpha}. \end{cases} \quad (5)$$

Add them up, and we get

$$x_t - \sigma^t x_0 \leq \frac{b_1}{\alpha} (1 + \sigma + \sigma^2 + \dots + \sigma^{t-1}). \quad (6)$$

As  $\sigma \in (0, 1)$ , it is easy to obtain the following inequality for any given initial value  $x_0$ :

$$\limsup_{t \rightarrow \infty} x_t \leq \frac{b_1}{\alpha} \frac{1}{1 - \sigma} = \frac{b_1}{\alpha d_1}. \quad (7)$$

Similarly, for  $y_t$ , we have

$$\limsup_{t \rightarrow \infty} y_t \leq \frac{b_2}{\beta d_2}. \quad (8)$$

Therefore,

$$\Gamma = \left\{ (x, y) \in \mathbb{R}^2 \mid 0 \leq x \leq \frac{b_1}{\alpha d_1}, 0 \leq y \leq \frac{b_2}{\beta d_2} \right\} \quad (9)$$

is a positive invariant.

Next, we analyze the existence and stability of the equilibria to (3). Note that (3) is not defined at the origin. In order to study the dynamical behavior of solutions to (3) near the origin, we define an auxiliary function:

$$f(x, y) = \begin{cases} \frac{b_2 y}{1 + \beta(x + y)} \frac{y}{x + y} + (1 - d_2)y, & (x, y) \neq (0, 0), \\ 0, & (x, y) = (0, 0). \end{cases} \quad (10)$$

Thus, (3) can be modified as

$$\begin{cases} x_{t+1} = \frac{b_1 x_t}{1 + \alpha(x_t + y_t)} + (1 - d_1)x_t, \\ y_{t+1} = f(x_t, y_t). \end{cases} \quad (11)$$

Thus,  $E_0(0, 0)$  can be regarded as an equilibrium of (3). The other equilibria of (3) satisfy the following algebraic equations:

$$\begin{cases} x = \frac{b_1 x}{1 + \alpha(x + y)} + (1 - d_1)x, \\ y = \frac{b_2 y}{1 + \beta(x + y)} \frac{y}{x + y} + (1 - d_2)y. \end{cases} \quad (12)$$

There are two nonnegative boundary equilibria of model (12),  $E_1((1/\alpha)((b_1/d_1) - 1), 0)$  and  $E_2(0, (1/\beta)((b_2/d_2) - 1))$ , provided  $b_1 > d_1$  and  $b_2 > d_2$ . Besides, a positive equilibrium

$$E_3 \left( \frac{1}{\alpha} \left( \frac{b_1}{d_1} - 1 \right) \left( 1 - \frac{d_2}{b_2} \left[ 1 + \frac{\beta}{\alpha} \left( \frac{b_1}{d_1} - 1 \right) \right] \right), \frac{d_2}{\alpha b_2} \left( \frac{b_1}{d_1} - 1 \right) \left[ 1 + \frac{\beta}{\alpha} \left( \frac{b_1}{d_1} - 1 \right) \right] \right) \quad (13)$$

exists if  $b_1 > d_1, b_2 > d_2$ , and  $(1/\beta)((b_2/d_2) - 1) > (1/\alpha)((b_1/d_1) - 1)$ .

**Theorem 1.** For model (3), we have the following conclusions.

- (a) If  $b_1 \leq d_1, b_2 \leq d_2$ , then  $E_0$  is globally asymptotically stable.
- (b) If  $b_1 > d_1, b_2 \leq d_2$ , then  $E_0$  is unstable and  $E_1$  is globally asymptotically stable.
- (c) If  $b_1 \leq d_1, b_2 > d_2$ , then  $E_0$  is unstable and  $E_2$  is globally asymptotically stable.

*Proof.* The Jacobian of model (3) is

$$J = \begin{pmatrix} \frac{b_1(1 + \alpha y)}{[1 + \alpha(x + y)]^2} + 1 - d_1 & \frac{-\alpha b_1 x}{[1 + \alpha(x + y)]^2} \\ \frac{-b_2 y^2 [1 + 2\beta(x + y)]}{[1 + \beta(x + y)]^2 (x + y)^2} & \frac{b_2 y(2x + y) + 2b_2 \beta x y (x + y)}{[1 + \beta(x + y)]^2 (x + y)^2} + 1 - d_2 \end{pmatrix}. \quad (14)$$

The Jacobians evaluated at  $E_1$  and  $E_2$  read as

$$J_1 = \begin{pmatrix} \frac{d_1^2}{b_1} + 1 - d_1 & \frac{d_1^2}{b_1} - d_1 \\ 0 & 1 - d_2 \end{pmatrix}, \quad (15)$$

$$J_2 = \begin{pmatrix} \frac{b_1}{1 + (\alpha/\beta)((b_2/d_2) - 1)} + 1 - d_1 & 0 \\ \frac{d_2^2}{b_2} - 2d_2 & \frac{d_2^2}{b_2} + 1 - d_2 \end{pmatrix}, \quad (16)$$

respectively. Their eigenvalues appear along the diagonals. Recall that an equilibrium is globally asymptotically stable if

it is locally asymptotically stable and all orbits tend to the equilibrium as  $t \rightarrow \infty$ .

- (a) If  $b_1 \leq d_1, b_2 \leq d_2$ , there is no nonnegative equilibrium except for  $E_0$ . When  $b_1 < d_1, b_2 < d_2$ , from (3), we have

$$\begin{aligned} 0 \leq x_{t+1} &\leq (b_1 - d_1 + 1)x_t, \\ 0 \leq y_{t+1} &\leq (b_2 - d_2 + 1)y_t, \end{aligned} \quad (17)$$

the system is monotonically decreasing, and if  $t \rightarrow \infty$ , then  $x_t \rightarrow 0, y_t \rightarrow 0$ , so that  $E_0$  is globally asymptotically stable. Furthermore, when  $b_1 = d_1, b_2 = d_2$ , from (3), we have

$$x_{t+1} = \left( \frac{b_1}{1 + \alpha(x_t + y_t)} + 1 - d_1 \right) x_t, \quad (18)$$

$$y_{t+1} = \left( \frac{b_2}{1 + \beta(x_t + y_t)} \frac{y_t}{x_t + y_t} + 1 - d_2 \right) y_t.$$

Obviously,  $x_{t+1} = x_t$ ,  $y_{t+1} = y_t$  if and only if  $x_t = y_t = 0$  for all  $t \geq 0$ . Otherwise, we claim that  $0 \leq x_{t+1} < x_t$  and  $0 \leq y_{t+1} < y_t$  for all  $t \geq 0$ . It follows that  $\lim_{t \rightarrow +\infty} x_t$  and  $\lim_{t \rightarrow +\infty} y_t$  exist and must be zero. Therefore,  $E_0$  is globally asymptotically stable. For the remaining cases, i.e.,  $b_1 < d_1, b_2 = d_2$  and  $b_1 = d_1, b_2 < d_2$ , the conclusion can be verified similarly.

- (b) If  $b_1 > d_1, b_2 \leq d_2$ , there are two equilibria,  $E_0$  and  $E_1$ . When  $y_t = 0$ , from the first equation of model (3), we have

$$x_{t+1} = \left( \frac{b_1}{1 + \alpha x_t} + 1 - d_1 \right) x_t. \quad (19)$$

Clearly,  $b_1/(1 + \alpha x_t) + 1 - d_1 > 1$  if and only if  $x_t < (1/\alpha)((b_1/d_1) - 1)$ . It follows that the solution emanating from the  $X$ -axis with  $0 < x_0 < (1/\alpha)((b_1/d_1) - 1)$  will be away from  $E_0$  along the  $X$ -axis, so  $E_0$  is unstable. The eigenvalues of  $J_1$  belong to the interval  $(0, 1)$ , and hence  $E_1$  is locally asymptotically stable. In addition, according to a theorem due to Liu and Elaydi [24], all bounded orbits will eventually converge to an equilibrium; thus, all orbits will converge to  $E_1$ . Therefore,  $E_1$  is globally asymptotically stable.

- (c) If  $b_1 \leq d_1, b_2 > d_2$ , there are two equilibria,  $E_0$  and  $E_2$ . In this case, we can prove the results in a similar way to case (b), so we omit it.  $\square$

From now on, we assume that  $b_1 > d_1, b_2 > d_2$ . By a similar argument, we know that  $E_0$  is unstable. Therefore, in the sequel, we will mainly study the boundary equilibria  $E_1, E_2$  and positive equilibrium  $E_3$ .

We claim that  $E_3$  exists if and only if

$$\begin{aligned} b_1 &> d_1, \\ b_2 &> d_2, \end{aligned} \quad (20)$$

$$\frac{1}{\beta} \left( \frac{b_2}{d_2} - 1 \right) > \frac{1}{\alpha} \left( \frac{b_1}{d_1} - 1 \right).$$

We analyze it graphically, from the first equation of (12), we can obtain the perpendicular isoclines

$$y = -x + \frac{1}{\alpha} \left( \frac{b_1}{d_1} - 1 \right), \quad (21)$$

denoted by  $L_1$ , which is a segment of lines with slope  $-1$  and intercept  $(1/\alpha)((b_1/d_1) - 1)$ . From the second equation of (12), we can obtain the horizontal isoclines

$$\beta x^2 + 2\beta x y + \beta y^2 + x + (1 - (b_2/d_2))y = 0, \quad (22)$$

denoted by  $L_2$ , which is a parabola, and it goes through three fixed points  $(0, 0)$ ,  $(-1/\beta, 0)$ , and  $(0, (1/\beta)((b_2/d_2) - 1))$ . We distinguish two cases depending on the position of  $L_1$  and  $L_2$  as shown in Figure 1. The inequalities satisfied by the coefficients that correspond to these cases can be listed as follows:

Case A

$$\begin{aligned} b_1 &> d_1, \\ b_2 &> d_2, \end{aligned} \quad (23)$$

$$\frac{1}{\beta} \left( \frac{b_2}{d_2} - 1 \right) < \frac{1}{\alpha} \left( \frac{b_1}{d_1} - 1 \right).$$

In this case, there exist three equilibria  $E_0, E_1$ , and  $E_2$ , but  $E_3$  does not exist.

Case B

$$\begin{aligned} b_1 &> d_1, \\ b_2 &> d_2, \end{aligned} \quad (24)$$

$$\frac{1}{\beta} \left( \frac{b_2}{d_2} - 1 \right) > \frac{1}{\alpha} \left( \frac{b_1}{d_1} - 1 \right).$$

In this case, there exist four equilibria  $E_0, E_1, E_2$ , and  $E_3$ , the positive equilibrium  $E_3$  is the intersection of  $L_1$  and  $L_2$ .

For the above two cases, a feasible biological interpretation of the conditions is that if  $(1/\beta)((b_2/d_2) - 1) < (1/\alpha)((b_1/d_1) - 1)$ , then the environment is more favorable for infected mosquitoes, and we say that Wolbachia infection has a fitness benefit. On the contrary, if  $(1/\beta)((b_2/d_2) - 1) > (1/\alpha)((b_1/d_1) - 1)$ , then the environment is less favorable for infected mosquitoes, and we claim that the infection has a fitness cost [10]. The stability analysis of the equilibria in both cases will be shown in the following theorem.

**Theorem 2.** Suppose  $b_1 > d_1, b_2 > d_2$ . Then, we have the following conclusions.

- In the fitness benefit case  $(1/\beta)((b_2/d_2) - 1) < (1/\alpha)((b_1/d_1) - 1)$ ,  $E_2$  is a saddle and  $E_1$  is globally asymptotically stable.
- In the fitness cost case  $(1/\beta)((b_2/d_2) - 1) > (1/\alpha)((b_1/d_1) - 1)$ , both  $E_1$  and  $E_2$  are locally asymptotically stable while  $E_3$  is a saddle.

*Proof*

- Case A: from  $J_2$  (see (16)), we know that  $E_2$  is a saddle and is unstable and the stable manifold is the  $Y$ -axis. From the stable manifold theory and Hartman-Grobman theorems [25, 26], it follows that no

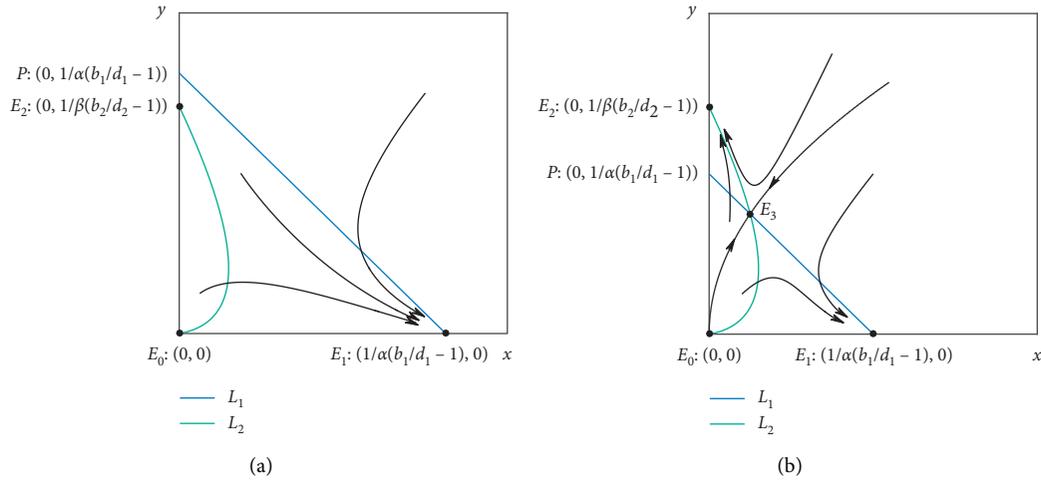


FIGURE 1: The two possible cases of  $L_1$  and  $L_2$ . (a) Case A. (b) Case B.

solution can approach  $E_2$ . By Liu and Elaydi's theorem, all solutions must approach  $E_1$ . Besides, the eigenvalues of  $J_1$  (see (15)) are positive and less than 1, so  $E_1$  is locally asymptotically stable. Therefore,  $E_1$  is globally asymptotically stable.

(b) Case B: all of the eigenvalues of  $J_1$  (see (15)) and  $J_2$  (see (16)) are positive and less than 1, so both  $E_1$  and  $E_2$  are locally asymptotically stable.

The stability of  $E_3$  is discussed below. The Jacobian at  $E_3$  takes the form

$$J_3 = \begin{pmatrix} \frac{d_1^2(1 + (d_2/b_2)((b_1/d_1) - 1)[1 + (\beta/\alpha)((b_1/d_1) - 1)])}{b_1} + 1 - d_1 \left( \frac{d_1^2 - d_1}{b_1} \right) \left( 1 - \frac{d_2}{b_2} \left[ 1 + \frac{\beta}{\alpha} \left( \frac{b_1}{d_1} - 1 \right) \right] \right) & \\ -\frac{d_2^2[1 + (2\beta/\alpha)((b_1/d_1) - 1)]}{b_2} & -\frac{d_2^2[1 + (2\beta/\alpha)((b_1/d_1) - 1)]}{b_2} + 1 + d_2 \end{pmatrix}. \quad (25)$$

According to the Jury criteria [27], the equilibrium  $E_3$  is locally asymptotically stable if the Jury condition

$$|\text{tr } J_3| < 1 + \det J_3 < 2, \quad (26)$$

holds, where  $\text{tr } J_3$  is the trace and  $\det J_3$  is the determinant of  $J_3$ . If at least one of these inequalities is reversed, then the

equilibrium is unstable. The inequalities are equivalent to the following three inequalities.

- (1)  $1 + \det J_3 < 2$ ,
- (2)  $-1 - \det J_3 < \text{tr } J_3$ ,
- (3)  $\text{tr } J_3 < 1 + \det J_3$ .

By a direct calculation, it shows that

$$\det J_3 = \frac{d_1^2(1 + d_2)(1 + (d_2/b_2)((b_1/d_1) - 1)[1 + (\beta/\alpha)((b_1/d_1) - 1)])}{b_1} - \frac{d_2^2[1 + (2\beta/\alpha)((b_1/d_1) - 1)]}{b_2} + (1 - d_1)(1 + d_2),$$

$$\text{tr } J_3 = \frac{d_1^2(1 + (d_2/b_2)((b_1/d_1) - 1)[1 + (\beta/\alpha)((b_1/d_1) - 1)])}{b_1} - \frac{d_2^2[1 + (2\beta/\alpha)((b_1/d_1) - 1)]}{b_2} + 2 - d_1 + d_2. \quad (27)$$

Using these formulas, we find that inequality (3) is equivalent to

$$\frac{d_1^2 d_2 (1 + (d_2/b_2)((b_1/d_1) - 1)[1 + (\beta/\alpha)((b_1/d_1) - 1)])}{b_1} - d_1 d_2 > 0, \quad (28)$$

and the reverse inequality holds in Case B, so that  $E_3$  is unstable.

In what follows, we prove that  $E_3$  is a saddle.

Inequality (2) is equivalent to

$$d_1(2+d_2)\left(\frac{d_1}{b_1}\left(1+\frac{d_2}{b_2}\left(\frac{b_1}{d_1}-1\right)\left[1+\frac{\beta}{\alpha}\left(\frac{b_1}{d_1}-1\right)\right]\right)-1\right) + 2d_2\left(1-\frac{d_2}{b_2}\left[1+\frac{2\beta}{\alpha}\left(\frac{b_1}{d_1}-1\right)\right]\right) + 4 > 0. \quad (29)$$

We will prove that it holds in Case B.

Let's analyze the two complicated parts of the above equation. Obviously, the inequality

$$-1 < \frac{d_1}{b_1}\left(1+\frac{d_2}{b_2}\left(\frac{b_1}{d_1}-1\right)\left[1+\frac{\beta}{\alpha}\left(\frac{b_1}{d_1}-1\right)\right]\right) - 1 < 0, \quad (30)$$

---


$$\begin{aligned} & d_1(2+d_2)\left(\frac{d_1}{b_1}\left(1+\frac{d_2}{b_2}\left(\frac{b_1}{d_1}-1\right)\left[1+\frac{\beta}{\alpha}\left(\frac{b_1}{d_1}-1\right)\right]\right)-1\right) + 2d_2\left(1-\frac{d_2}{b_2}\left[1+\frac{2\beta}{\alpha}\left(\frac{b_1}{d_1}-1\right)\right]\right) + 4 \\ & \geq d_1(2+d_2)\left(\frac{d_1}{b_1}\left(1+\frac{d_2}{b_2}\left(\frac{b_1}{d_1}-1\right)\left[1+\frac{\beta}{\alpha}\left(\frac{b_1}{d_1}-1\right)\right]\right)-1\right) + 4 \\ & > -d_1(2+d_2) + 4 > 0. \end{aligned} \quad (31)$$

Consequently, we only need to prove  $-1 - \det J_3 < \text{tr } J_3$  holds when  $(1/\alpha)((b_1/d_1)-1) < (1/\beta)((b_2/d_2)-1) < (2/\alpha)((b_1/d_1)-1)$ . By using this condition, we have

---


$$\begin{aligned} & d_1(2+d_2)\left(\frac{d_1}{b_1}\left(1+\frac{d_2}{b_2}\left(\frac{b_1}{d_1}-1\right)\left[1+\frac{\beta}{\alpha}\left(\frac{b_1}{d_1}-1\right)\right]\right)-1\right) + 2d_2\left(1-\frac{d_2}{b_2}\left[1+\frac{2\beta}{\alpha}\left(\frac{b_1}{d_1}-1\right)\right]\right) + 4 \\ & \geq d_1(2+d_2)\left(\frac{d_1}{b_1}\left(1+\frac{d_2}{b_2}\left(\frac{b_1}{d_1}-1\right)\left[1+\frac{\beta}{2\beta}\left(\frac{b_2}{d_2}-1\right)\right]\right)-1\right) + 2d_2\left(1-\frac{d_2}{b_2}\left[1+\frac{2\beta}{\beta}\left(\frac{b_2}{d_2}-1\right)\right]\right) + 4 \\ & \geq d_1(2+d_2)\left(\frac{d_1}{b_1}\left[1+\frac{d_2}{b_2}\left(\frac{b_1}{d_1}-1\right)\frac{1}{2}\left(\frac{b_2}{d_2}+1\right)\right]-1\right) + 2d_2\left(1-\frac{d_2}{b_2}\left[1+2\left(\frac{b_2}{d_2}-1\right)\right]\right) + 4 \\ & \geq d_1(2+d_2)\left[\frac{1}{2}\frac{d_1}{b_1}\left(\frac{b_1}{d_1}+1\right)-1\right] + 2d_2\left[1-\frac{d_2}{b_2}\left(2\frac{b_2}{d_2}-1\right)\right] + 4 \\ & > -\frac{1}{2}d_1(2+d_2) - 2d_2 + 4 > 0. \end{aligned} \quad (32)$$

The last inequality employs the condition  $0 < d_2 < d_1 < 1$ .

Now, we consider the characteristic quadratic polynomial of  $J_3$ , namely,

$$p(\lambda) = \lambda^2 - (\text{tr } J_3)\lambda + \det J_3. \quad (33)$$

holds in Case B. Also, we have

(i) If  $(1/\beta)((b_2/d_2)-1) < (2/\beta)((b_1/d_1)-1)$ , then  $1 - (d_2/b_2)[1 + (2\beta/\alpha)((b_1/d_1)-1)] < 0$ .

(ii) If  $(1/\beta)((b_2/d_2)-1) = (2/\alpha)((b_1/d_1)-1)$ , then  $1 - (d_2/b_2)[1 + (2\beta/\alpha)((b_1/d_1)-1)] = 0$ .

(iii) If  $(1/\beta)((b_2/d_2)-1) > (2/\alpha)((b_1/d_1)-1)$ , then  $1 - (d_2/b_2)[1 + (2\beta/\alpha)((b_1/d_1)-1)] > 0$ .

If  $(1/\beta)((b_2/d_2)-1) > (2/\alpha)((b_1/d_1)-1)$  or  $(1/\beta)((b_2/d_2)-1) = (2/\alpha)((b_1/d_1)-1)$ , then

---

Clearly,  $p(1) = 1 - \text{tr } J_3 + \det J_3 < 0$  because the inequality (3) is reversed in Case B. Moreover,  $p(-1) = 1 + \text{tr } J_3 + \det J_3 > 0$  because the inequality (2) holds, and  $p(+\infty) = +\infty$ . Thus,  $p(\lambda)$  has a positive root  $\lambda > 1$  and a root between  $-1$  and  $1$ . Therefore,  $E_3$  is a saddle.  $\square$

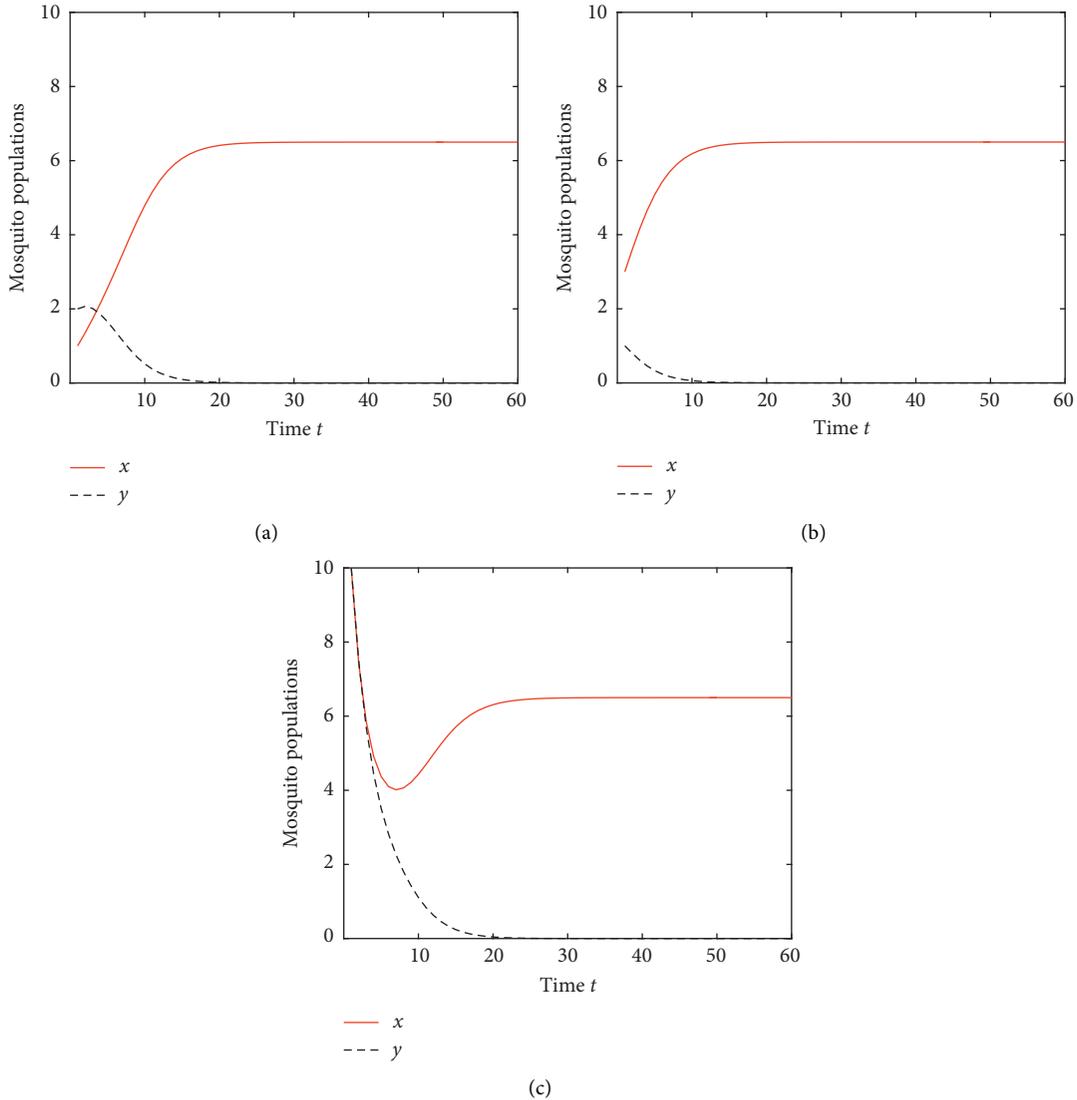


FIGURE 2: The red solid and the black dotted curves represent the numbers of infected and uninfected mosquitoes in *Wolbachia*, respectively. The parameter values are  $\alpha = \beta = 1, b_1 = 3, b_2 = 2, d_1 = 0.4,$  and  $d_2 = 0.3$ . The initial conditions are given by  $(x_0, y_0) = (1, 2)$  in (a),  $(x_0, y_0) = (3, 1)$  in (b), and  $(x_0, y_0) = (10, 10)$  in (c), and all of them show  $E_1$  is globally asymptotically stable in Case A.

The first part of Theorem 2 predicts that if the environment favors *Wolbachia*-infected populations, then successful invasion is ensured for any initial release size [28]. Biologically, the other case is more feasible when *Wolbachia*-infected populations have a fitness cost. In this case, model (3) possesses a saddle point  $E_3$ , whose stable curves separate the attraction regions of  $E_1$  and  $E_2$ . We illustrate our results by numerical simulations in the next section.

### 3. Numerical Results

In order to show the dynamic stability of the model (3), we use MATLAB technical computing software for numerical simulations. The simulations for (a) and (b) in Theorem 2 is mainly conducted by using different parameters. Some results are shown as follows.

From Figure 2 we see that in Case A, namely, the fitness benefit case,  $E_1$  is globally asymptotically stable. The result of (a) in Theorem 2 is verified. Whatever the initial value of *Wolbachia*-infected mosquito population  $x_t$  and uninfected mosquito population  $y_t$  are,  $y_t$  will extinct and  $x_t$  will persist, this means that the result of the competition is that *Wolbachia* successfully spreads throughout the mosquito population. In addition, it can be shown from the conditions that increasing the birth rate  $b_1$  and reducing the competition coefficient  $\alpha$  and the death rate  $d_1$  will be beneficial to this result.

From Figure 3, we see that in Case B, namely, the fitness cost case, both  $E_1$  and  $E_2$  are locally asymptotically stable, which is consistent with the result of (b) in Theorem 2. Each equilibrium has its own attractive regions and the initial values of *Wolbachia*-infected mosquitoes  $x_t$  and uninfected mosquitoes  $y_t$  will affect the trend of the solution; if the

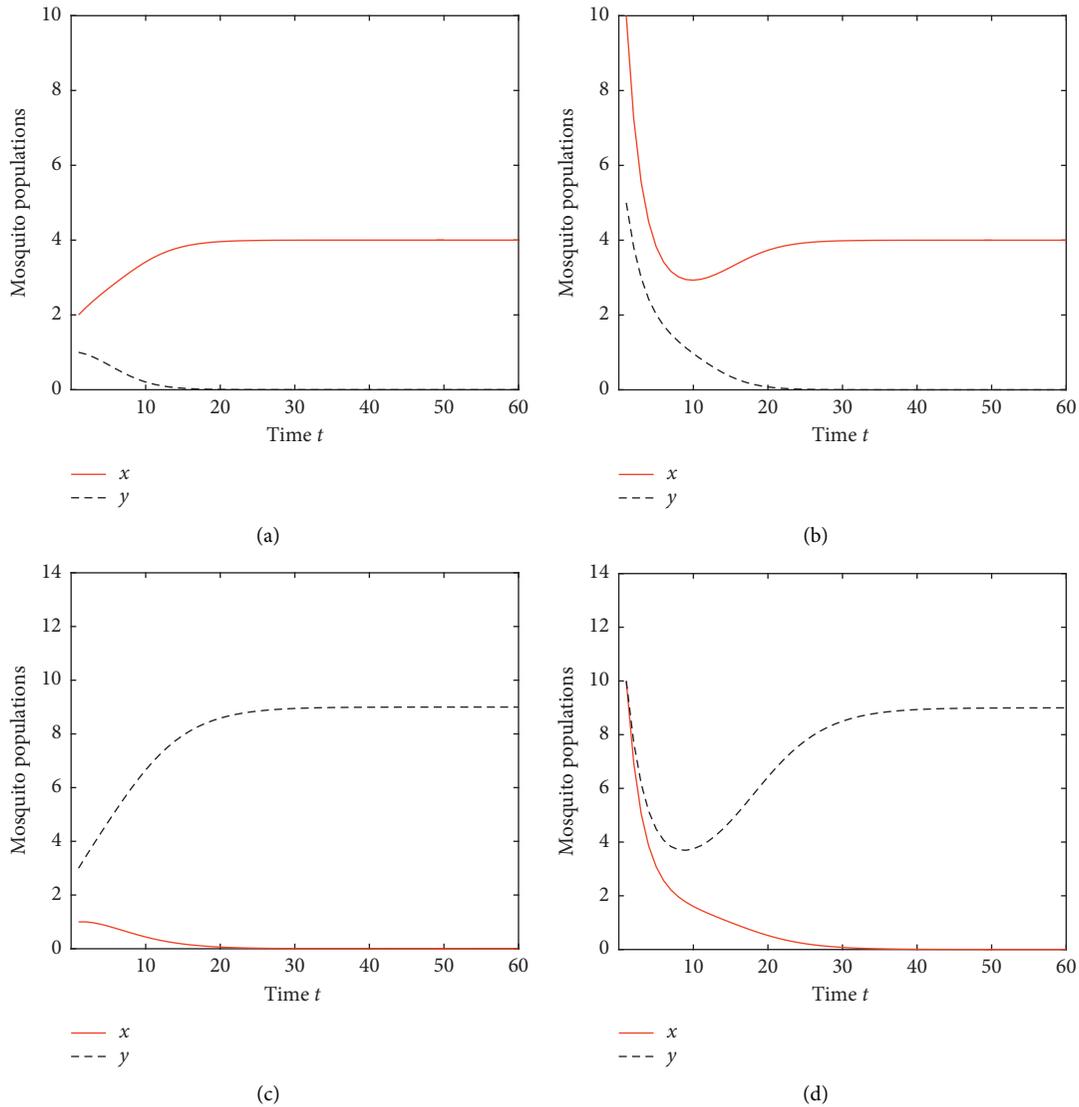


FIGURE 3: The red solid and the black dotted curves represent the numbers of infected and uninfected mosquitoes in *Wolbachia*, respectively. The parameter values are  $\alpha = \beta = 1, b_1 = 2, b_2 = 3, d_1 = 0.4$ , and  $d_2 = 0.3$ . It satisfies the condition of Case B, both  $E_1$  and  $E_2$  are locally asymptotically stable, and they have their own attractive regions. The solutions with different initial values will approach to different equilibria. The initial value  $(x_0, y_0) = (2, 1)$  and  $(x_0, y_0) = (10, 5)$  will lead to the solution approach  $E_1$  as  $t \rightarrow \infty$ , shown in (a) and (b), while the initial value  $(x_0, y_0) = (1, 3)$  and  $(x_0, y_0) = (10, 10)$  will lead to the solution approach  $E_2$  as  $t \rightarrow \infty$ , shown in (c) and (d).

solution approaches  $E_1$ , then  $y_t$  will become extinct and  $x_t$  will persist, that is to say the result of the competition is that *Wolbachia* successfully spreads throughout the mosquito population. On the contrary, if the solution approaches  $E_2$ , then  $x_t$  will go to extinct and  $y_t$  will persist, namely, *Wolbachia* diffusion fails.

From above, we find the factors that affect the competition results are the competition coefficient within (or between) species, the birth rate, the death rate, and the initial value of the population. Reducing the competition coefficient and the death rate of the population and increasing the birth rate and the initial value of the population will be beneficial to the lasting survival of the population. It also makes sense in biological terms.

Finally, we give an explanation on the stable manifold of  $E_3$ . Theorem 2 shows that  $E_3$  is a saddle whose stable manifold separates the attractive regions of  $E_1$  and  $E_2$ . However, the specific position of the stable manifold cannot be determined. Here, we use numerical simulation to roughly estimate the position of the stable curve by using different initial values, as shown in Figure 4, and observing which equilibrium that the solution will tend to. Through figure analysis, we claim that the stable curve can be expressed as a smooth function that starts at  $E_0$ , strictly increasing in the positive direction, and its image biased towards the  $X$ -axis. The stable manifold is composed of two separation curves with  $E_3$  as the dividing point. Therefore, the attraction region of  $E_2$  is larger than that of  $E_1$ .

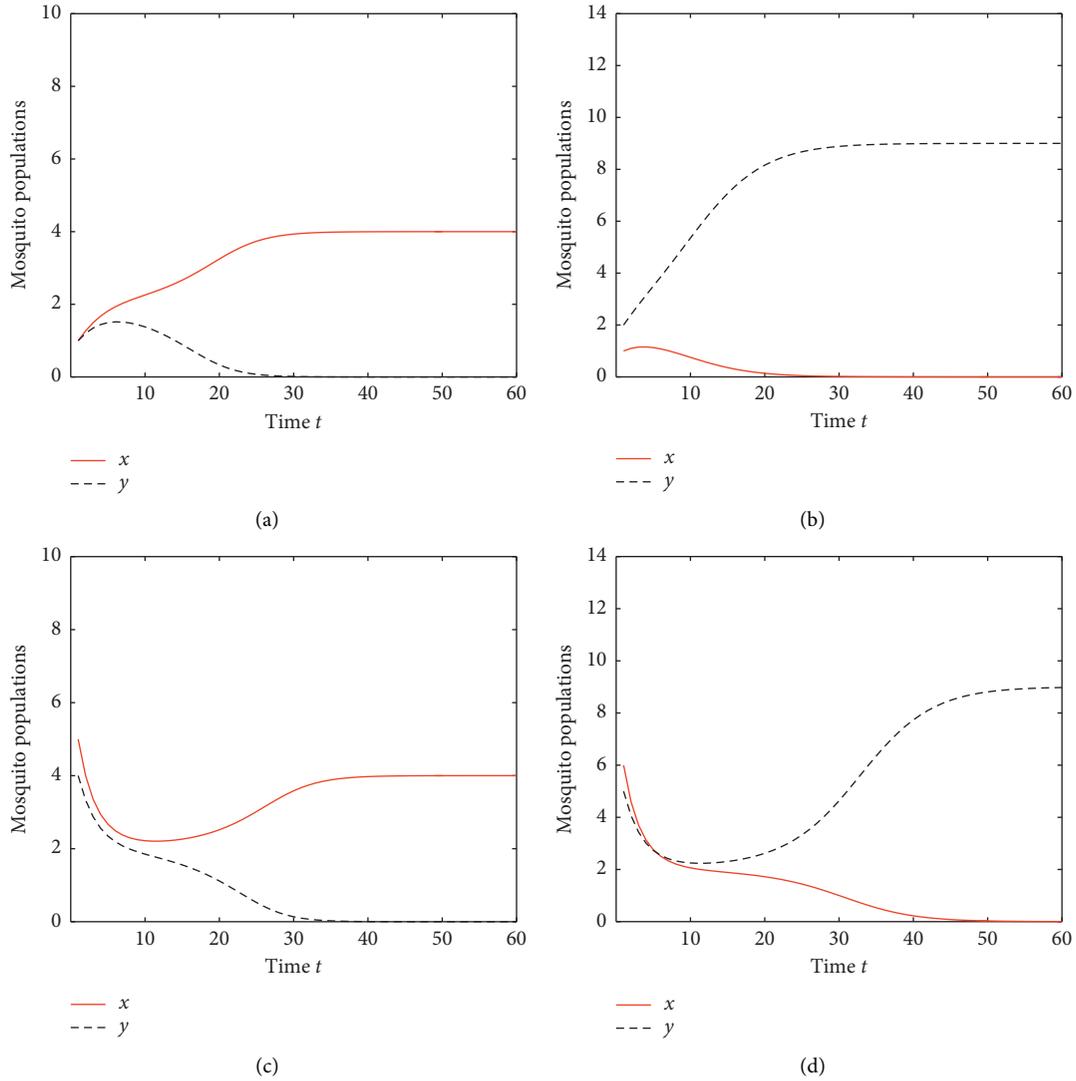


FIGURE 4: The parameters and some conclusions are given in Figure 3.  $E_3$  is the saddle, and its stable manifolds separate the attractive regions of  $E_1$  and  $E_2$ . The solutions with different initial values will approach to different equilibria. The initial value  $(x_0, y_0) = (1, 1)$  and  $(x_0, y_0) = (5, 4)$  will lead to the solution approaches  $E_1$  as  $t \rightarrow \infty$ , shown in (a) and (c), while the initial value  $(x_0, y_0) = (1, 2)$  and  $(x_0, y_0) = (6, 5)$  will lead to the solution approaches  $E_2$  as  $t \rightarrow \infty$ , shown in (b) and (d).

### 4. Conclusion and Discussion

Dengue fever is a mosquito-borne disease, which has great harm to human society. Due to the lack of vaccines and efficient clinical cures, we need to control mosquito population to block the spread of the disease. An innovative and effective method to control mosquitoes is to employ *Wolbachia*, which has led to a growing number of researchers building models to study the dynamics of *Wolbachia* transmission. Considering that the collection data of mosquitoes in the wild are discrete, we established a discrete competition model to study the conditions for *Wolbachia* to successful spread in mosquitoes.

Model (3) is a discrete competition model of overlapping generations of *Wolbachia*-infected mosquitoes population  $x_t$  and noninfected mosquitoes population  $y_t$ . We showed the global asymptotic properties of the four equilibria of the

model through elaborate analysis. First of all, the trivial equilibrium  $E_0$  is globally asymptotically stable when  $b_1 \leq d_1$  and  $b_2 \leq d_2$ , mosquito populations will go to extinct, otherwise  $E_0$  is unstable. Then, we obtain a complete result of  $E_1$  and  $E_2$ . If  $b_1 > d_1, b_2 \leq d_2$ , then  $E_1$  is globally asymptotically stable, which means that *Wolbachia*-infected mosquitoes population  $x_t$  will persist and noninfected mosquitoes  $y_t$  will become extinct, namely, *Wolbachia* successfully spreads. On the contrary, if  $b_1 \leq d_1, b_2 > d_2$ , then  $E_2$  is globally asymptotically stable, namely, *Wolbachia* fails to spread. Furthermore, we study the case when  $b_1 > d_1, b_2 > d_2$ . In the fitness benefit case, namely,  $(1/\beta)((b_2/d_2) - 1) < (1/\alpha)((b_1/d_1) - 1)$ , and then  $E_2$  is a saddle while  $E_1$  is globally asymptotically stable and  $E_3$  is not exist; that is, *Wolbachia* successfully spreads. In the fitness cost case, namely,  $(1/\beta)((b_2/d_2) - 1) < (1/\alpha)((b_1/d_1) - 1)$ , both  $E_1$  and  $E_2$  are locally asymptotically stable while  $E_3$  is a saddle,  $E_1$  and  $E_2$

have their own attractive regions, and the stable manifold of  $E_3$  is separated from their attracting domain. The size of the initial population value will affect its own persistence.

Numerical simulations are also provided to demonstrate these theoretical results. We mainly showed the simulation under condition  $b_1 > d_1, b_2 > d_2$ , and we found that the simulation results are consistent with the theoretical results. In particular, since we cannot determine the exact position of the stable manifold of  $E_3$ , we showed its approximate position through simulations.

There are some limitations of the model presented in this paper. When we built the model, we only took into account the competitive factors affecting the birth rate of the population, not the death rate. In fact, both intraspecific and interspecific competition can affect mortality in populations. Also, we assume  $c_{11} = c_{12} = \alpha$  and  $c_{21} = c_{22} = \beta$  to obtain a simpler model. It is obvious that if  $c_{11} \neq c_{12}, c_{21} \neq c_{22}$ , the model will be more reasonable and can better describe the actual situation of competition between two mosquito populations. However, it presents great challenges in equilibrium analysis.

## Data Availability

No data were used to support the study.

## Conflicts of Interest

The authors declare that they have no conflicts of interest.

## Acknowledgments

This work was partially supported by the National Natural Science Foundation of China (No. 11771104) and Program for Changjiang Scholars and Innovative Research Team in University (IRT16R16).

## References

- [1] J. L. Kyle and E. Harris, "Global spread and persistence of dengue," *Annual Review of Microbiology*, vol. 62, no. 1, pp. 71–92, 2008.
- [2] S. V. Bardina, P. Bunduc, S. Tripathi et al., "Enhancement of Zika virus pathogenesis by preexisting antinflavivirus immunity," *Science*, vol. 356, no. 6334, pp. 175–180, 2017.
- [3] H. Laven, "Cytoplasmic inheritance in *Culex*," *Nature*, vol. 177, no. 4499, pp. 141–142, 1956.
- [4] M. Hertig and S. B. Wolbach, "Studies on Rickettsia-like micro-organisms in insects," *The Journal of Medical Research*, vol. 44, no. 3, pp. 329–374, 1924.
- [5] Z. Xi, C. C. Khoo, S. L. Dobson et al., "*Wolbachia* establishment and invasion in an *Aedes aegypti* laboratory population," *Science*, vol. 310, no. 5746, pp. 326–328, 2005.
- [6] Z. Xi, J. L. Dean, C. Khoo, and S. L. Dobson, "Generation of a novel *Wolbachia* infection in *Aedes albopictus* (Asian tiger mosquito) via embryonic microinjection," *Insect Biochemistry and Molecular Biology*, vol. 35, no. 8, pp. 903–910, 2005.
- [7] M. G. Huang, J. W. Luo, L. C. Hu et al., "Assessing the efficiency of *Wolbachia*, driven, *Aedes*, mosquito suppression by delay differential equations," *Journal of Theoretical Biology*, vol. 440, pp. 1–11, 2017.
- [8] J. Yu, "Modeling mosquito population suppression based on delay differential equations," *SIAM Journal on Applied Mathematics*, vol. 78, no. 6, pp. 3168–3187, 2018.
- [9] J. K. Axford, A. G. Callahan, A. A. Hoffmann, H. L. Yeap, and P. A. Ross, "Fitness of wAlbB *Wolbachia* infection in *Aedes aegypti*: parameter estimates in an outcrossed background and potential for population invasion," *The American Journal of Tropical Medicine and Hygiene*, vol. 94, no. 3, pp. 507–516, 2016.
- [10] B. Zheng, M. X. Tang, and J. S. Yu, "Modeling *Wolbachia* spread in mosquitoes through delay differential equations," *SIAM Journal of Applied Mathematics*, vol. 74, pp. 734–770, 2014.
- [11] M. Huang, J. Yu, L. Hu, and B. Zheng, "Qualitative analysis for a *Wolbachia* infection model with diffusion," *Science China Mathematics*, vol. 59, no. 7, pp. 1249–1266, 2016.
- [12] M. Huang, M. Tang, and J. Yu, "*Wolbachia* infection dynamics by reaction-diffusion equations," *Science China Mathematics*, vol. 58, no. 1, pp. 77–96, 2015.
- [13] X. Zheng, D. Zhang, Y. Li et al., "Incompatible and sterile insect techniques combined eliminate mosquitoes," *Nature*, vol. 572, no. 7767, pp. 56–61, 2019.
- [14] M. Huang, M. Tang, J. S. Yu, and B. Zheng, "A stage structured model of delay differential equations for *Aedes* mosquito population suppression," *Discrete & Continuous Dynamical Systems—A*, 2019.
- [15] M. G. Huang, L. C. Hu, and B. Zheng, "Comparing the efficiency of *Wolbachia* driven *Aedes* mosquito suppression strategies," *Journal of Applied Analysis and Computation*, vol. 9, no. 1, pp. 211–230, 2019.
- [16] M. Huang, M. Tang, J. S. Yu, and B. Zheng, "The impact of mating competitiveness and incomplete cytoplasmic incompatibility on *Wolbachia*-driven mosquito population suppression," *Mathematical Biosciences and Engineering*, vol. 16, no. 5, pp. 4741–4757, 2019.
- [17] J. Yu and B. Zheng, "Modeling *Wolbachia* infection in mosquito population via discrete dynamical models," *Journal of Difference Equations and Applications*, vol. 25, no. 11, pp. 1549–1567, 2019.
- [18] B. Zheng, X. P. Liu, M. X. Tang et al., "Use of age-stage structural models to seek optimal *Wolbachia*-infected male mosquito releases for mosquito-borne disease control," *Journal of Theoretical Biology*, vol. 472, pp. 95–109, 2019.
- [19] L. C. Hu, M. X. Tang, Z. D. Wu et al., "The threshold infection level for *Wolbachia* invasion in random environments," *Journal of Differential Equations*, vol. 266, pp. 4377–4393, 2019.
- [20] J. M. Cushing, R. F. Costantino, B. Dennis et al., *Chaos in Ecology Theoretical Ecology Series*, Academic Press/Elsevier, San Diego, CA, USA, 2003.
- [21] J. M. Cushing, S. Leverage, N. Chitnis et al., "Some discrete competition models and the competitive exclusion principle," *Journal of Difference Equations and Applications*, vol. 10, no. 13–15, pp. 1139–1151, 2004.
- [22] P. H. Leslie and J. C. Gower, "The properties of a stochastic model for two competing species," *Biometrika*, vol. 45, no. 3–4, pp. 316–330, 1958.
- [23] J. H. Werren, L. Baldo, and M. E. Clark, "*Wolbachia*: master manipulators of invertebrate biology," *Nature Reviews Microbiology*, vol. 6, no. 10, pp. 741–751, 2008.
- [24] P. Liu and S. N. Elaydi, "Discrete competitive and cooperative models of Lotka-Volterra type," *Journal of Computational Analysis and Applications*, vol. 3, no. 1, pp. 53–73, 2001.

- [25] S. N. Elaydi, *An Introduction to Difference Equations*, Springer, New York, NY, USA, Second edition, 1999.
- [26] J. Guckenheimer and P. Holmes, *Nonlinear Oscillations, Dynamical Systems and Bifurcations of Vector Fields*, Springer-Verlag, Berlin, Germany, 1983.
- [27] H. Caswell, *Matrix Population Models: Construction, Analysis and Interpretation*, Sinauer Associates, Inc. Publisher, Sunderland, MA, USA, Second edition, 2001.
- [28] M. Turelli, "Cytoplasmic incompatibility in populations with overlapping generations," *Evolution*, vol. 64, no. 1, pp. 232–241, 2010.
- [29] D. Xiao and S. Ruan, "Global dynamics of a ratio-dependent predator-prey system," *Journal of Mathematical Biology*, vol. 43, no. 3, pp. 268–290, 2001.