Modelling diapause in mosquito population growth

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Abstract: Diapause, a period of arrested development caused by adverse environmental conditions, serves as a key survival mechanism for insects and other invertebrate organisms in temperate and tropical areas. In this paper, a novel modelling framework, motivated by mosquito development, is proposed to investigate the effects of diapause on seasonal population growth, where diapause period is taken as an independent growth process, during which the population dynamics are completely different from that in the normal developmental and post-diapause periods. More specifically, the annual growth period is divided into three intervals, and the population dynamics during each interval are described by different sets of equations. Using the mosquito species as a motivative example, we formulate two models of delay differential equations (DDE) to explicitly describe population growth with a single diapausing stage, either immature or adult ones. These two models can be further unified into one DDE model, on which the seasonal population abundances of two temperate mosquito species with different diapausing stages are analysed and simulated. Numerical results illustrate the key role on population persistence that diapause plays and predict that killing mosquitoes during the diapause period can lower but fail to prevent the occurrence of peak abundance in the following season. Instead, controlling mosquitoes during the normal growth period is much more efficient to decrease the outbreak size.

Key Words: Diapause, population growth, seasonality, delay differential equation

MSC: 37N25; 34K60; 92D40

1 Introduction

Diapause is a neurohormonally mediated dynamic state of low metabolic activity, associated with a reduced morphogenesis, increased resistance to environmental extremes and altered or reduced physical activity [42]. As an adapting mechanism to the unfavourable environmental conditions such as harsh winters and dry seasons, this process of physiological rest can be commonly found among invertebrate organisms, which includes temperate zone insects or some tropical species occasionally and their arthropod relatives [9, 23], such as mosquitoes [1], ticks [2], ladybirds [21], dragonflies [32], silkworms [20]. Recent extensive studies on different aspects of diapause contributed to understand how inherent mechanisms regulate organisms surviving through diapause [9, 11, 12, 17, 34] and the critical roles of diapause in evolutionary dynamics and molecular physiology [1, 10, 42]. For example, the regulation of hormonal schemes was discussed elaborately in [9, 12], exhibiting how hormones control organisms to shut down their growth and enter a period of diapause during adverse seasons. The authors in [11, 34] outlined the cold and desiccation tolerance mechanisms of overwintering insects in response to low temperature and limited water. Molecular mechanisms involved in diapause nutrient regulation were discussed in [17] to show how overwintering insects regulate the timing of entering diapause and the diapause durations based on their energy storage. Tauber et al. [42] provided a fundamental introduction about the importance of diapause from the perspective of ecology. Alekseev et al. [1] discussed the phenomenology of diapause and its significance in scientific and practical uses with a focus on aquatic insects. Denlinger and Armbruster [10] offered a comprehensive overview of diapause summarising the past and recent progresses in the evolutionary dynamics and molecular physiology of diapause with an emphasis on mosquitoes.

The aforementioned contributions illustrated the effects of diapause stage on linking the favourable and adverse seasons, and synchronising the life cycle of organisms with seasonal environmental variations [10, 41]. Mathematical models are believed to be efficient and indispensable tools for better understanding of population dynamics. However, few population models focus on exploring the effects of diapause on population persistence. In this paper, we attempt to investigate how diapause influences seasonal population patterns by constructing mathematically tractable models, with mosquito species as a motivating example. Mosquitoes act as pathogen vectors to transmit various infectious diseases including dengue fever, malaria, West Nile fever, Japanese encephalitis, Zika and chikunguya, which pose great challenges to human health [38]. Due to their epidemiological significance, the study of mosquitoes attracts increasing attention and makes mosquitoes to be the most concerned model group among aquatic insects. Even though there are huge investments in mosquito research, relatively a small number of population models evaluate the effects of diapause on mosquito persistence. A stage-structure, climate-driven population model incorporating the diapause effects was formulated in [5] to predict seasonal mosquito abundance over time, identify the main determinants of mosquito population dynamics and assess mosquito control strategies. This model was modified by optimising the parameters and transition functions in a follow-up work [43]. Based on these two models, a new fine-tuned model was constructed in [22] to explore the relationships between major climatic variables and diapause related parameters during the developmental cycle. Another temperature-dependent, delay-differential equation (DDE) model incorporating diapause was proposed to demonstrate the sensitivity of seasonal mosquito abundance patterns to annual changes in temperature, which links the effects of environmental change with the transmission of mosquito-borne disease [13]. In the models mentioned above, by using a piecewise function, the diapause period was regarded as an independent dynamic process during which the population dynamics are completely different from that in the normal growth period. This idea is fairly reasonable since considerable research suggests that not only the developmental rate but also the reproduction and mortality are altered when organisms enter into diapause [10, 18, 36]. Following this point of view and incorporating the extended maturation duration due to diapause, a novel and comprehensive modelling framework will be proposed in the current manuscript. Although the motivative example of this paper is the mosquito species, our modelling framework can be applied to other species including ticks [2], silkworms [20] and flesh flies [15], which are capable of diapause to survive through unfavourable seasons.

The occurrence of diapause is caused by the advent of adverse environmental conditions such as winter seasons in temperate zones and dry seasons in tropic areas. As such, the organisms surviving through diapause must experience a fixed period of latency before their normal growth resumes [10]. In addition, the observations in [10, 23, 25] indicate that normal growth cannot resume immediately after the termination of diapause. It would make sense to classify the annual growth period into three intervals, that is, the normal growth period, the diapause period and the post-diapause period.

Population dynamics during each interval are described by different sets of differential equations, which are completely different from previous models. Since mosquito diapause is restricted to a single stage for most species, on either adult stage or immature (egg or larval) stage [4, 10], we attempt to investigate two distinct cases of mosquito diapause separately, that is, adult diapause and immature diapause. Consequently, the population is structured into immature and matured age classes to explicitly describe different diapausing life stages. Two distinct DDE models are formulated from the continuous age-structured partial differential equations (PDEs) to explicitly describe mosquito growth with either diapausing adults or immatures. Furthermore, we formulate a unified DDE model, which can reflect population dynamics with adult diapause and immature diapause respectively, by assuming different parameters related to diapause. The formulations of three models are derived elaborately in Section 2. The theoretical analysis on the unified model including the well-posedness of the solutions and global stability of the trivial and positive periodic solutions is presented in the Appendix section. Numerical results are performed in Section 3 to show the seasonality of population abundances of two temperate mosquito species, the sensitivity of the diapause-related parameters and implications for controlling mosquito population. Discussions are provided in the final section.

2 Model formulation

We first derive the formulation of the model describing the growth of population with only one diapausing stage, either adult or immature diapause ones. A unified model capable of describing both adult and immature diapause cases is then proposed. The mosquito population is stratified into two different age classes: immature ($I(t)$) and mature ($M(t)$) classes with a threshold age τ, which represents the development duration from egg to adult. Within each age group, all individuals share the same birth and death rates. We denote the population density at time t of age a by $u(a, t)$. Then the population sizes for immature and adult individuals are represented respectively by the following integration:

$$I(t) = \int_0^\tau u(a,t)da, \quad M(t) = \int_\tau^\infty u(a,t)da. \tag{2.1}$$

The annual growth period consists of three intervals, that is, the normal growth period, the diapause period and the post-diapause period, the lengths of which are denoted by T_1, T_2 and T_3 respectively. Here, we assume that the post-diapause period lasts for only one developmental duration, i.e. $T_3 = \tau$. The length of the (irrespective of adult diapause or immature) diapause duration is assumed to be τ_d, i.e. $T_2 = \tau_d$. Biological observations indicate that $\tau_d > \tau$ [10, 35]. It then follows that the length of the remaining period, i.e. the normal growth period, is $T_1 = 1-\tau-\tau_d$. In this paper, we set the starting time $t = 0$ of the annual growth period at the termination of the post-diapause period.

During the normal growth period, there is no difference in the model formulations between these two different diapause mechanisms. The McKendrick-von Foerster equation can be used to describe the dynamics of an age-structured population (see, e.g., [7, 16, 28] and the references therein):

$$\begin{cases} \left(\dfrac{\partial}{\partial a} + \dfrac{\partial}{\partial t}\right) u(a,t) &= -\mu(a)u(a,t), \\ u(0,t) &= b(M(t)), \\ u(a,0) &= u_0(a). \end{cases} \tag{2.2}$$

The birth rate function is $b(M(t))$, assumed to be dependent only on the adult population size and $u_0(a)$ is the initial age distribution. The death rates during the normal growth period are stage-dependent, and $\mu(a) = \mu_I$ for $a < \tau$ while $\mu(a) = \mu_M$ for $a \geq \tau$. In view of (2.2), differentiating the integral equations in (2.1) with respect to time t on both sides yields

$$\frac{dI(t)}{dt} = u(0,t) - u(\tau,t) - \mu_I I(t) = b(M(t)) - u(\tau,t) - \mu_I I(t),$$
$$\frac{dM(t)}{dt} = u(\tau,t) - u(\infty,t) - \mu_M M(t).$$

It is natural to assume that $u(\infty,t) = 0$ as no individual can live forever. To close the system, we need to figure out $u(\tau,t)$, the maturation rate at time t, which can be achieved by the technique of integration along characteristics (see for example [39]). To proceed, let $\xi^s(t) = u(t-s,t)$, then for $t - s \leq \tau$, we have

$$\frac{d\xi^s(t)}{dt} = -\mu(t-s)\xi^s(t),$$

where $\xi^s(s) = u(0,s) = b(M(s))$. Therefore, setting $s = t - \tau$ (≥ 0), we have the following expression for $u(\tau,t)$ when $t \geq \tau$,

$$u(\tau,t) = b(M(t-\tau))e^{-\mu_I \tau}.$$

The following system describes the population dynamics taking into consideration of seasonal effects during the normal growth period, i.e. when $n \leq t \leq n + T_1 = n + 1 - \tau - \tau_d$, here n (≥ 0) is an integer representing the n-th year:

$$\frac{dI(t)}{dt} = b(M(t)) - b(M(t-\tau))e^{-\mu_I \tau} - \mu_I I(t),$$
$$\frac{dM(t)}{dt} = b(M(t-\tau))e^{-\mu_I \tau} - \mu_M M(t).$$

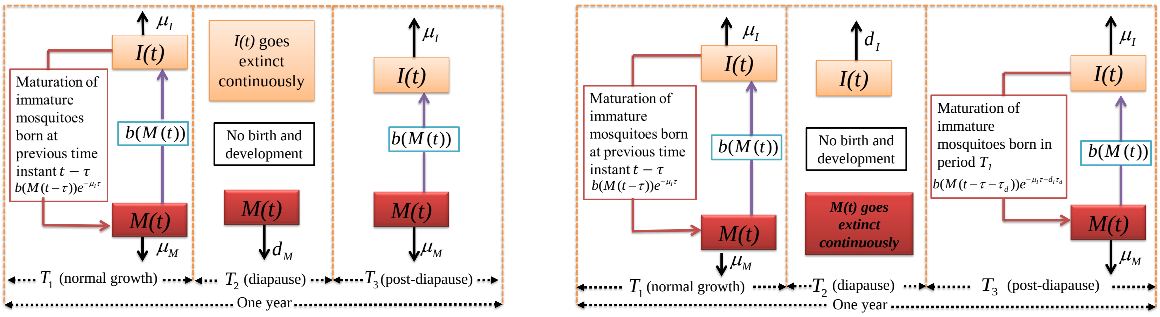
However, the population dynamics during the diapause and post-diapause periods are completely different for two diapause cases. In the next subsection, we start from the model formulation for adult diapause case.

2.1 Adult diapause

Once the diapause period is initiated, all individuals cease their developmental activities due to harsh environmental conditions. For adult diapause case, adult individuals can survive with a diapausing mortality rate d_M while the immature population becomes extinct [37]. Consequently, we assume that the number of immatures $I(t)$ decreases to zero continuously during the diapause period, i.e. when $n+1-\tau-\tau_d \leq n+1-\tau$, and moreover, $I(t) \equiv 0$ when $t \in [n+1-2\tau, n+1-\tau]$. During the post-diapause period, i.e. when $n+1-\tau \leq t \leq n+1$, the maturation rate is 0 as no immature survives through the diapause period. The annual growth of the mosquito population when adults enter into diapause is illustrated in Fig. 1(a). In this case, the population dynamics subject to seasonal effects can be described by the following system (A), consisting of (A1), (A2) and (A3).

(1) During the normal growth period T_1, i.e. when $t \in [n, n+1-\tau-\tau_d]$:

$$\begin{cases} \dfrac{dI(t)}{dt} = b(M(t)) - b(M(t-\tau))e^{-\mu_I \tau} - \mu_I I(t), \\ \dfrac{dM(t)}{dt} = b(M(t-\tau))e^{-\mu_I \tau} - \mu_M M(t). \end{cases} \tag{A1}$$



(a) Diagram for adult diapause

(b) Diagram for immature diapause

Figure 1: Diagrams depicting the annual growth of mosquito populations with single diapausing stage. The one year period, is divided into three intervals with different growth rates for immatures $I(t)$ and adults $M(t)$ on different intervals. Moreover, the lengths of these three intervals T_1, T_2, T_3 are $1-\tau_d-\tau$, τ_d and τ respectively.

(2) During the adult diapause period T_2, i.e. when $t \in [n+1-\tau-\tau_d, n+1-\tau]$, there is no developmental activity, immatures go extinct and adults survive through diapause:

$$\begin{cases} I(t) \text{ decreases to zero continuously and } I(t) \equiv 0, \ \forall\, t \in [n+1-2\tau, n+1-\tau], \\ \dfrac{dM(t)}{dt} = -d_M M(t). \end{cases} \tag{A2}$$

(3) During the post-diapause period T_3, i.e. when $t \in [n+1-\tau, n+1]$, no immatures develop to adults since the longest age for newborns in this period is τ:

$$\begin{cases} \dfrac{dI(t)}{dt} &= b(M(t)) - \mu_I I(t), \\ \dfrac{dM(t)}{dt} &= -\mu_M M(t). \end{cases} \tag{A3}$$

2.2 Immature diapause

In the case that immature individuals diapause, the annual growth of mosquito population is illustrated in Fig. 1(b). During the diapause period, all individuals stop growing, immatures (eggs or larvae) enter into diapause with a diapausing mortality rate d_I while the adult population goes extinct due to harsh environmental conditions [26, 44]. Therefore, we assume that $M(t)$ decreases to zero continuously during the diapause period, i.e. when $n+1-\tau-\tau_d \le t \le n+1-\tau$ and moreover, $M(t) \equiv 0$ when $t \in [n+1-2\tau, n+1-\tau]$. Different from the adult diapause case, the maturation rate during the post-diapause period is $b(M(t-\tau-\tau_d))e^{-\mu_I\tau - d_I\tau_d}$ other than 0. The dynamics of seasonal mosquito population when immatures enter into diapause can be described by the following system (I), consisting of (I1), (I2) and (I3).

(1) During the normal growth period T_1, i.e. when $t \in [n, n+1-\tau-\tau_d]$:

$$\begin{cases} \dfrac{dI(t)}{dt} &= b(M(t)) - b(M(t-\tau))e^{-\mu_I\tau} - \mu_I I(t), \\ \dfrac{dM(t)}{dt} &= b(M(t-\tau))e^{-\mu_I\tau} - \mu_M M(t). \end{cases} \tag{I1}$$

(2) During the immature diapause period T_2, i.e. when $t \in [n+1-\tau-\tau_d, n+1-\tau]$, no adult gives birth since all adults die:

$$\begin{cases} \dfrac{dI(t)}{dt} = -d_I I(t), \\ M(t) \text{ decreases to zero continuously and } M(t) \equiv 0, \ \forall\, t \in [n+1-2\tau, n+1-\tau]. \end{cases} \tag{I2}$$

(3) During the post-diapause period T_3, i.e. when $t \in [n+1-\tau, n+1]$, juveniles born at previous time instant $t-\tau-\tau_d$ survive through the diapause period and mature into adults at time t:

$$\begin{cases} \dfrac{dI(t)}{dt} &= b(M(t)) - b(M(t-\tau-\tau_d))e^{-\mu_I\tau - d_I\tau_d} - \mu_I I(t), \\ \dfrac{dM(t)}{dt} &= b(M(t-\tau-\tau_d))e^{-\mu_I\tau - d_I\tau_d} - \mu_M M(t). \end{cases} \tag{I3}$$

2.3 A unified model

In this subsection, we will explore the formulation of a unified model, which is capable of describing both the immature (Model (I)) and adult (Model (A)) diapause cases respectively. The annual growth of mosquito population is shown in Fig. 2.

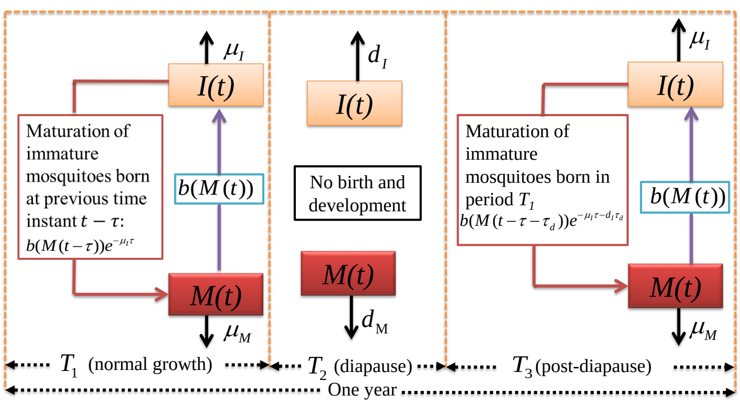


Figure 2: Diagram illustrating the annual growth for the mosquito population when both immatures and adults can survive through diapause. The one year period is divided into three intervals with different growth rates for immatures $I(t)$ and adults $M(t)$ on different intervals. Moreover, the lengths of these three different intervals T_1, T_2, T_3 are $1-\tau_d-\tau$, τ_d and τ respectively.

(1) During the normal growth period T_1, i.e. when $n \le t \le n + T_1 = n+1-\tau-\tau_d$, the population dynamics are described by the following system, which are the same as previous two cases.

$$\begin{cases} \dfrac{dI(t)}{dt} &= b(M(t)) - b(M(t-\tau))e^{-\mu_I\tau} - \mu_I I(t), \\ \dfrac{dM(t)}{dt} &= b(M(t-\tau))e^{-\mu_I\tau} - \mu_M M(t). \end{cases} \tag{U1}$$

(2) Afterwards, all mosquitoes evolve into the diapause period with the advent of unfavourable seasons. During this period T_2, the development of all individuals is arrested and we assume both immature and mature mosquitoes can survive through the diapause period suffering the mortality rate d_I and d_M, respectively. Then, the population dynamics for mosquitoes during the diapause period (i.e. when $n+1-\tau_d-\tau \le t \le n+1-\tau$) are described by the following system:

$$\begin{cases} \dfrac{dI(t)}{dt} &= -d_I I(t), \\ \dfrac{dM(t)}{dt} &= -d_M M(t). \end{cases} \tag{U2}$$

(3) For the post-diapause period T_3, i.e. when $n+1-\tau \le t \le n+1$, the population dynamics can be represented by the following system:

$$\begin{cases} \dfrac{dI(t)}{dt} &= b(M(t)) - b(M(t-\tau-\tau_d))e^{-\mu_I\tau - d_I\tau_d} - \mu_I I(t), \\ \dfrac{dM(t)}{dt} &= b(M(t-\tau-\tau_d))e^{-\mu_I\tau - d_I\tau_d} - \mu_M M(t). \end{cases} \tag{U3}$$

By assuming $d_I \gg 1$ ($d_M \gg 1$), we can investigate the population dynamics for individuals experiencing adult (resp. immature) diapause in the previous cases via this unified model. In fact, when only adults diapause, $I(t)$ declines to zero very quickly in (U2), as expressed in (A2). Moreover, the term $b(M(t-\tau-\tau_d))e^{-\mu_I\tau-d_I\tau_d}$ is close to zero in (U3), which approximates to (A3). Similarly, when immatures diapause by assuming $d_M \gg 1$, the dynamics of system (I) can be approximated by those of system (U). In summary, we may use system (U) to reflect the dynamics of systems (A) and (I) and conduct theoretical analysis on the unified model (U). We defer the theoretical analysis of the unified model to the Appendix section, where the detailed proofs of the well-posedness of the solutions and global stability of the trivial and positive periodic solutions in terms of the threshold value $\mathcal{R}$ are provided. The persistence and extinction of population is totally dependent on the sign of $\mathcal{R}-1$. When $\mathcal{R}>1$, the population will eventually oscillate at an annual cycle. In the rest of the paper, we attempt to explore the roles of diapause on seasonal population growth and predict reasonable implications in terms of mosquito control by performing a series of numerical simulations.

3 Numerical results

In this section, some numerical simulations are carried out to show how the mosquito population fluctuates with the diapause-related parameters. In this paper, we focus on simulating the population dynamics of two temperate mosquito species. One is *Aedes albopictus*, only the immature individuals (restricted in egg stage) of which can survive by entering diapause with the advent of unfavourable seasons [46]. The other is *Culex pipiens*, only the adults of which undergo diapause to maintain viability in response to harsh environment conditions [46]. The seasonal patterns of these two mosquito species with different diapausing stages will be simulated. The sensitivity analysis is then performed to exhibit how diapause-related parameters affect the population dynamics. Some implications for controlling mosquitoes can be obtained from the further check of the integrated effects of the diapausing and natural death rates.

Parameter values are adopted from existing biological literatures. In virtue of the habitats for *Aedes albopictus* and *Culex pipiens* existing in similar latitudes [29], there may be subtle differences between these two species in the developmental rates during the normal growth and diapause periods, and therefore, related parameters for these two species are set as the same. Due to the lack of diapause-related parameters, some reasonable assumptions are made based on current understanding of mosquito diapause. Since the two species are mostly distributed in temperate zone, diapause serves as an overwintering strategy. As such, the duration of diapause period particularly depends on the length of winter season, which was fixed as 3 months for both immature and adult diapause cases. During the diapause period, the mortality rates of immatures and adults rely on their diapausing ability. For diapausing immatures (adults), we presume that the mortality rate during diapause period is slightly larger than that in normal growth duration even though their resistance to harsh environment conditions is enhanced [19, 34]. The mortality rate for non-diapausing mosquitoes is assumed as ten-fold of the death rate during the normal developmental period. In consideration of the density dependent mosquito reproduction, the well-known Beverton-Holt function may be a good choice for the birth rate function, which is widely applied in modelling the recruitment of fishes [3] and insects [24]. In this paper, the birth rate function is constructed as a special case of Beverton-Holt function, that is, $b(M) = pM/(q + M^n)$, which only depends on the adult population M with the maximum recruitment rate $p = 120$ (month^{-1}), the maximum capacity related parameter $q = 5$ and the dimensionless parameter $n = 0.5$. The detailed descriptions of parameters are provided in Table 1.

Table 1: Parameter values of the model for mosquito population dynamics

Parameter	Definition	Range	Value	Reference
τ	Developmental duration for immature mosquitoes (month)	$0.4 \sim 1$	0.5	[35]
τ_d	Diapause period for immature (mature) mosquitoes (month)	$2.5 \sim 5$	3	[10]
μ_I	Mortality rate for immature mosquitoes during normal growth period (month^{-1})	$0.3 \sim 1.8$	0.6	[6, 8, 31]
μ_M	Mortality rate for mature mosquitoes during normal growth period (month^{-1})	$0.6 \sim 2.1$	0.7	[6, 8, 31]
d_I	Mortality rate for immature mosquitoes during diapause period (month^{-1})	≥ 0.8	Diapause: 0.8 Otherwise: 6	Assumed
d_M	Mortality rate for mature mosquitoes during diapause period (month^{-1})	≥ 0.9	Diapause: 0.9 Otherwise: 7	Assumed

3.1 Seasonal population pattern

We first check the seasonality of the population abundance for *Aedes albopictus* and *Culex pipiens* with different stages entering diapause respectively. For each species, the population dynamics of immatures and adults are simulated on the unified model (U) by adjusting the diapause-related death rates d_I and d_M in Table 1. Moreover, we plot the curves of the periodic solutions to the other two models (A) and (I) (illustrated as dotted lines in Figs. 3(a) and 3(b)) since further check is needed to verify whether our unified model (U) can characterise the dynamics of them. The curves of the periodic solutions to the unified model (depicted as dashed lines in Figs. 3(a) and 3(b)) overlap with those simulated by the other two models, which validate that our unified model (U) is reasonable to characterise the dynamics of population experiencing immature and mature diapause respectively. In what follows, all simulations are carried out on the unified model (U).

Fig. 3 shows that the population dynamics of *Aedes albopictus* and *Culex pipiens* eventually stabilise at seasonal patterns, that is, fluctuating periodically between maximum and minimum values. The mosquito abundance bears a dramatic increase and reaches the peak at the end of the normal growth period, then experiences a sharp decline when diapause period begins. The subtle differences in post-diapause period between these two mosquito species begin to emerge when we zoom in on the annual population pattern (Figs. 3(d) and 3(c)). The numbers of both immature and adult drop substantially in the diapause period. Unlike the immatures, the minimum adult *Culex pipiens* population size appears at the end of post-diapause period as the decreasing trend in the diapause period is still maintained until the end of the post-diapause period (Fig. 3(c)). For *Aedes albopictus*, the population sizes of immature and adult *Aedes albopictus* both undergo similar decline. However, different from *Culex pipiens*, the number of *Aedes* immatures and adults both bounce back immediately after the termination of diapause (Fig. 3(d)). Different diapausing strategies contribute to the subtle difference between these two species. For *Culex pipiens*, no immature individuals surviving at the end of the diapause period leading to zero maturation rate during the post-diapause period, which results in further decline in the number of adults. After one developmental duration (the post-diapause period), the number of adults starts to increase as the new-born immatures attain maturity and develop into adults. However, for *Aedes albopictus*, immatures survive through diapause. At the end of the diapause period, some immatures born $\tau + \tau_d$ time earlier survive and develop into adults, leading to the increased number of adults during the post-diapause period. Owing to these newly matured adults which can give birth, the number of immatures can resume growing after the diapause period ends.

The global stability of the periodic solutions, which was rigorously approved in the Appendix, can be demonstrated intuitively by two phase portraits of systems with respect to immature and adult diapause cases. The phase portraits sketched in Fig. 4 show similar qualitative features. All solutions with different initial conditions converge towards a stable positive periodic solution, which can be seen as the solid closed curve in Fig. 4. The stable periodic orbit in Fig. 4(b) passing the bottom boundary of the axis related to adult population size implies that adult *Aedes albopictus* die out while immatures enter diapause, whereas, for *Culex pipiens* experiencing adult diapause, the periodic orbit may reach the leftmost boundary of the axis referring to the extinction of immatures (shown in Fig. 4(a)).

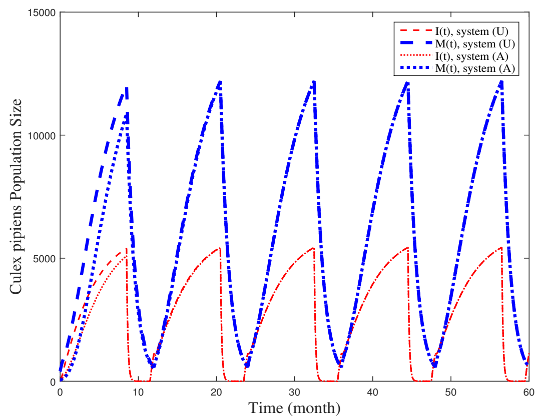
These simulations are as expected and further demonstrate that the modelling framework is valid to capture the dynamical behaviour of diapausing species. In the next subsection, sensitivity analysis reveals how the mosquito population dynamics change due to the variations of specific parameters related to diapause.

3.2 Sensitivity analysis

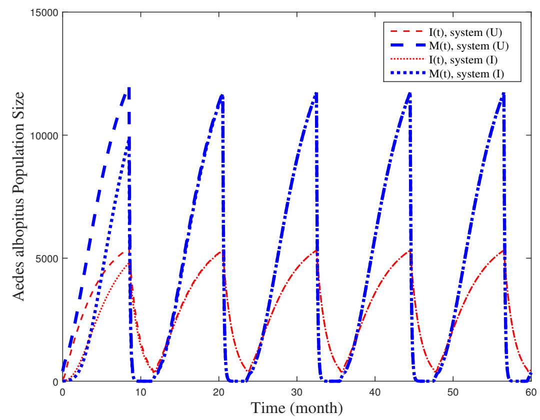
The survivability of mosquitoes under adverse environmental conditions is believed to be the vital factor preserving the population size and maintaining the succeeding normal development [34]. The sensitivity analysis mainly investigates the impacts of the mortality rates during diapause period and the length of diapause duration, which are strongly relevant to the diapausing survivability.

3.2.1 Effects of the diapausing death rates

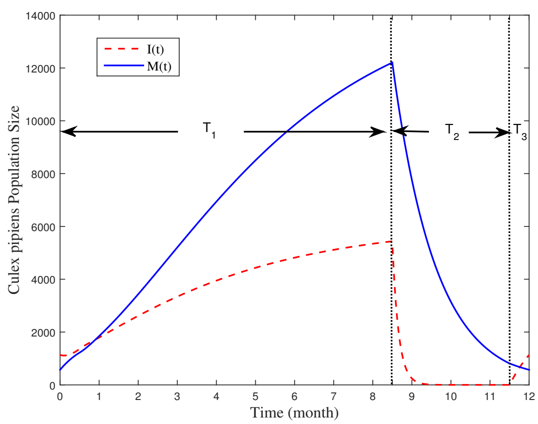
Maximum population abundance as one index characterising mosquito population abundance is mainly concerned to evaluate the effects of the diapausing death rates on population growth. For the adult diapause case, all immature *Culex pipiens* die at the end of the diapause period while some adults can survive through diapause. In this case, the survivability of diapausing adults other than



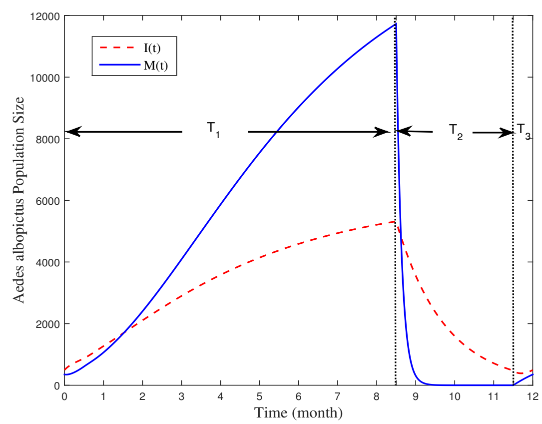
(a) Adult diapause



(b) Immature diapause

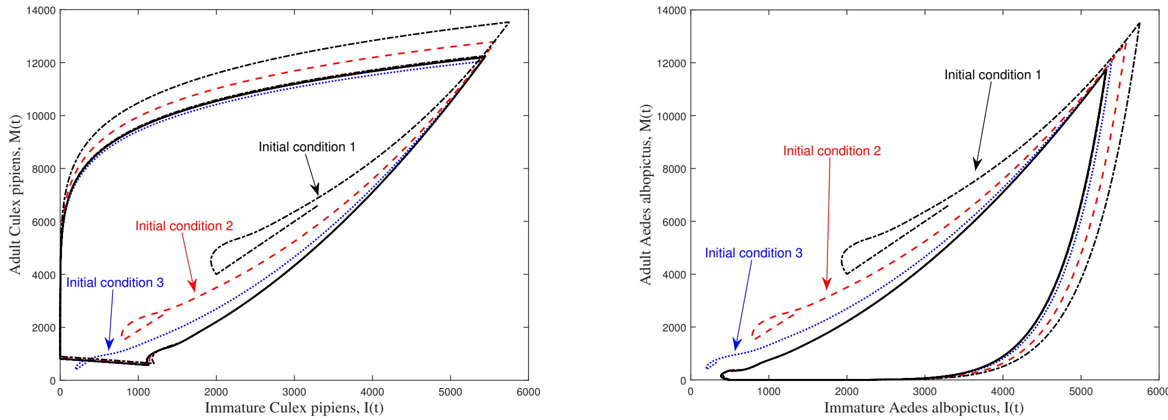


(c) Adult diapause



(d) Immature diapause

Figure 3: Simulated mosquito population abundance. (a) Population dynamics for *Culex pipiens*: immature population (shown as fine red lines) and adult population (bold blue lines), simulated by systems (A) (shown as dotted lines) and (U) (dashed lines). Here, $d_I = 6$, $d_M = 0.9$. (b) Population dynamics for *Aedes albopictus* population dynamics: immature population (shown as fine red lines) and adult population (bold blue lines), simulated by systems (I) (shown as dotted lines) and (U) (dashed lines). Here, $d_I = 0.8$, $d_M = 7$. (c) *Culex pipiens* population dynamics in one period with adult diapause. (d) *Aedes albopictus* population dynamics in one period with immature diapause. T_1, T_2 and T_3 represent the durations of the normal growth period, diapause period and post-diapause period respectively. The values of all other parameters are following Table 1.



(a) Adult diapause

(b) Immature diapause

Figure 4: Phase portraits for systems with respect to the adult and immature diapause case respectively. (a) In the case of adult *Culex pipiens* diapause, phase-portraits of solutions with three different positive initial conditions. (b) In this case, $d_I = 0.8$, $d_M = 7$. In the case of immature *Aedes albopictus* diapause, phase-portraits of solutions with three different positive initial conditions. Here, $d_I = 6$, $d_M = 0.9$. The values of all other parameters are following Table 1. For these two cases, all solutions with different initial conditions converge to a positive periodic solution (shown as the solid closed curve).

immatures during the diapause period is crucial for subsequent population growth. The variations of maximum adult and immature *Culex pipiens* population sizes are examined respectively by varying the adult diapausing death rate d_M and fixing the immatures dying at a non-diapausing rate, i.e. $d_I = 6$. However, in the case of immature *Aedes albopictus* entering diapause, the ability of the immatures surviving though diapause becomes the major concern. Consequently, we vary the immature diapausing rate d_I while fix the adult death rate during the diapause period as $d_M = 7$ to investigate how the maximum adult and immature *Aedes albopictus* population sizes change.

The consequences of varying diapausing mortality rates d_M and d_I for two diapause cases are illustrated in Figs. 5(a) and 5(b), the curves in which clearly show that increasing the survivability of diapausing mosquitoes may benefit the succeeding normal growth, which is embodied in the larger maximum adult and immature population abundances with lower diapausing mortality rate. The decreasing trend of the maximum population abundance for both diapause cases (illustrated in Figs. 5(a) and 5(b)) slows down when the diapausing rates are greater than some threshold value. The possible reason is that diapausing death rates only determine the survivability during the diapause period. Once the population size drops substantially to a very small number at the end of the diapause period, the impact of the increased diapausing adult death rate on the population dynamics is not significant.

3.2.2 Effects of the diapause duration

In addition to the diapausing death rates, the length of the diapause duration τ_d also plays an important role on population growth. Global climate change is believed to affect the timing of critical diapause periods [33]. For each diapause case, we examine how the adult and immature population dynamics fluctuate with changing τ_d. The curves in Figs. 5(c) and 5(d) describe the annual population patterns during one year period with three different values of τ_d, which clearly show that the lengthened diapause period lowers the peak population abundance and brings forward the peak time of each stage. The possible reason is that longer diapause duration results in relatively low survivability during diapause period and shortens the normal growth period for mosquito population to rebound. The results in this subsection further demonstrates that increase in the survival ability during the diapause period with shorter diapausing duration will be beneficial to the following normal population growth.

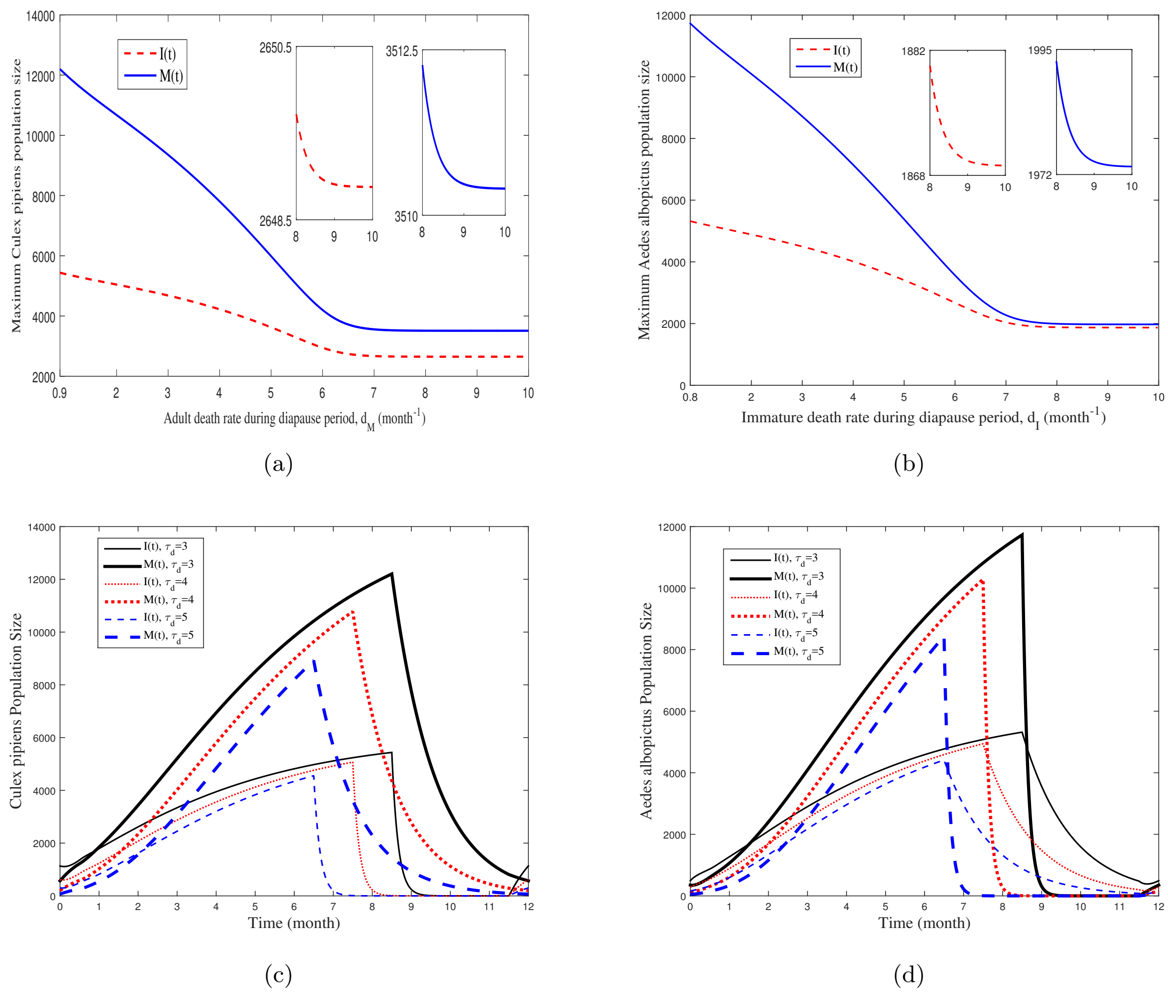


Figure 5: Sensitivity analysis of the diapause-related parameters. (a) Maximum *Culex pipiens* population size varies with changing d_M. (b) Maximum *Aedes albopictus* population size varies with changing d_I. (c) Population dynamics for *Culex pipiens* in one period when $\tau_d = 3$ (shown as solid lines), $\tau_d = 4$ (shown as dotted lines) and $\tau_d = 5$ (shown as dashed lines): adult population (shown as bold lines) and immature population (shown as fine lines). Here, $d_I = 6$ and $d_M = 0.9$. (d) Population dynamics for *Aedes albopitus* in one period when $\tau_d = 3$ (shown as solid lines), $\tau_d = 4$ (shown as dotted lines) and $\tau_d = 5$ (shown as dashed lines): adult population (shown as bold lines) and immature population (shown as fine lines). Here, $d_I = 0.8$ and $d_M = 7$.

It is worth noting that the decline in the peak population abundance for both cases (as shown in Figs. 5(a) and 5(b)) becomes inconspicuous when the diapausing death rate is above some threshold value. The peak population sizes for both immatures and adults tend to keep unchanged at a positive value rather than zero even if the death rate becomes very large, which means that the extremely low survivability during the diapause period is still hard to drive population extinction. Once the environment conditions become suitable for development, the mosquito population will resume growing rapidly as long as there are few mosquitoes surviving through the environmentally harsh period. On account of the short developmental durations for mosquitoes, the normal growth period is long enough for mosquitoes to rebound and new outbreaks of mosquitoes will emerge again. The above sensitivity analysis indicates that the mosquito population growth can benefit from the enhanced diapausing survivability. Diapause plays a significant role in preventing the extinction of the population from harsh environmental conditions.

3.3 Controlling adult mosquito population

It is well-known that all mosquito-borne pathogens such as dengue, West Nile, Japanese encephalitis, Zika and chikunguya viruses are transmitted by adult mosquitoes [38], controlling or reducing the adult mosquito population size is an indispensable tool to fight against the transmission of the mosquito-borne diseases. Based on the sensitivity analysis in previous subsection, the larger decline in the peak adult population size indicates that reducing the survivability by increasing the diapausing death rate may be an alternative way to lower the peak of adult population size and prevent the transmission of the infectious diseases. However, for the sake of controlling efficiency, focusing on killing mosquitoes during the diapause period alone may not be an effective strategy as it is impossible to wipe out all the mosquitoes. It would be better to integrate mosquito control measures in the normal growth period. To verify this conjecture, we perform a series of numerical simulations to investigate the integrated effects of the natural death rates and the diapausing death rates on the peak adult population sizes of both species.

The surfaces depict the fluctuations of peak adult *Culex pipiens* (illustrated in Fig. 6) and *Aedes albopictus* (shown in Fig. 7) population sizes respectively. For each species, the peak shows apparent decreasing trend when the normal and diapausing death rates are increasing respectively. In accordance with the aforementioned results, the peak adult *Culex pipiens* drops substantially when d_M is less than 5 and remains unchanged when the diapausing death rate is greater than 5 (see Figs. 6(b) and 6(d)). The narrower range of variations in the natural death rate lead to the same decline in the peaks of both species (see contour plots in Figs. 6(b), 6(d), 7(b) and 7(d)), which indicates that reducing the immature or adult death rate during the normal growth period is more effective than reducing the diapausing death rate to control the peaks of these two species. The contour plots in Figs. 6(f) and 7(f) suggest that increasing the adult death rate other than immature death rate during the normal growth period is relatively more efficient to reduce the adult outbreak size for both species. Compared with the effects of diapausing adult death rate on the peak of adult *Culex pipiens*, the diapausing immature death rate d_I has relatively larger effects on the peak of adult *Aedes albopictus* (see Figs. 6 and 7). Even though increasing the mortality rate during the diapause period will lower the peak of adult population, the more efficient way to control the adult outbreak size is to increase the mortality rate during the normal developmental period, particularly the adult natural death rate.

4 Discussion

Diapause, a transition strategy in response to the adverse environment conditions, is believed to play significant roles in preserving population size and maintaining the population growth. The effects of this survival mechanisms on species persistence remain unclear so far. In this paper, we attempted to explore this question by constructing mathematically tractable models, where diapause period is taken as an independent dynamic process, during which the population growth is completely different from that in the normal developmental and post-diapause periods. Consequently, the annual growth period is divided into three different intervals, with respective sets of equations in each interval. To explicitly describe population growth with different diapausing stages, we

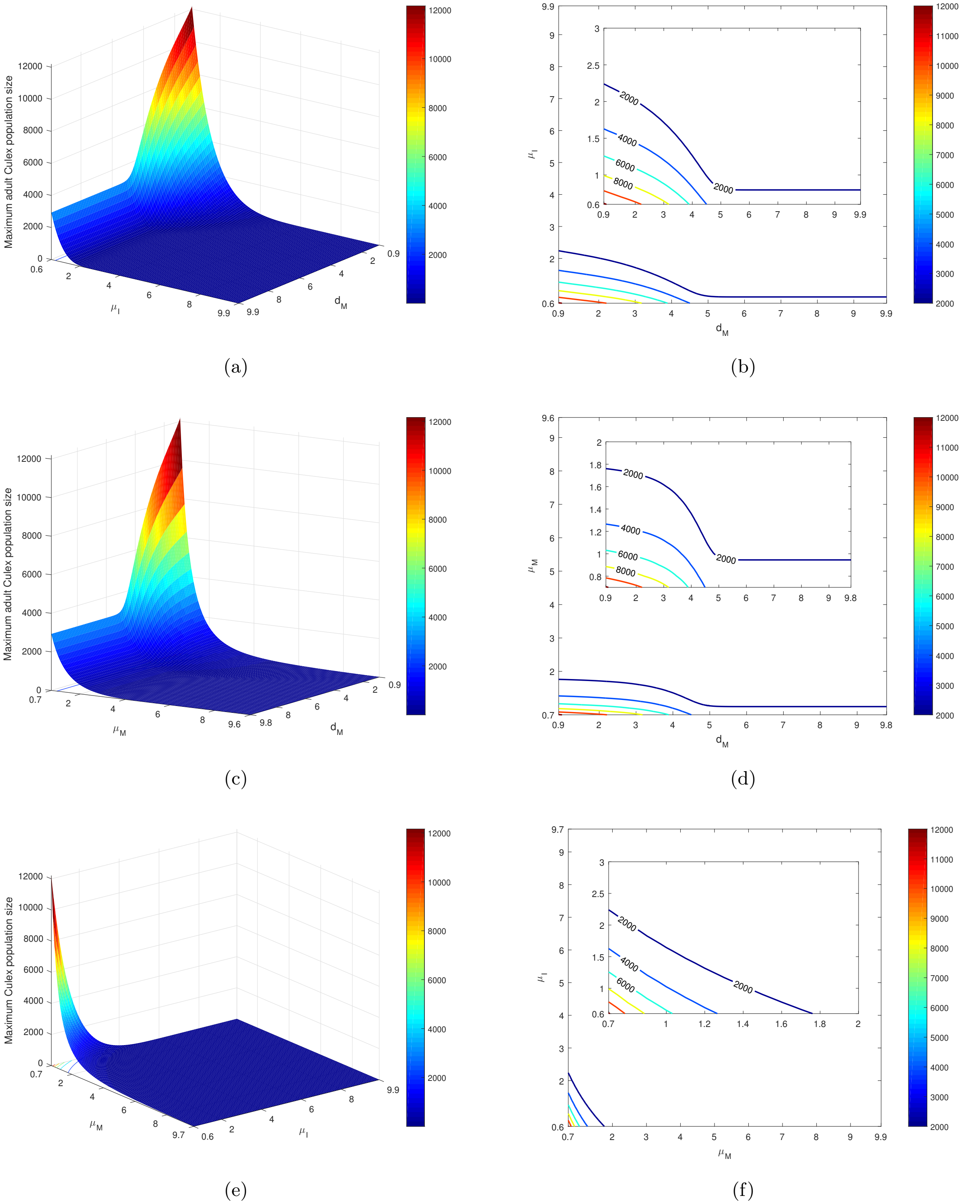
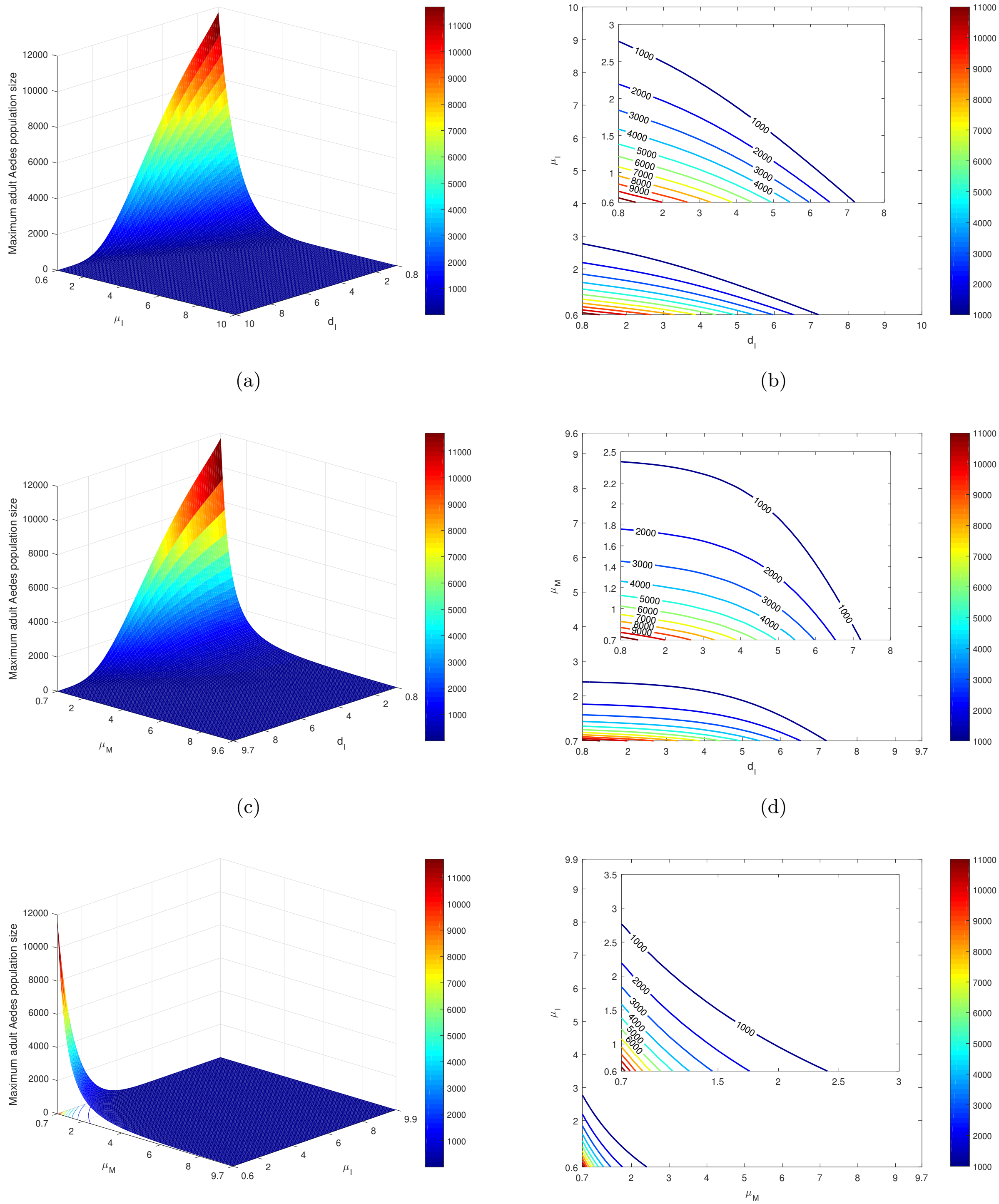


Figure 6: The surfaces (a, c, e) and contour plots (b, d, f) depicting the variations of peak adult *Culex pipiens* population size with varying death rates. Here, $d_I = 6$, the values of all other parameters are following Table 1. (a, b) The peak varies with changing μ_I and d_M. (c, d) The peak varies with changing μ_M and d_M. (e, f) The peak varies with changing μ_I and μ_M. In this case, we fix $d_M = 0.9$.



(a) (b) (c) (d) (e) (f)

Figure 7: The surfaces (a, c, e) and contour maps (b, d, f) describing the fluctuations of peak adult *Aedes albopictus* population size with varying death rates. Here, $d_M = 7$, the values of all other parameters are following Table 1. (a, b) The peak varies with changing μ_I and d_I. (c, d) The peak varies with changing μ_M and d_I. (e, f) The peak varies with changing μ_I and μ_M. In this case, we fix $d_I = 0.8$.

constructed three different models motivated by mosquitoes: model (A) with consideration of the adult diapause case; model (I) taking into account the immature diapause case; and the unified model (U) characterising both diapausing cases respectively. The well-posedness of the solutions to unified model (U) was investigated by the decoupled adult system. Rigorous analysis on population dynamics was performed. Moreover, we explored the threshold dynamics involving the global stability in terms of an index $\mathcal{R}$ dependent on model parameters by applying the theory of monotone dynamical systems.

In addition to the theoretical analysis, the numerical simulations were carried out on the unified model (U) to simulate the population dynamics of two temperate mosquito species respectively, that is, *Aedes albopictus* experiencing immature diapause and *Culex pipiens* undergoing adult diapause. The simulated mosquito population abundance of these two species from the unified model and the other two models support our expectations that the unified model (U) remains valid to describe the dynamics of diverse mosquito populations with different diapausing stages. The sensitivity analysis was then performed to check how the diapause-related parameters influence the population dynamics of these two mosquito species. The fluctuations of maximum population size as one index characterising mosquito population dynamics was mainly concerned. Our results indicate that increasing the survivability during diapause period by either reducing the diapausing death rate or shortening the length of diapause period may benefit the following normal growth, which is embodied in the larger outbreak size with lower diapausing mortality rate and shorter diapause duration. These sensitivity results further demonstrated that mosquito diapause is crucial for the sake of population persistence.

Adult mosquitoes as the main agent of many mosquito-borne diseases pose a big threat to human life. Controlling the adult population size is believed to be an effective way to prevent the disease transmission. Hence, we further investigated the integrated effects of the diapausing and natural death rates on the peak adult population sizes for these two species. These results indicate that the more effective approach to reduce the outbreak size of these two species is to increase the death rate during the normal growth period especially that for adults, rather than the diapausing death rate. As an assistant intervention, killing mosquitoes during the diapause period is feasible to lower the peak and average adult population sizes, which can prevent the massive outbreaks of mosquitoes to some extent.

Although the density-dependent self-regulation is accounted by assuming that the per-capita birth rate is a decreasing function of the adult density, the intra-specific competition among immatures is ignored during the normal population growth in the current study. In mosquitoes, intra-specific competition often occurs during the immature stage [45]. One feasible way to incorporate the immature intra-specific competition is to change the death term in (2.2) into immature density dependent such as $\mu(a) + g(I(t))$, where $g(I(t))$ represents the additional deaths due to intra-specific competition among immatures [14]. Then, the resulted model will contain a term involving the survivability due to intra-specific competition, i.e. $\exp(-\int_0^\tau g(I(t-\tau+r))dr)$, which brings challenges to the theoretical analysis of the model. In this case, it is impossible to decouple the adult population size $M(t)$ from the whole system, which makes the model much more difficult to analyse. Moreover, it would be more reasonable to incorporate time varying death rates, lengths of maturation and the diapause period, which are strongly relate to the variations of environmental conditions such as temperature, humidity and photoperiod. These improvements will result in a more complex DDE model with time-dependent periodic delays, which gives rise new challenges to the derivation of the model formulations and the theoretical analysis of the model. These interesting topics will be considered in our future work.

Data accessibility

This article has no additional data.

Author's contributions.

Y. L. conceived the modelling framework and theoretical analysis. K. L. carried the analyses theoretically and numerically. Y. L. and K. L. drafted the manuscript. D. H., D. G. and S. R. helped refine the manuscript.

Competing interests.

The authors declare no competing interests.

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Appendices: Model analysis

Since the equations for $M(t)$ can be decoupled in system (U), it suffices to analyse the equations for adult population in the unified model:

$$\begin{cases} \dfrac{dM(t)}{dt} = b(M(t-\tau))e^{-\mu_I \tau} - \mu_M M(t), & t \in [n, n+1-\tau-\tau_d], \\ \dfrac{dM(t)}{dt} = -d_M M(t), & t \in [n+1-\tau-\tau_d, n+1-\tau], \\ \dfrac{dM(t)}{dt} = b(M(t-\tau-\tau_d))e^{-\mu_I \tau - d_I \tau_d} - \mu_M M(t), & t \in [n+1-\tau, n+1], \end{cases} \tag{4.1}$$

where $n \in \mathbb{N}$. It is worth noting that only one-sided derivative is considered at all break points in our model.

We make the following biologically plausible assumptions on the birth rate and the periods, which are justified in existing literature [27]:

(H1) $b(M)$ is a non-negative locally Lipschitz continuous function in M. In particular, we assume that $b(M)$ is strictly increasing with respect to $M > 0$. Furthermore, $b(0) = 0$ and there exists $\overline{M} > 0$ such that $b(M)e^{-\mu_I \tau} > \mu_M M$ when $0 < M < \overline{M}$, and $b(M)e^{-\mu_I \tau} < \mu_M M$ whenever $M > \overline{M}$.

(H2) $2\tau + \tau_d < 1$.

In fact, any desired birth rate function can be constructed with appropriate parameter values alternatively. In general, our assumption for the birth rate function can be deduced from Fig. 8. Furthermore, the mosquito diapause is usually initiated when the cold and dry season comes and halted when the environment is suitable for reproduction and development [10]. The length of the diapause period may range from 3 to 5 months among different species and geographies. The lifespan of mosquitoes is very short, which varies with different species and is averaged at around 2-4 weeks [35]. Thus, it is reasonable to assume that the dimensionless parameters (divided by one year), the developmental duration and the period for diapause, satisfy assumption (H2).

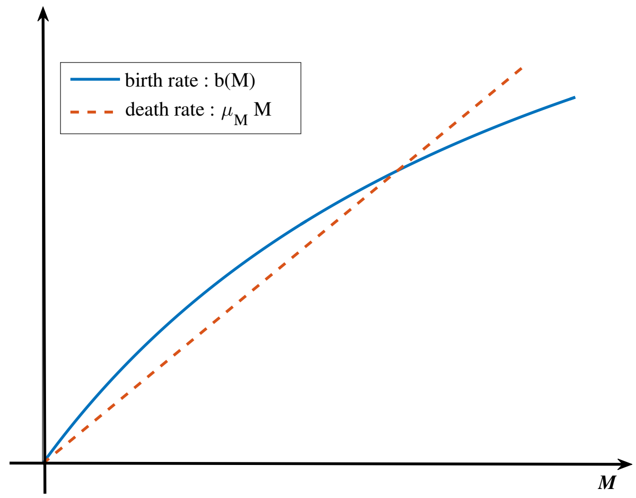

Figure 8: A schematic illustration of the birth rate function that satisfies assumption (H1).

Appendix A : The well-posedness

Based on the variation of constant formulae, system (4.1) can be written as the following equivalent integral form:

$$M(t) = e^{-\mu_M(t-n)}\left[\int_n^t b(M(s-\tau))e^{-\mu_I\tau}e^{\mu_M(s-n)}ds + M(n)\right], \qquad t \in [n, n+1-\tau_d-\tau], \tag{4.2a}$$

$$M(t) = e^{-d_M(t-(n+1-\tau-\tau_d))}M(n+1-\tau-\tau_d), \qquad t \in [n+1-\tau-\tau_d, n+1-\tau], \tag{4.2b}$$

$$M(t) = e^{-\mu_M(t-(n+1-\tau))}\left[\int_{n+1-\tau}^t b(M(s-(\tau+\tau_d)))e^{-\mu_I\tau-d_I\tau_d}e^{\mu_M(s-(n+1-\tau))}ds + M(n+1-\tau)\right], \quad t \in [n+1-\tau, n+1]. \tag{4.2c}$$

Define $Y = C([-\tau, 0], \mathbb{R}_+)$ with the usual supremum norm. For a function $u(\cdot) \in C([-\tau, \infty), \mathbb{R}_+)$, define $u_t \in Y$ by $u_t(\theta) = u(t+\theta)$, $\forall \theta \in [-\tau, 0], t \geq 0$. In what follows, the well-posedness of system (4.1) is established.

Theorem 4.1. *Suppose that assumptions (H1) and (H2) hold, then for any $\phi \in Y$, system (4.1) admits a unique non-negative and bounded solution $u(t, \phi)$ with $u_0 = \phi$ on $[0, \infty)$.*

Proof. Denote f by

$$f(t, M(t), M(t-\tau)) = b(M(t-\tau))e^{-\mu_I\tau} - \mu_M M(t).$$

For any given $\rho \geq 1$ and any $\phi \in Y$ satisfying $0 \leq \phi \leq \rho\overline{M}$, where $\overline{M}$ is defined in the assumption (H1), system (4.1) becomes the initial-value problem for the following ordinary differential equation (ODE) on $t \in [0, \tau]$:

$$\frac{dM(t)}{dt} = f(t, M(t), \phi(t-\tau)), \quad M(0) = \phi(0), \quad \forall\, t \in [0, \tau].$$

It follows from assumption (H1) that f is Lipschitz in M, then system (4.1) admits a unique solution on its maximal interval of existence. It can be easily checked by differentiation that (4.2a) with $n = 0$ satisfies system (4.1) on $[0, \tau]$. Moreover, it follows from the assumption (H1) that the following holds for $t \in [0, \tau]$:

$$\begin{aligned} u(t) =& e^{-\mu_M t}\left[\int_0^t b(u(s-\tau))e^{-\mu_I \tau}e^{\mu_M s}ds + u(0)\right] \\ =& e^{-\mu_M t}\left[\int_0^t b(\phi(s-\tau))e^{-\mu_I \tau}e^{\mu_M s}ds + \phi(0)\right] \\ \leq& e^{-\mu_M t}\left[\int_0^t b(\rho\overline{M})e^{-\mu_I \tau}e^{\mu_M s}ds + \rho\overline{M}\right] \\ =& \frac{b(\rho\overline{M})e^{-\mu_I \tau}}{\mu_M}e^{-\mu_M t}(e^{\mu_M t} - 1) + e^{-\mu_M t}\rho\overline{M} \\ \leq& \rho\overline{M}(1 - e^{-\mu_M t}) + e^{-\mu_M t}\rho\overline{M} = \rho\overline{M}. \end{aligned}$$

Hence, system (4.1) admits a unique solution $u(t) \in [0, \rho\overline{M}]$ for $t \in [0, \tau]$. Furthermore, the existence of a unique solution $u(t, \phi)$ can be extended to $[0, 1 - \tau - \tau_d]$ by the method of induction.

For $t \in [1 - \tau - \tau_d, 1 - \tau]$, the solution of system (4.1) can be determined uniquely by the initial-value problem for the following linear ODE:

$$\frac{dM(t)}{dt} = -d_M M(t), \quad M(1 - \tau - \tau_d) = u(1 - \tau - \tau_d), \quad \forall\, t \in [1 - \tau - \tau_d, 1 - \tau],$$

which implies that (4.2b) with $n = 0$ is the solution of system (4.1) on $[1 - \tau - \tau_d, 1 - \tau]$. In view of (4.2b) with $n = 0$, we have the solution $0 \leq u(t) \leq \rho\overline{M}$. It then follows that system (4.1) has a unique solution $u(t, \phi)$ on $[0, 1 - \tau]$.

Denote g by

$$g(t, M(t), M(t - (\tau + \tau_d))) = b(M(t - (\tau + \tau_d)))e^{-\mu_I \tau - d_I \tau_d} - \mu_M M(t).$$

For $t \in [1 - \tau, 1]$, the solution of system (4.1) must satisfy the initial-value problem for the following ODE:

$$\frac{dM(t)}{dt} = g(t, M(t), M(t - (\tau + \tau_d))), \quad M(1 - \tau) = u(1 - \tau), \quad \forall\, t \in [1 - \tau, 1].$$

According to assumption (H1), g is also Lipschitz in M. It then follows that there is a unique solution on its maximal interval of existence for system (4.1). It is easy to verify by differentiation that (4.2c) with $n = 0$ satisfies system (4.1) on $[1 - \tau, 1]$. Furthermore, based on assumption (H1), for all $t \in [1 - \tau, 1]$, we have

$$\begin{aligned} u(t) =& e^{-\mu_M (t-(1-\tau))}\left[\int_{1-\tau}^t b(u(s - (\tau + \tau_d)))e^{-\mu_I \tau - d_I \tau_d}e^{\mu_M (s-(1-\tau))}ds + u(1 - \tau)\right] \\ \leq& e^{-\mu_M (t-(1-\tau))}\left[\int_{1-\tau}^t b(\rho\overline{M})e^{-\mu_I \tau}e^{\mu_M (s-(1-\tau))}ds + \rho\overline{M}\right] \\ =& \frac{b(\rho\overline{M})e^{-\mu_I \tau}}{\mu_M}e^{-\mu_M (t-(1-\tau))}(e^{\mu_M (t-(1-\tau))} - 1) + e^{-\mu_M (t-(1-\tau))}\rho\overline{M} \\ \leq& \rho\overline{M}(1 - e^{-\mu_M (t-(1-\tau))}) + e^{-\mu_M (t-(1-\tau))}\rho\overline{M} = \rho\overline{M}. \end{aligned}$$

Thus, system (4.1) admits a unique solution $u(t, \phi)$ on $[0, 1]$.

Next, we can show the existence of a unique solution $0 \le u(t,\phi) \le \rho\overline{M}$ with $0 \le u_0 = \phi \le \rho\overline{M}$ for all $t \ge 0$ by applying the method of steps on each interval $[n, n+1]$. Since ρ can be chosen sufficiently large, it then follows that system (4.1) admits a unique solution $u(t,\phi)$ with $u_0 = \phi \in Y$ on $[0,\infty)$. □

Appendix B: Threshold dynamics

In order to investigate the global dynamics of system (4.1), we employ the theory of strongly monotone and sub-homogeneous semiflows in [47, Section 2.3]. Define Φ_t as the periodic semiflow for system (4.1) on Y; that is, $\Phi_t(\phi)(\theta) = u_t(\theta,\phi) = u(t+\theta,\phi)$ for $t \ge 0$, $\theta \in [-\tau, 0]$, where $u(t,\phi)$ is the unique solution of system (4.1) on $[0,\infty)$ with $u_0 = \phi \in Y$. The following lemma implies that Φ_t is a 1-periodic semiflow on Y.

Lemma 4.2. *Φ_t is a 1-periodic map on Y, that is, (i) $\Phi_0 = I$, where I is the identity map; (ii) $\Phi_{t+1} = \Phi_t \circ \Phi_1$, $\forall t \ge 0$; (iii) $\Phi_t(\phi)$ is continuous in $(t,\phi) \in [0,\infty) \times Y$.*

Proof. It is obvious that property (i) is true. Property (iii) can be easily verified by applying a standard argument [30, Theorem 8.5.2]. Now, we show that property (ii) holds. For any $\phi \in Y$ and all $t \ge 0$, let $v(t) = u(t+1,\phi)$ and $w(t) = u(t, u_1(\phi))$ with $v(\theta) = u(\theta+1,\phi) = w(\theta)$ for $\theta \in [-\tau, 0]$. For all $t \in [n, n+1-\tau-\tau_d]$ with $n \in \mathbb{N}$, we have

$$\begin{aligned}\frac{dv(t)}{dt} = \frac{du(t+1,\phi)}{dt} =& b(u(t+1-\tau),\phi))e^{-\mu_I \tau} - \mu_M u(t+1,\phi)\\ =& b(v(t-\tau))e^{-\mu_I \tau} - \mu_M v(t)\end{aligned}$$

and for all $t \in [n+1-\tau-\tau_d, n+1-\tau]$:

$$\begin{aligned}\frac{dv(t)}{dt} =& -d_M u(t+1,\phi)\\ =& -d_M v(t)\end{aligned}$$

and for all $t \in [n+1-\tau, n+1]$:

$$\begin{aligned}\frac{dv(t)}{dt} = \frac{du(t+1,\phi)}{dt} =& b(u(t+1-(\tau+\tau_d),\phi))e^{-\mu_I\tau - d_I\tau_d} - \mu_M u(t+1,\phi)\\ =& b(v(t-(\tau+\tau_d)))e^{-\mu_I\tau - d_I\tau_d} - \mu_M v(t).\end{aligned}$$

This indicates that $v(t)$ is a solution of system (4.1) with the same initial condition as another solution $w(t)$. The uniqueness of the solution indicates that $v(t) = u(t+1;\phi) = w(t) = u(t, u_1(\phi))$, $\forall t \ge 0$. Thus, $u_t \circ u_1(\phi) = u_{t+1}(\phi)$, which further implies that $\Phi_{t+1} = \Phi_t \circ \Phi_1$, $\forall t \ge 0$. □

The next two lemmas show that the periodic semiflow Φ_t is eventually strongly monotone and strictly subhomogeneous on Y.

Lemma 4.3. *For any ϕ and ψ in Y with $\phi > \psi$ (that is, $\phi(s) \ge \psi(s)$ for $s \in [-\tau, 0]$ with $\phi \not\equiv \psi$), there are two solutions $u(t,\phi)$ and $v(t,\psi)$ of system (4.1) with $u_0 = \phi$ and $v_0 = \psi$, respectively, that satisfy $u(t,\phi) > v(t,\psi)$ for all $t > \tau + \tau_d$, and hence $\Phi_t(\phi) \gg \Phi_t(\psi)$ on Y for all $t > 2(\tau + \tau_d)$.*

Proof. For any ϕ and ψ in Y with $\phi > \psi$, it can be easily shown that $u(t) \ge v(t)$ for all $t \ge 0$ by applying the comparison argument [40, Theorem 5.1.1] on each interval $[n, n+1]$ for all $n \in \mathbb{N}$. In view of (4.2a) with $n = 0$ and assumption (H1), we have

$$\begin{aligned} u(\tau) &= e^{-\mu_M \tau}\left[\int_0^\tau b(u(s-\tau))e^{-\mu_I\tau}e^{\mu_M s}ds + u(0)\right] \\ &= e^{-\mu_M \tau}\left[\int_0^\tau b(\phi(s-\tau))e^{-\mu_I\tau}e^{\mu_M s}ds + \phi(0)\right] \\ &> e^{-\mu_M \tau}\left[\int_0^\tau b(\psi(s-\tau))e^{-\mu_I\tau}e^{\mu_M s}ds + \psi(0)\right] \\ &= v(\tau). \end{aligned}$$

By the continuity of the solution, there must exist some $\xi \in (\tau, 1-\tau-\tau_d]$ such that $u(t) > v(t)$ for all $t \in (\tau, \xi)$. This claim can be further extended to all $t \in (\tau, 1-\tau-\tau_d]$. If we assume the contrary, then there exists a $t_0 \in (\tau, 1-\tau-\tau_d]$ such that $u(t) > v(t)$ for all $\tau < t < t_0$ and $u(t_0) = v(t_0)$. However,

$$\begin{aligned} u(t_0) &= e^{-\mu_M(t_0-\tau)}\left[\int_\tau^{t_0} b(u(s-\tau))e^{-\mu_I\tau}e^{\mu_M(s-\tau)}ds + u(\tau)\right] \\ &\geq e^{-\mu_M(t_0-\tau)}\left[\int_\tau^{t_0} b(v(s-\tau))e^{-\mu_I\tau}e^{\mu_M(s-\tau)}ds + u(\tau)\right] \\ &> e^{-\mu_M(t_0-\tau)}\left[\int_\tau^{t_0} b(v(s-\tau))e^{-\mu_I\tau}e^{\mu_M(s-\tau)}ds + v(\tau)\right] \\ &= v(t_0), \end{aligned}$$

which is a contradiction. For $t \in [1-\tau-\tau_d, 1-\tau]$, it follows from (4.2b) that

$$u(t) = e^{-d_M(t-(1-\tau-\tau_d))}u(1-\tau-\tau_d) > e^{-d_M(t-(1-\tau-\tau_d))}v(1-\tau-\tau_d) = v(t).$$

For $t \in [1-\tau, 1]$, based on assumption (H1) and (4.2c), we have

$$\begin{aligned} u(t) =& e^{-\mu_M(t-(1-\tau))}\left[\int_{1-\tau}^t b(u(s-(\tau+\tau_d)))e^{-\mu_I\tau-d_I\tau_d}e^{\mu_M(s-(1-\tau))}ds + u(1-\tau)\right] \\ \geq& e^{-\mu_M(t-(1-\tau))}\left[\int_{1-\tau}^t b(v(s-(\tau+\tau_d)))e^{-\mu_I\tau-d_I\tau_d}e^{\mu_M(s-(1-\tau))}ds + u(1-\tau)\right] \\ >& e^{-\mu_M(t-(1-\tau))}\left[\int_{1-\tau}^t b(v(s-(\tau+\tau_d)))e^{-\mu_I\tau-d_I\tau_d}e^{\mu_M(s-(1-\tau))}ds + v(1-\tau)\right]. \end{aligned}$$

Subsequently, we can show that $u(t) > v(t)$ for all $t > \tau$ by applying the method of induction on each interval $[n, n+1]$ with $1 \leq n \in \mathbb{N}$. In particular, $s - \tau > 0$ and $s - (\tau + \tau_d) > 0$ hold when $s > \tau + \tau_d$, then we have $u(s-\tau) > v(s-\tau)$ and $u(s-(\tau+\tau_d)) > v(s-(\tau+\tau_d))$ for $s > \tau + \tau_d$. Thus, it easily follows that $u(t) > v(t)$ for all $t > \tau + \tau_d$. Therefore, the solution map Φ_t is strongly monotone on Y when $t > 2(\tau + \tau_d)$. □

We need to make additional assumptions on the birth rate function before investigating the sub-homogeneity of Φ_t.

(H3) The birth rate $b(M)$ can be expressed as $b(M) = B(M)M$, where $B(M)$ is the per-capita birth rate and is strictly decreasing with respect to $M(> 0)$.

Lemma 4.4. *For any $\phi \gg 0$ in Y and any $\lambda \in (0,1)$, we have $u(t, \lambda\phi) > \lambda u(t, \phi)$ for all $t > \tau + \tau_d$, and therefore, $\Phi_1^n(\lambda\phi) \gg \lambda\Phi_1^n(\phi)$ in Y for any integer n with $n > 2(\tau + \tau_d)$.*

Proof. Let $u(t,\phi)$ be the unique solution of system (4.1) with $u_0 = \phi \gg 0$ in Y. Denote $w(t) = u(t,\lambda\phi)$ and $v(t) = \lambda u(t,\phi)$, then for all $\theta \in [-\tau, 0]$, $w(\theta) = \lambda\phi(\theta) = v(\theta)$. Since $\phi \gg 0$, the proof of Theorem 4.1 implies that $v(t) > 0$ and $w(t) > 0$ hold for all $t \geq 0$. In consideration of assumption (H3), it follows that $v(t)$ satisfies the following system of differential equations:

$$\begin{cases} \dfrac{dv(t)}{dt} = B(\dfrac{1}{\lambda}v(t-\tau))v(t-\tau)e^{-\mu_I\tau} - \mu_M v(t), \quad t \in [n, n+1-\tau-\tau_d], \\ \dfrac{dv(t)}{dt} = -d_M v(t), \qquad\qquad t \in [n+1-\tau-\tau_d, n+1-\tau], \\ \dfrac{dv(t)}{dt} = B(\dfrac{1}{\lambda}v(t-(\tau+\tau_d)))v(t-(\tau+\tau_d))e^{-\mu_I\tau-d_I\tau_d} - \mu_M v(t), \\ \qquad\qquad t \in [n+1-\tau, n+1], \end{cases}$$

where $n \in \mathbb{N}$. Then, the corresponding equivalent integral form is shown as follows:

$$\begin{aligned} v(t) =& e^{-\mu_M(t-n)}\left[\int_n^t B(\frac{1}{\lambda}v(s-\tau))v(s-\tau)e^{-\mu_I\tau}e^{\mu_M(s-n)}ds + v(n)\right], \\ & \qquad t \in [n, n+1-\tau-\tau_d], \\ v(t) =& e^{-d_M(t-(n+1-\tau-\tau_d))}v(n+1-\tau-\tau_d), \qquad t \in [n+1-\tau-\tau_d, n+1-\tau], \\ v(t) =& e^{-\mu_M(t-(n+1-\tau))}\left[\int_{n+1-\tau}^t B(\frac{1}{\lambda}v(s-(\tau+\tau_d)))v(s-(\tau+\tau_d))\right. \\ & \left.\times\, e^{-\mu_I\tau-d_I\tau_d}e^{\mu_M(s-(n+1-\tau))}ds + v(n+1-\tau)\right], \qquad t \in [n+1-\tau, n+1]. \end{aligned} \tag{4.3}$$

For all $t \in (0, \tau]$, it follows from assumption (H3) and the first equation of (4.3) that

$$\begin{aligned} v(t) =& e^{-\mu_M t}\left[\int_0^t B(\frac{1}{\lambda}v(s-\tau))v(s-\tau)e^{-\mu_I\tau}e^{\mu_M s}ds + v(0)\right] \\ =& e^{-\mu_M t}\left[\int_0^t B(\phi(s-\tau))w(s-\tau)e^{-\mu_I\tau}e^{\mu_M s}ds + w(0)\right] \\ <& e^{-\mu_M t}\left[\int_0^t B(\lambda\phi(s-\tau))w(s-\tau)e^{-\mu_I\tau}e^{\mu_M s}ds + w(0)\right] \\ =& e^{-\mu_M t}\left[\int_0^t B(w(s-\tau))w(s-\tau)e^{-\mu_I\tau}e^{\mu_M s}ds + w(0)\right] \\ =& w(t). \end{aligned}$$

Then, there must exist some $\xi_1 \in (\tau, 1-\tau-\tau_d]$ such that $0 < v(t) < w(t)$ for all $t \in (\tau, \xi_1)$ due to the continuity of the solution. This claim can be further extended to all $t \in (\tau, 1-\tau-\tau_d]$. If not, then there exists a $t_1 \in (\tau, 1-\tau-\tau_d]$ such that $v(t) < w(t)$ for all $\tau < t < t_1$ and $v(t_1) = w(t_1)$.

However,

$$
\begin{aligned}
w(t_1) =& e^{-\mu_M(t_1-\tau)}\left[\int_\tau^{t_1} b(w(s-\tau))e^{-\mu_I\tau}e^{\mu_M(s-\tau)}ds + w(\tau)\right] \\
>& e^{-\mu_M(t_1-\tau)}\left[\int_\tau^{t_1} b(v(s-\tau))e^{-\mu_I\tau}e^{\mu_M(s-\tau)}ds + v(\tau)\right] \\
=& e^{-\mu_M(t_1-\tau)}\left[\int_\tau^{t_1} B(v(s-\tau))v(s-\tau)e^{-\mu_I\tau}e^{\mu_M(s-\tau)}ds + v(\tau)\right] \\
>& e^{-\mu_M(t_1-\tau)}\left[\int_\tau^{t_1} B(\frac{1}{\lambda}v(s-\tau))v(s-\tau)e^{-\mu_I\tau}e^{\mu_M(s-\tau)}ds + v(\tau)\right] \\
=& v(t_1),
\end{aligned}
$$

which is a contradiction. For all $t \in [1-\tau-\tau_d, 1-\tau]$, in view of the second equation of (4.3), we have

$$
v(t) = e^{-d_M(t-(1-\tau-\tau_d))}v(1-\tau-\tau_d) < e^{-d_M(t-(1-\tau-\tau_d))}w(1-\tau-\tau_d) = w(t).
$$

For all $t \in [1-\tau, 1]$, assumption (H3) and the third equation of (4.3) imply that

$$
\begin{aligned}
w(t) =& e^{-\mu_M(t-(1-\tau))}\left[\int_{1-\tau}^{t} b(w(s-(\tau+\tau_d)))e^{-\mu_I\tau-d_I\tau_d}e^{\mu_M(s-(1-\tau))}ds + w(1-\tau)\right] \\
>& e^{-\mu_M(t-(1-\tau))}\left[\int_{1-\tau}^{t} b(v(s-(\tau+\tau_d)))e^{-\mu_I\tau-d_I\tau_d}e^{\mu_M(s-(1-\tau))}ds + v(1-\tau)\right] \\
=& e^{-\mu_M(t-(1-\tau))}\Big[\int_{1-\tau}^{t} B(v(s-(\tau+\tau_d)))v(s-(\tau+\tau_d))e^{-\mu_I\tau-d_I\tau_d}e^{\mu_M(s-(1-\tau))}ds \\
&+ v(1-\tau)\Big] \\
>& e^{-\mu_M(t-(1-\tau))}\Big[\int_{1-\tau}^{t} B(\frac{1}{\lambda}v(s-(\tau+\tau_d)))v(s-(\tau+\tau_d))e^{-\mu_I\tau-d_I\tau_d}e^{\mu_M(s-(1-\tau))}ds \\
&+ v(1-\tau)\Big] \\
=& v(t).
\end{aligned}
$$

Similarly on each interval $(n, n+1]$, which induces that $0 < v(t) < w(t)$ for all $t \in (n, n+1]$ with $n \in \mathbb{N}$. Note that $s-\tau > 0$ and $s-(\tau+\tau_d) > 0$ hold when $s > \tau+\tau_d$, which imply that $w(s-\tau) > v(s-\tau)$ and $w(s-(\tau+\tau_d)) > v(s-(\tau+\tau_d))$ for $s > \tau+\tau_d$. Thus, we have $w(t) > v(t)$ for any $t > \tau+\tau_d$, that is, $u(t, \lambda\phi) > \lambda u(t, \phi)$ for all $t > \tau+\tau_d$, and hence, $\Phi_1^n(\lambda\phi) = \Phi_n(\lambda\phi) \gg \lambda\Phi_n(\phi) = \lambda\Phi_1^n(\phi)$ holds for all integer n satisfying $n > 2(\tau+\tau_d)$.

□

Motivated by the theory of threshold dynamics in [47] (or those in [48]) for strongly monotone and strictly sub-homogeneous semiflows, we investigate the global dynamics for system (4.1) in the rest of this section. Based on assumption (H1), it is easy to verify that system (4.1) has a population extinction equilibrium 0. Then, the corresponding linearised system is

$$
\begin{cases}
\dfrac{dM(t)}{dt} = b'(0)e^{-\mu_I\tau}M(t-\tau) - \mu_M M(t), & t \in [n, n+1-\tau-\tau_d], \\
\dfrac{dM(t)}{dt} = -d_M M(t), & t \in [n+1-\tau-\tau_d, n+1-\tau], \\
\dfrac{dM(t)}{dt} = b'(0)e^{-\mu_I\tau-d_I\tau_d}M(t-(\tau+\tau_d)) - \mu_M M(t), & t \in [n+1-\tau, n+1],
\end{cases}
\tag{4.4}
$$

where $n \in \mathbb{N}$. For any given $t \geq 0$, let $P(t)$ be the solution map of the linear system (4.4) on Y. Then, $P(1)$ is the Poincaré map associated with system (4.4) with its spectral radius denoted as $\mathcal{R}$.

We now prove the main result of this section, that is, the global stability of system (4.1) in terms of $\mathcal{R}$.

Theorem 4.5. *The following statements hold for system (4.1):*

(i) If $\mathcal{R} \leq 1$, then 0 is globally asymptotically stable in Y.

(ii) If $\mathcal{R} > 1$, then system admits a unique positive 1-periodic solution $M^*(t)$, which is globally asymptotically stable in $Y \setminus \{0\}$.

Proof. For a fixed integer n_1 satisfying $n_1 > 2(\tau + \tau_d)$, it follows from Lemma 4.2 that Φ_t can be a n_1-periodic semiflow on Y. In view of Lemmas 4.3 and 4.4, Φ_{n_1} is a strongly monotone and strictly subhomogeneous map on Y. Let $D\Phi_{n_1}(0)$ be the Fréchet derivative of Φ_{n_1} at 0 if it exists, and denote the spectral radius of this linear operator $D\Phi_{n_1}(0)$ as $r(D\Phi_{n_1}(0))$. In light of Theorem 2.3.4 in [47], we have:

(i) If $r(D\Phi_{n_1}(0)) \leq 1$, then 0 is globally asymptotically stable for system (4.1) in Y.

(ii) If $r(D\Phi_{n_1}(0)) > 1$, then system (4.1) admits a unique positive n_1-periodic solution $M^*(t)$, which is globally asymptotically stable in $Y \setminus \{0\}$.

Since $r(D\Phi_{n_1}(0)) = r(P(n_1)) = (r(P(1)))^{n_1} = \mathcal{R}^{n_1}$, it then follows that the above statements remain valid when the threshold value is $\mathcal{R}$. Moreover, it is necessary to show that $M^*(t)$ is 1-periodic. Let $\phi^* = M^*(0)$ in $Y \setminus \{0\}$, then we have $\Phi_{n_1}(\phi^*) = \phi^*$. Since

$$\Phi_1^{n_1}(\Phi_1(\phi^*)) = \Phi_1(\Phi_1^{n_1}(\phi^*)) = \Phi_1(\Phi_{n_1}(\phi^*)) = \Phi_1(\phi^*),$$

the uniqueness of the positive fixed point of $\Phi_1^{n_1} = \Phi_{n_1}$ implies that $\Phi_1(\phi^*) = \phi^*$. Thus, $M^*(t)$ is a positive period-1 solution for system (4.1) with $M^*(0) = \phi^*$.

□

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