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COMPARING THE EFFICIENCY OF WOLBACHIA DRIVEN AEDES MOSQUITO SUPPRESSION STRATEGIES*

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Abstract *Wolbachia* is an endosymbiotic bacterium which manipulates host reproduction by cytoplasmic incompatibility, and restrains the transmission of dengue virus in *Aedes* mosquitoes. A novel strategy for dengue control involves releasing *Wolbachia* infected males into nature to suppress wild *Aedes* mosquito population. We develop a model of delay differential equations, integrating larval density-dependent competition and diapausing eggs, to compare the efficiency of different suppression strategies. The global asymptotical stability of the complete suppression state identifies the releasing amount threshold ascertaining suppression. Based on the experimental data for *Aedes albopictus* population in Guangzhou, our simulations show that the mosquito density in the highest peak season can be reduced by more than 95% when the number of released males is above the releasing threshold. The best time to initiate the suppression is in early March, lasting until the end of June, followed by the parallel releasing policy from July to November. However, the egg bank has neglectable effects on the control of dengue vector in Guangzhou.

Keywords Dengue fever, Wolbachia, cytoplasmic incompatibility, population suppression strategy.

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1. Introduction

Dengue fever, a mosquito-borne febrile disease caused by a flavivirus with four serotypes, is regarded as one of the most severe arbovirus diseases. In the past 50 years, dengue incidence has increased 30 fold, with over 390 million people infected

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annually in the tropical and subtropical regions worldwide [1, 29]. Dengue fever reemerged in Guangdong Province in 1979 after being absent for about 30 years in mainland China [30]. Since then, it has got worse both in extent and severity, and cases have been reported in Guangdong every year [30]. An unprecedented outbreak of dengue fever occurred in Guangdong, especially in Guangzhou, in 2014. The dengue cases were more than 10 times of the total cases in previous 10 years with 6 death cases [16]. Dengue was characterized as an imported epidemic disease and was not confirmed as an endemic in mainland China [29]. Although the current vector control strategies, including insecticide spraying and community-based source reduction, has taken some effect in a short time period, innovative prevention and control methods with long-term effect are still needed to control dengue. *Wolbachia*, an endosymbiotic bacterium which can block the replication of dengue virus in *Aedes* mosquitoes, has become a new weapon to combat dengue. This is feasible because *Wolbachia* can manipulate the host reproduction by cytoplasmic incompatibility (CI): Eggs produced from wild females mating with *Wolbachia* infected males do not hatch. This makes *Wolbachia* infected males be the killer of wild females. In Guangzhou, *Wolbachia*-infected *Aedes albopictus* males have been reared in a factory, and been released in several isolated natural or residential areas since March, 2015. The CI mechanism has suppressed more than 95% of wild *Aedes albopictus* population, the main vector of dengue in China in these areas [27].

To assess and compare the efficiency of different mosquito suppression strategies, we develop a mathematical model integrating density-dependent competition among immature stages of *Aedes* mosquitoes since it has been frequently documented that intraspecific competition increased the mortality rate in larval stage, lengthened their development time, and influenced the female size (wing length) and fecundity [19, 20, 25, 26]. Our model consists of delay differential equations by considering the waiting time from mating to eclosion of mosquitoes, usually about 7∼20 days [15, 18, 19].

To proceed, let $A(t)$ be the size of adult mosquitoes, and $L(t)$ be the size of larvae at time t. The wild population is invaded by released male mosquitoes, denoted by $R(t)$, carrying a *Wolbachia* strain that can induce complete CI. As a maternally transmitted bacterium [28, 31], there exist no *Wolbachia*-infected females. Let τ_1 be the average waiting time from the eclosion to the hatching of first instar larvae, and τ_2 the average development time of larvae and pupae. Then the average duration in one reproduction cycle is $\tau_1 + \tau_2$. We assume that the fecundity is proportional to the number of female adults, and the rates of stage transitions, from eggs to larvae, and from larvae to pupae, are proportional to the population sizes in the previous stage. Let β denote the average number of larvae produced by one female adult without the interference of CI. As in classical studies [4, 8–12, 14, 23, 32–35], the probability of CI is the number of released infected males over the total number of males $R(t)/(R(t) + A(t)/2)$. Thus, the birth function of larvae is given by $\beta A^2(t - \tau_1)/[2(A(t - \tau_1) + 2R(t - \tau_1))]$. To incorporate the strong intraspecific competition in the larval stage, we introduce a density-dependent competition function

$$f(L) = m\left(1 + \frac{L}{K_L}\right)L \tag{1.1}$$

to account for the death of larvae, where $m > 0$ is the constant minimum larval mortality rate, and K_L measures the carrying capacity in a unit breeding area for larvae [3, 22]. Let μ denote the pupation rate of larvae, and α denote the eclosion rate of pupae. Since adult mosquitoes only weakly density restricted, we use the mortality rate $\delta > 0$ to describe the death of adults. This leads to the model

$$\begin{cases} \dfrac{dL(t)}{dt} = \dfrac{\beta}{2} \cdot \dfrac{A^2(t-\tau_1)}{A(t-\tau_1)+2R(t-\tau_1)} - m\left(1+\dfrac{L(t)}{K_L}\right)L(t) - \mu L(t), \\ \dfrac{dA(t)}{dt} = \alpha\mu L(t-\tau_2) - \delta A(t). \end{cases} \tag{1.2}$$

Wolbachia infected *Aedes albopictus* males mate with wild females effectively for about three days after released. In the field trial of mosquito suppression in Guangzhou, the infected males are released every three days such that the loss of crossable infected males in the field is compensated by new releasing, and keeps the number of copulatory infected males in wild almost a constant. This motivates us to use a fixed releasing policy in the model which manages the abundance of released *Wolbachia*-infected males a constant independent of the population size of wild mosquitoes. Let $R(t) \equiv R$. Upon rescaling the parameters in (1.2),

$$\begin{gathered} \alpha \to \frac{m+\mu}{\delta}\alpha, \quad \tau_1 \to (m+\mu)\tau_1, \quad \tau_2 \to (m+\mu)\tau_2, \quad R \to \frac{2m}{\mu K_L}R, \\ b = \frac{\beta\mu}{2(m+\mu)^2}, \quad x(t) = \frac{m}{(m+\mu)K_L}L(\frac{t}{m+\mu}), \quad y(t) = \frac{m}{\mu K_L}A(\frac{t}{m+\mu}), \end{gathered} \tag{1.3}$$

(1.2) can be rewritten as

$$\begin{cases} \dfrac{dx(t)}{dt} = \dfrac{by^2(t-\tau_1)}{y(t-\tau_1)+R} - x(t)(1+x(t)), \\ \dfrac{dy(t)}{dt} = \dfrac{\delta}{m+\mu}(\alpha x(t-\tau_2) - y(t)). \end{cases} \tag{1.4}$$

We study the dynamics of (1.4) supplemented with the initial value functions

$$x(t) = \phi(t) > 0, \quad y(t) = \varphi(t) > 0, \quad t \in [-\max\{\tau_1, \tau_2\}, 0]. \tag{1.5}$$

The stability analysis of the equilibria of (1.4) is provided in Section 2. We establish the releasing threshold over which the wild mosquito population will be eliminated eventually. Since the life table parameters are sensitive to temperature and precipitation, there is an apparent gap between this theoretical threshold level and the releasing threshold in the field trial for mosquito suppression. We fill up this gap in Section 3. In conformity to the daily meteorological data in Guangzhou, we divide one year into five periods, and estimate the life table parameters of *Aedes albopictus* in each period based on the field data. Our analysis shows that the model (1.4) captures several critical features of the seasonal abundance of natural *Aedes albopictus* population in Guangzhou [15, 18, 19]. To measure the mosquito suppression efficiency, we use suppression rate $\gamma \in [0, 1]$, a ratio of the *Aedes* number of suppressed population over the wild *Aedes* number, recorded at the day when the last and highest peak of the natural population is observed [13]. The simulation shows that if the released amount of infected males is no less than the releasing threshold, then the mosquito density in the highest peak season can be reduced by more than 95%.

Different from the fixed releasing policy, the parallel releasing policy manages the released number of infected males to stay in a constant ratio to the density of wild mosquitoes. For the parallel releasing policy, by letting $r = R(t)/A(t)$, and renaming L as x, A as y, and $\beta/2$ as b, we rewrite (1.2) as

$$\begin{cases} \dfrac{dx(t)}{dt} = \dfrac{b}{1+2r}\, y(t-\tau_1) - m\left(1 + \dfrac{x(t)}{K_L}\right) x(t) - \mu x(t), \\ \dfrac{dy(t)}{dt} = \alpha\mu x(t-\tau_2) - \delta y(t). \end{cases} \tag{1.6}$$

It is very interesting to assess and compare the suppression efficiency of the two releasing policies. By comparing the suppression dynamics of (1.4) and (1.6), for a similar suppression effect, our analysis shows that the more efficient and economical suppression strategy is highly dependent on the abundance of wild *Aedes* population. The fixed releasing policy needs less released number of males than the parallel releasing policy when the wild *Aedes albopictus* population is large, while the parallel releasing policy needs less infected males than that of the fixed releasing policy when the wild *Aedes albopictus* population is small. Since *Aedes albopictus* adults grow rapidly in the Spring and reach their first peak at about the end of May, the optimal time point to initiate the suppression is the beginning of March. By integrating the two releasing policies, the most efficient and economical suppression strategy is utilizing the fixed releasing policy from March to June, and then the parallel releasing policy from July to November. We use different initial larval numbers with same initial adult numbers to characterize the influence of egg bank on the suppression dynamics. Although a large amount of initial larvae will change the wild *Aedes* population dynamics before July hugely, our analysis shows that egg bank has little impact on natural *Aedes* population after August. Since the high-incidence season of dengue in Guangzhou are from August to October, egg bank has limit influence on the control situation of dengue fever in Guangzhou.

2. Global stability of the complete suppression state

To offer a simple and transparent view on the equilibria and classify its stability, we first consider the following system without time delays

$$\begin{cases} \dfrac{dx(t)}{dt} = \dfrac{by^2(t)}{y(t)+R} - x(t)(1+x(t)), \\ \dfrac{dy(t)}{dt} = \dfrac{\delta}{m+\mu}(\alpha x(t) - y(t)). \end{cases} \tag{2.1}$$

Define

$$\begin{aligned} &R^* = \alpha(\sqrt{\alpha b} - 1)^2,\ x^* = \sqrt{\alpha b} - 1,\ x_1 = \frac{\alpha^2 b - \alpha - R - \sqrt{(\alpha^2 b - \alpha - R)^2 - 4\alpha R}}{2\alpha} \\ &x_2 = \frac{\alpha^2 b - \alpha - R + \sqrt{(\alpha^2 b - \alpha - R)^2 - 4\alpha R}}{2\alpha},\ \text{and } y^* = \alpha x^*,\ y_i = \alpha x_i,\ i = 1, 2. \end{aligned} \tag{2.2}$$

We classify its local dynamics in $\mathbb{R}_+^2 = \{(x, y) : x \geq 0, y \geq 0\}$ in the following theorem.

Theorem 2.1. *Let $R \geq 0$ and all other parameters be positive in (2.1). Then $\mathbb{R}_+^2$ is positively invariant, within which all solutions remain bounded. Furthermore, we have:*

(1) If $\alpha b \leq 1$ or $R > R^*$, then the origin $E_0(0,0)$ is the only equilibrium point, and is globally asymptotically stable in $\mathbb{R}_+^2$.

(2) If $\alpha b > 1$ and $R = R^*$, then (2.1) has two equilibrium points: $E_0(0,0)$ and a positive equilibrium point $E^*(x^*, y^*)$. E^* is unstable, and E_0 is globally asymptotically stable in $\mathbb{R}_+^2 \setminus E^*$.

(3) If $\alpha b > 1$ and $R < R^*$, then (2.1) has three equilibrium points $E_0(0,0)$, $E_1(x_1, y_1)$ and $E_2(x_2, y_2)$. E_1 is a saddle point, and E_0 and E_2 are local asymptotically stable.

Proof. Let $(x(t), y(t))$ be a solution of (2.1) with $(x(0), y(0)) \in \mathbb{R}_+^2$. Let $x = 0$ and $y > 0$ in the first equation of (2.1). We find $dx(t)/dt > 0$. Similarly, $dy(t)/dt > 0$ when $x > 0$ and $y = 0$. As a result, we see that $\mathbb{R}_+^2$ is positively invariant. Along the solution $(x(t), y(t))$, we have $x(t)$, $y(t) \geq 0$ for all $t > 0$, and

$$\begin{aligned}\frac{d}{dt}\left(\frac{\delta}{m+\mu}x + by\right) &= \frac{\delta}{m+\mu}\left[\frac{by^2}{y+R} - x(1+x)\right] + \frac{b\delta}{m+\mu}(\alpha x - y) \\ &\leq \frac{\delta}{m+\mu}[by - x(1+x)] + \frac{b\delta}{m+\mu}(\alpha x - y) \qquad (2.3) \\ &= -\frac{\delta}{m+\mu}x(x+1-\alpha b),\end{aligned}$$

which is negative when $x > \alpha b - 1$. It shows clearly that $x(t)$ must be bounded. By using the second equation of (2.1), it is further seen that $y(t)$ is also bounded.

We first enumerate the equilibrium points of system (2.1), which satisfy

$$\frac{by^2}{y+R} - x(1+x) = 0, \quad \text{and} \quad y = \alpha x. \tag{2.4}$$

Apparently, the origin $E_0(0,0)$ is an equilibrium point, and is the only one on the two axes. If (x, y) is an equilibrium point of (2.1) with positive x and y, then

$$\alpha x^2 - (\alpha^2 b - \alpha - R)x + R = 0. \tag{2.5}$$

The discriminant of this quadratic equation is

$$\Delta_R = (\alpha^2 b - \alpha - R)^2 - 4\alpha R = (R - \alpha(\sqrt{\alpha b} + 1)^2)(R - R^*).$$

Obviously, if $R^* < R < \alpha(\sqrt{\alpha b} + 1)^2$, then $\Delta_R < 0$ and (2.5) has no real root. We note

$$\alpha(\sqrt{\alpha b} + 1)^2 - \alpha(\alpha b - 1) = 2\alpha(1 + \sqrt{\alpha b}) > 0,$$

and

$$R^* - \alpha(\alpha b - 1) = 2\alpha(1 - \sqrt{\alpha b}). \tag{2.6}$$

If $R \geq \alpha(\sqrt{\alpha b} + 1)^2$, then $R > \alpha(\alpha b - 1)$, and (2.5) has no positive solution. Similarly, (2.5) has no positive solution when $\alpha b \leq 1$. Hence system (2.1) has exactly one equilibrium E_0 if and only if

$$\alpha b \leq 1 \quad \text{or} \quad R > R^*.$$

Let $\alpha b > 1$. (2.1) has three equilibria $E_0(0,0)$, $E_1(x_1, y_1)$ and $E_2(x_2, y_2)$ if and only of

$$\Delta_R > 0 \quad \text{and} \quad \alpha^2 b - \alpha - R > 0. \tag{2.7}$$

It follows from (2.6) that $R^* < \alpha(\alpha b - 1)$ when $\alpha b > 1$. Thus (2.7) is equivalent to

$$\alpha b > 1 \quad \text{and} \quad 0 \le R < R^*. \tag{2.8}$$

Particularly, (2.1) has two equilibria $E_0(0,0)$ and $E^*(x^*, y^*)$ with

$$x^* = \frac{\alpha^2 b - \alpha - R}{2\alpha} \quad \text{and} \quad y^* = \alpha x^*$$

if and only of

$$\Delta_R = 0 \quad \text{and} \quad \alpha^2 b - \alpha - R > 0. \tag{2.9}$$

By using $\alpha(\sqrt{\alpha b} + 1)^2 > \alpha(\alpha b - 1)$, $\alpha b > 1$ and (2.6), we see that (2.9) is equivalent to $R = R^*$, and so

$$x^* = \frac{\alpha^2 b - \alpha - R}{2\alpha} = \frac{\alpha^2 b - \alpha - \alpha(\sqrt{\alpha b} - 1)^2}{2\alpha} = \sqrt{\alpha b} - 1.$$

Hence system (2.1) has two equilibria E_0 and E^* if and only if

$$\alpha b > 1 \quad \text{and} \quad R = R^*.$$

Next, we consider the stability of the equilibria. For the case when $\alpha b \le 1$, E_0 is the only equilibrium. Let $V(t) = \delta x/(m + \mu) + by$. (2.3) implies that $dV/dt < 0$, when $x > 0$. In the case $x = 0$, we have

$$\frac{dV}{dt} = -\frac{b\delta}{m + \mu} y < 0,$$

when $y > 0$. Hence $V(t) \to 0$ as $t \to \infty$, and E_0 is globally asymptotically stable.

Let $R > R^*$. The Jacobian matrix of system (2.1) is

$$J = \begin{pmatrix} -1 - 2x \dfrac{2by}{y + R} & -\dfrac{by^2}{(y + R)^2} \\ \\ \dfrac{\alpha\delta}{m + \mu} & -\dfrac{\delta}{m + \mu} \end{pmatrix}.$$

It follows from the Jacobian matrix J_{E_0} at E_0

$$J_{E_0} = \begin{pmatrix} -1 & 0 \\ \\ \dfrac{\alpha\delta}{m + \mu} & -\dfrac{\delta}{m + \mu} \end{pmatrix},$$

that the two eigenvalues of J_{E_0} are

$$\lambda_1 = -1 \quad \text{and} \quad \lambda_2 = -\frac{\delta}{m+\mu}.$$

Hence E_0 is always local asymptotically stable for any releasing constant $R \geq 0$. Since there is no interior equilibrium point, there can be no closed orbits and E_0 is globally asymptotically stable in $\mathbb{R}_+^2$.

For the case when $\alpha b > 1$ and $R = R^*$, we have (2.1) has a locally stable equilibrium $E_0(0,0)$ and a positive equilibrium $E^*(x^*, y^*)$. The stability of E^* is under-determined by the eigenvalue method. We consider the trajectory $\mathfrak{L} = \{(x(t), y(t))|t \geq 0\}$ on the line $y = \alpha x$,

$$\frac{dx}{dt}\Big|_{y=\alpha x} = -\frac{x}{x + (\sqrt{\alpha b} - 1)^2}(x + 1 - \sqrt{\alpha b})^2 < 0.$$

Along the line $y = \alpha x$, the solution trajectory $\mathfrak{L}$ always tends to E_0, and so E^* is unstable. Denote $f(x,y)$ and $g(x,y)$ the two functions in the two equations of (2.1). The divergence of the vector field (f,g) satisfies

$$\frac{\partial f}{\partial x} + \frac{\partial g}{\partial y} = -1 - 2x - \frac{\delta}{m+\mu} < 0.$$

The Bendixson-Dulac theorem implies that (2.1) does not admit any (nontrivial) periodic solution. Since E_0 is the only (locally) stable equilibrium point in $\mathbb{R}_+^2$ when $R > R^*$, the classical Poincaré - Bendixson theorem implies that E_0 is globally asymptotically stable in $\mathbb{R}_+^2$.

For the case when $\alpha b > 1$ and $R < R^*$, (2.1) has three equilibria E_0, E_1 and E_2. The Jacobian matrix J_{E_1} at E_1 takes the form

$$J_{E_1} = \begin{pmatrix} -1 - 2x_1 & \dfrac{2by_1}{y_1 + R} - \dfrac{by_1^2}{(y_1 + R)^2} \\ \\ \dfrac{\alpha\delta}{m+\mu} & -\dfrac{\delta}{m+\mu} \end{pmatrix}.$$

Hence the eigenvalues λ_1 and λ_2 satisfy

$$\lambda_1 + \lambda_2 = -1 - 2x_1 - \frac{\delta}{m+\mu} < 0,$$

and

$$\lambda_1 \cdot \lambda_2 = \frac{\delta}{m+\mu}\Big[1 + 2x_1 - \alpha\Big(\frac{2by_1}{y_1 + R} - \frac{by_1^2}{(y_1 + R)^2}\Big)\Big]. \tag{2.10}$$

Since (x_1, y_1) is the solution of (2.4), we have

$$\frac{by_1}{y_1 + R} = \frac{x_1(1 + x_1)}{y_1} = \frac{x_1(1 + x_1)}{\alpha x_1} = \frac{1 + x_1}{\alpha}.$$

By substituting it into (2.10), we have

$$\begin{aligned}\lambda_1 \cdot \lambda_2 &= \frac{\delta}{m+\mu}[1 + 2x_1 - \alpha(2\frac{1 + x_1}{\alpha} - b\frac{(1 + x_1)^2}{(\alpha b)^2})] \\ &= \frac{\delta}{\alpha b(m+\mu)}(x_1 + 1 + \sqrt{\alpha b})(x_1 + 1 - \sqrt{\alpha b}).\end{aligned}$$

It follows from the condition $R < R^*$ in (2.8) and

$$\begin{aligned} &(R^* - R)^2 - [(\alpha^2 b - \alpha - R)^2 - 4\alpha R] \\ &= (R - R^*)^2 - (R - R^*)(R - \alpha(\sqrt{\alpha b} + 1)^2) \\ &= 4\alpha\sqrt{\alpha b}(R - R^*) < 0 \end{aligned}$$

that

$$R^* - R < \sqrt{(\alpha^2 b - \alpha - R)^2 - 4\alpha R}.$$

Hence

$$x_1 + 1 - \sqrt{\alpha b} = \frac{1}{2\alpha}[R^* - R - \sqrt{(\alpha^2 b - \alpha - R)^2 - 4\alpha R}] < 0,$$

and $\lambda_1 \cdot \lambda_2 < 0$, and E_1 is an unstable saddle point.

Now, we consider the local stability of E_2. The Jacobian matrix of E_2 is

$$J_{E_2} = \begin{pmatrix} -1 - 2x_2 \dfrac{2by_2}{y_2 + R} - \dfrac{by_2^2}{(y_2 + R)^2} \\ \\ \dfrac{\alpha\delta}{m + \mu} & -\dfrac{\delta}{m + \mu} \end{pmatrix}.$$

Similarly to the analysis on the eigenvalues of E_1, the eigenvalues λ_1 and λ_2 of the Jacobian matrix of E_2 satisfy

$$\lambda_1 + \lambda_2 = -1 - 2x_2 - \frac{\delta}{m + \mu} < 0,$$

$$\lambda_1 \cdot \lambda_2 = \frac{\delta}{\alpha b(m + \mu)}(x_2 + 1 + \sqrt{\alpha b})(x_2 + 1 - \sqrt{\alpha b}).$$

By using the condition $R < R^*$ in (2.8) and

$$x_2 + 1 - \sqrt{\alpha b} = \frac{1}{2\alpha}[R^* - R + \sqrt{(\alpha^2 b - \alpha - R)^2 - 4\alpha R}],$$

we have $\lambda_1 \cdot \lambda_2 > 0$ and both of λ_1 and λ_2 have negative real parts, and so E_2 is local asymptotically stable. □

Now we come back to (1.4) supplemented with the initial functions given in (1.5). We give the positivity and boundedness of the solutions of (1.4) and (1.5). The proof is similar to that in the proof of Lemma 2.1 in [13], so we omit it.

Lemma 2.1. *Let $R \geq 0$ and all other parameters be positive in (2.1). The initial value problem (1.4) and (1.5) has a unique solution $(x(t), y(t))$ defined for all $t \geq 0$, that is positive and satisfies*

$$\hat{x} = \limsup_{t\to\infty} x(t) \leq x_2 \quad \text{and} \quad \hat{y} = \limsup_{t\to\infty} y(t) \leq y_2. \tag{2.11}$$

Now, we analyze the stabilities of the equilibria for system (1.4).

Theorem 2.2. *Let $R \geq 0$ and all other parameters be positive in (1.4). For the initial value problem (1.4) and (1.5), we have*

(1) *If $\alpha b \leq 1$, then E_0 is globally asymptotically stable.*

(2) *If $\alpha b > 1$ and $R < \alpha(\sqrt{\alpha b} - 1)^2$, then E_0 and E_2 are local asymptotically stable, and E_1 is unstable.*

Proof. (1) Let $\alpha b \leq 1$, and $(x(t), y(t))$ be the solution of the initial value problem (1.4) and (1.5). By Lemma 2.1, $x(t)$ and $y(t)$ are positive and bounded. Rewrite system (1.4) as

$$\begin{cases} \dfrac{d}{dt}\left(x(t) + b\displaystyle\int_{t-\tau_1}^{t} \frac{y^2(s)}{y(s)+R}ds\right) = \dfrac{by^2(t)}{y(t)+R} - x(t)(1+x(t)), \\ \dfrac{d}{dt}\left(y(t) + \dfrac{\alpha\delta}{m+\mu}\displaystyle\int_{t-\tau_2}^{t} x(s)ds\right) = \dfrac{\delta}{m+\mu}(\alpha x(t) - y(t)). \end{cases}$$

Define a Liapunov-type function $V(t)$ as

$$V(t) = \frac{\delta}{m+\mu}\left(x(t) + b\int_{t-\tau_1}^{t} \frac{y^2(s)}{y(s)+R}ds\right) + b\left(y(t) + \frac{\alpha\mu}{m+\mu}\int_{t-\tau_2}^{t} x(s)ds\right). \quad (2.12)$$

Then V is positive for all $t \geq 0$. Along the solution $(x(t), y(t))$, we have

$$\frac{dV}{dt} = -\frac{\delta}{m+\mu}\left[\frac{bRy(t)}{y(t)+R} + x(t)(x(t) + 1 - \alpha b)\right].$$

It follows from $\alpha b \leq 1$ that

$$\frac{dV}{dt} < 0,$$

and $V(t)$ decays to zero as $t \to \infty$. Hence $(x(t), y(t)) \to E_0$ as $t \to \infty$, and so E_0 is globally asymptotically stable.

(2) Let $\alpha b > 1$ and $R < \alpha(\sqrt{\alpha b} - 1)^2$. (1.4) has three equilibria $E_0(0, 0)$, $E_1(x_1, y_1)$ and $E_2(x_2, y_2)$. The characteristic equation of the linearization system of (1.4) is

$$(\lambda + \frac{\delta}{m+\mu})(\lambda + 1 + 2x)|_E - \frac{\alpha\delta}{m+\mu}(\frac{2by}{y+R} - b(\frac{y}{y+R})^2)|_E e^{-\lambda(\tau_1+\tau_2)} = 0, \quad (2.13)$$

where $E = E_0$, E_1 and E_2. It is easy to check that the characteristic equation (2.13) at E_0 has two negative eigenvalues -1 and $-\delta/(m + \mu)$. Hence E_0 is locally asymptotically stable.

We use the absolute stability criterion to prove the local stability of E_2 [21]. Substitute $E_2(x_2, y_2)$ into the characteristic equation (2.13), and let

$$p(\lambda) = (\lambda + \frac{\delta}{m+\mu})(\lambda + 1 + 2x_2), \quad q = -\frac{\alpha\delta}{m+\mu}(\frac{2by_2}{y_2+R} - b(\frac{y_2}{y_2+R})^2),$$

where x_2 is defined in (2.2), and $y_2 = \alpha x_2$. Obviously, $p(\lambda)$ has two negative real roots $-1 - 2x_2$ and $-\frac{\delta}{m+\mu}$. On the other hand, by the analysis of local stability of E_2 for the ODE system (2.1) in Theorem 2.1, we have

$$p(0) - |q| = \frac{\delta}{m+\mu}(1 + 2x_2) - \frac{\alpha\delta}{m+\mu}\left(\frac{2by_2}{y_2+R} - b(\frac{y_2}{y_2+R})^2\right) > 0.$$

It follows from the absolute stability criterion that E_2 is locally asymptotically stable irrelevant of the delays τ_1 and τ_2.

Now we verify the instability of E_1. By Theorem 2.1, E_1 is an unstable saddle point when $\tau_1 = \tau_2 = 0$. As $\tau = \tau_1 + \tau_2$ increases from zero to infinity, if E_1 changes stability at some τ, then there would exist at least one pair of conjugate pure imaginary roots of the characteristic equation

$$\left(\lambda+\frac{\delta}{m+\mu}\right)(\lambda+1+2x_1)-\frac{\alpha\delta}{m+\mu}\left(\frac{2by_1}{y_1+R}-b(\frac{y_1}{y_1+R})^2\right)e^{-\lambda(\tau_1+\tau_2)}=0. \tag{2.14}$$

Let $\lambda_\pm = \pm iw(\tau^*)$ a pair of pure imaginary roots of (2.14) at $\tau = \tau^* > 0$. By Theorem 2.2 in [2], the eigenvalue λ of (2.14) crosses the imaginary axis from left to right when $\theta(\tau^*) > 0$, or from right to left when $\theta(\tau^*) < 0$, where

$$\theta(\tau^*) = \operatorname{sign}\left\{\mathfrak{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}|_{\lambda=iw(\tau^*)}\right\}.$$

It is well known that [2]

$$\theta_\pm(\tau) = \operatorname{sign}\{\pm\sqrt{\Delta}\}\,\operatorname{sign}D_\pm(\tau), \tag{2.15}$$

where

$$\begin{aligned}
\Delta &= \left[(1+2x_1)^2 - \frac{\delta^2}{(m+\mu)^2}\right]^2 + \left(\frac{\delta(1+x_1)}{\alpha b(m+\mu)}\right)^2(x_1+1-2\alpha b)^2,\\
D_+ &= \frac{d^2}{2}\left[-(1+2x_1)^2 - \frac{\delta^2}{(m+\mu)^2} + \sqrt{\Delta}\right],\\
D_- &= \frac{d^2}{2}\left[-(1+2x_1)^2 - \frac{\delta^2}{(m+\mu)^2} - \sqrt{\Delta}\right],\\
d &= -\frac{\alpha\delta}{m+\mu}\left[\frac{2by_1}{y_1+R} - b(\frac{y_1}{y_1+R})^2\right].
\end{aligned}$$

It is obvious that $w_-^2 < 0$, and $w_+^2 > 0$ is equivalent to $\Delta > [(1+2x_1)^2 + (\frac{\delta}{m+\mu})^2]^2$, which holds if and only of $(1+x_1)^2 > 2\alpha b(2+3x_1)$, or

$$(1+x_1-3\alpha b)^2 > 9\alpha^2b^2 - 2\alpha b.$$

By the conditions $\alpha b > 1$ and $0 \le R < R^*$, we have $9\alpha^2b^2 - 2\alpha b = \alpha b(9\alpha b-2) > 0$, and $w_+^2 > 0$ if and only if $1+x_1-3\alpha b < -\sqrt{9\alpha^2b^2-2\alpha b}$ or $1+x_1-3\alpha b > \sqrt{9\alpha^2b^2-2\alpha b}$.

By substituting x_1 into the inequation $1+x_1-3\alpha b > \sqrt{9\alpha^2b^2-2\alpha b}$, we have

$$\alpha - 5\alpha^2b - R > \sqrt{(\alpha^2b-\alpha-R)^2-4\alpha R} + 2\alpha\sqrt{9\alpha^2b^2-2\alpha b} > 0,$$

which implies $5\alpha^2b + R < \alpha$, and so

$$0 < \alpha(5\alpha b-1) + R < 0.$$

This contradiction implies that $1+x_1-3\alpha b < \sqrt{9\alpha^2b^2-2\alpha b}$. Similarly, by substituting x_1 into the inequation $1+x_1-3\alpha b < -\sqrt{9\alpha^2b^2-2\alpha b}$, we have

$$2\alpha\sqrt{9\alpha^2b^2-2\alpha b} - \sqrt{(\alpha^2b-\alpha-R)^2-4\alpha R} < 5\alpha^2b + R - \alpha. \tag{2.16}$$

It is easy to verify that

$$2\alpha\sqrt{9\alpha^2b^2 - 2\alpha b} > \sqrt{(\alpha^2 b - \alpha - R)^2 - 4\alpha R}.$$

Hence (2.16) implies

$$3\alpha^3 b^2 - 3\alpha bR < \sqrt{(9\alpha^2b^2 - 2\alpha b)((\alpha^2 b - \alpha - R)^2 - 4\alpha R)}. \tag{2.17}$$

It follows from the conditions $\alpha b > 1$ and $R < R^*$ that

$$3\alpha^3 b^2 - 3\alpha bR > 3\alpha b[\alpha^2 b - \alpha(\sqrt{\alpha b} - 1)^2] = 3\alpha^2 b(2\sqrt{\alpha b} - 1) > 0.$$

By (2.17), we have

$$2((\alpha^2 b - \alpha - R)^2 - 4\alpha R) < -9\alpha^2 b(2\alpha^2 b - \alpha + 2R).$$

Since $(\alpha^2 b - \alpha - R)^2 - 4\alpha R > 0$ and $\alpha b > 1$, we get

$$0 > 2\alpha^2 b - \alpha + 2R = \alpha^2 b + 2R + \alpha(\alpha b - 1) > 0.$$

This contradiction shows that $w_+^2 < 0$, and so $D_+ > 0$ and $D_- < 0$. Therefore,

$$\theta_+ = \mathrm{sign}\{\sqrt{\Delta}\}signD_+ = 1 \times (-1) = -1 < 0,$$
$$\theta_- = \mathrm{sign}\{-\sqrt{\Delta}\}signD_- = -1 \times (-1) = 1 > 0.$$

By using Theorem 2.2 in [2], one of the eigenvalue λ of (2.14) at E_1 crosses the imaginary axis from left to right, and another from right to left at any possible pure imaginary roots $\lambda_\pm = \pm iw(\tau^*)$. Since E_1 is a saddle point when τ_1 and τ_2 disappear by Theorem 2.1, the above analysis implies that at least one eigenvalue of E_1 has positive real part, and so E_1 is unstable for (1.4) with positive delays. □

We note that Theorem 2.2 does not reveal the stability of E_0 when $R \geq R^*$. As shown in [13], for the parallel releasing policy, the delays do not change the stability of the equilibria of (1.6). For the fixed releasing policy, by comparing Theorems 2.1 and 2.2, we conjecture that the delays also do not change the stability of the equilibria of (1.4), and E_0 is globally asymptotically stable when $R \geq R^*$ for (1.4). Our numerical simulation in Section 3.2 shows this conjecture is true.

3. Implication on *Aedes* population suppression

In order to design and optimize the population suppression strategy, we need to compare the advantages and disadvantages of the parallel releasing policy and fixed releasing policy. In this section, we assess quantitatively the effects of different suppression strategies on natural *Aedes* population suppression by using our model integrated with experimental data.

3.1. A life table for *Aedes albopictus*

We list important parameters for *Aedes albopictus* population in Table 1. Most of the values listed are taken from measurements of *Aedes albopictus* population in Guangzhou [15,18,19,36,37]. By the development periods of mosquitoes in different stages, we estimate τ_1 by $\tau_e + \tau_a/2$, and τ_2 by $\tau_l + \tau_p$. To compare with the parallel releasing policy (1.6), we use (1.2) to assess the effect of fixed releasing policy, and rewrite the parameters as in (1.3).

Para.	Definition	Lab.	Field	Reference
δ_e	Egg mortality rate (day^{-1})	(0.03, 0.14)	(0.03, 0.14)	[15,24]
N	Number of eggs laid by a female	(230, 409)	(29, 225)	[18,19]
τ_a	Mean longevity of female	(25.5, 40.9)	(4.8, 36.7)	[15,19,36]
b	Hatching rate (day^{-1})	(2.42, 7.78)	(0.28, 4.23)	$b=\frac{N(1-\delta_e)}{2\tau_a}$
m	Minimum larva mortality rate (day^{-1})	(0.03, 0.1)	(0.03, 0.1)	[3,22,24]
μ	Pupation rate (day^{-1})	(0.32, 0.68)	(0.05, 0.15)	[15,22,24]
α	Pupa survival rate (day^{-1})	(0.92,0.97)	(0.90,0.97)	[3,7,22,24]
δ	Adult female mortality rate (day^{-1})	(0.03, 0.1)	(0.05, 0.15)	[3,15,22,24]
τ_e	Development period of egg	(3.7, 5.1)	(8.3, 18.3)	[15,19,36]
τ_l	Development period of larva	(5.2, 7.6)	(12.0, 27.7)	[15,19,36]
τ_p	Development period of pupa	(2.2, 3.4)	(2.3, 8.6)	[15,19,36]

Table 1. The life table of *Aedes albopictus*. Most of the laboratory data and field data are collected in Guangzhou, and the average temperature ranges from $20°C$ to $35°C$ [13].

3.2. Assessing the stability of E_0 when $\bar{R} \geq \bar{\alpha}(\sqrt{\bar{\alpha}b}-1)^2$

We assess quantitatively the stability of E_0 when the releasing number $\bar{R} \geq \bar{\alpha}(\sqrt{\bar{\alpha}b}-1)^2$ in this section. By using the variable substitution (1.3), the condition

$$\bar{R} \geq \bar{\alpha}(\sqrt{\bar{\alpha}b}-1)^2 \quad \Leftrightarrow \quad R \geq \frac{\alpha\mu(m+\mu)}{2km\delta}\Big(\sqrt{\frac{\alpha b\mu}{\delta(m+\mu)}}-1\Big)^2. \tag{3.1}$$

Take the following life table parameters of *Aedes albopictus*

$$\begin{aligned} &b=2.5, \quad m=0.07, \quad \mu=0.12, \quad K_L=500, \quad \alpha=0.95,\\ &\delta=0.09, \quad \tau_1=25, \quad \tau_2=30. \end{aligned} \tag{3.2}$$

By substituting these data in (3.2) into (3.1), we get

$$R=\frac{\alpha\mu(m+\mu)K_L}{2m\delta}\left(\sqrt{\frac{\alpha b\mu}{\delta(m+\mu)}}-1\right)^2 \approx 8167.$$

As shown in Fig. 1, we find that solution $(x(t), y(t))$ converges to E_0 for (1.2) when the releasing number $R=8200$.

3.3. Comparing the efficiency of different releasing strategies

In conformity to the daily average temperature and precipitation data in Guangzhou (China meteorological data sharing service system: http://data.cma.cn/), we divide one year into five periods: March to May, June to July, August to September, October to November, and December to February. The average temperature and precipitation display similar pattern in each stages. As shown in [13], and supported by the experimental data in [3,15,17–19,36,37], we set the initial data as $\phi(t)=5000$ and $\psi(t)=100$ in $[-\max\{\tau_1,\tau_2\},0]$, $K_L=500$, and specify all other parameters within the five time periods in Table 2.

To compare the suppression effect of different releasing policies, we first let $R=0$ and approximate the population dynamics of natural *Aedes albopictus* in Guangzhou. In fact, systems (1.2) and (1.6) are the same system when $R=r=$

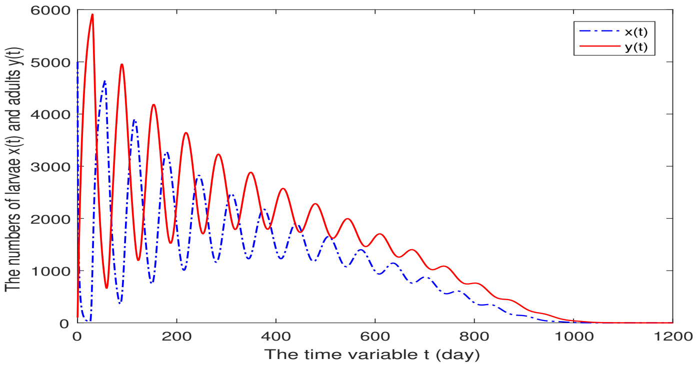

Figure 1. E_0 is globally asymptotically stable for (1.4) when $\bar{R} \geq \bar{\alpha}(\sqrt{\bar{\alpha} b}-1)^2$. Take $R = 8200$, $\phi(t) = 5000$ and $\psi(t) = 100$ for $t \in [-30, 0]$, and all other parameters as in (3.2).

Para.	Mar. to May	Jun. to Jul.	Aug. to Sep.	Oct. to Nov.	Dec. to Mar.
b	2.5	1	3	0.5	0
m	0.07	0.08	0.07	0.09	0.1
μ	0.12	0.13	0.14	0.11	0.05
α	0.95	0.93	0.97	0.92	0.9
δ	0.09	0.12	0.11	0.14	0.15
τ_1	25	13	11	20	30
τ_2	30	18	15	25	35

Table 2. The parameters of the natural *Aedes albopictus* population in Guangzhou.

0. As shown in Fig. 2, (1.2) with these specified parameter values in Table 2 captures several critical features of the seasonal abundance of natural population of *Aedes albopictus* in Guangzhou [15, 18, 19]. In close agreement with the field data [15, 18, 19], the numbers of larvae and adults show similar patterns and both develop two apparent peaks, the lower peak occurring between the last part of May and the first half of June, and the larger occurring between the last part of September and the first half of October. Due to the outbreak of diapausing egg hatching in the early of March and overlapping generations, the larvae and adults behave differently in the first stage.

To suppress wild *Aedes albopictus* population successfully, the released number depending on the life table parameters which vary in the five periods during one year, we define the released number vector $\Re := (R_1, R_2, R_3, R_4, R_5)$, where R_i denotes the released number in the i-th period for $i = 1, 2, 3, 4, 5$. Since the dengue high-incidence season in Guangzhou is coincide with the second peak of wild *Aedes albopictus* population, it is necessary to suppress the mosquitoes effectively in the second peak. We use an index introduced in [13], the *suppression rate* $\gamma \in [0, 1]$ associating with a given released number vector $\Re$, to measure the suppression efficiency. We define γ as the ratio of the mosquito number in the suppressed population over the wild mosquito number without suppression, recorded at the day when the second peak of the natural population is observed. We say that the population suppression is successful if $\gamma \leq 5\%$.

By substituting the life table parameter values in Table 2 into (3.1), we obtain

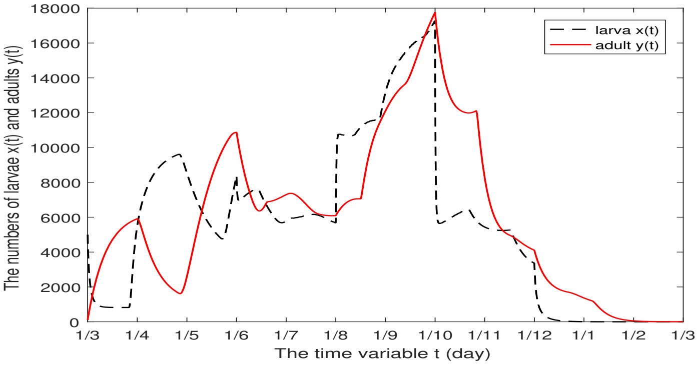

Figure 2. Monthly changes of natural *Aedes albopictus* larvae and adults in Guangzhou. The two curves are simulated numerically by Equations (1.2) with $R = 0$, $K_L = 500$, the initial data $\phi(t) = 5000$ and $\psi(t) = 100$ for $t \in [-35, 0]$, and all the other parameters as in Table 2.

the threshold released number vector $\Re^* = (8167, 1024, 9479, 48, 113)$. As shown in Fig. 3, when a released number $\Re = (8200, 1200, 9500, 100, 150)$ close to $\Re^*$ is applied, the suppression rate $\gamma = 10.49\%$ indicates that we need enlarge the released amount to suppress successfully in short periods. For example, the released number $\Re = (12000, 1600, 14000, 100, 0)$ gives $\gamma = 4.83\%$. To obtain a similar suppression effect, the most economical method is to increase the released number in second period. As shown in Fig. 3, we can still manage to make $\gamma < 5\%$ if the released number $\Re = (9800, 2500, 10000, 100, 0)$. Specifically, the simulation shown in Fig. 3 indicates that the suppression is still successful with the suppression rate $\gamma = 4.9\%$ when the same released number $R = 5800$ in the first 3 periods.

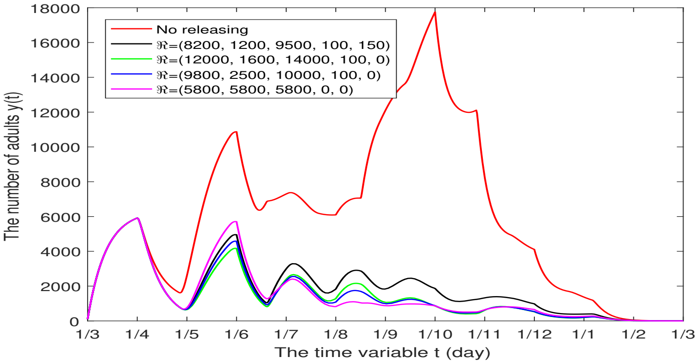

Figure 3. *Wolbachia* can suppress wild *Aedes albopictus* population successfully with different released number vectors. With the same initial data and parameter values as in Fig. 2, the suppression rate $\gamma = 10.49\%$ for $\Re = (8200, 1200, 9500, 100, 150)$, $\gamma = 4.83\%$ for $\Re = (12000, 1600, 14000, 100, 0)$, $\gamma = 4.92\%$ for $\Re = (9800, 2500, 10000, 100, 0)$, and $\gamma = 4.90\%$ for $\Re = (5800, 5800, 5800, 0, 0)$.

It is instructive to compare the releasing threshold levels of different suppression strategies. The ratio of releasing threshold of fixed releasing policy over that of parallel releasing policy is connected with the life table parameters, and is very complex to analyze. Since the suppression rate γ is connected with the released

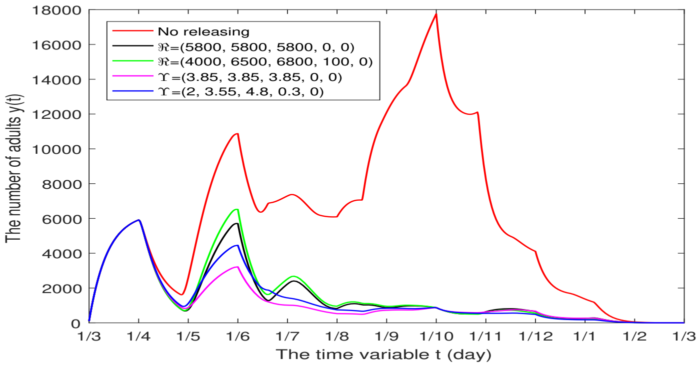

Figure 4. Comparison of different suppression strategies with similar suppression efficiency. With the same initial data and parameter values as in Fig. 2, the suppression rate $\gamma = 4.90\%$ for $\Re = (5800, 5800, 5800, 0, 0)$, and $\gamma = 4.95\%$ for $\Re = (4000, 6500, 6800, 100, 0)$ for fixed releasing policy, and $\gamma = 4.97\%$ for $\Upsilon = (3.85, 3.85, 3.85, 0, 0)$, and $\gamma = 4.96\%$ for $\Upsilon = (2, 3.55, 4.8, 0.3, 0)$ for parallel releasing policy.

numbers in different periods and life table parameter values which are sensitive to temperature and precipitation, there are infinite releasing ways to obtain a similar or even the same suppression effect. In summary, for similar suppression rate, the needed released number of parallel releasing policy is much larger than that of fixed releasing policy when the number of natural *Aedes albopictus* is large. To the contrary, the released number of fixed releasing policy is larger than that of parallel releasing policy when the number of natural *Aedes albopictus* is small.

Similar to $\Re$, we use $\Upsilon := (r_1, r_2, r_3, r_4, r_5)$ denote the released rate vector for the parallel releasing policy, where r_i denotes the releasing rate in the i-th period for $i = 1, 2, 3, 4, 5$. Take the same releasing rate for parallel releasing policy and the same released number for fixed releasing policy in the first three stages for example. As shown in Fig. 4, the released rate vector $\Upsilon = (3.85, 3.85, 3.85, 0, 0)$ for parallel releasing policy gives the suppression rate $\gamma = 4.97\%$, and the released number vector $\Re = (5800, 5800, 5800, 0, 0)$ for fixed releasing policy gives $\gamma = 4.90\%$. The released number of males for parallel releasing policy is larger than that for fixed releasing policy in the most of time before the middle of June. As shown in Fig. 4, the released number for parallel releasing policy is almost 4 times that for fixed releasing policy in the end of April, and is more than 2 times in the beginning of June. By previous suppression, the population size of *Aedes albopictus* becomes much smaller after the middle of June. The released number of infected males for fixed releasing policy is almost more than two folds that for parallel releasing policy. To suppress the *Aedes albopictus* efficiently and economically in Guangzhou, by integrating the two releasing policies, the best strategy is initiate the suppression in the beginning of March, and utilize the fixed releasing policy from March to June, and utilize the parallel releasing policy from July to November.

3.4. Assessing the impact of egg bank

The recurring arrival of cold and dry winter is a harsh challenge to the survival and reproduction of mosquitoes [5]. *Aedes albopictus* surmount this challenge by laying diapause eggs, which offers a mechanism for bridging unfavorable seasons and serves to synchronize development within populations, thus directly affecting disease transmission cycles [5]. Diapause eggs serve as a reservoir which accumulate into *egg bank*, which hatch in a suitable environmental conditions in next favorable season, and generate abundant larvae in a few days. Liu et al [18] reported that *Aedes albopictus* in Guangzhou begin to oviposit diapause eggs in the late of October and sustain to January, and most of the diapause eggs hatch in the early of March.

It inspires us to characterise the influence of egg bank on wild *Aedes albopictus* population by different initial larval numbers in the early of March. As shown in Fig. 5, the number of adult mosquitoes show up three peaks. The highest peak raise in the early of April, the second highest peak raise in the early of May, and the third peak appear in the early of October as the case without egg bank. The highest peak in the early of April induced by the synthetic actions of egg bank and delays, and it cannot be suppressed by releasing *Wolbachia* infected males. As shown in Fig. 5, egg bank has little impact on the number of adults after August, and the number of adults in the third peak nearly the same as that of without considering egg bank.

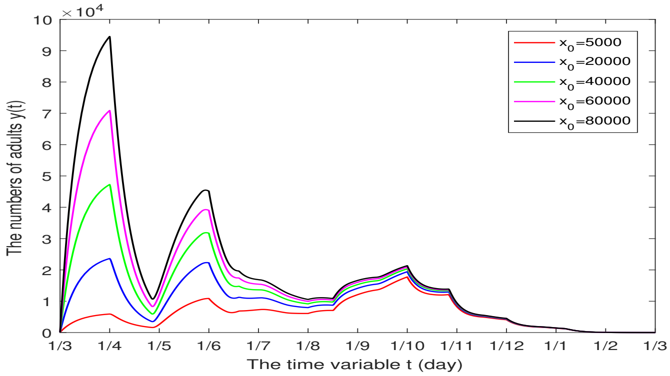

Figure 5. The influence of egg bank on the dynamics of natural *Aedes albopictus* population in Guangzhou. With the same initial number of adults and parameter values as in Fig. 2, the influence on the dynamics of wild *Aedes albopictus* population of the initial number of larvae mainly focus on the first two periods.

Coinciding with the huge number of *Aedes albopictus* in September and October, the underlying mechanisms of dengue high-incidence season in Guangzhou need to be identified. Since egg bank has limit influence on the dynamics of *Aedes albopictus* population in August and afterward, it will be relatively easy to suppress the *Aedes albopictus* population in the September and October. However, the number of adult mosquitoes on the second highest peak induced by the synthetic actions of egg bank and overlapping generations, and it is very difficult to suppress. To quantify the suppression efficiency of the second and third peaks, similar to the definition of suppression rate γ, we define γ_1 and γ_2 as the suppression rates on the second and third peaks, recorded at the day when the second and third peaks of the natural population is observed, respectively. Take the initial data $\phi(t) = 50000$ and $\psi(t) = 100$ for $t \in [-35, 0]$ for example, as shown in Fig. 6, the suppression rates $\gamma_1 = 74.55\%$ and $\gamma_2 = 4.95\%$ for $\Re = (20000, 20000, 20000, 200, 0)$ which only suppresses successfully in the third peak. To suppress *Aedes albopictus* population in the early of June successfully, we need to release a mountain of *Wolbachia* infected males in

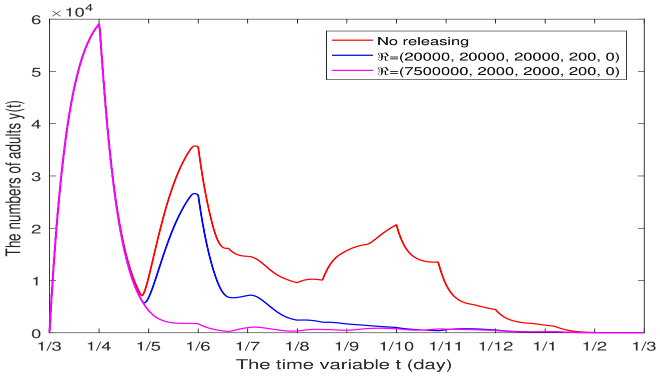

Figure 6. The influence of egg bank on the suppression dynamics of *Aedes albopictus* population in Guangzhou. With the initial data $\phi(t) = 50000$ and $\psi(t) = 100$ for $t \in [-35, 0]$, and all other parameter values as in Fig. 2, the suppression rates $\gamma_1 = 74.55\%$ and $\gamma_2 = 4.95\%$ for $\Re = (20000, 20000, 20000, 200, 0)$, and $\gamma_1 = 4.97\%$ and $\gamma_2 = 3.78\%$ for $\Re = (7500000, 2000, 2000, 200, 0)$.

the first time period, which generates the subsequent population suppressing easily. For example, the releasing number vector $\Re = (7500000, 2000, 2000, 200, 0)$ gives $\gamma_1 = 4.97\%$ and $\gamma_2 = 3.78\%$.

3.5. Discussions

Although lacking sustainability, vector control strategies, including community-based source reduction and insecticide spraying, remain the mainstay of dengue control in the past few decades. A promising avenue to control dengue involves an endosymbiotic bacterium *Wolbachia*. By releasing *Wolbachia*-infected male *Aedes* mosquitoes, we can suppress wild mosquito population, the vector of dengue virus, and thus control dengue. Larval density-dependent competition in immature stage is the main regulatory mechanism of natural *Aedes* mosquito population, which elevated mortality rate, delayed development time, and influenced the female size (wing length) and fecundity [19, 20, 25, 26]. Furthermore, *Wolbachia* infection status has relatively little impact on immature *Aedes albopictus* performance [6]. Fixed releasing policy and parallel releasing policy are the main strategies used in the field trials of population suppression. The complexity of natural *Aedes* mosquito population dynamics motivated us to assess and compare the efficiency of different suppression strategies. For this purpose, we integrated larval density-dependent competition and different releasing policies into delay differential equation models. Our analysis indicates that the suppression dynamics of fixed releasing policy is more complicated than that of parallel releasing policy.

In accordance with the daily meteorological data in Guangzhou, mainly the average daily temperature and precipitation data, we divided each year into five periods, and estimated the life table parameters of *Aedes albopictus*, the main vector of dengue in Guangzhou, in each period from field data. The model captures several critical features of the seasonal abundance of natural *Aedes albopictus* population in Guangzhou [15, 18, 19]. Our analysis shows that if the number of released infected males is no less than the releasing threshold under the specific circumstances, then the mosquito density in the highest peak season can be reduced by more than 95%.

To suppress wild *Aedes albopictus* effectively, we compare the number of released males for the two releasing policies. To gain similar suppression rate, the more economical suppression strategy, which need less released mosquitoes, is determined by the number of natural *Aedes albopictus*. The fixed releasing policy is much more economical than parallel releasing policy when the natural *Aedes albopictus* population is large, while the parallel releasing policy is much more economical than fixed releasing policy when the natural *Aedes albopictus* population is small. According to the seasonal abundance of natural *Aedes albopictus* population in Guangzhou, the best time to initiate the suppression is the early of March, which will reduce the mosquito population size greatly after June, and reduce the vectors of dengue fever from August to October effectively. The best efficient and economical strategy to suppress *Aedes albopictus* in Guangzhou is integrating the two releasing policies: Utilize the fixed releasing policy from March to June, and utilize the parallel releasing policy from July to November.

Offering a mechanism to bridge unfavorable natural conditions, diapause eggs serve as a reservoir which accumulates into egg bank. Since most of diapause eggs hatch in the early of March in Guangzhou [18], we characterise the influence of egg bank on the suppression dynamics by different initial larval numbers. With a large amount of initial larvae, by the synthetic actions of egg bank and overlapping generations, the number of natural adult mosquitoes show up three peaks: The highest peak raise in the early of April, and the other two peaks raise in the same time as the case without considering egg bank. Our analysis shows that egg bank has little impact on natural population after August, and the number of adults in the third peak nearly the same as that of without considering egg bank. Thus it is relatively easy to suppress the *Aedes albopictus* population in the September and October, but is very difficult to suppress the population in the second peak in the beginning of June. Since dengue high-risk season in Guangzhou is from August to October, egg bank has limit influence on the control situation of dengue fever in Guangzhou.

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References

[1] S. Bhatt, P. W. Gething, O. J. Brady, J. P. Messina, A. W. Farlow, C. L. Moyes, J. M. Drake, J. S. Brownstein, A. G. Hoen, O. Sankoh, M. F. Myers, D. B. George, T. Jaenisch, G. R. W. Wint, C. P. Simmons, T. W. Scott, J. J. Farrar and S. I. Hay, *The global distribution and burden of dengue*, Nature, 2013, 496, 504–507.

[2] E. Beretta and Y. Kuang, *Geometric stability switch criteria in delay differential systems with delay dependent parameters*, SIAM J. Math. Anal., 2002, 33, 1144–1165.

[3] P. Cailly, A. Tran, T. Balenghien, G. L'Ambert, C. Toty and P. Ezanno, *A climate driven abundance model to assess mosquito control strategies*, Ecol. Model., 2012, 227, 7–17.

[4] E. Caspari and G. S. Watson, *On the evolutionary importance of cytoplasmic sterility in mosquitoes*, Evolution, 1959, 13, 568–570.

[5] D. L. Denlinger and P. A. Armbruster, *Mosquito diapause*, Annu. Rev. Entomol., 2014, 59, 73–93.

[6] L. Gavotte, D. Mercer, R. Vandyke, J. W. Mains and S. L. Dobson, *Wolbachia infection and resource competition effects on immature Aedes albopictus (Diptera: Culicidae)*, J. Med. Entomol., 2009, 46(3), 451–459.

[7] P. A. Hancock, V. L. White, A. G. Callahan, C. H. J. Godfray and A. A. Hoffmann, *Density-dependent population dynamics in Aedes aegypti slow the spread of wMel Wolbachia*, J. Appl. Ecol., 2016, 53, 785–793.

[8] L. Hu, M. Tang, Z. Wu, Z. Xi and J. Yu. *The threshold infection level for Wolbachia invasion in random environments*, J. Diff. Equ., 2019, 266(7), 4377–4393.

[9] L. Hu, M. Huang, M. Tang, J. Yu and B. Zheng. *Wolbachia spread dynamics in multi-regimes of environmental conditions*, J. Theor. Biol., 2019, 462, 247–258.

[10] L. Hu, M. Huang, M. Tang, J. Yu and B. Zheng, *Wolbachia spread dynamics in stochastic environments*, Theor. Popul. Biol., 2015, 106, 32–44.

[11] M. Huang, M. Tang and J. Yu, *Wolbachia infection dynamics by reaction-diffusion equations*, Sci. China Math., 2015, 58, 77–96.

[12] M. Huang, J. Yu, L. Hu and B. Zheng, *Qualitative analysis for a Wolbachia infection model with diffusion*, Sci. China Math., 2016, 59, 1249–1266.

[13] M. Huang, J. Lou, L. Hu, B. Zheng and J. Yu, *Assessing the efficiency of Wolbachia driven Aedes mosquito suppression by delay differential equations*, J. Theor. Biol., 2018, 440, 1–11.

[14] M. J. Keeling, F. M. Jiggins and J. M. Read, *The invasion and coexistence of competing Wolbachia strains*, Heredity, 2003, 91, 382–388

[15] Y. Li, F. Kamara, G. Zhou, S. Puthiyakunnon, C. Li, Y. Liu, Y. Zhou, G. Yan and X. Chen, *Urbanization inreases Aedes albopictus larval habitats and accelerates mosquito development and survivorshop*, PLoS Negl. Trop. Dis., 2014, 8(11), e3301.

[16] H. Lin, T. Liu, T. Song, L. Lin, J. Xiao, J. Lin, J. He, H. Zhong, W. Hu, A. Deng, Z. Peng, W. Ma and Y. Zhang, *Community involvement in dengue outbreak control: An integrated rigorous intervention strategy*, PLoS Negl. Trop. Dis., 2016, 10(8), e0004919.

[17] Z. Liu, Y. Zhang and Y. Yang, *Population dynamics of Aedes (Stegomyia) albopictus (Skuse) under laboratory conditions*, Acta Entomol. Sin., 1985, 28(3), 274–280.

[18] F. Liu, C. Zhou and P. Lin, *Studies on the population ecology of Aedes albopictus 5. The seasonal abundance of natural population of Aedes albopictus in Guangzhou*, Acta Sci. Natur. Universitatis Sunyatseni, 1990, 29(2), 118–122.

[19] F. Liu, C. Yao, P. Lin and C. Zhou, *Studies on life table of the natural population of Aedes albopictus*, Acta Sci. Natur. Universitatis Sunyatseni, 1992, 31(3), 84–93.

[20] R. A. Ross, N. M. Endersby, H. L. Yeap and A. A. Hoffmann, *Larval competition extends developmental time and decreases adult size of wMelPop Wolbachia infected Aedes aegypti*, Am. J. Trop. Hyg., 2014, 9(1), 198–205.

[21] H. L. Smith, *An introduction to delay differential equations with applications to life sciences*, Springer, New York, 2011.

[22] A. Tran, G. L'Ambert, G. Lacour, M. Demarchi, M. Cros, P. Cailly, M. A. Kientz, T. Balenghien and P. Ezanno, *A rainfall and temperature driven abundance model for Aedes albopictus populations*, Int. J. Environ. Res. Public Health, 2013, 10, 1698–1719.

[23] M. Turelli and A. A. Hoffmann, *Rapid spread of an inherited incompatibility factor in California Drosophila*, Nature, 1991, 353, 440–442.

[24] J. Waldock, N. L. Chandra, J. Lelieveld, Y. Proestos, E. Michael, G. Christophides and P. E. Parham, *The role of environment variables on Aedes albopictus biology and Chikungunya epidemiology*, Pathogens and Global Health., 2013, 107, 224–240.

[25] R. K. Walsh, C. Bradley, C. S. Apperson and F. Gould, *An experimental field study of delayed density dependence in natural populations of Aedes albopictus*, PLoS One, 2012, 7, e35959.

[26] R. K. Walsh, L. Facchinelli, J. M. Ramsey, J. G. Bond and F. Gould, *Assessing the impact of density dependence in field populations of Aedes aegypti*, J. Vect. Ecol., 2011, 36(2), 300–307.

[27] E. Waltz, *US reviews plan to infect mosquitoes with bacteria to stop disease*, Nature, 2016, 89(1), 450–451.

[28] T. Walker, P. H. Johnson, L. A. Moreika, I. Iturbe-Ormaetxe, F. D. Frentiu, C. J. Mcmeniman, Y. S. Leong, Y. Dong, J. Axford, P. Kriesner, A. L. Lloyd, S. A. Ritchie, S. L. O'Neill and A. A. Hoffmann, *The wMel Wolbachia strain blocks dengue and invades caged Aedes aegypti populations*, Nature, 2011, 476, 450–453.

[29] WHO, *Global strategy for dengue prevention and control 2012-2020*, Geneva: World Health Organization, 2012.

[30] J. Wu, Z. Lun, A. A. James and X. Chen, *Dengue fever in mainland China*, Am. J. Trop. Med. Hyg., 2010, 83(3), 664–671.

[31] Z. Xi, C. C. Khoo and S. L. Dobson, *Wolbachia establishment and invasion in an Aedes aegypti laboratory population*, Science, 2005, 310, 326–328.

[32] J. Yu, *Modeling mosqutio population suppression based on delay differential equations*, SIAM J. Appl. Math., 2018, 78(6), 3168–3187.

[33] B. Zheng, M. Tang and J. Yu, *Modeling Wolbachia spread in mosquitoes through delay differential equation*, SIAM J. Appl. Math., 2014, 74, 743–770.

[34] B. Zheng, M. Tang, J. Yu and J. Qiu, *Wolbachia spreading dynamics in mosquitoes with imperfect maternal transmission*, J. Math. Biol. 2018, 76, 235–263.

[35] B. Zheng, J. Yu, Z. Xi and M. Tang, *The annual abundance of dengue and Zika vector Aedes albopictus and its stubbornness to suppression*, Ecol. Model., 2018, 387, 38–48.

[36] Z. Zhong and G. He, *The life table of laboratory Aedes albopictus under various temperatures*, Academic J. Sun Yat-sen University of Medical Sciences, 1988, 9(3), 35–39.

[37] Z. Zhong and G. He, *The life and fertility table of Aedes albopictus under different temperatures*, Acta Entom. Sinica, 1990, 33(1), 64–70.