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ORIGINAL ARTICLE

Threshold Dynamics of a Temperature-Dependent Stage-Structured Mosquito Population Model with Nested Delays

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Abstract Mosquito-borne diseases remain a significant threat to public health and economics. Since mosquitoes are quite sensitive to temperature, global warming may not only worsen the disease transmission case in current endemic areas but also facilitate mosquito population together with pathogens to establish in new regions. Therefore, understanding mosquito population dynamics under the impact of temperature is considerably important for making disease control policies. In this paper, we develop a stage-structured mosquito population model in the environment of a temperature-controlled experiment. The model turns out to be a system of periodic delay differential equations with periodic delays. We show that the basic reproduction number is a threshold parameter which determines whether the mosquito population goes to extinction or remains persistent. We then estimate the parameter values for *Aedes aegypti*, the mosquito that transmits dengue virus. We verify the analytic result by numerical simulations with the temperature data of Colombo, Sri Lanka where a dengue outbreak occurred in 2017.

Keywords Mosquito · Climate change · Periodic delay · Dengue · Basic reproduction ratio · Population dynamics

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1 Introduction

Mosquito is the vector that transmits numerous diseases including malaria, dengue, West Nile virus, Chikungunya and Zika. These mosquito-borne diseases cause a major public health concern and a significant economic burden in tropical and subtropical regions of the world. For instance, 2.4 billion people around the world are at risk of malaria, which is transmitted by *Anopheles* mosquitoes. There are more than 275 million malaria cases and over 438,000 malaria deaths every year, according to the 2015 World Malaria Report (see http://www.who.int/malaria/publications/worldmalaria-report-2015/en/). Dengue fever, which is mainly transmitted by *Aedes aegypti*, is another mosquito-borne disease that seriously threatens over one third of the world's population. The World Health Organization (WHO) estimates that there are 50 to 100 million infections every year, including 500,000 dengue haemorrhagic fever cases and 22,000 deaths.

Global warming together with increased global connectivity and population movements has affected the distribution of both the pathogens and the vectors and has accordingly facilitated the mosquito-borne disease transmission to new geographic regions (Liu-Helmersson et al. 2014; Tatem et al. 2006; Wilder-Smith and Gubler 2008). This has brought new challenge to the prediction of epidemic outbreaks and the control of the diseases. Due to the lack of effective malaria and dengue vaccines, most public policies for the control of those diseases focus on minimizing the mosquito population. Therefore, studying the mosquito population dynamics and its relevance to temperature is fundamental to understanding mosquito-borne disease transmission dynamics and the design of effective mosquito control strategies.

Mosquitoes go through four distinct stages during their life time: egg, larva, pupa and adult. The first three immature stages take place in the water while the adult live on land in the air. After hatching of eggs comes the first larval instar, which is followed by three moults, leading, respectively, to the second, third and fourth larval instars. Then pupation gives rise to the pupa. At last, emergence of the pupa results in the appearance of the adult, male or female. The copulation of the male and the female leads to the fertilization of the female and then the oviposition occurs if the adult female had a sufficient blood meal (Christophers 1960; Simoy et al. 2015).

Considerable evidences have shown that temperature has a great impact on both the mosquito life and the disease transmission cycles (see Beck-Johnson et al. 2013; Simoy et al. 2015 and the references therein). With higher temperatures in the favourable survival range of mosquitoes, the length of the gonotrophic cycle (the egg-laying time) decreases, causing an increase in egg number (Costa et al. 2010). Increasing temperature also leads to decreases in the lengths of each immature stage, the adult life span and the extrinsic incubation period, resulting in higher rates of disease transmission (Hopp and Foley 2001).

Numerous mathematical models incorporating the mosquito stage structure have been proposed to study the impact of climatic factors on the dynamics of mosquito population or mosquito-borne infectious disease transmissions (see, e.g. Abdelrazec and Gumel 2017; Ewing et al. 2016; Ngarakana-Gwasira et al. 2014; Simoy et al. 2015; Wang et al. 2016, 2017 and the references therein). Some of them are delay differential equations models in which the delays are employed to describe the mosquito stage durations or the extrinsic incubation period (from the uptake of pathogens by a mosquito until the mosquito becomes infectious). Since the lengths of each mosquito stage duration and the extrinsic incubation period vary with temperature, several models with periodic delays have been developed (see, e.g. Beck-Johnson et al. 2013; Wang and Zhao 2017a). We refer the readers to (Lou and Zhao 2017; McCauley et al. 1996; Molnár et al. 2013; Rittenhouse et al. 2016; Wu et al. 2015) for more population models with time-dependent delays. Most of the researchers did not study the asymptotic behaviour of the models due to the difficulty induced by time varying delays. Recently, Lou and Zhao (2017) studied the global dynamics of a host-macroparasite model with seasonal developmental durations by introducing a periodic semiflow on a suitably chosen phase space. By using the similar method in (Lou and Zhao 2017), Wang and Zhao (2017a) investigated the global dynamics of a malaria transmission model with periodic time delays. An increasing number of researchers have carried out temperature-controlled experiments to explore the impact of temperature on mosquito life cycle (see, e.g. Marinho et al. 2016; Shapiro et al. 2017; Yang et al. 2009). They estimated values and derived formulas for entomological parameters, which provide great help for numerical simulations and case studies.

Recently, Beck-Johnson et al. (2013) proposed a stage-structured mosquito population model to study the potential effect of temperature on malaria transmission. Their model consists of four delay differential equations, corresponding to the four stages of mosquitoes. They transformed the delay equations onto the physiological timescale so that the temperature-dependent delays become constants. In this paper, we use the model in Beck-Johnson et al. (2013) as a base to derive a temperature-dependent stage-structured mosquito population model for the scenario of a temperature-controlled experiment. Our model turns out to be a system of delay differential equations. In particular, the delays are time-periodic functions and one delay is nested in another one. We hope the analytic and numerical results of this paper can provide some help for future field studies and laboratory experiments in developing and testing control methods against different stages of mosquitoes.

The rest of this paper is organized as follows. In the next section, we derive the model. In Sect. 3, we show the threshold dynamics of the model in terms of the basic reproduction number. In Sect. 4, we parameterize the model with data about *Aedes agypti* mosquitoes and implement numerical simulations using the temperature data of Colombo, Sri Lanka where an outbreak of dengue occurred in 2017. In the last section, we give a brief discussion about the results and their implications and propose some possible future works.

2 Model Formulation

The purpose of this section is to derive a stage-structured mosquito population model in the environment of a temperature-controlled experiment. In laboratory experiments, mosquitoes are usually provided with sufficient food and water and there are no predators. Thus, we do not consider intraspecific competition. Motivated by the model proposed by Beck-Johnson et al. (2013), we start formulating our model from the following system:

$$
\begin{aligned}
\frac{\mathrm{d}E(t)}{\mathrm{d}t} &= R_E(t) - R_L(t) - \delta_E(t)E(t),\\
\frac{\mathrm{d}L(t)}{\mathrm{d}t} &= R_L(t) - R_P(t) - \delta_L(t)L(t),\\
\frac{\mathrm{d}P(t)}{\mathrm{d}t} &= R_P(t) - R_A(t) - \delta_P(t)P(t),\\
\frac{\mathrm{d}A(t)}{\mathrm{d}t} &= kR_A(t) - \delta_A(t)A(t),
\end{aligned}
\tag{1}
$$

where the variables $E(t)$, $L(t)$, $P(t)$ and $A(t)$ represent the numbers of eggs, larvae, pupae and adult female mosquitoes at time t, respectively. Here $R_E(t)$ is the recruitment rate of eggs, $R_L(t)$ the transition rate from the egg to the larval stage, $R_P(t)$ the transition rate from the larval stage to the pupal stage, and $R_A(t)$ the transition rate from the pupal stage to the adult stage. The per capita mortality rates of the four stages are represented by $\delta_x(t)$ with $x = E, L, P, A$, respectively, and k is the proportion of new adult mosquitoes that are females. To derive the model, we use the arguments similar to those in Nisbet and Gurney (1983), Omori and Adams (2011) and Wang and Zhao (2017a). Let q be the development level of mosquitoes such that q increases at a temperature-dependent rate $\gamma_x(T(t)) = \gamma_x(t)$ where $x = E$, L or P. Suppose $q = q_E = 0$ at the start of stage E, $q = q_L$ at the transition from E to L, $q = q_P$ at the transition from L to P, $q = q_A$ at the transition from P to A. Let $\rho(q,t)$ be the density of mosquitoes with development level q at time t. Then $R_L(t) = \gamma_E(t)\rho(q_L,t)$, $R_P(t) = \gamma_L(t)\rho(q_P,t)$, $R_A(t) = \gamma_P(t)\rho(q_A,t)$.

Let $J(q,t)$ be the flux, in the direction of increasing q, of mosquitoes with development level q at time t. Then we have the equations (see, e.g. Kot 2001)

$$
\begin{aligned}
\frac{\partial\rho(q,t)}{\partial t} &= -\frac{\partial J(q,t)}{\partial q} - \delta_E(t)\rho(q,t), \quad q \in [q_E, q_L],\\
\frac{\partial\rho(q,t)}{\partial t} &= -\frac{\partial J(q,t)}{\partial q} - \delta_L(t)\rho(q,t), \quad q \in [q_L, q_P],\\
\frac{\partial\rho(q,t)}{\partial t} &= -\frac{\partial J(q,t)}{\partial q} - \delta_P(t)\rho(q,t), \quad q \in [q_P, q_A].
\end{aligned}
$$

Since $J(q,t) = \rho(q,t)\gamma_E(t)$, $q \in [q_E, q_L]$, we have

$$
\frac{\partial\rho(q,t)}{\partial t} = -\frac{\partial}{\partial q}[\rho(q,t)\gamma_E(t)] - \delta_E(t)\rho(q,t) \quad q \in [q_E, q_L]. \tag{2}
$$

System (2) has the boundary condition

$$
\rho(q_E,t) = \frac{R_E(t)}{\gamma_E(t)} = \frac{b(t)A(t)}{\gamma_E(t)},
$$

where $b(t)$ is the oviposition rate. To solve system (2) with this boundary condition, we introduce a new variable

$$
\xi = h(t) := q_E + \int_0^t \gamma_E(s)\mathrm{d}s.
$$

Let $h^{-1}(\xi)$ be the inverse function of $h(t)$, and define

$$\hat{\rho}(q,\xi)=\rho(q,h^{-1}(\xi)),\ \hat{\delta}_E(\xi)=\delta_E(h^{-1}(\xi)),\ \hat{\gamma}_E(\xi)=\gamma_E(h^{-1}(\xi)).$$

In view of (2), we then have

$$\frac{\partial\hat{\rho}(q,\xi)}{\partial\xi}=-\frac{\partial\hat{\rho}(q,\xi)}{\partial q}-\frac{\hat{\delta}_E(\xi)}{\hat{\gamma}_E(\xi)}\hat{\rho}(q,\xi). \tag{3}$$

This equation is identical in form to the standard von Foerster equation (see Nisbet and Gurney 1982). Let $V(s)=\hat{\rho}(s+q-\xi,s)$. It follows from (3) that

$$\frac{\mathrm{d}V(s)}{\mathrm{d}s}=-\frac{\hat{\delta}_E(s)}{\hat{\gamma}_E(s)}V(s).$$

Since $\xi-(q-q_E)\le\xi$, we have

$$V(\xi)=V(\xi-(q-q_E))e^{-\int_{\xi-(q-q_E)}^{\xi}\frac{\hat{\delta}_E(s)}{\hat{\gamma}_E(s)}\mathrm{d}s},$$

and hence,

$$\hat{\rho}(q,\xi)=\hat{\rho}(q_E,\xi-q+q_E)e^{-\int_{\xi-q+q_E}^{\xi}\frac{\hat{\delta}_E(s)}{\hat{\gamma}_E(s)}\mathrm{d}s}.$$

Define $\tau_E(q,t)$ to be the time taken to grow from development level q_E to level q by mosquitoes who arrive at development level q at time t. Since $\frac{\mathrm{d}q}{\mathrm{d}t}=\gamma_E(t)$ for $q\in[q_E,q_L]$, it follows that

$$q-q_E=\int_{t-\tau_E(q,t)}^{t}\gamma_E(s)\mathrm{d}s,\quad q\in[q_E,q_L], \tag{4}$$

and hence,

$$h(t-\tau_E(q,t))=h(t)-\int_{t-\tau_E(q,t)}^{t}\gamma_E(s)\mathrm{d}s=h(t)-(q-q_E).$$

By change of variable $s=h(\alpha)$, we then see that

$$\int_{\xi-q+q_E}^{\xi}\frac{\hat{\delta}_E(s)}{\hat{\gamma}_E(s)}\mathrm{d}s=\int_{t-\tau_E(q,t)}^{t}\delta_E(\alpha)\mathrm{d}\alpha.$$

It follows that

$$\begin{aligned}\rho(q,t) &= \hat{\rho}(q,h(t))\\ &= \rho(q_E, t-\tau_E(q,t))e^{-\int_{t-\tau_E(q,t)}^{t}\delta_E(\alpha)\mathrm{d}\alpha}\\ &= \frac{b(t-\tau_E(q,t))A(t-\tau_E(q,t))}{\gamma_E(t-\tau_E(q,t))}e^{-\int_{t-\tau_E(q,t)}^{t}\delta_E(\alpha)\mathrm{d}\alpha}.\end{aligned}$$

Denoting $\tau_E(t)=\tau_E(q_L,t)$, we have

$$\gamma_E(t)\rho(q_L,t) = b(t-\tau_E(t))A(t-\tau_E(t))\frac{\gamma_E(t)}{\gamma_E(t-\tau_E(t))}e^{-\int_{t-\tau_E(t)}^{t}\delta_E(\alpha)}\mathrm{d}\alpha.$$

Letting $q=q_L$ in (4) we get

$$q_L - q_E = \int_{t-\tau_E(t)}^{t}\gamma_E(s)\mathrm{d}s \tag{5}$$

Taking the derivative with respect to t on both sides of (5) we obtain

$$1-\tau_E'(t) = \frac{\gamma_E(t)}{\gamma_E(t-\tau_E(t))}.$$

It follows that

$$R_L(t) = b(t-\tau_E(t))A(t-\tau_E(t))(1-\tau_E'(t))e^{-\int_{t-\tau_E(t)}^{t}\delta_E(\alpha)\mathrm{d}\alpha}$$

and $1-\tau_E'(t)>0$.

Define $\tau_L(q,t)$ and $\tau_P(q,t)$ to be the time taken to grow from development levels q_L and q_P, respectively, to level q by mosquitoes that arrive at development level q at time t. We then have

$$q - q_L = \int_{t-\tau_L(q,t)}^{t}\gamma_L(s)\mathrm{d}s \tag{6}$$

and

$$q - q_P = \int_{t-\tau_P(q,t)}^{t}\gamma_P(s)\mathrm{d}s \tag{7}$$

Define $\tau_L(t)=\tau_L(q_P,t)$, $\tau_P(t)=\tau_P(q_A,t)$. Letting $q=q_P$ in (6) and $q=q_A$ in (7), we have

$$q_P - q_L = \int_{t-\tau_L(t)}^{t}\gamma_L(s)\mathrm{d}s, \tag{8}$$

and

$$q_A - q_P = \int_{t-\tau_P(t)}^{t}\gamma_P(s)\mathrm{d}s. \tag{9}$$

Taking the derivative with respect to t on both sides of (8) and (9) we have

$$1 - \tau_L'(t) = \frac{\gamma_L(t)}{\gamma_L(t - \tau_L(t))} > 0,$$

and

$$1 - \tau_P'(t) = \frac{\gamma_P(t)}{\gamma_P(t - \tau_P(t))} > 0.$$

Since $J(q,t) = \rho(q,t)\gamma_L(t), q \in [q_L, q_P]$ and $J(q,t) = \rho(q,t)\gamma_P(t), q \in [q_P, q_A]$, we have

$$\begin{aligned}
\frac{\partial \rho(q,t)}{\partial t} &= -\frac{\partial}{\partial q}[\rho(q,t)\gamma_L(t)] - \delta_L(t)\rho(q,t) \quad q \in [q_L, q_P],\\
\frac{\partial \rho(q,t)}{\partial t} &= -\frac{\partial}{\partial q}[\rho(q,t)\gamma_P(t)] - \delta_P(t)\rho(q,t) \quad q \in [q_P, q_A].
\end{aligned}$$

By similar arguments to what are used in deriving the form of $R_L(t)$, we obtain

$$R_P(t) = \gamma_L(t)\rho(q_P,t) = R_L(t - \tau_L(t))(1 - \tau_L'(t))e^{-\int_{t-\tau_L(t)}^{t}\delta_L(\alpha)\mathrm{d}\alpha},$$

and

$$R_A(t) = \gamma_P(t)\rho(q_A,t) = R_P(t - \tau_P(t))(1 - \tau_P'(t))e^{-\int_{t-\tau_P(t)}^{t}\delta_P(\alpha)\mathrm{d}\alpha}.$$

In virtue of (5), (8) and (9), it easily follows that if $\gamma_x(t)$ is a periodic function, then so is $\tau_x(t)$ with the same period ($x = E$, L or P).

Substituting the expressions of $R_L(t)$, $R_P(t)$ and $R_A(t)$ into system (1) and denoting

$$\begin{aligned}
m_E(t) &= t - \tau_E(t),\\
h_L(t) &= t - \tau_L(t),\\
h_E(t) &= m_E(h_L(t)) = h_L(t) - \tau_E(h_L(t)) = t - \tau_L(t) - \tau_E(t - \tau_L(t))\\
g_P(t) &= t - \tau_P(t),\\
g_L(t) &= h_L(g_P(t)) = g_P(t) - \tau_L(g_P(t)) = t - \tau_P(t) - \tau_L(t - \tau_P(t))\\
f(t) &= m_E(g_L(t)) = g_L(t) - \tau_E(g_L(t))\\
&= t - \tau_P(t) - \tau_L(t - \tau_P(t)) - \tau_E(t - \tau_P(t) - \tau_L(t - \tau_P(t)))
\end{aligned}$$

we arrive at the following model system:

$$\begin{aligned}
\frac{\mathrm{d}E(t)}{\mathrm{d}t} &= b(t)A(t) - b(m_E(t))A(m_E(t))(1 - \tau_E'(t))e^{-\int_{m_E(t)}^{t}\delta_E(\alpha)\mathrm{d}\alpha} - \delta_E(t)E(t),\\
\frac{\mathrm{d}L(t)}{\mathrm{d}t} &= b(m_E(t))A(m_E(t))(1 - \tau_E'(t))e^{-\int_{m_E(t)}^{t}\delta_E(\alpha)\mathrm{d}\alpha} - b(h_E(t))A(h_E(t))\\
&\quad \cdot (1 - \tau_E'(h_L(t)))e^{-\int_{h_E(t)}^{h_L(t)}\delta_E(\alpha)\mathrm{d}\alpha}(1 - \tau_L'(t))e^{-\int_{h_L(t)}^{t}\delta_L(\alpha)\mathrm{d}\alpha}\\
&\quad - \delta_L(t)L(t),
\end{aligned}$$

Table 1 Biological interpretations for parameters of model (10)

Parameters	Description
$b(t)$	Oviposition rate
$\delta_E(t)$	Per capita mortality rate of eggs
$\delta_L(t)$	Per capita mortality rate of larvae
$\delta_P(t)$	Per capita mortality rate of pupae
$\delta_A(t)$	Per capita mortality rate of adults
$\tau_E(t)$	Duration of the egg stage
$\tau_L(t)$	Duration of the larva stage
$\tau_P(t)$	Duration of the pupa stage
k	Proportion of new adult mosquitoes that are females

$$\begin{aligned}
\frac{\mathrm{d}P(t)}{\mathrm{d}t} &= b(h_E(t))A(h_E(t))(1-\tau_E'(h_L(t)))e^{-\int_{h_E(t)}^{h_L(t)}\delta_E(\alpha)\mathrm{d}\alpha}(1-\tau_L'(t))\\
&\quad\cdot e^{-\int_{h_L(t)}^{t}\delta_L(\alpha)\mathrm{d}\alpha} - b(f(t))A(f(t))(1-\tau_E'(g_L(t)))e^{-\int_{f(t)}^{g_L(t)}\delta_E(\alpha)\mathrm{d}\alpha}\\
&\quad\cdot(1-\tau_L'(g_P(t)))e^{-\int_{g_L(t)}^{g_P(t)}\delta_L(\alpha)\mathrm{d}\alpha}(1-\tau_P'(t))e^{-\int_{g_P(t)}^{t}\delta_P(\alpha)\mathrm{d}\alpha}\\
&\quad-\delta_P(t)P(t),\\
\frac{\mathrm{d}A(t)}{\mathrm{d}t} &= kb(f(t))A(f(t))(1-\tau_E'(g_L(t)))e^{-\int_{f(t)}^{g_L(t)}\delta_E(\alpha)\mathrm{d}\alpha}(1-\tau_L'(g_P(t)))\\
&\quad\cdot e^{-\int_{g_L(t)}^{g_P(t)}\delta_L(\alpha)\mathrm{d}\alpha}(1-\tau_P'(t))e^{-\int_{g_P(t)}^{t}\delta_P(\alpha)\mathrm{d}\alpha} - \delta_A(t)A(t),
\end{aligned}\tag{10}$$

where k is a positive constant and $b(t)$, $\delta_E(t)$, $\delta_L(t)$, $\delta_P(t)$, $\delta_A(t)$, $\tau_E(t)$, $\tau_L(t)$, $\tau_P(t)$ are positive, continuous and ω-periodic functions for some $\omega > 0$. The biological interpretations for the parameters of model (10) are listed in Table 1.

It is easy to see that the functions

$$\begin{aligned}
a_1(t) &:= e^{-\int_{t-\tau_E(t)}^{t}\delta_E(\alpha)\mathrm{d}\alpha},\\
a_2(t) &:= e^{-\int_{t-\tau_L(t)-\tau_E(t-\tau_L(t))}^{t-\tau_L(t)}\delta_E(\alpha)\mathrm{d}\alpha},\\
a_3(t) &:= e^{-\int_{t-\tau_L(t)}^{t}\delta_L(\alpha)\mathrm{d}\alpha},\\
a_4(t) &:= e^{-\int_{t-\tau_P(t)-\tau_L(t-\tau_P(t))}^{t-\tau_P(t)}\delta_L(\alpha)\mathrm{d}\alpha},\\
a_5(t) &:= e^{-\int_{t-\tau_P(t)}^{t}\delta_P(\alpha)\mathrm{d}\alpha},\\
a_6(t) &:= e^{-\int_{t-\tau_P(t)-\tau_L(t-\tau_P(t))-\tau_E(t-\tau_P(t)-\tau_L(t-\tau_P(t)))}^{t-\tau_P(t)-\tau_L(t-\tau_P(t))}\delta_E(\alpha)\mathrm{d}\alpha},
\end{aligned}$$

are also ω-periodic. Thus, model (10) can be written as $u'(t) = F(t, u_t)$ with $F(t+\omega, \phi) = F(t, \phi)$, and hence, it is an ω-periodic system of functional differential equations.

3 Threshold Dynamics

In this section, we study the global dynamics of system (10). The basic reproduction number, denoted by R_0, is the threshold quantity which measures the average expected number of new female adult offsprings produced by a single female adult mosquito during its life time (Abdelrazec and Gumel 2017). Ever since the works on R_0 by Diekmann et al. (1990) and van den Driessche and Watmough (2002), there have been many studies on the theory and applications of R_0 for population models in a periodic environment (see, e.g. Bacaër and Ait Dads 2012; Bacaër and Guernaoui 2006; Inaba 2012; Thieme 2009; Wang and Zhao 2008; Zhao 2017a, b and the references therein). In what follows, we use the theory in Zhao (2017a) to derive the basic reproduction number R_0. Since each of the first three equations of system (10) is decoupled from the other equations and the fourth equation is also decoupled from the other three, it suffices to study the fourth, i.e. the following equation:

$$\begin{aligned}\frac{\mathrm{d}A(t)}{\mathrm{d}t} &= kb(f(t))A(f(t))(1-\tau_E'(g_L(t)))e^{-\int_{f(t)}^{g_L(t)}\delta_E(\alpha)\mathrm{d}\alpha}(1-\tau_L'(g_P(t)))\\ &\quad\cdot e^{-\int_{g_L(t)}^{g_P(t)}\delta_L(\alpha)\mathrm{d}\alpha}(1-\tau_P'(t))e^{-\int_{g_P(t)}^{t}\delta_P(\alpha)\mathrm{d}\alpha}-\delta_A(t)A(t),\end{aligned} \tag{11}$$

Denote

$$\begin{aligned}B(t) &= kb(f(t))(1-\tau_E'(g_L(t)))e^{-\int_{f(t)}^{g_L(t)}\delta_E(\alpha)\mathrm{d}\alpha}(1-\tau_L'(g_P(t)))e^{-\int_{g_L(t)}^{g_P(t)}\delta_L(\alpha)\mathrm{d}\alpha}\\ &\quad\cdot(1-\tau_P'(t))e^{-\int_{g_P(t)}^{t}\delta_P(\alpha)\mathrm{d}\alpha}.\end{aligned}$$

Then system (11) can be rewritten as

$$\frac{\mathrm{d}A(t)}{\mathrm{d}t} = B(t)A(f(t)) - \delta_A(t)A(t). \tag{12}$$

Let $\hat{\tau} = \max\{\max_{t\in[0,\omega]}\tau_E(t), \max_{t\in[0,\omega]}\tau_L(t), \max_{t\in[0,\omega]}\tau_P(t)\}$, $C = C([-3\hat{\tau},0],\mathbb{R})$, $C^+ = C([-3\hat{\tau},0],\mathbb{R}_+)$. Then (C, C^+) is an ordered Banach space equipped with the maximum norm and the partial order induced by the positive cone C^+. For any given continuous function $v : [-3\hat{\tau},\sigma) \to \mathbb{R}$ with $\sigma > 0$, we define $v_t \in C$ by

$$v_t(\theta) = v(t+\theta), \quad \forall\theta \in [-3\hat{\tau}, 0]$$

for any $t \in [0,\sigma)$.

Equation (12) is linear with the recruitment represented by $F : \mathbb{R} \to \mathcal{L}(C,\mathbb{R})$ defined by

$$F(t)\varphi = B(t)\varphi(-\tau_P(t) - \tau_L(t-\tau_P(t)) - \tau_E(t-\tau_P(t)-\tau_L(t-\tau_P(t)))).$$

The evolution of the existing adult population is governed by the periodic ordinary differential equation

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = -\delta_A(t)u(t).$$

Let $\Phi(t, s)$, $t \geq s$, be the evolution operator of the above linear system, that is, $\Phi(t, s)$ satisfies

$$\frac{\partial}{\partial t}\Phi(t, s) = -\delta_A(t)\Phi(t, s),\ \forall t \geq s, \quad \text{and} \quad \Phi(s, s) = 1,\ \forall s \in \mathbb{R}.$$

It then easily follows that $\Phi(t, s) = e^{-\int_s^t \delta_A(r)dr}$.

Let C_ω be the ordered Banach space of all continuous and ω-periodic functions from $\mathbb{R}$ to $\mathbb{R}$, which is equipped with the maximum norm and the positive cone $C_\omega^+ := \{v \in C_\omega : v(t) \geq 0, \forall t \in \mathbb{R}\}$.

Suppose that $v \in C_\omega$ is the initial number of adult female mosquitoes. Then for any given $s \geq 0$, $F(t-s)v_{t-s}$ is the number of female mosquitoes that are newly recruited into adult stage per unit time at time $t-s$, which are produced by the adult female mosquitoes who were introduced over the time interval $[t-s-3\hat{\tau}, t-s]$. Then $\Phi(t, t-s)F(t-s)v_{t-s}$ is the number of those adult female mosquitoes who newly became adult at time $t-s$ and remain alive at time t. It follows that

$$\int_0^\infty \Phi(t, t-s)F(t-s)v_{t-s}\mathrm{d}s = \int_0^\infty \Phi(t, t-s)F(t-s)v(t-s+\cdot)\mathrm{d}s$$

is the number of accumulative new adult females at time t produced by all those adult female mosquitoes introduced at all previous time to t.

Define a linear operator $L : C_\omega \to C_\omega$ by

$$[Lv](t) = \int_0^\infty \Phi(t, t-s)F(t-s)v(t-s+\cdot)\mathrm{d}s, \quad \forall t \in \mathbb{R}, \quad v \in C_\omega.$$

Following (Zhao 2017a), we define $R_0 = r(L)$, the spectral radius of L.

By Hale and Verduyn Lunel (1993, Theorem 6.1.1) and Smith (1995, Theorem 5.2.1), we obtain the following result for linear system (12).

Lemma 1 *For any $\varphi \in C$, system (12) has a unique solution $y(t, \varphi)$ for $t \geq 0$ with $y_0 = \varphi$; moreover, if $\varphi \in C^+$, then $y(t, \varphi) \geq 0$ for all $t \geq 0$.*

Let $\hat{P}(t)$ be the solution maps of system (12) on C, that is, $\hat{P}(t)\varphi = y_t(\varphi)$, $t \geq 0$, where $y(t, \varphi)$ is the unique solution of (12) with $y_0 = \varphi \in C$. Then $\hat{P} := \hat{P}(\omega)$ is the Poincaré map associated with linear system (12). Let $r(\hat{P})$ be the spectral radius of $\hat{P}$. By Zhao (2017a, Theorem 2.1), we have the following result.

Lemma 2 *$R_0 - 1$ has the same sign as $r(\hat{P}) - 1$.*

Let

$$\Omega := C([-\tau_P(0) - \tau_L(-\tau_P(0)) - \tau_E(-\tau_P(0) - \tau_L(-\tau_P(0))), 0], \mathbb{R}_+).$$

We then have the following preliminary result for system (12).

Lemma 3 *For any $\varphi \in \Omega$, system* (12) *has a unique solution $z(t, \varphi)$ with $z_0 = \varphi$, and $z_t(\varphi) \in \Omega$ for all $t \geq 0$.*

Proof Since $g_P(t) = t - \tau_P(t)$, $g_L(t) = g_P(t) - \tau_L(g_P(t))$, $f(t) = g_L(t) - \tau_E(g_L(t))$, $1 - \tau'_P(t) > 0$, $1 - \tau'_L(t) > 0$ and $1 - \tau'_E(t) > 0$, it then easily follows that $g_P(t)$, $g_L(t)$ and $f(t)$ are strictly increasing in t.

Let $\bar{\tau} = \min\{\min_{t\in[0,\omega]} \tau_E(t), \min_{t\in[0,\omega]} \tau_L(t), \min_{t\in[0,\omega]} \tau_P(t)\}$. For any $t \in [0, \bar{\tau}]$, we have

$$\begin{aligned}
&-\tau_P(0) \leq g_P(t) \leq \bar{\tau} - \tau_P(\bar{\tau}) \leq \bar{\tau},\\
&\Rightarrow -\tau_P(0) - \tau_L(-\tau_P(0)) \leq g_L(t) \leq \bar{\tau} - \tau_L(\bar{\tau}) \leq \bar{\tau},\\
&\Rightarrow -\tau_P(0) - \tau_L(-\tau_P(0)) - \tau_E(-\tau_P(0) - \tau_L(-\tau_P(0))) \leq f(t)\\
&\leq \bar{\tau} - \tau_E(\bar{\tau}) \leq \bar{\tau} - \bar{\tau} = 0,
\end{aligned}$$

and hence,

$$z(f(t)) = \varphi(f(t)).$$

Therefore, we have the following ordinary differential equation for $t \in [0, \bar{\tau}]$:

$$\frac{\mathrm{d}z(t)}{\mathrm{d}t} = B(t)\varphi(f(t)) - \delta_A(t)z(t).$$

Given $\varphi \in \Omega$, the solution $z(t)$ of the above equation exists for $t \in [0, \bar{\tau}]$. In other words, we have obtained values of $\psi(\theta) = z(\theta)$ for $\theta \in [-\tau_P(0) - \tau_L(-\tau_P(0)) - \tau_E(-\tau_P(0) - \tau_L(-\tau_P(0))), \bar{\tau}]$.

For any $t \in [\bar{\tau}, 2\bar{\tau}]$, we have

$$\begin{aligned}
&-\tau_P(0) = 0 - \tau_P(0) \leq \bar{\tau} - \tau_P(\bar{\tau}) \leq g_P(t) \leq 2\bar{\tau} - \tau_P(2\bar{\tau}) \leq 2\bar{\tau},\\
&\Rightarrow -\tau_P(0) - \tau_L(-\tau_P(0)) \leq g_L(t) \leq 2\bar{\tau} - \tau_L(2\bar{\tau}) \leq 2\bar{\tau},\\
&\Rightarrow -\tau_P(0) - \tau_L(-\tau_P(0)) - \tau_E(-\tau_P(0) - \tau_L(-\tau_P(0))) \leq f(t)\\
&\leq 2\bar{\tau} - \tau_E(2\bar{\tau}) \leq 2\bar{\tau} - \bar{\tau} = \bar{\tau},
\end{aligned}$$

and hence, $z(f(t)) = \psi(f(t))$. Solving the following ordinary differential equation for $t \in [\bar{\tau}, 2\bar{\tau}]$ with $z(\bar{\tau}) = \psi(\bar{\tau})$:

$$\frac{\mathrm{d}z(t)}{\mathrm{d}t} = B(t)\psi(f(t)) - \delta_A(t)z(t),$$

we then get the solution $z(t)$ on $[\bar{\tau}, 2\bar{\tau}]$. Repeating this procedure for $t \in [2\bar{\tau}, 3\bar{\tau}]$, $[3\bar{\tau}, 4\bar{\tau}], \ldots$, it then follows that for any $\varphi \in \Omega$, system (12) has a unique solution $z(t, \varphi)$ with $z_0 = \varphi$ and $z_t(\varphi) \in \Omega$ for all $t \geq 0$. □

Remark 1 By the uniqueness of solutions in Lemmas 1 and 3, it follows that for any $\psi \in C_+$ and $\phi \in \Omega$ with $\psi(\theta) = \phi(\theta)$ for all $\theta \in [-\tau_P(0) - \tau_L(-\tau_P(0)) -$

$\tau_E(-\tau_P(0)-\tau_L(-\tau_P(0))), 0]$, we have $y(t,\psi)=z(t,\phi)$ for all $t\geq 0$, where $y(t,\psi)$ and $z(t,\phi)$ are solutions of system (12) satisfying $y_0=\psi$ and $z_0=\phi$, respectively.

Let $P(t)$ be the solution maps of system (12) on Ω, that is, $P(t)\varphi=z_t(\varphi)$, $t\geq 0$, where $z(t,\varphi)$ is the unique solution of system (12) with $z_0=\varphi\in\Omega$. By the arguments similar to those in Lou and Zhao (2017, Lemma 3.5), we have the following result.

Lemma 4 *$P(t):\Omega\to\Omega$ is an ω-periodic semiflow in the sense that $(i)P(0)=I$; $(ii)P(t+\omega)=P(t)\circ P(\omega)$, $\forall t\geq 0$; $(iii)P(t)\varphi$ is continuous in $(t,\varphi)\in[0,\infty)\times\Omega$.*

Let $P=P(\omega)$ be the Poincaré map of the linear system (12) on the space Ω, and $r(P)$ be its spectral radius. Then we have the following threshold type result for system (12).

Lemma 5 *The following statements are valid:*

(i) *If $r(P)<1$, then $\lim_{t\to\infty}A(t,\varphi)=0$ for any $\varphi\in\Omega$.*
(ii) *If $r(P)>1$, then $\lim_{t\to\infty}A(t,\varphi)=+\infty$ for any $\varphi\in\Omega\setminus\{0\}$.*

Proof For any given $\varphi,\psi\in\Omega$ with $\varphi\geq\psi$, let $\bar{u}(t)=u(t,\varphi)$ and $u(t)=u(t,\psi)$ be the unique solutions of system (12) with $u_0=\varphi$ and $u_0=\psi$, respectively. Let $\bar{\tau}=\min\{\min_{t\in[0,\omega]}\tau_E(t), \min_{t\in[0,\omega]}\tau_L(t), \min_{t\in[0,\omega]}\tau_P(t)\}$.

Since for any $t\in[0,\bar{\tau}]$,

$$-\tau_P(0)-\tau_L(-\tau_P(0))-\tau_E(-\tau_P(0)-\tau_L(-\tau_P(0)))\leq f(t)\leq 0,$$

we have $\bar{u}(f(t))=\varphi(f(t))$ and $u(f(t))=\psi(f(t))$ for all $t\in[0,\bar{\tau}]$, and hence, $\bar{u}(f(t))\geq u(f(t))$ for all $t\in[0,\bar{\tau}]$. In view of $\bar{u}(0)=\varphi(0)\geq\psi(0)=u(0)$, the comparison theorem for cooperative ordinary differential equation systems implies that $\bar{u}(t)\geq u(t)$ for all $t\in[0,\bar{\tau}]$. Repeating this procedure for $t\in[\bar{\tau},2\bar{\tau}],[2\bar{\tau},3\bar{\tau}],\ldots$, it follows that $u(t,\varphi)\geq u(t,\psi)$ for all $t\geq 0$. This implies that $P(t):\Omega\to\Omega$ is monotone for each $t\geq 0$. Next we show that the solution map $P(t):\Omega\to\Omega$ is eventually strongly monotone. Let $\varphi,\psi\in\Omega$ satisfy $\varphi>\psi$. Denote $u(t,\varphi)=\bar{y}(t)$ and $u(t,\psi)=y(t)$.

Since $f(t)$ is continuous and strictly increasing in t, there exists a unique solution to the equation $f(t)=0$. Denote the unique solution of $f(t)=0$ as $\bar{t}$, i.e. $f(\bar{t})=0$. We first prove that $\bar{y}(t_0)>y(t_0)$ for some $t_0\in[0,\bar{t}]$. Otherwise, we have $\bar{y}(t)=y(t)$ for all $t\in[0,\bar{t}]$, and hence, $\frac{\mathrm{d}\bar{y}(t)}{\mathrm{d}t}=\frac{dy(t)}{dt}$ for all $t\in(0,\bar{t})$. Thus, we have $B(t)[\bar{y}(f(t))-y(f(t))]=0$, $\forall t\in[0,\bar{t}]$. It follows that $\bar{y}(f(t))=y(f(t))$ for all $t\in[0,\bar{t}]$, that is, $\varphi(\theta)=\psi(\theta)$ for all $\theta\in[-\tau_P(0)-\tau_L(-\tau_P(0))-\tau_E(-\tau_P(0)-\tau_L(-\tau_P(0))),0]$, which contradicts the assumption that $\varphi>\psi$.

Let

$$g(t,x):=B(t)y(f(t))-\delta_A(t)x.$$

Since

$$\begin{aligned}\frac{\mathrm{d}\bar{y}(t)}{\mathrm{d}t}&=B(t)\bar{y}(f(t))-\delta_A(t)\bar{y}(t)\\&\geq B(t)y(f(t))-\delta_A(t)\bar{y}(t)\\&=g(t,\bar{y}(t)),\end{aligned}$$

we have

$$\frac{\mathrm{d}\bar{y}(t)}{\mathrm{d}t} - g(t, \bar{y}(t)) \geq 0 = \frac{\mathrm{d}y(t)}{\mathrm{d}t} - g(t, y(t)), \ \ \forall t \geq t_0.$$

Since $\bar{y}(t_0) > y(t_0)$, the comparison theorem for ordinary differential equations (Walter 1997, Theorem 4) implies that $\bar{y}(t) > y(t)$ for all $t \geq t_0$. It follows that

$$\bar{y}_t > y_t, \quad \forall t > \bar{t} - f(0).$$

This shows that $P(t) : \Omega \to \Omega$ is strongly monotone for any $t > \bar{t} - f(0)$. It follows from (Hale and Verduyn Lunel 1993, Theorem 3.6.1) that the linear operator $P(t)$ is compact on Ω. Choose an integer n_0 such that $n_0\omega > \bar{t} - f(0)$. Since $P^{n_0} = P(n_0\omega)$, (Liang and Zhao 2007, Lemma 3.1) implies that $r(P)$ is a simple eigenvalue of P having a strongly positive eigenvector, and the modulus of any other eigenvalue is less than $r(P)$. It then follows from (Wang and Zhao 2017b, Lemma 1) that there is a positive ω-periodic function $\bar{v}(t)$ such that $v^*(t) = e^{\frac{\ln r(P)}{\omega}t}\bar{v}(t)$ is a positive solution of system (12).

In the case $r(P) < 1$, we have $\lim_{t\to\infty} v^*(t) = 0$. For any $\varphi \in \Omega$, choose a sufficiently large number $K > 0$ such that $\varphi \leq Kv_0^*$. Then by the comparison theorem, we have

$$A(t, \varphi) \leq Kv^*(t), \quad \forall t \geq 0.$$

Hence, $\lim_{t\to\infty} A(t, \varphi) = 0$. This proves statement (i).

In the case $r(P) > 1$, we have $\lim_{t\to\infty} v^*(t) = \infty$. For any $\varphi \in \Omega \setminus \{0\}$, we can choose a sufficiently small real number $\delta > 0$ such that $\varphi(\theta) \geq \delta v^*(\theta), \theta \in [f(0), 0]$. Then by the comparison theorem, we have $A(t, \varphi) \geq \delta v^*(t)$ for all $t \geq 0$. Hence, $\lim_{t\to\infty} A(t, \varphi) = \infty$. This proves statement (ii). □

By the same arguments as in Lou and Zhao (2017, Lemma 3.8), we have $r(P) = r(\hat{P})$. Combining Lemmas 2 and 5 we have the following result on the global dynamics of system (12).

Theorem 1 *The following statements are valid for system* (12)*:*

(i) *If $R_0 < 1$, then the zero solution is globally attractive for system* (12) *in Ω;*
(ii) *If $R_0 > 1$, then all nontrivial solutions of system* (12) *go to infinity eventually.*

In the rest of this section, we derive the dynamics for the variables $E(t)$, $L(t)$ and $P(t)$ in system (10). Under the compatibility conditions

$$\begin{aligned} E(0) &= \int_{-\tau_E(0)}^{0} b(\xi)A(\xi)e^{-\int_\xi^0 \delta_E(s)\mathrm{d}s}\mathrm{d}\xi, \\ L(0) &= \int_{-\tau_L(0)}^{0} R_L(\xi)e^{-\int_\xi^0 \delta_L(s)\mathrm{d}s}\mathrm{d}\xi, \\ P(0) &= \int_{-\tau_P(0)}^{0} R_P(\xi)e^{-\int_\xi^0 \delta_P(s)\mathrm{d}s}\mathrm{d}\xi, \end{aligned} \tag{13}$$

we can solve $E(t)$, $L(t)$ and $P(t)$ as

$$\begin{aligned} E(t) &= \int_{t-\tau_E(t)}^{t} b(\xi)A(\xi)e^{-\int_{\xi}^{t}\delta_E(s)\mathrm{d}s}\mathrm{d}\xi, \\ L(t) &= \int_{t-\tau_L(t)}^{t} R_L(\xi)e^{-\int_{\xi}^{t}\delta_L(s)\mathrm{d}s}\mathrm{d}\xi, \\ P(t) &= \int_{t-\tau_P(t)}^{t} R_P(\xi)e^{-\int_{\xi}^{t}\delta_P(s)\mathrm{d}s}\mathrm{d}\xi, \end{aligned} \tag{14}$$

In the case where $R_0 < 1$, we have $\lim_{t\to\infty} A(t) = 0$. It then follows from (14) that

$$\lim_{t\to\infty}(E(t), L(t), P(t)) = 0.$$

In the case where $R_0 > 1$, we have $\lim_{t\to\infty} A(t) = +\infty$. From (14) it is easy to show that

$$\lim_{t\to\infty}(E(t), L(t), P(t)) = +\infty.$$

Consequently, we have the following result on the global dynamics of system (10).

Theorem 2 *The following statements are valid for system* (10)*:*

(i) *If* $R_0 < 1$*, then* $(0, 0, 0, 0)$ *is globally attractive for system* (10)*;*
(ii) *If* $R_0 > 1$*, then the nontrivial solutions of system* (10) *go to infinity eventually.*

Remark 2 (On the dichotomy of either 0 or infinity) It is impossible for the mosquito population grows to infinity in natural environment. We get such a result when $R_0 > 1$ in Theorem 2 because our model is based on a laboratory experiment environment and the density-dependent mortality is ignored. We will further discuss possible extensions along this line in Sect. 5.

4 Numerical Simulations

Dengue is endemic in Sri Lanka, an island country in South Asia. According to the report of the Epidemiology Unit of the Ministry of Health (MoH) Sri Lanka, there are 80732 dengue fever cases including 215 deaths from 1 January to 7 July 2017. World Health Organization (WHO) is supporting the MoH Sri Lanka to ensure comprehensive and efficient response measures. In this section, we use the temperature data of Colombo, Sri Lanka (given in Table 2) to derive the formulas for the periodic parameters. Then we numerically calculate the basic reproduction number and verify the analytic result obtained in the last section. Assuming that the sex ratio of adult mosquitoes is $1:1$, we take $k = 1/2$.

Using the Curve Fitting Toolbox in MATLAB we get the following function which approximately describes how temperature varies seasonally in Colombo, Sri Lanka (See Fig. 1 for the fitted curve).

Table 2 Monthly mean temperature for Colombo, Sri Lanka (in °C)

Month	Jan	Feb	Mar	Apr	May	June
Temperature	26.45	27.26	28.36	28.58	28.64	27.92
Month	**Jul**	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**
Temperature	27.64	27.64	27.6	27.34	27.02	26.75

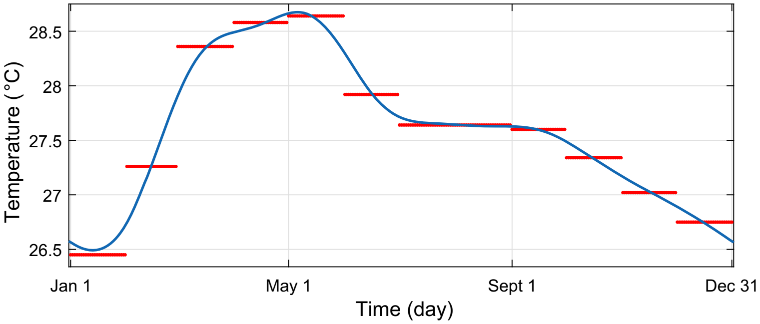


Fig. 1 (Color figure online) Fitted curve for temperature of Colombo, Sri Lanka

$$
\begin{aligned}
T(t) = &-0.6248\cos(2\pi t/365) + 0.4664\sin(2\pi t/365) - 0.4392\cos(4\pi t/365)\\
&- 0.1597\sin(4\pi t/365) + 0.006974\cos(6\pi t/365) - 0.09078\sin(6\pi t/365)\\
&- 0.03427\cos(8\pi t/365) - 0.08193\sin(8\pi t/365) + 0.05021\cos(10\pi t/365)\\
&- 0.05556\sin(10\pi t/365) + 0.01499\cos(12\pi t/365)\\
&+ 0.02312\sin(12\pi t/365) + 27.6.
\end{aligned}
$$

Recently, Yang et al. (2009) conducted a temperature-controlled experiment to assess the effects of temperature on the *Aedes aegypti* population. Based on their experimental results, they adjusted the oviposition rate, the mortality rate of aquatic stages (larval and pupal) and the mortality rate of adult females, respectively, by the following polynomials:

$$
\begin{aligned}
b(T) &= -5.4 + 1.8T - 0.2124T^2 + 1.015\times 10^{-2}T^3 - 1.515\times 10^{-4}T^4,\\
\delta(T) &= b_0 + b_1T + b_2T^2 + b_3T^3 + b_4T^4,\\
\delta_A(T) &= c_0 + c_1T + c_2T^2 + c_3T^3 + c_4T^4,
\end{aligned}
$$

where T is the temperature (in $^\circ C$) and $b_0 = 2.13$, $b_1 = -3.797\times 10^{-1}$, $b_2 = 2.457\times 10^{-2}$, $b_3 = -6.778\times 10^{-4}$, $b_4 = 6.794\times 10^{-6}$, $c_0 = 8.692\times 10^{-1}$, $c_1 = -1.590\times 10^{-1}$, $c_2 = 1.116\times 10^{-2}$, $c_3 = -3.408\times 10^{-4}$, $c_4 = 3.809\times 10^{-6}$. Plugging in the temperature function $T(t)$ into $b(T)$, $\delta(T)$ and $\delta_A(T)$ we get the oviposition rate function $b(t)$ and mortality rate functions $\delta(t)$ (for larval and pupal stages) and $\delta_A(t)$ (for adult) as follows.

$$
\begin{aligned}
b(t) = &-0.3461\cos(2\pi t/365) - 0.2318\cos(4\pi t/365) - 0.0143\cos(6\pi t/365)\\
&- 0.01718\cos(8\pi t/365) + 0.02681\cos(10\pi t/365)\\
&+ 0.007914\cos(12\pi t/365) + 0.2167\sin(2\pi t/365)\\
&- 0.07796\sin(4\pi t/365) - 0.04793\sin(6\pi t/365)\\
&- 0.05344\sin(8\pi t/365) - 0.02979\sin(10\pi t/365)\\
&+ 0.006904\sin(12\pi t/365) + 7.942,\\
\delta(t) = &\ 0.000513\cos(2\pi t/365) - 0.0006237\sin(2\pi t/365)\\
&+ 0.0003774\cos(4\pi t/365) + 0.0002605\sin(4\pi t/365)\\
&- 0.0001673\cos(6\pi t/365) + 7.95\times 10^{-5}\sin(6\pi t/365)\\
&- 2.573\times 10^{-6}\cos(8\pi t/365) + 1.985\times 10^{-5}\sin(8\pi t/365)\\
&- 7.88\times 10^{-5}\cos(10\pi t/365) + 1.501\times 10^{-5}\sin(10\pi t/365)\\
&- 2.842\times 10^{-6}\cos(12\pi t/365) - 7.536\times 10^{-5}\sin(12\pi t/365)\\
&+ 2.815\times 10^{-5}\cos(14\pi t/365) - 5.796\times 10^{-6}\sin(14\pi t/365) + 0.05847,\\
\delta_A(t) = &\ 0.000961\cos(2\pi t/365) + 0.0006243\cos(4\pi t/365)\\
&+ 9.585\times 10^{-5}\cos(6\pi t/365) + 4.681\times 10^{-5}\cos(8\pi t/365)\\
&- 6.948\times 10^{-5}\cos(10\pi t/365) - 2.454\times 10^{-5}\cos(12\pi t/365)\\
&- 0.0005156\sin(2\pi t/365) + 0.000163\sin(4\pi t/365)\\
&+ 0.0001273\sin(6\pi t/365) + 0.0001716\sin(8\pi t/365)\\
&+ 8.356\times 10^{-5}\sin(10\pi t/365)\\
&- 3.562\times 10^{-6}\sin(12\pi t/365) + 0.0273.
\end{aligned}
$$

However, obtaining the overall mortality rate function $\delta(t)$ for larval and pupal stages together is not enough. We need the respective mortality rate functions for each stage of mosquitoes. To this end, we have to estimate the length of each stage. Indeed, it is also necessary to know the expressions of such duration functions $\tau_E(t)$, $\tau_L(t)$ and $\tau_P(t)$ to finish the numerical simulations. Marinho et al. (2016) collected samples of *Aedes aegypti* in three cities in Brazil and assessed their life cycles under different constant temperatures. The means of duration (days) of each stage under these constant temperatures are listed in Table 3. We take the average of the three duration values of these three cities at each temperature as the value of the duration corresponding to that temperature, and then adjust the relationship between the duration and the temperature by the following polynomials (see Fig. 2 for the graphs of these functions).

$$
\begin{aligned}
\tau_E(T) &= -0.000282T^4 + 0.03009T^3 - 1.14T^2 + 17.59T - 82.56,\\
\tau_L(T) &= -0.0006582T^4 + 0.06869T^3 - 2.575T^2 + 40.08T - 200.2,\\
\tau_P(T) &= -0.0002051T^4 + 0.01981T^3 - 0.6765T^2 + 9.3T - 36.67.
\end{aligned}
$$

Table 3 Means of development duration (days). Reproduced with permission from Marinho et al. (2016)

Regions	16 °C	22 °C	28 °C	33 °C	36 °C	Overall mean
Egg						
Campina Grande	13.4	7.68	3.35	2.70	3.66	5.86
João Pessoa	10.4	5.16	3.15	2.61	3.48	5.03
Patos	11.5	7.92	3.32	4.23	2.59	5.92
Average of the three cities	11.7667	6.92	3.2733	3.18	3.2433	5.6033
Larva						
Campina Grande	20.51	13.40	6.16	6.70	5.17	10.39
João Pessoa	19.86	12.49	7.20	6.12	5.26	10.19
Patos	20.19	12.12	7.25	7.12	5.43	10.42
Average of the three cities	20.1867	12.67	6.87	6.6467	5.2867	10.3333
Pupa						
Campina Grande	6.97	3.68	2.08	2.51	1.29	3.30
João Pessoa	5.95	3.25	2.16	2.69	1.50	3.11
Patos	7.06	3.38	2.51	1.88	1.30	3.22
Average of the three cities	6.66	3.4367	2.25	2.36	1.3633	3.21

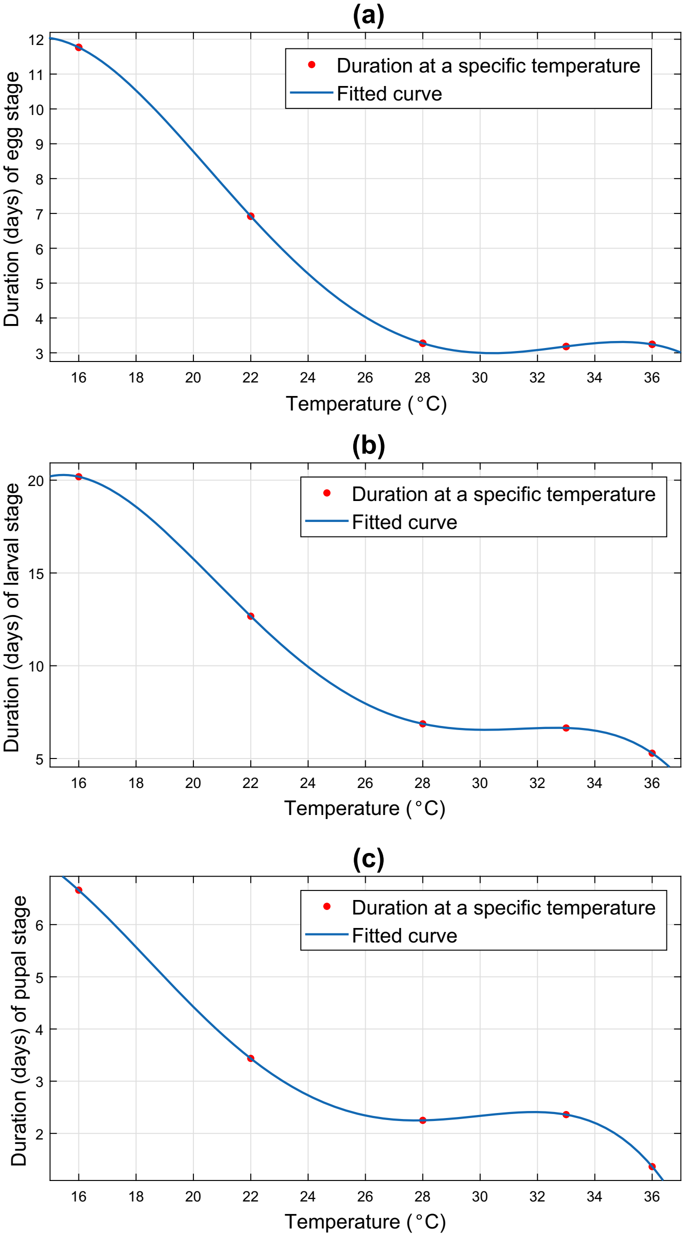


Fig. 2 (Color figure online) Fitted curve of development duration functions with respect to temperatures

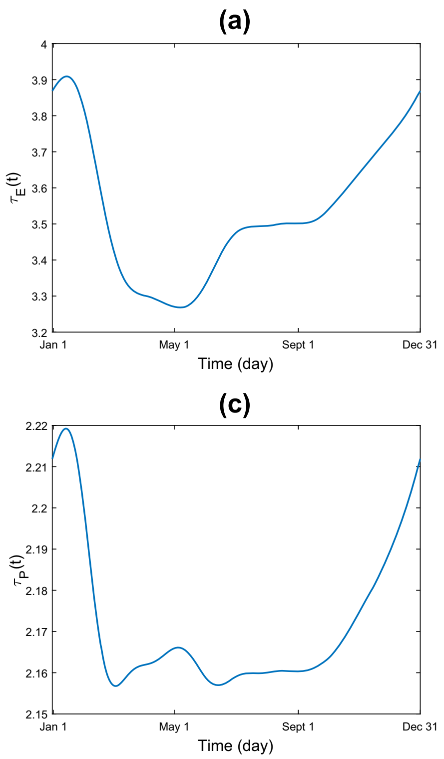


Fig. 3 (Color figure online) Development duration functions for the three aquatic stages of mosquitoes

By using the formula of the temperature function $T(t)$, we get the following duration functions in terms of time t (see Fig. 3 for the graphs).

$$\begin{aligned}
\tau_E(t) = {} & 0.1972\cos(2\pi t/365) - 0.1102\sin(2\pi t/365) + 0.1309\cos(4\pi t/365)\\
& + 0.0384\sin(4\pi t/365) + 0.01632\cos(6\pi t/365) + 0.02702\sin(6\pi t/365)\\
& + 0.0112\cos(8\pi t/365) + 0.03287\sin(8\pi t/365) - 0.01341\cos(10\pi t/365)\\
& + 0.01845\sin(10\pi t/365) - 0.004763\cos(12\pi t/365)\\
& - 0.001001\sin(12\pi t/365) - 0.003726\cos(14\pi t/365)\\
& + 0.0002592\sin(14\pi t/365) + 3.535,\\
\tau_L(t) = {} & 0.3011\cos(2\pi t/365) - 0.1639\sin(2\pi t/365) + 0.1995\cos(4\pi t/365)\\
& + 0.05676\sin(4\pi t/365) + 0.02762\cos(6\pi t/365) + 0.0412\sin(6\pi t/365)\\
& + 0.01768\cos(8\pi t/365) + 0.05094\sin(8\pi t/365) - 0.01979\cos(10\pi t/365)\\
& + 0.02873\sin(10\pi t/365) - 0.00741\cos(12\pi t/365)\\
& - 0.0005297\sin(12\pi t/365) - 0.006148\cos(14\pi t/365)\\
& + 0.0005606\sin(14\pi t/365) + 6.759,
\end{aligned}$$

$$\begin{aligned}\tau_P(t) = {} & 0.01964\cos(2\pi t/365) - 0.001059\sin(2\pi t/365) + 0.01194\cos(4\pi t/365)\\ & - 0.001411\sin(4\pi t/365) + 0.008138\cos(6\pi t/365)\\ & + 0.002024\sin(6\pi t/365) + 0.002489\cos(8\pi t/365)\\ & + 0.005095\sin(8\pi t/365) + 0.0002754\cos(10\pi t/365)\\ & + 0.002864\sin(10\pi t/365) - 0.0005423\cos(12\pi t/365)\\ & + 0.0022\sin(12\pi t/365) - 0.001453\cos(14\pi t/365)\\ & + 0.0004463\sin(14\pi t/365) - 0.0004065\cos(16\pi t/365)\\ & - 0.0002446\sin(16\pi t/365) - 0.0002068\cos(18\pi t/35)\\ & - 0.000118\sin(18\pi t/365) + 2.172.\end{aligned}$$

By averaging the overall means (the rightmost column of Table 3) of each stage duration, we estimated the length of each aquatic stage (egg, larva, pupa) as follows:

$$\begin{aligned}\bar{\tau}_E &= \frac{5.86 + 5.03 + 5.92}{3} = 5.6033,\\ \bar{\tau}_L &= \frac{10.39 + 10.19 + 10.42}{3} = 10.3333,\\ \bar{\tau}_P &= \frac{3.3 + 3.11 + 3.22}{3} = 3.2100.\end{aligned}$$

Let $1/\mu_L$ and $1/\mu_P$ be the proportions of the acquatic (larval and pupal) development time that larval and pupal stages make up, respectively. Then

$$\begin{aligned}\mu_L &\approx \frac{\bar{\tau}_L + \bar{\tau}_P}{\bar{\tau}_L} = 1.3106,\\ \mu_P &\approx \frac{\bar{\tau}_L + \bar{\tau}_P}{\bar{\tau}_P} = 4.2191\end{aligned}$$

and

$$\frac{1}{\mu_L} + \frac{1}{\mu_P} = 1.$$

It follows that

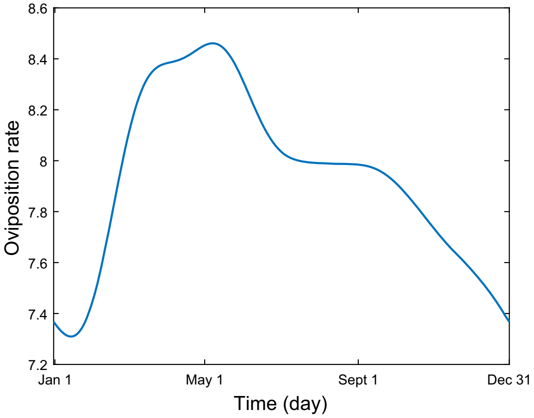
$$\delta_L(t) = \mu_L \delta(t) \quad \text{and} \quad \delta_P(t) = \mu_P \delta(t).$$

Further, we assume that

$$\delta_E(t) = \frac{\mu_E}{\mu_L}\delta_L(t),$$

where $\mu_E \approx \frac{\bar{\tau}_L}{\bar{\tau}_E}\mu_L = \frac{10.3333}{5.6033} \times 1.3106 = 2.4170$. The graphs of the oviposition rate function and the mortality rate functions are given in Figs. 4 and 5, respectively. To numerically calculate R_0, we use (Zhao 2017a, Theorem 2.2), (Liang et al. 2017,

Fig. 4 (Color figure online) Oviposition rate of mosquitoes



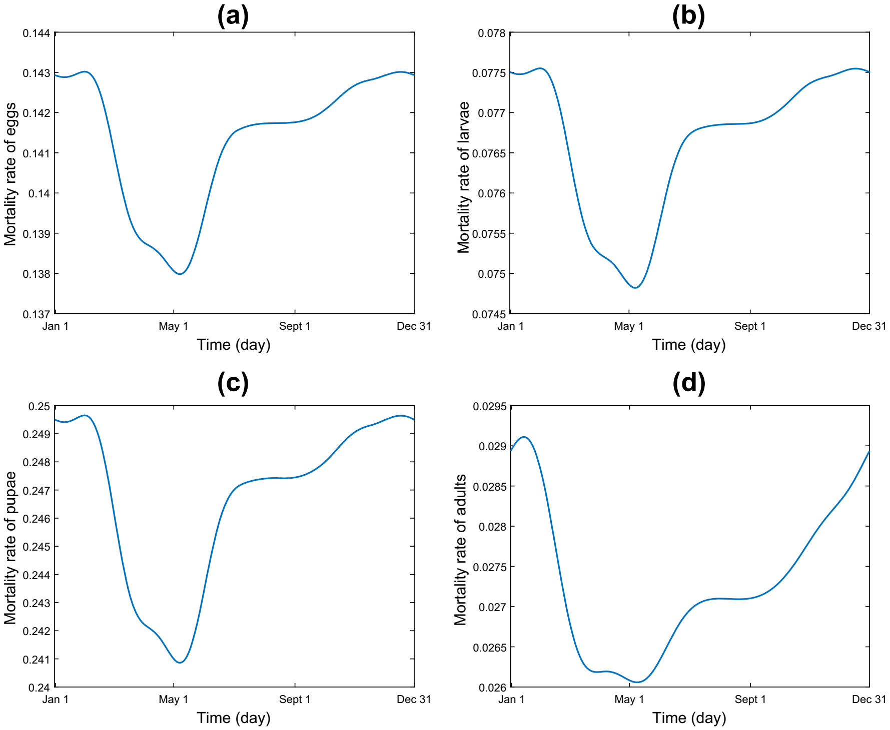
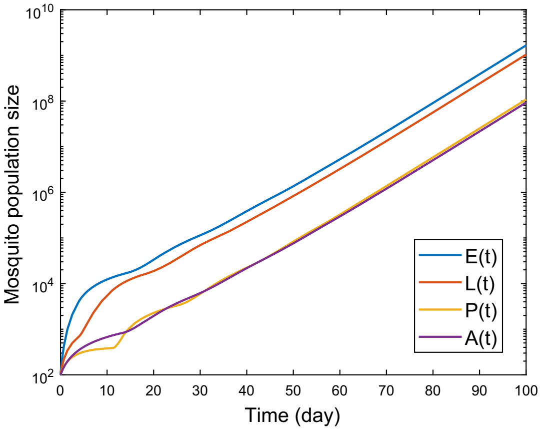


Fig. 5 (Color figure online) Mortality rate of mosquitoes

Lemma 2.5) and the bisection method. Using the above-estimated parameter values, we obtain $R_0 = 30.8563$. Figure 6 shows that the mosquito population keeps growing in this case.

Next, we investigate the effects of two possible measures for controlling mosquito population. The first strategy is to reduce the oviposition rate, which may be realized

Fig. 6 (Color figure online) Long-term behaviour of the solution. Here $R_0 = 30.8563$



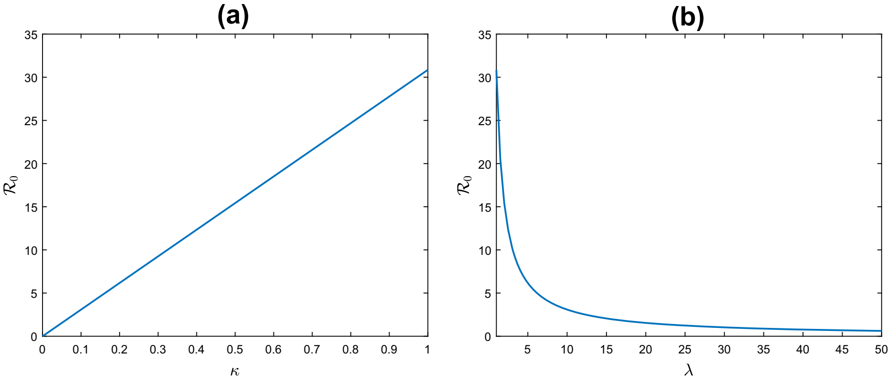


Fig. 7 (Color figure online) **a** R_0 as a function of κ, **b** R_0 as a function of λ

by elimination of mosquito breeding sites such as containers and discarded tires. By multiplying $b(t)$ by κ, $\kappa \in [0, 1]$ and keeping the other parameter values the same as those in Fig. 6, we can observe that R_0 is an increasing function of κ as shown in Fig. 7a. The second strategy is by increasing the mortality of adults, which may be obtained by indoor spraying of insecticide aerosol products. By multiplying $\delta_A(t)$ by λ, $\lambda \in [1, 50]$ and fixing the other parameter values the same as those in Fig. 6, we see that R_0 is a decreasing function of λ in Fig. 7b. Figure 7 indicates that decreasing the egg production rate and increasing the mortality of adults are probably effective methods in controlling mosquito population and it gives a quantitative evaluation of these two strategies. In Fig. 8, we choose two special values of κ and λ to see the effects of these two control measures. In Fig. 8a, we set $\kappa = 0.02$. In this case, $R_0 = 0.6171$ and we see that the mosquito population dies out eventually. In Fig. 8b, by fixing $\lambda = 50$, we get $R_0 = 0.6180$. In this case, the mosquito population also goes to extinction as time elapses. The numerical simulation results in Figs. 6 and 8 are consistent with the analytic result in Theorem 2.

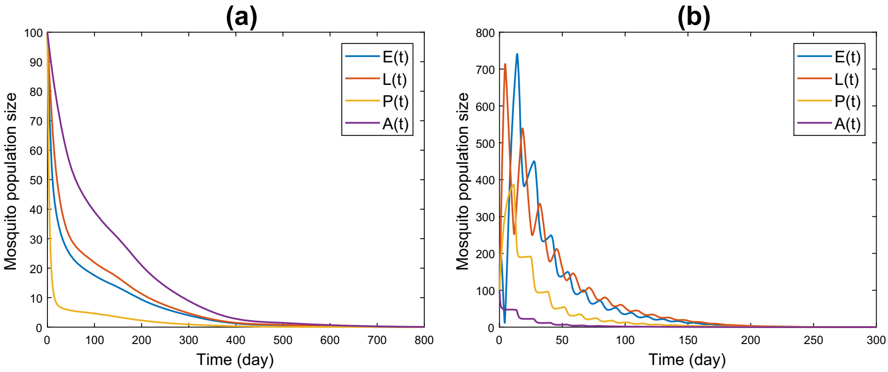


Fig. 8 (Color figure online) **a** $\kappa = 0.02$, $R_0 = 0.6171$, **b** $\lambda = 50$, $R_0 = 0.6180$

5 Discussion

In this paper, we developed a periodic delay differential equations model to estimate mosquito population size of each stage under the influence of temperature. Since each of the first three equations are decoupled from others, we convert the mathematical analysis of the model system into that of the last equation which is for the adult female mosquitoes. Then we derived the basic reproduction number R_0 for the model system. By using the theory of monotone dynamical systems and the comparison method, we showed the threshold dynamics of the system in terms of R_0. Biologically, the analytic result implies that the mosquito population goes to extinction eventually if $R_0 < 1$ and keeps growing to positive infinity if $R_0 > 1$. According to the recent laboratory experiment by Yang et al. (2009) and the field exploration result by Marinho et al. (2016), we obtained the function relationships between the entomological parameters and the temperature. Then we expressed the parameters as time-periodic functions using the temperature data from Colombo, Sri Lanka. The simulation results about long-term behaviours of the solutions are consistent with the analytic result. We also assessed two control measures quantitatively by showing the potential of reducing R_0. We found that both decreasing the oviposition rate and increasing the mortality rate of adult mosquitoes are effective measures in controlling mosquito population size. In order to decrease the oviposition rate, it is helpful to reduce mosquito breeding sites by elimination of discarded tires and draining of unnecessary containers (Thomé et al. 2010). Insecticide-treated bed nets and indoor residual spraying play important roles in adult mosquito control. With the emergence of insecticide resistance in recent years, new control measures are urgently needed to substantially and sustainably reduce mosquito-borne disease transmission and the disease-related economic burden. In particular, it is recommended that integrated control strategy rather than a single intervention method should be employed.

Our model is based on the environment of a temperature-controlled experiment in which the intraspecific competition of mosquitoes is excluded. The model can be extended to describe mosquito population dynamics in natural environment. In that case, however, it is necessary to incorporate the density-dependent larval competition which has been considered an important determinant of mosquito population dynamics (Ewing et al. 2016; Fang et al. 2016; Legros et al. 2009). Indeed, larval competition can affect adult longevity which has a significant impact on malaria transmission dynamics due to the long extrinsic incubation period (the development time of malaria parasites in a mosquito before the mosquito becomes infectious) (Fang et al. 2016). Larval competition may also alter susceptibility of adult mosquitoes to dengue infection (Alto et al. 2008). We refer readers to (Fang et al. 2016; Liu et al. 2017) for more details about intra- and interspecific competition among mosquito larvae, as well as other insect and amphibian species. Incorporation of the density-dependent larval mortality is also helpful for us to explore successful larval control measures. Larval mosquitoes undergo four moult substages. In order to estimate mosquito population size more accurately, we can develop a model which includes all the four substages of larval mosquitoes.

In addition to temperature, rainfall also dramatically influences mosquito population dynamics and disease outbreaks in natural environment. Some researchers have studied the effects of temperature and rainfall on mosquito population and disease transmission dynamics (see, e.g. Abdelrazec and Gumel 2017; Wang et al. 2016, 2017). It would be very interesting yet challenging to incorporate the effects of temperature and rainfall simultaneously in a delay differential equations model of mosquito population dynamics. For better understanding of vector population or disease transmission dynamics, we call for a good collection of data from biological and ecological researchers. For example, our simulation result would be better if we knew the accurate relationship between the mortality of each stage and the temperature. The method to analyse the asymptotic behaviour of solutions in this paper can also be used to study other linear periodic delay differential equations with periodic time delays.

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