



The annual abundance of dengue and Zika vector *Aedes albopictus* and its stubbornness to suppression



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ARTICLE INFO

Keywords:

Aedes albopictus
Population dynamics
Age-stage structure
Insecticide resistance

ABSTRACT

The mosquito *Aedes albopictus* is a competent vector for more than 25 arboviruses, including dengue and Zika, and the sole vector for the 2014 unprecedented dengue outbreak in southern China. Due to the lack of a deep understanding of how its seasonal abundance is tied to environments, current methods have failed to control its prevalence and expansion on a large scale. In this paper, we develop a comprehensive model of difference equations that incorporates mosquito age at the four developmental stages, egg diapause, larval density competition, and the meteorological data for temperature, precipitation, and humidity, to predict the mosquito abundance over time in southern China. The generated temporal profile is robust against the variation of initial inputs, and matches well with the measurements in a northeast district in Guangzhou in 2013 and 2014 with a correlation coefficient $R^2 \approx 0.9511$. We find that chemical interventions have only a temporary effect; once the intervention is terminated, mosquito population bounces back quickly. Moreover, improper adulticide applications facilitate a fast spread of insecticide resistance. The resistance spread is quantified and the optimal intensity and frequency of chemical interventions are simulated. These findings remain to be tested by more real data and our methods can be adapted to other geographic areas and/or mosquito species for designing better mosquito control strategies.

1. Introduction

The Asian tiger mosquito, *Aedes albopictus*, is notoriously the most invasive insect with a global distribution (Estrada-Franco and Craig, 1995). It is a competent vector for more than 25 arboviruses, including dengue and Zika (Baldacchino et al., 2015). The 2014 unprecedented dengue outbreak in Guangdong Province, China, with 45,171 reported cases, has put *Ae. albopictus* under the spotlight (Cheng et al., 2016; Meng et al., 2015; Wang et al., 2017). Due to the lack of commercially available vaccines for either dengue or Zika, current disease control methods focus on suppressing the prevalence of vectors and their capacity to transmit viruses (Baldacchino et al., 2015; Faraji and Unlu, 2016). Source reduction appears to be the most prioritized approach for *Ae. albopictus* control (Estrada-Franco and Craig, 1995; Meng et al., 2015), but the continual creation of ubiquitous larval sources due to the warm and humid weather has made this approach very challenging in southern China. Applying insecticides has remained a primary strategy in China, with more than 250 million kg of insecticides being sprayed

annually since 1997. In the campaign to combat the 2014 dengue outbreak, more than 27,000 kg of pyrethroids were used for ultra-low volume spraying in over 3291 km² of land in Guangzhou, along with massive human resources and funds (> 30 million US dollars) (Wang et al., 2017).

Chemical interventions provide a rapid, but not sustainable, suppression of mosquito populations. Due to the evolutionary plasticity and ecological adaptability, insecticide application has facilitated *Ae. albopictus* to develop insecticide resistance (Baldacchino et al., 2015). Although the knowledge of its biology has been greatly enhanced, and many control methods have been developed, the prevalence and expansion of *Ae. albopictus* have not been effectively controlled on a large scale (Faraji and Unlu, 2016). The population dynamics of the invasive species is tightly tied to climatic conditions, temperature and rainfalls in particular. In southern China, the population of *Ae. albopictus* follows essentially the same yearly growth pattern (Liu et al., 1992; Yan et al., 2010). When the rainy and warm season starts in the middle of March, the adult population emerges due to the hatching of diapausing eggs,

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and grows rapidly until reaching a peak in late May or early June. It then decreases for one to two months, mainly due to the density-induced larval death in hot summer. The moderate temperature in the fall helps the population bounce back and reach the second peak in September or October, after which the abundance decays sharply and eventually vanishes in dry winter. It remains unclear and highly non-trivial to understand how the climatic conditions interplay with *Ae. albopictus* to regulate its population dynamics (Monaghan et al., 2018; Petrić et al., 2017; Wang et al., 2016). A deep understanding is essential to help integrate current knowledge and translate it into more effective control approaches, and recognize the correlation between mosquito-borne diseases and the growth or decline of vector populations (Cailly et al., 2012; Cheng et al., 2016; Jia et al., 2016; Juliano, 2007; Tran et al., 2013).

In this work, we develop a mathematical model of difference equations that tracks the daily mosquito abundances of eggs, larvae, pupae, and adults, with the age specified in each stage. The basic idea underlying our model is rather simple: The number of eggs of age $n = 1$ is increased by oviposition; the numbers of mosquitoes of age $n = 1$ in other stages are increased by stage transitions; and the numbers of mosquitoes of age $n > 1$ are decreased due to mortality. The inclusion of ages and the four life stages presents a novel feature of our model comparing to the difference equation models of mosquito populations in the literature; see (Li, 2013; Li and Li, 2018) and the references therein. In addition, the delicate effect of weather conditions on the survival and transition rates, egg diapause, and the density restriction in the larval stage are integrated into equations. In our model, both the time variable t and the age variable n have “day” as their unit. It provides a convenient and transparent incorporation of the meteorological data for temperature and precipitation, and the experimental data that are often recorded on a daily basis. It also allows us to define explicitly the time period for egg diapause, and specify precisely the developmental stage durations that were often overlooked in most mathematical models.

Based on an extensive review of current knowledge on mosquito biology, we estimate the seasonal oviposition rate and daily transition and survival rates that change with the environmental conditions. Egg diapause is treated by dividing each year into unfavorable and favorable seasons during which eggs are discriminated by different daily survival and hatching rates. The density restriction on larval growth is elaborated by analyzing the nonlinear dependence of the threshold larval density on temperature and precipitation, and its linear dependence on larval resources. The simulated temporal profile of adult abundances is robust against the variation of the initial input, and matches well with the experimental data collected in a northeast district in Guangzhou in 2013 and 2014. It captures critical features commonly observed in previous surveillance in Guangzhou. We find that chemical interventions can only temporarily suppress the mosquito population: A significant, but not perfect, suppression of mosquito population by chemical interventions within one year brings on almost negligible impact in subsequent years. By incorporating a resistance gene with a recessive trait at a single locus of two alleles in our model, we show that the control efficacy does not always increase in the intensity or the frequency of adulticide application. We further identify the optimal intensity and frequency of chemical interventions to maximize the control efficacy. Our model can be extended to other geographic areas and/or different mosquito species by modifying the system parameter values for designing better mosquito control strategies.

2. The model

2.1. Basic Framework

In their life cycle, *Aedes* mosquitoes undergo four developmental stages: egg(E), larva(L), pupa(P) and adult(A). Eggs hatch to larvae,

which, after four sub-stages, grow into pupae, and adults emerge from the mature pupae. The first three stages are largely aquatic, and the adults are terrestrial. In our model, we use difference equations to track daily cohorts of mosquitoes in all stages, with age included in each stage, to account for their different responses to environments. The survival pressure due to population density is the severest for larvae among all stages (Lord, 1998); and the temperature is crucial for egg hatching but is not essential for egg survival (Khatchikian et al., 2010).

Let S denote a generic stage: $S = E, L, P, A$. The experimental data in the past two decades suggest that eggs, larvae, pupae, and adults are almost evenly distributed in sex. This motivates us to assume the 1:1 sex ratio in all stages and count only female individuals. The number of mosquitoes on stage S of age n on a given day t is denoted by $S(n, t)$, where $n \geq 1$ and $t \geq 0$ are integers. The number in the next day, $S(n + 1, t + 1)$, is reduced from $S(n, t)$ due to death or stage transitions. Let S_{-1} denote the preceding stage of S , meaning that

$$E_{-1} = A, \quad L_{-1} = E, \quad P_{-1} = L, \quad \text{and} \quad A_{-1} = P.$$

The newborn mosquitoes on the next day, counted by $S(1, t + 1)$, are accumulated from transition of mosquitoes in the stage S_{-1} of various ages on Day t . These considerations set the basic framework of our model in the following equations:

$$S(n + 1, t + 1) = \text{Daily survival rate} \cdot (1 - \text{Daily stage transition rate}) \cdot S(n, t). \tag{2.1}$$

$$S(1, t + 1) = \sum_{n=1}^{\infty} \text{Daily stage transition rate} \cdot S_{-1}(n, t). \tag{2.2}$$

When $S = A$, the term “Daily stage transition rate”, or oviposition rate, needs to be removed in (2.1) because oviposition does not cause the death of the mother.

For mathematical convenience, we introduce a characteristic function as follows. Let $a \leq b$ be two non-negative real numbers. We define

$$1_{[a,b]}(x) = \begin{cases} 1, & x \in [a, b], \\ 0, & x \notin [a, b]. \end{cases} \tag{2.3}$$

2.2. Eggs

We begin with the equation of $E(1, t + 1)$ for newborn eggs. It was observed that *Ae. albopictus* females took their first blood meals two days after emergence, and the first gonotrophic cycle after a blood meal lasted three to five days at a warm temperature (Estrada-Franco and Craig, 1995). Let $m(t)$ denote the average daily oviposition rate for adult females in their oviposition period. Then (2.2) gives

$$E(1, t + 1) = \sum_{n=5}^{30} m(t)A(n, t). \tag{2.4}$$

To set the equation of $E(n + 1, t + 1)$ by (2.1), we include egg diapause as a major factor determining the survival and hatch rates. Egg diapause is a stable state of hatching arrest that occurs when embryonic development has been completed but the fully formed first instar larva remains within the chorion of the egg (Vinogradova, 2007). It is mainly induced by photoperiod and low temperature, and the arrest will not be terminated until the reactivation of development by favorable climate conditions. As in the temperate zones in Europe and North America, *Ae. albopictus* in Guangzhou experiences high larval and almost complete adult mortality during winter and survives winter as diapausing eggs (Liu et al., 1992; Yan et al., 2010).

We divide each year into unfavorable and favorable seasons, depending on whether or not the eggs laid within the season are diapausing (unfavorable) or non-diapausing (favorable). In Guangzhou, few adults are found in January and February, and most eggs produced from mid-October to December diapause due to short photoperiod and low-temperature (Liu et al., 1992; Yan et al., 2010). We define the

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