Appl. Math. J. Chinese Univ.
2025, 40(1): 122-136

Global asymptotic stability in a delay stage structured model for mosquito population suppression

HUANG Mu-gen[1] YU Jian-she[2,*]

Abstract. A promising avenue to control mosquito-borne diseases such as dengue, malaria, and Zika involves releasing male mosquitoes carrying the bacterium *Wolbachia* in wild areas to drive female sterility by a mechanism called cytoplasmic incompatibility (CI). In this work, we initiate a preliminary assessment of how the combined impact of dispersal, incomplete CI and mating competitiveness on mosquito population suppression by a delay differential equation model. Our theoretical analyses indicate that the immigration of eggs plays a significant role in the suppression dynamics. For the case without egg immigration, we identify a threshold dispersal rate v^* of adult mosquitoes, threshold CI density ξ^*, and threshold release ratio r^*. A successful mosquito suppression would be established only when $v < v^*$, $\xi > \xi^*$, and $r(t) \geq r^*$ uniformly. The immigration of eggs causes the threshold dynamics to be invalid, and warns an absolute failure of population suppression. The monotonicity of the adult steady-state in the dispersal rate and CI intensity indicates that choosing a suitable *Wolbachia* strain with strong CI intensity, or bringing down the dispersal rate of mosquitoes by blocking the suppression zones is a feasible strategy to obtain a better suppression level.

§1 Introduction

Dengue is one of the most medically important mosquito-borne diseases, with over 390 million cases reported annually in tropical and subtropical regions in the world [2]. With growing urbanization and economic globalization, the incidence of the life-threatening dengue hemorrhagic fever and dengue shock syndrome has elevated over 500-fold since the 1950s [16].

Received: 2021-03-04. Revised: 2023-05-16.

MR Subject Classification: 92B05, 37N25, 34D23, 92D30.

Keywords: dengue fever, *Wolbachia*, cytoplasmic incompatibility, population suppression, delay differential equations.

Digital Object Identifier(DOI): https://doi.org/10.1007/s11766-025-4396-5.

Supported by the National Natural Science Foundation of China(12226414, 11471085, 11631005, 12171112).

[*] Corresponding author.

Dengue has become the main public health issue in China, exemplified by a total of 37,354 cases in Guangzhou in 2014, and a total of 22,599 cases in 550 counties of 28 provinces in 2019, with *Aedes albopictus* incriminated as the sole transmission vector [19]. Besides the considerable biting nuisance, *Aedes albopictus*, one of the most invasive mosquito species worldwide, is a competent vector of more than 25 viruses, including dengue, chikungunya, and Zika [1].

With no licensed vaccine and specific medication available, the widely used dengue control strategies involve vector elimination, including chemical-based insecticide spraying and time consuming community-based source reduction [6]. However, these traditional methods are insufficient to control dengue, as shown by the continued growth of dengue cases worldwide. Fortunately, the incompatible insect technique (IIT) based on the endosymbiotic maternally-inherited bacterium *Wolbachia* is an environmentally friendly pest control method driven by cytoplasmic incompatibility (CI), that induces sterility of wild females when they mate with *Wolbachia*-infected males [26]. By the mass release of infected males to mate with wild females, thereby reducing or eliminating the population, this method has been applied successfully in the field trial for *Aedes albopictus* suppression in Guangzhou [31].

The suppression efficiency relies critically on several factors, such as (i) CI intensity ξ, the ability of *Wolbachia* to induce zygotic death from incompatible mating. Evidence from the *Aedes albopictus* suppression field trial in Guangzhou showed that the *wPip* strain brought incomplete CI such that a small percentage of eggs from the incompatible mating of infected males with uninfected females hatched normally [28]. (ii) Mating competitiveness θ of infected males compared to wild males. Although the *Wolbachia*-infected males and uninfected males were observed to be equally competitive in a laboratory, *wPip* reduced the mating competitiveness of infected males by 25%-50% compared to wild males in the field trials [28]. (iii) The dispersal of wild mosquitoes from outside to the control area. Lower levels of suppression were observed in less isolated zones nearer transportation routes with frequent traffic such as ongoing bridge construction and shipping harbor, which suggests that human activities facilitate mosquito dispersal into the control area and compromise the efficiency of *Aedes albopictus* elimination [31]. Mosquito dispersal serves the purpose of egg-laying, feeding, or sheltering, usually involving only short distances. Mark-release-recapture experiments showed that *Aedes* mosquitoes are poor flyers as their range of active dispersal is generally assumed to be limited to 50-500 m, variation is driven by heterogeneity in the availability of oviposition sites and blood-feeding opportunities [5, 7, 18, 23]. Egg migration through human activities remains the main pattern of long-distance dispersal [24].

Mathematical models based on differential equations have been developed to study how the suppression efficiency of the IIT method in an isolated suppression target area is impacted by various factors, for example, the maturity lags [3, 12, 27], spatial diffusion [10, 11], and the randomness of climatic conditions [9, 14, 29, 30]. In [13], including only the terrestrial (adult), we initiate a preliminary assessment of the impact of CI intensity and mating competitiveness of released males on the suppression efficiency. However, the dispersal of wild mosquitoes to the suppression area from surrounding neighborhoods has not been included in most models, which causes an inconvenience in directly testing mosquito dispersal on the suppression efficiency [31]. This paper aims to develop a theoretical framework for studying the impacts of wild mosquito dispersal, combined with CI intensity and mating competitiveness, on the efficiency of population suppression.

It has been observed that density-induced intra-specific competition occurs mostly in the larval stage, for which the larvae need food to supply nutrition and become pupae by metamorphosis. Insufficient nutrition and/or overcrowding during the larval stage had a detrimental effect on larval development, and consequently on the fecundity of adult females [4, 15, 17, 22]. To test directly the density restriction on population growth, we divide mosquitoes into larval and adult stages, and denote $L(t)$ and $A(t)$ as the size of larvae and adults in the control area, respectively, equally distributed in sex. Let $R(t)$ be the number of releasing *Wolbachia*-infected males, and $D(t)$ be the average daily dispersal wild males from the outside of the suppression area. In terms of the mating competitiveness θ and omitting the dispersal of released males, the incompatible mating probability of a wild female equals the number $\theta R(t)$ of infected males over the total number $A(t)/2 + D(t) + \theta R(t)$ of males in random mating. Assuming a wild female produced daily average β first-instar larvae in compatible mating, and incorporating the CI intensity ξ defined above, the expected number of first-instar larvae produced by a local female is

$$\beta \cdot (1 - \frac{\theta R}{A/2 + D(t) + \theta R}) + \beta(1-\xi) \cdot \frac{\theta R}{A/2 + D(t) + \theta R}.$$

The exact dispersal pattern of mosquitoes remains obscure, which is enhanced by the complex interaction of released males and the wild populations. To initiate a preliminary assessment of how wild mosquito dispersal impacts the suppression efficiency, we assume $D(t) = vA(t)$ with $v > 0$ being a constant. Experimental data suggest that most females mate within 24 hours after emergence, and then we assume that copulation occurred before the wild females' dispersal [7, 18, 23]. Assume the immigration eggs hatched daily c first instar larvae. Integrating the total number of females $A/2$, the mated dispersal females $D(t)$, and the average development period τ_1 from the eclosion of female adults to the hatching of first instar larvae of next-generation, we obtain the production rate of larvae at time t

$$\frac{\beta}{2} \cdot \frac{(1+2v)A(t-\tau_1) + 2(1-\xi)\theta R(t-\tau_1)}{(1+2v)A(t-\tau_1) + 2\theta R(t-\tau_1)} A(t-\tau_1) + v\beta A(t-\tau_1) + c.$$

We use the logistic model to describe the impairment of larval density-dependent population regulation with $f(L) = m(1 + L/K_L)L$, where m is the natural mortality rate, and K_L is the density-dependent mortality rate constant of larvae. Assume linear stage transitions and natural death in adults with pupation rate μ of larvae and eclosion rate α of pupae, and mortality rate δ of adults. Integrating the average development durations of larvae and pupae τ_2, we derive the following system of delay differential equations

$$\begin{cases} \frac{dL(t)}{dt} = \frac{\beta}{2} \frac{(1+2v)A(t-\tau_1)+2(1-\xi)\theta R(t-\tau_1)}{(1+2v)A(t-\tau_1)+2\theta R(t-\tau_1)} A(t-\tau_1) + v\beta A(t-\tau_1) - f(L(t)) - \mu L(t) + c, \\ \frac{dA(t)}{dt} = \alpha\mu L(t-\tau_2) - \delta A(t) + vA(t). \end{cases} \tag{1}$$

Motivated by the field trial of *Aedes albopictus* population suppression in Guangzhou, which managed the release intensity of infected males to increase proportionally with the density of the local population, we use a parallel release policy in our model and let $r(t) = R(t)/A(t)$, which reduces (1) to

$$\begin{cases} \frac{dL(t)}{dt} = \frac{\beta}{2}\frac{1+2v+2(1-\xi)\theta r(t-\tau_1)}{1+2v+2\theta r(t-\tau_1)}A(t-\tau_1) + v\beta A(t-\tau_1) - m(1+\frac{L(t)}{K_L})L(t) - \mu L(t) + c, \\ \frac{dA(t)}{dt} = \alpha\mu L(t-\tau_2) - \delta A(t) + vA(t). \end{cases} \tag{2}$$

In accordance with their biological meanings and the low mobility of *Aedes* populations, we assume that the parameters β, m, K_L, μ, α, τ_1 and τ_2 are positive, and

$$\xi \in [0,1], \quad \theta \geq 0, \quad r(t) \geq 0, \quad c \geq 0, \quad \text{and} \quad \delta > v \geq 0. \tag{3}$$

We will study the dynamics of (2) under the initial conditions

$$x(t) = \phi(t) > 0, \quad y(t) = \psi(t) > 0, \quad t \in [t_0 - \tau, t_0], \quad \tau = \max\{\tau_1, \tau_2\}. \tag{4}$$

By using a standard argument, see for instance Lemma 2.1 in [12], it can be shown that the solution $(L(t), A(t))$ of the initial value problem (2) and (4) is positive and bounded for all $t \geq t_0$.

In Section 2, by studying the global dynamics of (2) and (4), we assess the combined impact of dispersal, CI intensity, and mating competitiveness on mosquito population suppression. Our theoretical analysis indicates that the immigration of eggs plays a significant role in the suppression dynamics. For the case without immigration of eggs such that $c = 0$, we identify the threshold dispersal rate v^* of adult mosquitoes, threshold CI density ξ^*, and threshold release ratio r^* with

$$v^* = \frac{\delta}{1+2b_0\delta}, \quad \xi^* = 1 + 2v - \frac{1}{b_1}, \quad \text{and} \quad r^* = \frac{(1+2v)\xi^*}{2\theta(\xi - \xi^*)},$$

where $b_0 = \alpha\beta\mu/(2\delta(m+\mu))$ and $b_1 = \delta b_0/(\delta - v)$. Only when $v < v^*$, $\xi > \xi^*$, and $r(t) \geq r^*$ uniformly, the wild mosquito population would be eliminated ultimately. Otherwise, population suppression is improbable no matter how many infected males are released. The threshold dynamics described above for $c = 0$ is no longer valid when egg immigration is included in our model. Furthermore, the global asymptotical stability of the unique positive equilibrium $E_r^*(L_r^*, A_r^*)$ warns an absolute failure of population suppression. It is further supported by our numerical examples in Section 3 which show that the immigration of eggs leads to the adult equilibrium A_r^* being bounded below by a positive constant A_∞^* independence from $r(t)$. By the monotonicity of A_r^* in the dispersal rate c and v, and CI intensity ξ, to obtain a better suppression level, we can choose some suitable *Wolbachia* strain with strong CI intensity, or bring down the dispersal rate of mosquitoes by blocking the suppression zones.

§2 Global stability analysis of the equilibria

2.1 The threshold dynamics when $c = 0$

We first consider the threshold dynamics of population suppression when $c = 0$ and $v \geq 0$. As $\alpha\beta\mu/2$ measures the average reproduction rate, and $\delta(m+\mu)$ is the average mortality rate in the total life cycle of mosquitoes, it holds in normal environmental conditions that

$\alpha\beta\mu/2 > \delta(m+\mu)$, that is,

$$b_0 = \frac{\alpha\beta\mu}{2\delta(m+\mu)} > 1. \tag{5}$$

Denote

$$b_1 = \frac{\alpha\beta\mu}{2(\delta - v)(m+\mu)} = \frac{\delta}{\delta - v} b_0. \tag{6}$$

The basic assumption (5) implies that $b_1 \geq b_0 > 1$ when $v \geq 0$. Let $r(t) \equiv r \geq 0$ and $E_r^*(L_r^*, A_r^*)$ be an equilibrium of (2). Then L_r^* is the zero of

$$g(L,r) = \frac{m}{K_L}L^2 - (m+\mu)[b_1(2v + \frac{1+2v+2(1-\xi)\theta r}{1+2v+2\theta r}) - 1]L - c, \tag{7}$$

and $A_r^* = \alpha\mu L_r^*/(\delta - v)$. When $c > 0$, it is obvious that $g(L,r)$ has a unique positive zero

$$L_r^* = \frac{K_L}{2m}[(m+\mu)(b_1(2v + \frac{1+2v+2(1-\xi)\theta r}{1+2v+2\theta r}) - 1) + \sqrt{\Delta_r}], \tag{8}$$

where

$$\Delta_r = (m+\mu)^2(b_1(2v + \frac{1+2v+2(1-\xi)\theta r}{1+2v+2\theta r}) - 1)^2 + \frac{4mc}{K_L}.$$

For the case $c = 0$, besides the complete suppression state $E_0(0,0)$, (2) has a positive equilibrium $E_r^*(L_r^*, A_r^*)$ if and only if

$$b_1(2v + \frac{1+2v+2(1-\xi)\theta r}{1+2v+2\theta r}) - 1 > 0,$$

or equivalently,

$$b_1(1+2v+2(1-\xi)\theta r) > (1-2b_1 v)(1+2v+2\theta r). \tag{9}$$

The basic assumption (3) reveals that (9) holds for all $\xi \in [0,1]$ and $r \geq 0$ when

$$v \geq \frac{1}{2b_1} = \frac{(\delta - v)(m+\mu)}{\alpha\beta\mu} \Leftrightarrow v \geq v^* = \frac{\delta}{1+2b_0\delta}. \tag{10}$$

Otherwise, if $0 \leq v < v^*$, then (9) holds if and only if

$$((1+2v)b_1 - 1)(1+2v) > 2\theta(1 - (1+2v-\xi)b_1)r. \tag{11}$$

The inequality in (11) holds for any $r \geq 0$ when $1 - (1+2v-\xi)b_1 \leq 0$, that is

$$\xi \leq \xi^* = 1 + 2v - \frac{1}{b_1} > 0. \tag{12}$$

If $\xi > \xi^*$, then (11) holds if and only if

$$r < r^* = (1+2v)\frac{(1+2v)b_1 - 1}{2\theta(1-(1+2v-\xi)b_1)} = (1+2v)\frac{\xi^*}{2\theta(\xi - \xi^*)}. \tag{13}$$

When $c = 0$, the above analyses show that (2) has two nonnegative equilibrium $E_0(0,0)$ and $E_r^*(L_r^*, A_r^*)$ when $v \geq v^*$, or $v < v^*$ and $\xi \leq \xi^*$, or $v < v^*$, $\xi > \xi^*$, and $r < r^*$. In this case, a similar method as in the proof of Theorem 2.2 in [14] shows that $E_r^*(L_r^*, A_r^*)$ is globally asymptotically stable. If $v < v^*$, $\xi > \xi^*$, and $r \geq r^*$, similarly to the proof of Theorem 2.3 below, we can prove that the unique nonnegative equilibrium $E_0(0,0)$ is globally asymptotically stable. Hence v^* defines the threshold dispersal rate level of adult mosquitoes. If the dispersal rate of adults is kept at a high level with $v \geq v^*$, a complete population suppression is improbable. When $v < v^*$, we identify the threshold CI intensity ξ^* over which a successful population suppression is possible. If $v < v^*$ and $\xi > \xi^*$, we identify the threshold release ratio r^* over which all wild mosquitoes in the control area will be eliminated ultimately. We summarize the threshold dynamics in the following theorem and omit its proof.

Theorem 2.1. *Let* $r(t) \equiv r \geq 0$, $c = 0$, *and (5) holds.*

(1) If one of the following conditions holds: (i) $v \geq v^*$, *(ii)* $v < v^*$ *and* $\xi \leq \xi^*$, *(iii)* $v < v^*$, $\xi > \xi^*$, *and* $r < r^*$, *then* $E_0(0,0)$ *is unstable and* $E_r^*(L_r^*, A_r^*)$ *is globally asymptotically stable;*

(2) If $v < v^*$, $\xi > \xi^*$, *and* $r \geq r^*$, *then* $E_0(0,0)$ *is globally asymptotically stable.*

2.2 The failure of a complete suppression when $c > 0$

In this part, we show that the immigration of eggs with $c > 0$ may cause a failure of a complete suppression. In fact, our next result proves that the numbers of larvae $L(t)$ and adults $A(t)$ have positive lower bounds.

Theorem 2.2. *Let* $c > 0$, $v \geq 0$, *and (5) hold. For each initial data* $\phi, \psi \in C([t_0-\tau, t_0], (0,\infty))$, *the solution* $(L(t), A(t))$ *of (2) satisfies*

$$0 < L_{\bar{r}}^* \leq \liminf_{t\to\infty} L(t) \leq \limsup_{t\to\infty} L(t) \leq L_{\underline{r}}^*, \tag{14}$$

and

$$0 < \frac{\alpha\mu}{\delta - v} L_{\bar{r}}^* \leq \liminf_{t\to\infty} A(t) \leq \limsup_{t\to\infty} A(t) \leq \frac{\alpha\mu}{\delta - v} L_{\underline{r}}^*, \tag{15}$$

where $\bar{r} = \sup_{[t_0-\tau,\infty)} r(t)$, $\underline{r} = \inf_{[t_0-\tau,\infty)} r(t)$, $L_{\bar{r}}^*$ *and* $L_{\underline{r}}^*$ *are defined in (8) with* r *replaced by* $\bar{r}$ *and* $\underline{r}$, *respectively.*

Proof. The nonnegativity of the release rate $r(t)$ verifies that $0 \leq \underline{r} \leq r(t) \leq \bar{r}$ for all $t \geq t_0$. The conditions $c > 0$, and (5) verify that $L_{\underline{r}}^*$ and $L_{\bar{r}}^*$ are well-defined and positive. The decreasing of $(1 + 2v + 2(1-\xi)\theta r)/(1 + 2v + 2\theta r)$ in r gives

$$\frac{1 + 2v + 2(1-\xi)\theta\bar{r}}{1 + 2v + 2\theta\bar{r}} \leq \frac{1 + 2v + 2(1-\xi)\theta r(s_n - \tau_1)}{1 + 2v + 2\theta r(s_n - \tau_1)} \leq \frac{1 + 2v + 2(1-\xi)\theta\underline{r}}{1 + 2v + 2\theta\underline{r}}$$

By using the fluctuation lemma, we can find two increasing and divergent sequences $\{s_n\}$ and $\{t_n\}$ along which $L(s_n) \to \underline{L} = \liminf_{t\to\infty} L(t)$, $L'(s_n) \to 0$, $A(t_n) \to \underline{A} = \liminf_{t\to\infty} A(t)$, and $A'(t_n) \to 0$, as $n \to \infty$. Taking the limits of (2) along these sequences gives

$$(\delta - v)\underline{A} = \liminf_{n\to\infty} \alpha\mu L(t_n - \tau_2) \geq \alpha\mu\underline{L}, \tag{16}$$

and

$$\begin{aligned} & \tfrac{m}{K_L}\underline{L}^2 + (m+\mu)\underline{L} - c \\ = \;& \liminf\nolimits_{n\to\infty} \tfrac{\beta}{2} \tfrac{1+2v+2(1-\xi)\theta r(s_n-\tau_1)}{1+2v+2\theta r(s_n-\tau_1)} A(s_n - \tau_1) + v\beta A(s_n - \tau_1) \\ \geq \;& \tfrac{\alpha\beta\mu}{2(\delta-v)}(2v + \tfrac{1+2v+2(1-\xi)\theta\bar{r}}{1+2v+2\theta\bar{r}})\underline{L}. \end{aligned} \tag{17}$$

The definition of $g(L, r)$ in (7) and inequality in (17) show that $g(\underline{L}, \bar{r}) \geq 0$, which implies $\underline{L} \geq L_{\bar{r}}^* > 0$, where $L_{\bar{r}}^*$ is defined in (8) with r replaced by $\bar{r}$. It follows the inequality in (16) that

$$\underline{A} \geq \frac{\alpha\mu}{\delta - v}\underline{L} \geq \frac{\alpha\mu}{\delta - v} L_{\bar{r}}^* > 0.$$

Let $\{s_n\}$ and $\{t_n\}$ again be the two sequences along which $L(s_n) \to \bar{L} = \limsup_{t\to\infty} L(t)$, $L'(s_n) \to 0$, $s_n \to \infty$, $A(t_n) \to \bar{A} = \limsup_{t\to\infty} A(t)$, $A'(t_n) \to 0$, and $t_n \to \infty$ as $n \to \infty$.

Taking the limits of (2) along these sequences leads to

$$(\delta-v)\bar{A}=\limsup_{n\to\infty}\alpha\mu L(t_n-\tau_2)\le\alpha\mu\bar{L}, \tag{18}$$

and

$$\begin{aligned}&\tfrac{m}{K_L}\bar{L}^2+(m+\mu)\bar{L}-c\\ =\;&\limsup\nolimits_{n\to\infty}\tfrac{\beta}{2}\tfrac{1+2v+2(1-\xi)\theta r(s_n-\tau_1)}{1+2v+2\theta r(s_n-\tau_1)}A(s_n-\tau_1)+v\beta A(s_n-\tau_1)\\ \le\;&\tfrac{\alpha\beta\mu}{2(\delta-v)}\big(2v+\tfrac{1+2v+2(1-\xi)\theta\underline{r}}{1+2v+2\theta\underline{r}}\big)\bar{L}.\end{aligned} \tag{19}$$

The inequality in (19) and the properties of $g(L,r)$ imply that $g(\bar{L},\underline{r})\le 0$. Hence $\bar{L}\le L^*_{\underline{r}}$, where $L^*_{\underline{r}}$ defined in (8) with r replaced by $\underline{r}$. The inequality on the right side of (15) follows from the inequality in (18) immediately. □

When the release ratio is managed to keep at almost a constant such that $r(t)\equiv r>0$, we have $\bar{r}=\underline{r}=r$ and $L^*_{\underline{r}}=L^*_{\bar{r}}=L^*_r$. In this case, (2) has a unique positive equilibrium $E^*_r(L^*_r,A^*_r)$, where L^*_r defined in (8), and $A^*_r=\alpha\mu L^*_r/(\delta-v)$. We show that $E^*_r(L^*_r,A^*_r)$ is globally asymptotically stable in the following theorem.

Theorem 2.3. *Let $c>0$, $v\ge 0$, $r(t)\equiv r\ge 0$, and (5) hold. Then $E^*_r(L^*_r,A^*_r)$ is globally asymptotically stable.*

Proof. To prove the global stability of $E^*_r(L^*_r,A^*_r)$, we first claim, for any $0<\varepsilon_1\le L^*_r$ and $\varepsilon_2>0$, if $L^*_r-\varepsilon_1<\phi(t)<L^*_r+\varepsilon_2$ and $A^*_r-\alpha\mu\varepsilon_1/(\delta-v)<\psi(t)<A^*_r+\alpha\mu\varepsilon_2/(\delta-v)$ on $[t_0-\tau,t_0]$, then

$$L^*_r-\varepsilon_1<L(t)<L^*_r+\varepsilon_2,\ A^*_r-\frac{\alpha\mu}{\delta-v}\varepsilon_1<A(t)<A^*_r+\frac{\alpha\mu}{\delta-v}\varepsilon_2,\ \text{for all } t\ge t_0. \tag{20}$$

Otherwise, let $\bar{t}>t_0$ be the last time at which $L=L^*_r-\varepsilon_1$, or $L=L^*_r+\varepsilon_2$, or $A=A^*_r-\alpha\mu\varepsilon_1/(\delta-v)$, or $A=A^*_r+\alpha\mu\varepsilon_2/(\delta-v)$. If $L(\bar{t})=L^*_r-\varepsilon_1$, then $L'(\bar{t})\le 0$, $A(\bar{t})\ge A^*_r-\alpha\mu\varepsilon_1/(\delta-v)$, $L(t)>L^*_r-\varepsilon_1$, and $A(t)>A^*_r-\alpha\mu\varepsilon_1/(\delta-v)$ for $t\in[t_0,\bar{t})$. Letting $t=\bar{t}$ in the first equation of (2) leads to

$$\begin{gathered}L'(\bar{t})=\\ \big(\tfrac{\beta}{2}\tfrac{1+2v+2(1-\xi)\theta r}{1+2v+2\theta r}+v\beta\big)A(\bar{t}-\tau_1)-m\big(1+\tfrac{L^*_r-\varepsilon_1}{K_L}\big)(L^*_r-\varepsilon_1)-\mu(L^*_r-\varepsilon_1)+c\le 0,\end{gathered}$$

which gives

$$\begin{aligned}\tfrac{m}{K_L}(L^*_r-\varepsilon_1)^2+(m+\mu)(L^*_r-\varepsilon_1)-c\;&\ge\;\big(\tfrac{\beta}{2}\tfrac{1+2v+2(1-\xi)\theta r}{1+2v+2\theta r}+v\beta\big)A(\bar{t}-\tau_1)\\ &>\;\big(\tfrac{\beta}{2}\tfrac{1+2v+2(1-\xi)\theta r}{1+2v+2\theta r}+v\beta\big)\big(A^*_r-\tfrac{\alpha\mu}{\delta-v}\varepsilon_1\big)\\ &=\;\tfrac{\alpha\beta\mu}{2(\delta-v)}\big(2v+\tfrac{1+2(1-\xi)\theta r}{1+2\theta r}\big)(L^*_r-\varepsilon_1).\end{aligned}$$

Hence $g(L^*_r-\varepsilon_1,r)>0$. By the definition of $g(L,r)$ in (7), we have for any $r\ge 0$,

$$g(L,r)<0,\quad L\in[0,L^*_r),\quad g(L^*_r,r)=0,\quad \text{and}\quad g(L,r)>0,\quad L>L^*_r,$$

which gives an obvious contradiction. The case $L(\bar{t})=L^*_r+\varepsilon_2$ can be proved similarly.

If $A(\bar{t})=A^*_r-\alpha\mu\varepsilon_1/(\delta-v)$, then $A'(\bar{t})\le 0$, $L(\bar{t})\ge L^*_r-\varepsilon_1$, $L(t)>L^*_r-\varepsilon_1$, and $A(t)>A^*_r-\alpha\mu\varepsilon_1/(\delta-v)$ for $t\in[t_0,\bar{t})$. Letting $t=\bar{t}$ in the second equation of (2) gives

$$\frac{dA(\bar{t})}{dt}=\alpha\mu L(\bar{t}-\tau_2)-\delta A(\bar{t})+vA(\bar{t})\le 0,$$

which leads to

$$(\delta - v)A(\bar{t}) = (\delta - v)(A_r^* - \frac{\alpha\mu}{\delta - v}\varepsilon_1) \geq \alpha\mu L(\bar{t} - \tau_2) > \alpha\mu(L_r^* - \varepsilon_1).$$

An obvious contradiction follows from the above inequality and the definition of $A_r^* = \alpha\mu/(\delta - v)L_r^*$. Those contradictions lead to the verification of the claim (20), which verifies the global stability of $E_r^*(L_r^*, A_r^*)$.

It follows from $r(t) \equiv r > 0$ that the lower limit $\underline{r}$ and upper limit $\bar{r}$ of the release ratio r satisfy $\underline{r} = \bar{r} = r$, which implies $L_{\underline{r}}^* = L_{\bar{r}}^* = L_r^*$. By using (14) in Theorem 2.2, we see that the lower limit $\underline{L}$ and upper limit $\bar{L}$ of the number of larvae $L(t)$ satisfy

$$\underline{L} = \bar{L} = L_r^*.$$

Similarly, by using (15) in Theorem 2.2, we obtain $\underline{A} = \bar{A} = A_r^*$. Hence

$$\lim_{t\to\infty} L(t) = L_r^*, \quad \text{and} \quad \lim_{t\to\infty} A(t) = A_r^*,$$

which verifies the global attractiveness of $E_r^*(L_r^*, A_r^*)$. The global asymptotical stability of $E_r^*(L_r^*, A_r^*)$ follows from its global stability and global attractiveness. □

§3 Application to *Aedes albopictus* population suppression

3.1 The dependence of the thresholds on parameters

In accordance with the biological meanings and the low mobility of *Aedes* populations, the basic assumptions (3) and (5) will be maintained in the discussion below. We first consider the case $c = 0$ and $v \geq 0$. In this case, our theoretical analysis identifies a threshold dispersal rate of adults

$$v^* = \frac{\delta(m + \mu)}{\alpha\beta\mu + m + \mu} = \frac{\delta}{1 + 2b_0\delta}, \tag{21}$$

which increases in the mortality rate constants m and δ, and decreases in the production rate constants β, μ, and α by nonlinear dependence. Our theoretical analysis indicates that a relatively low dispersal rate of adult mosquitoes is of the first importance prerequisite for a successful population suppression. When the dispersal rate of adults is large enough with $v \geq v^*$, the population suppression is, independent of other factors such as CI intensity, mating competitiveness and release ratio, absolutely improbable. When the dispersal of adults is kept at a lower level such that $v < v^*$, we find a threshold CI intensity

$$\xi^* = 1 + 2v - \frac{2(\delta - v)(m + \mu)}{\alpha\beta\mu} = 1 + 2v - \frac{1}{b_1} > 0, \tag{22}$$

increasing in α, β, μ, and v, and decreasing in m and δ. If the *Wolbachia* strain has relatively weak capability to induce zygotic death from incompatible mating with $\xi \leq \xi^*$, then a complete elimination of mosquitoes is improbable no matter how many infected males are released in the wild area. For the case $v < v^*$ and $\xi > \xi^*$, we identify a threshold release ratio r^* with

$$r^* = (1 + 2v)\frac{\xi^*}{2\theta(\xi - \xi^*)}, \tag{23}$$

above which a successful suppression is ascertained. r^* increases in α, β, μ, and v, and decreases in m, δ, θ, and ξ by nonlinear dependence. Although the CI intensity ξ and the mating competitiveness θ display a similarly inverse proportional relationship with the threshold release ratio r^*, the threshold dynamics in Theorem 2.1 is inclined to support a more important role of ξ than θ in population suppression. By the biological meaning, $\theta = 0$ indicates that all wild females refuse to mate with released males completely, and the used *Wolbachia* strain is ineffective. In practical application, the mating competitiveness θ of the chosen *Wolbachia* strain is larger than 0.5, and its variation has little impact on r^*. We use numerical examples to demonstrate further the dependence of the threshold release ratio r^* on CI intensity ξ and dispersal rate of adult mosquitoes v. By combining the field and laboratory data, we list the life table parameters of the *Aedes albopictus* population in the following Table 1.

Table 1. The life table parameters of *Aedes albopictus*. The parameter values are adapted to *Aedes albopictus* population in subtropical monsoon climate as in Guangzhou.

Para.	Definition	Value	Reference
N	Number of eggs laid by a female	$(29, 225)$	[20, 22, 33]
μ_E	Hatch rate of the egg (day^{-1})	$(0.06, 0.27)$	[17, 21, 25]
β	Mean larvae produced by a female (day^{-1})	$\beta = 2N\mu_E/\tau_A$	
m	Minimum larva mortality rate (day^{-1})	$(0.03, 0.1)$	[17, 25, 32, 33]
μ	Pupation rate (day^{-1})	$(0.05, 0.15)$	[17, 25, 32, 33]
α	Pupa survival rate (day^{-1})	$(0.90, 0.97)$	[8, 25, 32, 33]
δ	Adult female mortality rate (day^{-1})	$(0.05, 0.15)$	[17, 24, 25, 32]
τ_E	Development period of the egg (days)	(3.7, 18.3)	[17, 21, 32, 33]
τ_L	Development period of the larva (days)	(5.2, 27.7)	[17, 21, 32, 33]
τ_P	Development period of the pupa (days)	(1.5, 8.6)	[17, 21, 32, 33]
τ_A	Mean longevity of females (days)	(4.8, 40.9)	[17, 21, 32, 33]

To make it more specific and transparent, we fix the following parameter values

$$\beta = 4,\ m = 0.07,\ \mu = 0.1,\ \alpha = 0.95,\ \delta = 0.1,\ \tau_E = 4,\ \tau_L = 6,\ \tau_P = 2,\ \tau_A = 16. \tag{24}$$

In this case, $b_0 = \alpha\beta\mu/(2\delta(m+\mu)) = 11.18$, and the basic assumption (5) holds obviously. For the non-dispersal case with $c = v = 0$, when *Wolbachia* brings complete CI and has no impact on the mating competitiveness of infected males with $\xi = \theta = 1$, we estimate $\xi^* = 1 - 2\delta(m+\mu)/(\alpha\beta\mu) = 0.9105$ and $r^* = \xi^*/(2\theta(\xi - \xi^*)) = 5.0882$, which is consistent with the theoretically estimated values of $\xi^* = 0.9$ and $r^* = 5$ in [14, 27], and the practical release ratio 5 in the field trial of *Aedes albopictus* population suppression in Guangzhou [31]. We estimate from (24) that $v^* = \delta/(1+2b_0\delta) = 0.0309$, $\tau_1 \approx \tau_E + \tau_A/2 = 12$, and $\tau_2 = \tau_L + \tau_P = 8$. As K_L scaling with the number of breeding sizes in the inhabiting area, we take $K_L = 10^4$ as an example, which can be replaced by any other integer without changing the system dynamics. By the field trial data of *Aedes albopictus* suppression in Guangzhou and our theoretical analysis, we fix

$$\xi \in [0.9105, 1], \quad \theta \in [0.5, 1], \quad v \in [0, 0.0309], \quad c \geq 0. \tag{25}$$

We use a numerical example to demonstrate further the threshold dynamics when $c = 0$. With the parameters α, β, μ, m, and δ specified in (24), and $\theta = 0.75$, the threshold CI intensity

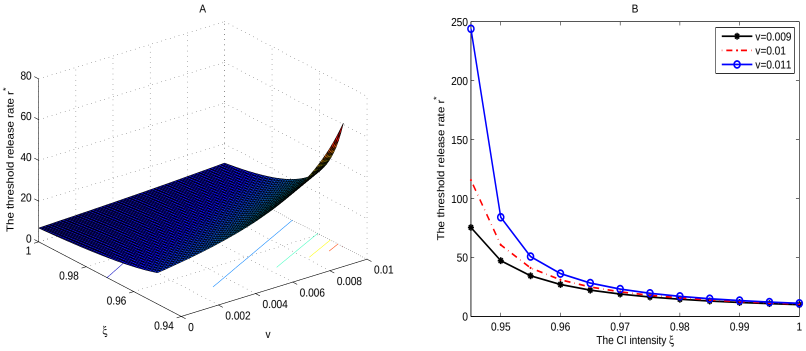

Figure 1. *The dependence of the threshold release ratio* r^* *on the CI intensity* ξ *and the dispersal rate of adult mosquitoes* v. The parameters α, β, μ, m, and δ are specified in (24), and $\theta = 0.75$. (A) r^* decreases in $\xi \in [0.95, 1]$ and increases in $v \in [0, 0.01]$ with the maximum $r^*(0.95, 0.01) = 60.69$ and the minimum $r^*(1, 0) = 6.78$. (B) For fixed $v = 0.009$, 0.01, 0.011, r^* is sensitive and elevates sharply when ξ is close to the threshold CI intensity $\xi^* = 0.9395$ when $v = 0.01$ and $\xi^* = 0.9424$ when $v = 0.011$.

$\xi^* = 0.9395$ for $v = 0.01$, and $\xi^* = 0.9424$ for $v = 0.011$. The dependence of the threshold release ratio $r^*(\xi, v)$ on the CI intensity $\xi \in [0.95, 1]$ and the adult dispersal rate $v \in [0, 0.01]$ is shown in Figure 1A, and its dependence on ξ for fixed $v = 0.009$, 0.01, 0.011 is shown in Figure 1B. $r^*(\xi, v)$ decreases in ξ and increases in v with the maximum $r^*(0.95, 0.01) = 60.69$ and the minimum $r^*(1, 0) = 6.78$. Figure 1B shows that $r^*(\xi, v)$ is sensitive and elevates sharply when ξ is close to the threshold CI intensity $\xi^*(v)$. It is interesting to find that $r^*(\xi, v)$ displays some similar sensitive pattern on v when ξ is closed to its threshold ξ^*. For example, when $\xi = 0.945$, a 10% increase in v from $v = 0.01$ to $v = 0.011$ results to 2.11 times increase in r^* from $r^*(0.945, 0.01) = 115.6$ to $r^*(0.945, 0.011) = 244$.

3.2 The individual impacts on the adult equilibrium

When $c > 0$, our theoretical analysis reveals that the threshold dynamics is invalid. In this case, if the release ratio $r(t)$ changes in time, then Theorem 2.2 showed that both the numbers of larvae $L(t)$ and adults $A(t)$ have positive lower bounds, which indicates that a complete elimination of the wild mosquito population is impossible no matter how many infected males are released. If the number of released males is managed to keep almost a constant ratio of the wild mosquitoes such that $r(t) \equiv r \geq 0$, then (2) has a unique positive equilibrium $E_r^*(L_r^*, A_r^*)$ with

$$L_r^* = \frac{K_L}{2m}[(m+\mu)(b_1(2v + \frac{1+2v+2(1-\xi)\theta r}{1+2v+2\theta r}) - 1) + (\Delta_r)^{1/2}],$$

and $A_r^* = \alpha\mu L_r^*/(\delta - v)$, where

$$\Delta_r = (m+\mu)^2(b_1(2v + \frac{1+2v+2(1-\xi)\theta r}{1+2v+2\theta r}) - 1)^2 + \frac{4mc}{K_L}.$$

Obviously, A_r^* increases in both of the dispersal rates $c \geq 0$ and $v \geq 0$, and decreases in both the mating competitiveness $\theta \geq 0$ and the CI intensity $\xi \in [0, 1]$. When $c > 0$, by the global asymptotical stability of the positive equilibrium $E_r^*(L_r^*, A_r^*)$ shown in Theorem 2.3, A_r^* indicates the sustained population size of adult mosquitoes in the studying area. For the special case $r(t) \equiv 0$, the wild mosquito population does not interfere with by *Wolbachia*. Theorem 2.3 demonstrates that A_r^* is the carrying capacity of wild adult mosquitoes in the inhabiting area.

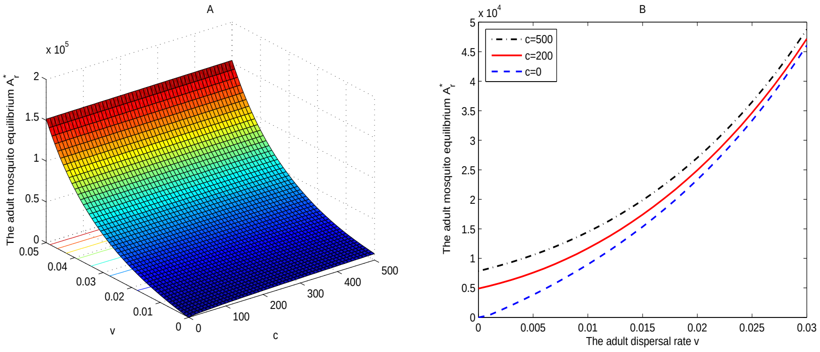

Figure 2. *The dependence of the adult equilibrium A_r^* on the dispersal rates c and v.* The parameters α, β, μ, m, and δ are specified in (24), $K_L = 10^4$, $\theta = 0.75$, $\xi = 0.95$, and $r(t) \equiv 16$. (A) A_r^* increases in both $c \geq 0$ and $v \geq 0$ with the minimum $A_r^*(0,0) = 0$. (B) For fixed $c = 500$, 200, 0, A_r^* is sensitive and increases convexly with a small increment of v.

Our theoretical analysis is inclined to support a more important role of the dispersal rate of adults than the dispersal rate of eggs in population suppression. To bring insight into the combined impact of CI intensity ξ, mating competitiveness θ, and dispersal rates c and v on population suppression, we study the dependence of the adult mosquito equilibrium A_r^* on these parameters. In Figure 2, we demonstrate the impact of dispersal rates c and v on the adult equilibrium A_r^*. Intuitively, A_r^* increases in both the dispersals of eggs and adults. With the parameters specified in (24), $K_L = 10^4$, $\theta = 0.75$, and $\xi = 0.95$, we have the threshold release ratio $r^* = 15.38$ when $c = v = 0$. In this case, the release rate $r(t) \equiv 16 > r^*$ verifies that $A_r^* = 0$ and the wild mosquitoes will be eliminated ultimately. As shown in Figure 2B, contrary to the relatively flat variation in c, the adult equilibrium A_r^* is sensitive to the dispersal rate v of adult mosquitoes. For example, for fixed $c = 200$, $A_r^*(c, v)$ elevates sharply from $A_r^*(200, 0) = 4892$ to $A_r^*(200, 0.03) = 47190$ as v increasing from $v = 0$ to $v = 0.03$. However, for fixed $v = 0.01$, $A_r^*(c, v)$ increases relatively flat from $A_r^*(0, 0.01) = 8978$ to $A_r^*(500, 0.01) = 14480$ as c elevating from $c = 0$ to $c = 500$.

The control of the simulated population is much less tolerant to CI intensity ξ than it is to their reduced mating competitiveness θ. As the mating competitiveness θ acts together with the release ratio $r(t)$ in the form of $\theta r(t - \tau_1)$, they relate reciprocally and a loss of θ can be compensated by a propositional increase in $r(t - \tau_1)$. The parameters α, β, μ, m, and δ specified in (24), $K_L = 10^4$, $c = 100$, $v = 0.01$, and $r(t) \equiv 65$. As shown in Figure 3A, compared to the flat variation in $\theta \in [0.5, 1]$, A_r^* exhibits a relatively sensitive change in $\xi \in [0.9, 1]$. For fixed $\xi = 0.95$, a 50% reduction in θ from $\theta = 1$ to $\theta = 0.5$ leads to a 33.59% increment in

A_r^* from $A_r^*(1, 0.95) = 3522$ to $A_r^*(0.5, 0.95) = 4705$. While a 10% reduction in ξ from $\xi = 1$ to $\xi = 0.9$ results in a 16.53 times increment in the equilibrium from $A_r^*(0.75, 1) = 941$ to $A_r^*(0.75, 0.9) = 16500$ when $\theta = 0.75$ as shown in Figure 3B.

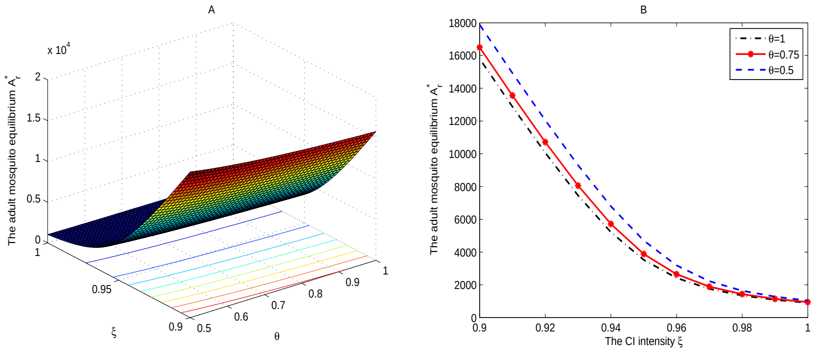

Figure 3. *The impact of CI intensity ξ and mating competitiveness θ on adult mosquito equilibrium A_r^*.* The parameter values are the same in Figure 2, except $c = 100$, $v = 0.01$, and $r(t) \equiv 65$. (A) A_r^* decreases in both $\xi \in [0.9, 1]$ and $\theta \in [0.5, 1]$ with the maximum $A_r^*(0.9, 0.5) = 1.788 \times 10^4$ and the minimum $A_r^*(1, 1) = 900$. (B) For fixed $\theta = 1$, 0.75, 0.5, A_r^* has a relatively flat variation when ξ is close to 1, but increases almost linearly when ξ decreases to 0.9.

3.3 Discussion

In contrary to the short-distance dispersal for egg-laying, blood-feeding, or sheltering, the immigration of eggs prompted by international travel and trade, especially the used tire trade, is the main long-distance invasion way of *Aedes albopictus* in the world [24]. Compared to the suppression in an isolated area, the dispersal of mosquitoes compromises suppression efficiency, and has a great influence on the suppression dynamics. In the field trial of *Aedes albopictus* suppression in Guangzhou, compared to complete elimination in isolated areas surrounded by vegetation, lower suppression levels were observed in less isolated zones nearer transportation routes with frequent traffic such as ongoing bridge construction and shipping harbor [31].

By introducing the dispersal of mosquitoes into the suppression model, we find that the immigration of eggs has changed the suppression dynamics completely. For the case without immigration of eggs with $c = 0$, the suppression dynamics with adult mosquito dispersal is similar to that in isolated zones. For the case $c = 0$, our theoretical analysis in Theorem 2.1 identifies the threshold dispersal rate $v^* = \delta/(1+2b_0\delta)$ of adult mosquitoes. When the dispersal of adults is large enough with $v \geq v^*$, complete elimination of mosquitoes is, independent of CI intensity and release ratio, absolutely improbable. When $v < v^*$, we find a threshold CI density $\xi^* = 1 + 2v - 1/b_1$, less than or equal to which causes a failure of complete suppression no matter how many infected males are released. When $v < v^*$ and $\xi > \xi^*$, we identify the threshold release ratio $r^* = (1 + 2v)\xi^*/(2\theta(\xi - \xi^*))$. The wild mosquito population will be eliminated completely when the release ratio $r(t) \geq r^*$ uniformly.

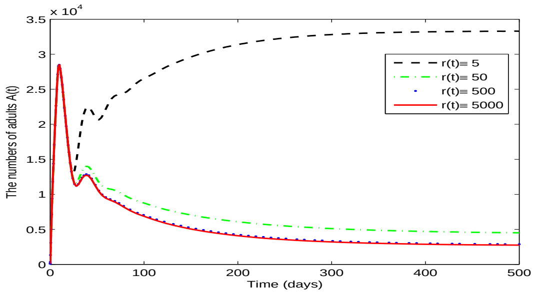

Figure 4. *The failure of suppression for any release ratio* $r(t)$ *when* $c > 0$. With the parameter values in (24), $K_L = 10^4$, $\theta = 0.75$, $\xi = 0.95$, $c = 100$, $v = 0.01$, and the initial values $\phi(t) \equiv 50000$ and $\psi(t) \equiv 100$ for $t \in [-12, 0]$, the curves were generated by (2) with different release ratios $r(t)$.

Interestingly, the threshold dynamics are invalid when $c > 0$. In this case, (2) has a unique positive equilibrium $E_r^*(L_r^*, A_r^*)$. The global asymptotical stability of $E_r^*(L_r^*, A_r^*)$ shown in Theorem 2.3 indicates that the immigration of eggs by human activities results to a failure of complete suppression no matter how many infected males are released. In fact, A_r^* decreases in r and $\lim_{r\to\infty} A_r^* = A_\infty^*$ with

$$A_\infty^* = \frac{\alpha\mu K_L}{2m(\delta - v)}[(m+\mu)(b_1(2v+1-\xi)-1) + ((m+\mu)^2(b_1(2v+1-\xi)-1)^2 + \frac{4mc}{K_L})^{1/2}].$$

As *Aedes albopictus* mosquitoes in Guangzhou overwinter from December to February mainly by diapause eggs, we take March 1 as the initial time $t_0 = 0$, and the initial number of larvae $\phi(t) \equiv 50000$ and adults $\psi(t) \equiv 100$ for $t \in [-12, 0]$ for simulation. With the parameter values specified in (24), $K_L = 10^4$, $\theta = 0.75$, $\xi = 0.95$, $c = 100$, and $v = 0.01$, we have $A_r^* = 299130$ for $r = 0$, and the limit of the wild adults is $A_\infty^* = 2652$. Since the maximum suppression rate is $2652/299130 = 8.9\%$, it is improbable to reach the general goal of suppression with a 95% reduction of the wild mosquitoes in the equilibrium. Since A_r^* increases in the dispersal rate c and v, and decreases in the CI intensity ξ, to obtain a better suppression level, we can choose some suitable *Wolbachia* strain with strong CI intensity, or bring down the dispersal rate of mosquitoes by blocking the suppression zones. As shown in Figure 4, when the release ratio increases from $r = 0$ to $r = 5$, the stabilized number of adults decreases from $A_r^* = 299130$ to $A_r^* = 33340$. The suppression levels keep almost the same when $r = 500$ and $r = 5000$.

Acknowledgements

We thank the two anonymous reviewers for their careful reading and valuable suggestions for the improvement of this manuscript.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

[1] F Baldacchino, B Caputo, F Chandre, et al. *Control methods against invasive Aedes mosquitoes in Europe: a review*, Pest Manag Sci, 2015, 71(11): 1471-1485.

[2] S Bhatt, P W Gething, O J Brady, et al. *The global distribution and burden of dengue*, Nature, 2013, 496: 504-507.

[3] L Cai, S Ai, G Fan. *Dynamics of delayed mosquitoes populations models with two different strategies of releasing sterile mosquitoes*, Math Biosci Eng, 2018, 15(5): 1181-1202.

[4] D Focks, D Haile. *Dynamic life table model for Aedes aegypti (Diptera: Culicidae): simulation results and validation*, J Med Entomol, 1993, 30 (6): 1018-1028.

[5] R M Freotas, C T Codeço, R L Olibeira, et al. *Daily survival rates and dispersal of Aedes aegypti females in Rio De Janeiro, Brazil*, Am J Trop Med Hyg, 2007, 76(4): 659-665.

[6] D Gao, Y Lou, D He, et al. *Prevention and Control of Zika as a Mosquito-Borne and Sexually Transmitted Disease: A Mathematical Modeling Analysis*, Sci Rep, 2016, 6: 28070.

[7] G L Goff, D Damiens, A H Ruttee, et al. *Field evaluation of seasonal trends in relative population sizes and dispersal pattern of Aedes albopictus males in support of the design of a sterile male release strategy*, Para Vect, 2019, 12: 81.

[8] P A Hancock, V L White, A G Callahan, et al. *Density-dependent population dynamics in Aedes aegypti slow the spread of wMel Wolbachia*, J Appl Ecol, 2016, 53(3): 785-793.

[9] L Hu, M Tang, Z Wu, et al. *The threshold infection level for Wolbachia invasion in random environments*, J Diff Equ, 2019, 266: 4377-4393.

[10] M Huang, M Tang, J Yu. *Wolbachia infection dynamics by reaction-diffusion equations*, Sci China Math, 2015, 58(1): 77-96.

[11] M Huang, J Yu, L Hu, et al. *Qualitative analysis for a Wolbachia infection model with diffusion*, Sci China Math, 2016, 59(7): 1249-1266.

[12] M Huang, J Lou, L Hu, et al. *Assessing the efficiency of Wolbachia driven Aedes mosquito suppression by delay differential equations*, J Theor Biol, 2018, 440: 1-11.

[13] M G Huang, M Tang, J Yu, et al. *The impact of mating competitiveness and incomplete cytoplasmic incompatibility on Wolbachia-driven mosquito population suppressio*, Math Bios Eng, 2019, 16(5): 4741-4757.

[14] M Huang, M X Tang, J S Yu, et al. *A stage structured model of delay differential equations for Aedes mosquito population suppression*, Discrete Contin Dyn Syst, 2020, 40(6): 3467-3484.

[15] P Jia, X Chen, J Chen, et al. *A climate driven mechanistic population model of Aedes albopictus with diapause*, Para Vect, 2016, 9: 175.

[16] J L Kyle, E Harris. *Global spread and persistence of dengue*, Annu Rev Microbiol, 2008, 62: 71-92.

[17] Y Li, F Kamara, G Zhou, et al. *Urbanization increases Aedes albopictus larval habitats and accelerates mosquito development and survivorship*, PLoS Negl Trop Dis, 2014, 8(11): e3301.

[18] C Liew, C F Curtis. *Horizontal and vertical dispersal of dengue vector mosquitoes, Aedes aegypti and Aedes albopictus, in Singapore*, Medical Veter Entom, 2004, 18: 351-360.

[19] Q Liu. *Dengue fever in China: new epidemical trend, challenges and strategies for prevention and control*, Chin J Vector Biol Control, 2020, 31(1): 1-6.

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

[21] F Liu, C Zhou, 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.

[22] F Liu, C Yao, P Lin, et al. *Studies on life table of the natural population of Aedes albopictus*, Acta Sci Natur Universitatis Sunyatseni, 1992, 31(3): 84-93.

[23] A Trájer, T Hammer, I Kacsala, et al. *Decoupling of active and passive reasons for the invasion dynamics of Aedes albopictus Skuse (Diptera: Culicidae): Comparisons of dispersal history in the Apennine and Florida peninsulas*, J Vector Ecol, 2017, 42(2): 233-242.

[24] L Vavassori, A Saddler, P Muller. *Active dispersal of Aedes albopictus: a mark-release-recapture study using self-marking units*, Paras Vectors, 2019, 12: 583.

[25] J Waldock, N L Chandra, J Lelieveld, et al. *The role of environment variables on Aedes albopictus biology and Chikungunya epidemiology*, Pathogens and Global Health, 2013, 107(5): 224-240.

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

[27] J Yu. *Modeling mosquito population suppression based on delay differential equations*, SIAM J Appl Math, 2018, 78(6): 3168-3187.

[28] D Zhang, X Zheng, Z Xi, et al. *Combining the sterile insect technique with the incompatible insect technique: I-impact of Wolbachia infection on the fitness of triple- and double-infected strains of Aedes albopictus*, PLoS One, 2015, 10(4): e0121126.

[29] X Zhang, S Tang, R A Cheke, et al. *Modeling the effects of augmentation strategies on the control of dengue fever with an impulsive differential equation*, Bull Math Biol, 2016, 78: 1968-2010.

[30] B Zheng, J Yu, Z Xi, et al. *The annual abundance of dengue and Zika vector Aedes albopictus and its stubbornness to suppression*, Ecol Model, 2018, 387: 38-48.

[31] X Zheng, D Zhang, Y Li, et al. *Incompatible and sterile insect techniques combined eliminate mosquitoes*, Nature, 2019, 572: 56-61.

[32] Z Zhong, 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.

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

[1] School of Statistics and Mathematics, Guangdong University of Finance and Economics, Guangzhou 510320, China.

[2] Guangzhou Center for Applied Mathematics, Guangzhou University, Guangzhou 510006, China.

Emails: mghuang@gdufe.edu.cn, jsyu@gzhu.edu.cn