ANALYSIS OF AGE-STRUCTURED POPULATION GROWTH FOR SINGLE SPECIES

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Certificate of Originality

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____________________________(Signed)

Kaihui Liu (Name of student)

Dedicate to my family.

Abstract

A wide variety of mathematical models have been proposed to investigate age-structured population growth for single species. Mathematical models allowing for more biotic and abiotic factors tend to better describe the complex behaviour of populations. In this thesis, we attempt to provide a comprehensive mathematical modelling framework and rigorous theoretical analysis for age-structured populations with the consideration of various factors regulating population growth such as seasonal variations, intra-specific competition, spatial movements and diapause. It is worth noting that developmental durations within each age group are assumed varying with time. Consequently, the model reduced from the classical Mckendrick-von Foerster equation takes the form of retarded delay differential or reaction-diffusion equations with time-dependent delays, which brings novel challenges to the theoretical analysis. By applying the well-developed theory of retarded functional differential or reaction diffusion equations and the theory of monotone dynamical system in periodic environment, we establish the well-posedness of the solutions and the global dynamics involving the global extinction, uniform persistence and global stability of the trivial and positive periodic solutions in terms of the basic reproduction number.

We begin this thesis with a brief introduction for the development of early and advanced age-structured population models in Chapter 1. Then, the methodologies employed in the theoretical analysis of age-structured models are reviewed. Finally, the motivations of this thesis are illustrated in detail. In Chapter 2, we provide some

requisite mathematical theories for this thesis, which refer to the theories related to monotone dynamical systems, uniform persistence and basic reproduction number in periodic environment.

The work presented in Chapter 3 mainly involves the investigation of the age-structured population growth based on the assumptions that the birth and death rate functions are dependent on density and periodic in time. In this work, we propose a generalised hyperbolic age-structured model, and give a detailed proof for the existence and uniqueness of the solution by applying the contraction mapping theorem on the integral form solution obtained through integration along characteristics. By assuming time-varying developmental durations and age thresholds and using tick population as a motivative example, we deduce an age-structured model of four coupled periodic delay differential equations (DDE) with time-dependent delays. When the immature intra-specific competition is ignored, we obtain a new reduced periodic DDE model system, the adult system of which can be decoupled. Based on this decoupled periodic delay differential equations, we show the global existence and uniqueness of the solution, define the basic reproduction number $\mathcal{R}_0$ and prove the global stability of the positive periodic solution in terms of $\mathcal{R}_0$ by defining a periodic solution semiflow on a suitable phase space and employing the theory of monotone dynamical systems. Under the consideration of immature intra-specific competition, the threshold dynamics including population extinction and uniform persistence in terms of $\mathcal{R}_0$ is established.

Chapter 4 is devoted to analyse an age-structured population model with the consideration of spatial movements, seasonal variations, intra-specific competition and time-varying maturation duration simultaneously. When the competition among immatures is negligible, the model takes the form of a system of reaction-diffusion equations with time-dependent delays, in which situation one equation for the adult population density is decoupled. The well-posedness of the decoupled system is established and the basic reproduction number $\mathcal{R}_0$ is defined and shown to determine the global attractivity of either the zero equilibrium (when $\mathcal{R}_0 \leqslant 1$) or a positive periodic solution ($\mathcal{R}_0 > 1$) by using the dynamical system approach on an appropriate phase space. When the immature intra-specific competition is included and the immature diffusion rate is negligible, the model is neither cooperative (where the comparison principle holds) nor reducible to a single equation. In this case, the threshold dynamics about the population extinction and uniform persistence are established by using the newly defined basic reproduction number $\widetilde{\mathcal{R}}_0$ as a threshold index.

In Chapter 5, we propose a novel modelling framework to investigate the effects of diapause on seasonal population growth. 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 subtropical areas. In this work, a novel modelling framework, motivated by mosquito species, 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. We formulate two models of delay differential equations (DDE) to explicitly describe mosquito population growth with a single diapausing stage, either immature or adult. These two models can be further unified into one DDE model, on which the well-posedness of the solution and the global stability of the trivial and positive periodic solution in terms of an index $\mathcal{R}$ are analysed. The seasonal population abundances of two temperate mosquito species with different diapausing stages are simulated to identify the essential 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. Our modelling framework may shed light on the diapause-induced variations in spatiotemporal distributions of different mosquito species.

Chapter 6 gives the conclusions of the results presented in this thesis and the discussions of the future work.

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Contents

List of Figures

List of Tables

Chapter 1

Introduction

Mathematical models have been extensively developed and effectively applied to the study of population growth, the recorded history of which can be dated back to thirteenth century when Leonardo Pisano (or Fibonacci) proposed the first mathematical model, the well-known Fibonacci sequence, with the problem of rabbit population as an example [8, 102]. Five centuries later, a pioneered work of Euler uncovered the geometric growth of human population, which inspired Malthus to formulate the most simple population model [22]. The Malthusian model assumed a constant per capita growth rate and suggested that the size of human population increases or decays exponentially with time in the case of ignoring the influences of overcrowding and limited resources [57]. Afterwards, by adding a term describing crowding effects or competition for resources into the Malthusian model, Verhulst proposed the logistic model, which predicted that the size of the population tends to a finite number under appropriate initial conditions other than infinity as time approaches to infinity [1, 17]. The dynamics predicted by the logistic model are in agreement with the behaviours of many populations. The development of mathematical formulation for population growth made little progress until Lotka and Volterra pioneered the modern ecology theory [62]. The classical population models including the Lotka-Volterra (or named predator-prey) equations and their generalisation have made great contributions to the study of population dynamics and ecology [26].

Simplifying assumptions are often made to formulate mathematically tractable models. Nevertheless, oversimplified assumptions in a model would limit the scope of its biological accuracy. The first common oversimplification in the aforementioned models is the assumption of homogeneity for individuals in a population, which means all individuals of the population are assumed to be physiologically identical. However, the population dynamics are very complex in the natural world, the individual developmental processes vary with many biotic and abiotic factors and therefore, a more realistic way characterising the differences between individuals is to formulate structured population models. The chronological age is one of the most natural and important structuring variables. In the natural world, the populations for many species of animals are structured by age. The human population is the best-known example. Age-distribution constitutes the most concerned topic in the study of demography since the age structure determines the future growth pattern of the population and has profound implications for government policy [23]. For example, juveniles have a relatively high developmental rate and low level of fecundity in comparison with adults. A larger proportion of the human population in elderly age classes leads to increasingly population aging and slower population growth. In consequence, the retirement systems and medical facilities must be developed by government to serve the elder people. Moreover, for some species of insects such as mosquitoes, in addition to the vital rates, the habitats of immature and mature individuals are completely different. It would be natural to associate with the effects of age structure by dividing the population into different age classes. Before proceeding to further investigations, it is imperative to give a brief introduction of age-structured population models.

1.1 Early age-structured population models

Age-structured models can be formulated mathematically in either discrete or continuous ways, each of which has advantages and drawbacks. Both discrete and continuous age-structured models have been widely applied in modelling population growth.

1.1.1 Discrete age-structured models

Leslie matrix model [68] is the classic representative discrete age-structured model. The population is first classified into a finite number of age groups, labeled by $i = 0, 1, \cdots, m$. The number of individuals within each age group is counted at discrete time steps, $t = 0, 1, \cdots$. At the t-th time step, the number of the population, denoted by $P(t)$, is described by a column vector, $P(t) = [P_0(t), P_1(t), \cdots, P_m(t)]^T$, where $P_i(t)(i = 0, 1, \cdots, m)$ represents the number of the population within the i-th age class at the t-th time step. The number of the population at the next time step $t+1$, $P(t+1)$, is deduced by the following difference equation:

$$P(t+1) = \mathbf{A}P(t),$$

where $\mathbf{A}$ is the *Leslie matrix* or *projection matrix* and the ijth entry of $\mathbf{A}$ is determined by the age-dependent reproductive, developmental and survival rates.

Compared to continuous age-structured models, matrix population models have the advantage that they are relatively tractable and easy to formulate, simulate and analyse. However, the matrix models are unable to describe the instantaneous rate of change and the dynamics occurring between different age groups and discrete time steps.

1.1.2 Continuous age-structured models

The first time-continuous model considering age as a continuous structuring variable was in the formulation of integral equations and introduced by Sharp and Lotka in 1911 [99], where they assumed that fertility and mortality rates are age-dependent. Based on similar idea, McKendrick in 1926 [84] proposed a first order partial differential equation (PDE) to describe the continuous variations of a population with respect to time and age. The dynamics of an age-structured population described by the McKendrick model is shown as follows:

$$\begin{cases} \Big(\dfrac{\partial}{\partial t} + \dfrac{\partial}{\partial a}\Big)\rho(t,a) = -\mu(a)\rho(t,a), \\ \rho(0,a) = \phi(a),\ \ a \geqslant 0, \\ \rho(t,0) = \int_0^\infty b(a)\rho(t,a)da,\ \ t \geqslant 0, \end{cases}$$

where $\rho(t,a)$ represents the density of the population at time t of age a, $\mu(a)$ and $b(a)$ are nonnegative age-dependent mortality and fertility rates, $\phi(a)$ is the nonnegative initial age-distribution of the population. This classical model is named as McKendrick-von Foerster model since the same partial differential equation was developed by von Foerster in 1959 to study cellular populations [120]. The investigation of the nonlinear modification and generalisation based on this classical model has attracted a great deal of attention in recent years. Interested readers can refer to the wonderful monographs to gain comprehensive understanding of age-structured models [26, 57, 70, 85, 122].

1.2 Generalised age-structured models in heterogeneous environment

Another common simplification in population models is the assumption of homogeneity for the environment that organisms inhabit, which is heterogeneously distributed in reality. Seasonal variations caused by climatic changes are considered as the dominant environmental factor shaping annual patterns of the population dynamics [112]. This is particular true for some insect species such as ticks, serving as the main vector spreading tick-borne diseases, the distribution and abundance of which are very sensitive to the climate conditions as they need relatively high humidity and moderate temperature to survive during their prolonged nonparasitic stages [89]. Incorporating seasonal effects in age-structured models would be a sensible choice to better investigate the population dynamics, with all the time-dependent parameter functions being periodic with the same period.

In the natural world, food and water resources may vary from place to place, which drive the organisms to keep drifting or dispersing. In addition to the seasonal effects, spatial diffusion affecting population dynamics and the structures of the communities are of particular interest to scientists. Due to limited available resources for individuals from the same species, intraspecific competition is a ubiquitous phenomenon in the population growth of a single species. Moreover, diapause, a period of suspended growth, serving as an surviving mechanism in response to harsh environmental conditions, plays significant roles on the persistences of insects or other invertebrate species. In this thesis, we attempt to investigate the age-structured population growth of single species subject to various factors such as the seasonal effects, intra-specific competition, spatial diffusion and diapause on individual growth, in particular, the birth, death and maturation rates.

1.3 Motivation

The analysis on age-structured models has attracted more attention than on other kinds of structured models such as size-structured models. This may be attributed to the predicted linear relation between age and time. Various mathematical methodologies have been applied to analyse the age-structured population models. The stable age distribution was identified in models with linear birth and death rates during early developmental period [73, 74]. By applying the methods of Volterra integral equations and Laplace transforms, rigorous analysis of linear age-structured models was established [11, 39]. For nonlinear age structured models, the existence, uniqueness and convergence to equilibrium of solutions was established by utilising a nonlinear Volterra integral equations approach [50], which was investigated sytematically in [57, 59, 85]. Another classical functional analytic approach, the theory for semigroups of operators in Banach spaces, was applied to the nonlinear age-structured models with increasingly complex nonlinearities (see the book of Webb for details [122]).

Although the operator semigroup theory and the theory of integral renewal equations are powerful tools to analyse age structured population models, the requisite sophisticated mathematical technics makes few analysts proficiently apply these two approaches in dynamical systems to gain heuristic biological insights. Gurney *et al.* advocated utilising the delay differential equations framework to model age-structured populations [49, 88]. For many species with various life stages, the influences of age differences among individuals within each age group may be trivial relative to that of intergroup differences. Consequently, the population can be divided into different age groups by different age thresholds. It is reasonable to assume the vital rates within one age group are independent of age, which means the vital rates are piecewise functions with jumps at age thresholds. The influences of age structure on population dynamics can be described by introducing time delays, that is, the developmental duration within each age group. In this case, the classical McKendrick-von Foerster model can be reduced into a system of delay differential (with discrete delays) or integral-differential equations (with distributed delays), which allows us to apply the well-developed theory of retarded functional differential equations to the complex dynamical systems to draw some useful conclusions.

The aim of this thesis is twofold. On one hand, we aim to provide a comprehensive modelling framework for age-structured populations growth with the consideration of time-dependent developmental durations in a general biological setting. In the natural word, the developmental durations of most species such as mosquitoes [100] and ticks [89] greatly rely on the temperature, which vary with time. The introduction of time-dependent maturation periods into the age-structured model will cause time-dependent age thresholds and lead to a system of functional differential equations with time-varying delays, the formulation of which is quite different from those with time-independent delay in [2] since we cannot indiscreetly replace the constant delay with time-changing delay. In this thesis, we start with the generalised McKendric-vonForster equation with age-dependent nonnegative fertility and mortality functions in periodical environment, then reduce it into a system of retarded functional or delay differential equations with periodic delays by introducing time-dependent developmental durations, as the work shown in Chapter 3 and 4. On the other hand, rigorous theoretical analysis is imperative to establish from the perspective of periodic dynamical systems. Monotone dynamics can be generated by some special class of retarded functional differential or reaction-diffusion equations, that is, the solutions of which preserve some kind of order relation on initial and boundary conditions [106]. This is particular suitable for the mathematical models describing biological population growth since the population sizes or densities are intrinsically positive, which facilitates the system gaining monotonicity or order-preserving properties [105]. In this thesis, we conduct our analysis on systems of retarded functional differential or reaction diffusion equations with time-varying delays in periodic environment. In light of the theory of retarded functional differential or reaction diffusion equations and monotone dynamical systems [135], we establish the well-posedness of the solutions and global dynamics involving the global extinction, uniform persistence and global stability of a positive periodic solution in terms of the basic reproduction number.

Chapter 2

Preliminaries

In this chapter, we present some terminologies and known results used in the rest of this thesis, which involve the theory of global attractors, uniform persistence, monotone dynamical systems and basic reproduction number for age-structured population models in periodic environments.

2.1 Global attractors and uniform persistence

Suppose X is a metric space with metric d. Let $f : X \to X$ be a continuous map and $X_0 \subset X$ an open set. Define $\partial X_0 := X \backslash X_0$, and $M_\partial := \{x \in \partial X_0 : f^n(x) \in \partial X_0, \forall n \geqslant 0\}$, which may be empty.

Definition 2.1. *A bounded set A is said to attract a bounded set B in X if*

$$\limsup_{n\to\infty,\ x\in B} \{d(f^n(x), A)\} = 0.$$

A subset $A \subset X$ is said to be an attractor for f if A is nonempty, compact and invariant ($f(A) = A$), and A attracts some open neighborhood of itself. A global attractor for $f : X \to X$ is an attractor that attracts every point in X. For a nonempty invariant set M, the set $W^s(M) := \{x \in X : \lim_{n\to\infty} d(f^n(x), M) = 0\}$ is called the stable set of M.

Recall that a continuous mapping $f : X \to X$ is said to be point dissipative if there is a bounded set B_0 in X such that B_0 attracts each point in X.

Theorem 2.1. *[135, Theorem 1.1.3] If $f : X \to X$ is compact and point dissipative, then there is a connected global attractor A that attracts each bounded set in X.*

Definition 2.2. *f is said to be uniformly persistent with respect to $(X_0, \partial X_0)$ if there exists an $\eta > 0$ such that $\liminf_{n\to\infty} d(f^n(x), \partial X_0) \geqslant \eta$ for all $x \in X_0$.*

Definition 2.3. *Let $A \subset X$ be a nonempty invariant set for f. We say A is internally chain-transitive if for any $a, b \in A$ and any $\epsilon > 0$, there is a finite sequence $x_1, \cdots, x_m$ in A with $x_1 = a, x_m = b$ such that $d(f(x_i), x_{i+1}) < \epsilon$, $1 \leqslant i \leqslant m-1$. The sequence $\{x_1, \cdots, x_m\}$ is called an ϵ-chain in A connecting a and b.*

Definition 2.4. *A lower semicotinuous function $p : X \to \mathbb{R}_+$ is called a generalized distance function for $f : X \to X$ if for every $x \in (X_0 \bigcap p^{-1}(0)) \bigcup p^{-1}(0, \infty)$, we have $p(f^n(x)) > 0$, $\forall n \geqslant 1$.*

Theorem 2.2. *[135, Theorem 1.3.2] (or [107, Theorem 3]) Let p be a generalized distance function for continuous map $f : X \to X$. Assume that*

(P1) f has a global attractor;

(P2) There exists a finite sequence $M = \{M_1, \cdots, M_k\}$ of disjoint, compact, and isolated invariant sets in ∂X_0 with the following properties:

- *(a) $\bigcap_{x\in M_\partial} \omega(x) \subset \bigcup_{i=1}^{k} M_i$, where $\omega(x)$ represents the omega limit set of x;*
- *(b) no subset of M forms a cycle in ∂X_0;*
- *(c) M_i is isolated in X;*
- *(d) $W^s(M_i) \bigcap p^{-1}(0, \infty) = \varnothing$ for each $1 \leqslant i \leqslant k$, where $W^s(M_i)$ is the stable set of M_i.*

Then there exists a $\delta > 0$ *such that for any compact chain transitive set* L *with* $L \not\subset M_i$*, for all* $1 \leqslant i \leqslant k$*, we have* $\min_{x \in L} p(x) > \delta$*. In particular,* f *is uniformly persistent in the sense that there exists an* $\eta > 0$ *such that* $\liminf_{n \to \infty} d(f^n(x), \partial X_0) \geqslant \eta$ *for all* $x \in X_0$*.*

Suppose $T > 0$, a family of mapping $\Phi(t) : X \to X$, $t \geqslant 0$, is called a T-periodic semiflow on X if it possesses the following properties:

(1) $\Phi(0) = I$, where I is the identity map on X;

(2) $\Phi(t + T) = \Phi(t) \circ \Phi(T)$, $\forall t \geqslant 0$;

(3) $\Phi(t)x$ is continuous in $(t, x) \in [0, \infty) \times X$.

The mapping $\Phi(T)$ is called the Poincaré map (or period map) associated with this periodic semiflow. In particular, if (2) holds for any $T > 0$, $\Phi(t)$ is called an autonomous semiflow.

Theorem 2.3. *[135, Theorem 3.1.1] Let* $\Phi(t)$ *be a* T*-periodic semiflow on* X *with* $\Phi(t)X_0 \subset X_0$*,* $\forall t \geqslant 0$*. Assume that* $S := \Phi(T)$ *is point dissipative in* X *and compact. Then the uniform persistence of* S *with respect to* $(X_0, \partial X_0)$ *implies that of* $\Phi(t) : X \to X$*.*

Recall that the Kuratowski measure of noncompactness, α, is defined by

$$\alpha(B) := \inf\{r : B \text{ has a finite cover of diameter } < r\}$$

for any bounded set B of X. It is not difficult to see that B is precompact if and only if $\alpha(B) = 0$. Let (X, d) be a complete space, and let $\rho : X \to \mathbb{R}_+$ be a continuous function. We define $M_0 := \{x \in X : \rho(x) > 0\}$ and $\partial M_0 := \{x \in X : \rho(x) = 0\}$.

Definition 2.5. *A continuous map* $f : X \to X$ *is said to be* ρ *uniformly persistent if there exists* $\epsilon > 0$ *such that* $\liminf_{n \to \infty} \rho(f^n(x)) \geqslant \epsilon$*,* $\forall x \in M_0$*. The map is said* *to be α-condensing (α-contraction of order k, $0 \leqslant k < 1$) if f takes bounded sets to bounded sets and $\alpha(f(B)) < \alpha(B)$ ($\alpha(f(B)) < k\alpha(B)$) for any nonempty closed bounded set $B \subset X$ with $\alpha(B) > 0$.*

Theorem 2.4. *[79, Theorem 4.1 and Theorem 4.7] Assume that $f : X \to X$ is α-condensing. If $f : M_0 \to M_0$ has a global attractor $A_0 \subset M_0$, then f has a fixed point $x_0 \in A_0$. The analogous result holds for an autonomous semiflow $\Phi(t)$: let $\Phi(t)$ be an autonomous semiflow on X with $\Phi(t)(M_0) \subset M_0$, $\forall t \geqslant 0$. Assume that $\Phi(t)$ is α-condensing for each $t > 0$, and that $\Phi(t) : M_0 \to M_0$ has a global attractor A_0. Then $\Phi(t)$ has an equilibrium $x_0 \in A_0$, i.e., $\Phi(t)x_0 = x_0$, $t \geqslant 0$.*

Theorem 2.5. *[79, Theorem 4.5] Assume that*

(1) $f : X \to X$ is point dissipative and ρ-uniformly persistent.

(2) f^{n_0} is compact for some integer $n_0 \geqslant 1$.

(3) Either f is α-condensing or f is convex k-contracting.

Then $f : M_0 \to M_0$ admits a global attractor A_0, and f has a fixed point in A_0.

2.2 Monotone dynamics

Let E be an ordered Banach space with an order cone P having nonempty interior $int(P)$. For $x, y \in E$, we write:

- $x \geqslant y$, if $x - y \in P$;
- $x > y$, if $x - y \in P\backslash\{0\}$;
- $x \gg y$, if $x - y \in int(P)$.

The order interval is defined as: $[a, b] := \{x \in E : a \leqslant x \leqslant b\}$, provided that $a < b$.

Definition 2.6. *Let U be a subset of E, and $f : U \to U$ a continuous map. The map f is said to be:*

- ***monotone*** *if $x \geqslant y$ implies that $f(x) \geqslant f(y)$;*
- ***strictly monotone*** *if $x > y$ implies that $f(x) \geqslant f(y)$;*
- ***strongly monotone*** *if $x > y$ implies that $f(x) \gg f(y)$.*

Recall that a subset K of E is said to be order convex if $[u, v] \in K$ whenever $u, v \in K$ satisfy $u < v$.

Definition 2.7. *Let $U \subset P$ be a nonempty, closed and order convex set. A continuous map $f : U \to U$ is said to be:*

- ***subhomogeneous*** *if $f(\lambda x) \geqslant \lambda f(x)$ for any $x \in U$ and $\lambda \in [0, 1]$;*
- ***strictly subhomogeneous*** *if $f(\lambda x) > \lambda f(x)$ for any $x \in U$ with $x \gg 0$ and $\lambda \in (0, 1)$;*
- ***strongly subhomogeneous*** *if $f(\lambda x) \gg \lambda f(x)$ for any $x \in U$ with $x \gg 0$ and $\lambda \in (0, 1)$.*

Theorem 2.6. *[135, Theorem 2.3.2] Assume that $f : U \to U$ satisfies either*

(i) f is monotone and strongly subhomogeneous; or

(ii) f is strongly monotone and strictly subhomogeneous.

If $f : U \to U$ admits a nonempty compact invariant set $K \subset int(P)$, then f has a fixed point $e \gg 0$ such that every nonempty compact invariant set of f in $int(P)$ consist of e.

Recall that a continuous mapping $f : X \to X$ is said to be asymptotically smooth if for any nonempty closed bounded set $B \subset X$ for which $f(B) \subset B$, there is a compact set $J \subset B$ such that J attracts B. Denote the Fréchet derivative of f at $u = a$ by $Df(a)$ if it exists, and let $r(D(f(a)))$ be the spectral radius of the linear operator $Df(a) : E \to E$.

Theorem 2.7. *(Threshold dynamics) [135, Theorem 2.3.4] Let* $V = [0, b]$ *with* $b \gg 0$*, and* $f : V \to V$ *be a continuous map. Assume that*

(1) $f : V \to V$ *satisfies either*

  (i) f *is monotone and strongly subhomogeneous; or*

  (ii) f *is strongly monotone and strictly subhomogeneous;*

(2) $f : V \to V$ *is asymptotically smooth, and every positive orbit of* f *in* V *is bounded;*

(3) $f(0) = 0$*, and* $Df(0)$ *is compact and strongly positive.*

Then there exists threshold dynamics:

(a) If $r(Df(0)) \leqslant 1$*, then every positive orbit in* V *converges to* 0*;*

(b) If $f(Df(0)) > 1$*, then there exists a unique fixed point* $u^* \gg 0$ *in* V *such that every positive orbit in* $V \backslash \{0\}$ *converges to* u^**.*

2.3 Basic reproduction number in periodic environment

In the study of population dynamics, one of the most important quantity is the basic reproduction number, $\mathcal{R}_0$, defined as the expected number of new offsprings born by a typical individual during its entire life. In a population, the basic reproduction number $\mathcal{R}_0$ serving as a threshold value to determine whether the population goes extinct (if $\mathcal{R}_0 \leqslant 1$) or keeps persistent uniformly (if $\mathcal{R}_0 > 1$).

In this section, we present the theory of basic reproduction number for abstract delay differential equations (including periodic and time-delayed reaction-diffusion models) developed in [134]. Let $\tau \geqslant 0$ be a given number, $X = C([-\tau, 0], \mathbb{R}^m)$, and $X^+ = C([-\tau, 0], \mathbb{R}^m_+)$. Then (X, X^+) is an ordered Banach space equipped with the maximum norm and the positive cone X^+. Let $F : \mathbb{R} \to \mathcal{L}(X, \mathbb{R}^m)$ be a map and $V(t)$ be a continuous $m \times m$ matrix function on $\mathbb{R}$. Assume that $F(t)$ and $V(t)$ are T-periodic in t for some real number $T > 0$. For a continuous function $u : [-\tau, \sigma) \to \mathbb{R}^m$ with $\sigma > 0$, define $u_t \in X$ by

$$u_t := u(t + \theta), \forall \theta \in [-\tau, 0]$$

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

By linearizing a population growth model at its population extinction equilibrium, we have the following linear and periodic function differential system:

$$\frac{du(t)}{dt} = F(t)u_t - V(t)u(t), \quad t \geqslant 0, \tag{2.1}$$

where $F(t)u_t$ describes the newly born individuals at time t linearly dependent on the reproductive individuals over the time interval $[t - \tau, t]$. Further, the internal evolution of individuals in the reproductive compartments (e.g., natural deaths, and movements among compartments) is described by the following linear ordinary differential system:

$$\frac{du(t)}{dt} = -V(t)u(t), \quad t \geqslant 0. \tag{2.2}$$

We assume that $F(t) : X \to \mathbb{R}^m$ is given by

$$F(t)\phi = \int_{-\tau}^{0} d[\eta(t, \theta)]\phi(\theta), \quad \forall t \in \mathbb{R},\ \phi \in X,$$

where $\eta(t,\theta)$ is an $m \times m$ matrix function which is measurable in $(t,\theta) \in \mathbb{R} \times \mathbb{R}$ and normalized so that $\eta(t,\theta) = 0$ for all $\theta \geqslant 0$ and $\eta(t,\theta) = \eta(t,-\tau)$ for all $\theta \leqslant -\tau$. Further, $\eta(t,\theta)$ is continuous from the left in θ on $(-\tau, 0)$ for each t, and the variation of $\eta(t,\cdot)$ on $[-\tau, 0]$ satisfies $Var_{[-\tau,0]}\eta(t,\cdot) \leqslant m(t)$ for some $m \in \mathbb{L}_1^{loc}((-\infty,\infty),\mathcal{R})$, the space of functions from $(-\infty,\infty)$ into $\mathbb{R}$ that are Lebesgue integrable on each compact set of $(-\infty,\infty)$. Since $F(t)$ is T-periodic in t, it follows that

$$\sup_{t\in\mathbb{R}}\|F(t)\| = \sup_{0\leqslant t\leqslant T}\|F(t)\| \leqslant \sup_{0\leqslant t\leqslant T} m(t).$$

We define the evolution operators $U(t,s)$ on X related to system (2.1) as

$$U(t,x)\phi = u_t(s,\phi), \quad \forall \phi \in X, \quad t \geqslant s, \ s \in \mathbb{R},$$

where $u(t,s,\phi)$ is a unique solution of (2.1) on $[s,\infty)$ with $u_s = \phi$, i.e. $u_t(s,\phi)(\theta) = u(t+\theta,s,\phi)$, $\forall \theta \in [-\tau, 0]$. Then, each operator $U(t,s)$ is continuous and

$$U(s,s) = I, \quad U(t,s)U(s,r) = U(t,r), U(t+T,s+T) = U(t,s), \quad \forall t \geqslant s \geqslant r. \tag{2.3}$$

Let $\Phi(t,s)$, $t \geqslant s$, be the evolution matrices corresponding to system (2.2), that is, $\Phi(t,s)$ satisfies

$$\frac{\partial}{\partial t}\Phi(t,s) = -V(t)\Phi(t,s), \quad \forall t \geqslant s, \quad \text{and} \quad \Phi(s,s) = I, \ \forall s \in \mathbb{R},$$

and $\omega(\Phi)$ be the exponential growth bound of $\Phi(t,s)$, that is,

$$\omega(\phi) = \inf\left\{\tilde{\omega} : \exists M \geqslant 1\text{such that}\|\Phi(t+s,s)\| \leqslant Me^{\tilde{\omega}t}, \ \forall s \in \mathbb{R}, \ t \geqslant 0\right\}.$$

We assume that the initial distribution of new born individuals, $v(t)$, is T-periodic in t to allow for the periodic environment. For any given $s \geqslant 0$, $F(t-s)v_{t-s}$ is the distribution of newly born individuals at time $t-s$, which is born by the reproductive individuals who were matured over the time interval $[t-s-\tau, t-s]$.

Then, $\Phi(t,t-s)F(t-s)v_{t-s}$ is the distribution of those newborns who were newly born at time $t-s$ and remain in the immature compartments at time t. It follows that

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

is the distribution of accumulative newborns at time t produced by all those reproductive individuals introduced at all previous times to t.

Let C_T be the ordered Banach space of all continuous and T-periodic functions form $\mathbb{R}$ to $\mathbb{R}^m$, which is equipped with the maximum norm and the positive cone $C_T^+ := \{v \in C_T : v(t) \geqslant 0, \forall t \in \mathbb{R}\}$. Then, we can define the following linear operator on C_T by

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

Then, the basic reproduction number for periodic system (2.1) is defined as the spectral radius of L based on the theory of next generation operators [34, 113, 118], i.e.

$$\mathcal{R}_0 := r(L).$$

The following theorem shows that $\mathcal{R}_0$ is a threshold value for the stability of the zero solution for periodic system (2.1). Recall that $U(T,0)$ is the Poincaré (period) map of system (2.1) on X.

Theorem 2.8. *[134, Theorem 2.1] The following statements are valid:*

(i) $\mathcal{R}_0 = 1$ *if and only if* $r(U(T,0)) = 1$.

(ii) $\mathcal{R}_0 > 1$ *if and only if* $r(U(T,0)) > 1$.

(ii) $\mathcal{R}_0 < 1$ *if and only if* $r(U(T,0)) < 1$.

Thus, $\mathcal{R}_0 - 1$ *has the same sign as* $r(U(T,0)) - 1$.

Chapter 3

Age-structured tick population growth subject to seasonal effects

3.1 Background

Ticks as the primary vector can transmit many tick-borne diseases such as anaplasmosis, babesiosis, Lyme disease, tularemia and so on [27]. For the sake of evaluating the risk of tick-borne diseases, the population growth of ticks has attracted increasing attentions. The lifecycle of ticks consists of four main stages, which are egg, larval, nymphal and adult stage. Seasonal effects are recognised as pervasive factors generating the annual patterns of tick population dynamics particularly the survivability during non-parasitic periods [90]. Consequently, a large amount of age-structured models incorporating seasonal variations have been proposed to investigate tick population growth. A computational model with delays dependent on temperature was formulated by Ogden and coauthors, who took into consideration of twelve tick mutually exclusive states to investigate the effect of temperature on tick population growth [89]. A continuous age-structured model of twelve ordinary differential equations was developed in [127] to study the persistence of tick population. Another similar continuous model with seasonal temperature-driven development and host biting rates estimated by temperature normals was formulated to evaluate different basic reproduction number at different locations of Eastern Canada [126]. By utilising the delay differential equations (DDE) framework, Fan et al. proposed a stage-structured DDE model to study the self-regulation in tick population growth [37]. With consideration of time dependent developmental durations, Wu et al. developed a periodic DDE model with temporally periodic delays for tick population in [128], where the chronological delays and the interstadial developmental delays were linked. They studied the nonnegativity and boundedness of solutions to such a system, defined the basic reproduction number $\mathcal{R}_0$ and computed it by a simple algorithm, which can be applied to different scenarios [128]. Nevertheless, they did not investigate the global dynamics, including the extinction, persistence and the global stability of the positive periodic solutions to the model system in terms of $\mathcal{R}_0$, which motivates us to provide a rigorous mathematical framework to study the population growth subject to seasonal variations on birth, death and development rates. Although the study is presented in terms of tick population, it is worth remarking that the theoretical framework is general enough for investigating population growths of other species.

We organise the rest of this chapter as follows. In Section 3.2, we propose a generalised hyperbolic age-structured model and show the existence and uniqueness of the solution to this system. Then, the reduced periodic age-structured DDE model with periodic delays from the hyperbolic model is derived in Section 3.3. When the host populations for immature ticks, such as deers, white-footed mice, chipmunks and shrews [92], are abundant and the density-dependent regulation of immature ticks can be ignored. In Section 3.4, we prove the global existence of the solutions to the new DDE model, define the basic reproduction number $\mathcal{R}_0$ as the spectral radius of the next generation operator and establish the global attractivity of a periodic positive solution by using the theory of monotone dynamical systems for the case $\mathcal{R}_0 > 1$. In the case of considering the immature intraspecific competition, detailed proof of tick extinction and persistence in terms of $\mathcal{R}_0$ is provided in Section 3.5. A brief discussion section is presented in the last section.

3.2 Generalised hyperbolic age-structured model and well posedness

In this section, we first generalise the McKendrick-von Foerster equation to obtain a periodic hyperbolic age-structured model, and then show some preliminary results related to this system including the uniqueness and existence of the solution. In order to study the long term dynamic behaviour, we reduce the generalised periodic hyperbolic system into a periodic age-structured DDE model with some reasonable assumptions.

3.2.1 A generalised hyperbolic age-structured model

Let $\rho(t,a)$ be the tick population density at time t of age a. The McKendrick-von Foerster equation (also named Lotka-McKendrick equation [57, 70, 122]) is known as a appropriate modelling framework for age structured population growth. In this work, we attempt to extend it to the following system by incorporating seasonal effects and intra-specific competitions.

$$\begin{cases} (\dfrac{\partial}{\partial t} + \dfrac{\partial}{\partial a})\rho(t,a) = -\mu\Big(t, a, \int_0^\infty q(t,s)\rho(t,s)ds\Big)\rho(t,a), \\ \rho(0,a) = \phi(a), \ a \geqslant 0, \\ \rho(t,0) = b\Big(t, \int_0^\infty p(t,s)\rho(t,s)ds\Big), \ t \geqslant 0. \end{cases} \tag{3.1}$$

Here, $b\left(t, \int_0^\infty p(t,s)\rho(t,s)ds\right)$ denotes the egg production rate, which depends on time t and population density $\rho(t,a)$ with a weight function $p(t,a)$, the per-capita mortality rate $\mu(t, a, \int_0^\infty q(t,s)\rho(t,s)ds)$ varies with time t, age a and the population density with another weight function $q(t,a)$. Here and in what follows, the variable parameter functions including the birth function b, death function μ and the weight functions q and p are all periodic in time t with the same period T, taking the seasonal effects on population growth into account. The function $\phi(\cdot)$ gives the non-negative bounded initial age distribution of the population. It is very natural to have the following general assumptions on the birth rate, death rate, initial and boundary conditions as well as kernel functions:

(B1) Both the birth rate $b\left(t, x\right)$ and the per-capita death rate $\mu\left(t, a, x\right)$ are non-negative and Lipschitzian functions with respect to the x variable with Lipschitzian constants $\bar{b}$ and $\bar{\mu}$ respectively. Moreover, there exists a positive constant $\mu_{\min}$ such that $\mu\left(t, a, x\right) \geqslant \mu_{\min} > 0$ for all x, $t \geqslant 0$ and $a \geqslant 0$.

(B2) The inherent relationships between boundary condition and initial condition must be satisfied, that is

$$\rho(0,0) = \phi(0) = b\left(0, \int_0^\infty p(0,s)\phi(s)ds\right).$$

(B3) $q(t,\cdot)$ and $p(t,\cdot)$ are assumed to be non-negative in $L[0,\infty]$.

Based on these assumptions, we can establish some preliminary results for the hyperbolic equation (3.1) as below.

3.2.2 Local existence and non-negativeness of solutions

In order to obtain the formulation of solutions for system (3.1), we will follow a more readily comprehensible method of characteristics (for example Li and Brauer [70] and [122]). Since the time variable t is involved in the right hand side of the hyperbolic equation and the boundary condition, a careful argument is needed and for reader's convenience.

Set $\hat{\rho}(h) := \rho(t_0+h, a_0+h)$ and $\hat{\mu}(h) := \mu(t_0+h, a_0+h, \int_0^\infty q(t_0+h, s)\rho(t_0+h, s)ds)$, where t_0 and a_0 are fixed. Differentiating $\hat{\rho}(h)$ with respect to h yields

$$\begin{aligned}\frac{d\hat{\rho}(h)}{dh} &= (\frac{\partial}{\partial t} + \frac{\partial}{\partial a})\rho(t_0+h, a_0+h) \\ &= -\mu(t_0+h, a_0+h, \int_0^\infty q(t_0+h, s)\rho(t_0+h, s)ds) \\ &= -\hat{\mu}(h)\hat{\rho}(h).\end{aligned} \tag{3.2}$$

Integrating (3.2) from 0 to h, we have

$$\hat{\rho}(h) = \hat{\rho}(0)\exp\Big(-\int_0^h \hat{\mu}(r)dr\Big),$$

that is

$$\begin{aligned}&\rho(t_0+h, a_0+h) \\ =&\rho(t_0, a_0)\exp\Big(-\int_0^h \mu(t_0+r, a_0+r, \int_0^\infty q(t_0+r, s)\rho(t_0+r, s)ds)dr\Big).\end{aligned}$$

In case where $a \geqslant t$, setting $(t_0, a_0) = (0, a-t)$ and $h = t$, it follows that

$$\begin{aligned}\rho(t,a) &= \rho(0, a-t)\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\rho(r,s)ds)dr\Big) \\ &= \phi(a-t)\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\rho(r,s)ds)dr\Big).\end{aligned}$$

Similarly, in case where $t > a$, setting $(t_0, a_0) = (t-a, 0)$ and $h = a$ yields

$$\begin{aligned}\rho(t,a) =&\rho(t-a, 0)\exp\Big(-\int_0^a \mu\Big(t-a+r, r, \int_0^\infty q(t-a+r, s)\rho(t-a+r, s)ds\Big)dr\Big) \\ =&b\Big(t-a, \int_0^\infty p(t-a, s)\rho(t-a, s)ds\Big) \\ &\times\exp\Big(-\int_0^a \mu\Big(t-a+r, r, \int_0^\infty q(t-a+r, s)\rho(t-a+r, s)ds\Big)dr\Big).\end{aligned}$$

Then, (3.1) can be rewritten as following equivalent integral equation:

$$\begin{aligned}\rho(t,a) =& b\Big(t-a, \int_0^\infty p(t-a,s)\rho(t-a,s)ds\Big)\\ & \times \exp\Big(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\rho(t-a+r,s)ds)dr\Big)\mathbf{1}_{\{t>a\}} \quad (3.3)\\ & + \phi(a-t)\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\rho(r,s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}},\end{aligned}$$

where the indicator function is shown as follows:

$$\mathbf{1}_{\{t>a\}} = \begin{cases} 1, & t > a \geqslant 0, \\ 0, & a \geqslant t \geqslant 0, \end{cases} \quad \text{and} \quad \mathbf{1}_{\{a\geqslant t\}} = \begin{cases} 0, & t > a \geqslant 0, \\ 1, & a \geqslant t \geqslant 0. \end{cases}$$

Next, we prove local existence and uniqueness of solutions to system (3.3) and hence to system (3.1) in the light of Theorem 2.1 in [18].

Theorem 3.1. *Let $x_0 = \phi(\cdot) \in L_+[0,\infty)$, then there exists $\epsilon > 0$ and an open neighborhood $B_0 \subset L[0,\infty)$ with $x_0 \in B_0$ such that there exists a unique continuous function, $\chi : [0,\epsilon) \times B_0 \to L[0,\infty)$, where $\chi(t,x)$ is the solution to system (3.3) with $\chi(0,x) = x$.*

Proof. Denote the set of all continuous functions from $[0,\epsilon) \times B_0$ to $L[0,\infty)$ as $\mathcal{Y} = C([0,\epsilon) \times B_0, L[0,\infty))$ with the norm $\|\cdot\|_{\mathcal{Y}}$ defined by

$$\|\psi\|_{\mathcal{Y}} = \sup_{t\in[0,\epsilon], x\in B_0} \int_0^\infty |\psi(t,x)(a)|da,$$

where $\epsilon > 0$ and $B_0 \subset L[0,\infty)$ is a neighborhood of x_0, which will be determined later. Let $\mathcal{B}$ be a subset of $\mathcal{Y}$ containing functions whose ranges lie in $B \subset L[0,\infty)$, where $B = \overline{U}(\phi(\cdot), r)$ is the closed ball of radius r centered around the initial function with the value of r to be determined later. Then, B is a complete metric space. Define an operator Λ on $\mathcal{B}$ as follows: for any $x = x(\cdot) \in B_0$ and $\eta \in \mathcal{B}$,

$$\begin{aligned}\Lambda(\eta)(t,x)(\cdot) =& b\Big(t-a, \int_0^\infty p(t-a,s)\eta(t-a,x)(s)ds\Big)\\ &\times \exp\Big(-\int_0^a \mu(t-a+r,r,\int_0^\infty q(t-a+r,s)\eta(t-a+r,x)(s)ds)dr\Big)\mathbf{1}_{\{t>a\}}\\ &+ x(a-t)\exp\Big(-\int_0^t \mu(r,a-t+r,\int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}}.\end{aligned} \tag{3.4}$$

If Λ admits a fixed point $u \in \mathcal{B}$ such that $\Lambda u(t,x)(\cdot) = u(t,x)(\cdot)$. Let $\tilde{\rho}(t,a) = u(t,x)(a)$, $\forall a \geqslant 0$, then we have

$$\begin{aligned}\tilde{\rho}(t,a) =& b\Big(t-a, \int_0^\infty p(t-a,s)\tilde{\rho}(t-a,s)ds\Big)\\ &\times \exp\Big(-\int_0^a \mu(t-a+r,r,\int_0^\infty q(t-a+r,s)\tilde{\rho}(t-a+r,s)ds)dr\Big)\mathbf{1}_{\{t>a\}}\\ &+ x(a-t)\exp\Big(-\int_0^t \mu(r,a-t+r,\int_0^\infty q(r,s)\tilde{\rho}(r,s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}}.\end{aligned}$$

Hence, $\tilde{\rho}(t,a)$ satisfies equation (3.3), i.e. $\tilde{\rho}(t,a)$ is a solution to (3.3) with $\tilde{\rho}(0,a) = \phi(a)$.

The subsequent proof is to show that Λ is a contraction mapping on $\mathcal{B}$, which ensures the existence of a unique fixed point of Λ on $\mathcal{B}$. This conclusion can be achieved by the following three steps.

Step (I): For any $\eta \in \mathcal{B}$, it follows from equation (3.4) that

$$\begin{aligned}
&\int_0^\infty |\Lambda(\eta)(t,x)(a)|\,da \\
=&\int_0^\infty \Big| b\Big(t-a, \int_0^\infty p(t-a,s)\eta(t-a,x)(s)ds\Big) \\
&\times \exp\Big(-\int_0^a \mu(t-a+r,r,\int_0^\infty q(t-a+r,s)\eta(t-a+r,x)(s)ds)dr\Big)\mathbf{1}_{\{t>a\}} \\
&+x(a-t)\exp\Big(-\int_0^t \mu(r,a-t+r,\int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}}\Big|\,da \\
\leqslant& b_{\max}\int_0^t e^{-\mu_{\min}a}da + \int_t^\infty \exp\Big(-\int_0^t \mu(r,a-t+r,\int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)\,|x(a-t)|\,da \\
\leqslant& b_{\max}\frac{1-e^{-\mu_{\min}t}}{\mu_{\min}} + \int_t^\infty e^{-\mu_{\min}t}|x(a-t)|da \\
\leqslant& b_{\max}\frac{1-e^{-\mu_{\min}t}}{\mu_{\min}} + \|x\| < \infty,
\end{aligned}$$

for all $t \in [0,\epsilon)$, where ϵ is sufficiently small number, $\|\cdot\|$ is defined as $\int_0^\infty |x(a)|da$, and $b_{\max} > 0$ is the maximal value of $b\left(t, \int_0^\infty p(t,s)\eta(t,x)(s)ds\right)$ on B_0 since the birth function is continuous in the closed region. Therefore, it can be concluded that $\Lambda(\eta) \in \mathcal{Y}$ for any $\eta \in \mathcal{B}$, that is, $\Lambda : \mathcal{B} \to \mathcal{Y}$.

Step (II): Set $B_0 = B(x_0, \frac{r}{2})$ with $x_0 = \rho(0,\cdot)$, then it follows that

$$
\begin{aligned}
&\|\Lambda(\eta)(t,x) - x_0\| \\
=&\int_0^\infty \bigg| b\Big(t-a, \int_0^\infty p(t-a,s)\eta(t-a,x)(s)ds\Big) \\
&\times \exp\Big(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\eta(t-a+r,x)(s)ds)dr\Big)\mathbf{1}_{\{t>a\}} \\
&+x(a-t)\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}} - \rho(0,a)\bigg| da \\
\leqslant& b_{\max}\frac{1-e^{-\mu_{\min}t}}{\mu_{\min}} + \int_0^\infty \bigg| x(a-t)\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big) \\
&\mathbf{1}_{\{a\geqslant t\}} - \rho(0,a)\bigg| da \\
\leqslant& b_{\max}\frac{1-e^{-\mu_{\min}t}}{\mu_{\min}} + \int_0^\infty \exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big) \\
&\mathbf{1}_{\{a\geqslant t\}}\Big| x(a-t) - \rho(0,a-t)\Big| da \\
&+\int_0^\infty \bigg| \exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}}\rho(0,a-t) - \rho(0,a)\bigg| da.
\end{aligned}
$$

Note that

$$
\begin{aligned}
&\int_0^\infty \exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}}|x(a-t) - \rho(0,a-t)|da \\
\leqslant& \|x(\cdot) - \rho(0,\cdot)\|,
\end{aligned}
$$

and

$$
\begin{aligned}
&\int_0^\infty \bigg| \exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}}\rho(0,a-t) - \rho(0,a)\bigg| da \\
\leqslant& \int_0^\infty \mathbf{1}_{\{a\geqslant t\}}\rho(0,a-t)\bigg| \exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big) - 1\bigg| da \\
&+\int_0^\infty \Big|\rho(0,a-t)\mathbf{1}_{\{a\geqslant t\}} - \rho(0,a)\Big| da.
\end{aligned}
$$

Hence the dominated-convergence theorem implies

$$\lim_{t\to 0}\int_0^\infty \mathbf{1}_{\{a\geqslant t\}}\rho(0,a-t)\left|\exp\Big(-\int_0^t \mu(r,a-t+r,\int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)-1\right|da=0.$$

Therefore, if ϵ is sufficiently small, the following inequality holds for all $t\in[0,\epsilon)$:

$$\int_0^\infty \mathbf{1}_{\{a\geqslant t\}}\rho(0,a-t)\left|\exp\Big(-\int_0^t \mu(r,a-t+r,\int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)-1\right|da<\frac{r}{16}.$$

Since the set of all continuous functions with compact support is dense in L, there exists a continuous function ξ with compact support in $[0,\infty)$ such that $\|\rho(0,\cdot)-\xi\|\leqslant\frac{r}{16}$. Besides, the function with compact support vanishes at the boundary, which indicates there exists a bounded and closed interval $I\subset[0,\infty)$ such that $\xi(y)=0$ for $\forall y\notin I$. Then,

$$\begin{aligned}
&\int_0^\infty |\rho(0,a-t)\mathbf{1}_{\{a\geqslant t\}}-\rho(0,a)|da\\
\leqslant&\int_0^t|\rho(0,a)|da+\int_t^\infty|\rho(0,a-t)-\rho(0,a)|da\\
\leqslant&\int_0^t|\rho(0,a)|da+\int_t^\infty|\rho(0,a-t)-\xi(a-t)|da\\
&+\int_t^\infty|\xi(a-t)-\xi(a)|da+\int_t^\infty|\xi(a)-\rho(0,a)|da\\
\leqslant&\int_0^t|\rho(0,a)|da+2\int_0^\infty|\xi(a)-\rho(0,a)|da+\int_I|\xi(a-t)-\xi(a)|da\\
\leqslant&\frac{r}{32}+\frac{r}{8}+\frac{r}{32}=\frac{3r}{16},
\end{aligned}$$

where ϵ should be very small.

Hence,

$$
\begin{aligned}
&\int_0^\infty \Big|\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}}\rho(0,a-t)-\rho(0,a)\Big|\,da\\
\leqslant&\int_0^\infty \mathbf{1}_{\{a\geqslant t\}}\rho(0,a-t)\Big|\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\Big)-1\Big|\,da\\
&+\int_0^\infty \big|\rho(0,a-t)\mathbf{1}_{\{a\geqslant t\}}-\rho(0,a)\big|\,da\\
<&\frac{r}{16}+\frac{3r}{16}=\frac{r}{4}.
\end{aligned}
$$

In summary, we have

$$\|\Lambda(\eta)(t,x)-x_0\|\leqslant b_{\max}\frac{1-e^{-\mu_{\min}t}}{\mu_{\min}}+\|x(\cdot)-\rho(0,\cdot)\|+\frac{r}{4}<\frac{r}{4}+\frac{r}{2}+\frac{r}{4}=r,$$

for all $t\in[0,\epsilon)$, where constant $\epsilon>0$ is small enough. Therefore, for any $\eta\in\mathcal{B}$, we have $\Lambda(\eta)\in\mathcal{B}$, that is $\Lambda:\mathcal{B}\to\mathcal{B}$.

Step (III): In the final step, we will show that Λ is a contraction mapping on $\mathcal{B}$

for ϵ small enough. For any $\eta_1, \eta_2 \in \mathcal{B}$, it then follows that

$$\begin{aligned}
&\|\Lambda(\eta_1)(t,x) - \Lambda(\eta_2)(t,x)\| \\
&\leqslant \int_0^\infty \Big| b\Big(t-a, \int_0^\infty p(t-a,s)\eta_1(t-a,x)(s)ds\Big) \\
&\quad \times \exp\Big(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\eta_1(t-a+r,x)(s)ds)dr\Big) \\
&\quad -b\Big(t-a, \int_0^\infty p(t-a,s)\eta_2(t-a,x)(s)ds\Big) \\
&\quad \times \exp\Big(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\eta_2(t-a+r,x)(s)ds)dr\Big)\Big| \mathbf{1}_{\{t>a\}} da \\
&\quad + \int_0^\infty \Big| x(a-t)\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta_1(r,x)(s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}} \\
&\quad -x(a-t)\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta_2(r,x)(s)ds)dr\Big)\mathbf{1}_{\{a\geqslant t\}}\Big| da \\
&\leqslant \int_0^t \Big| b\Big(t-a, \int_0^\infty p(t-a,s)\eta_1(t-a,x)(s)ds\Big) \\
&\quad -b\Big(t-a, \int_0^\infty p(t-a,s)\eta_2(t-a,x)(s)ds\Big)\Big| \\
&\quad \exp\Big(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\eta_1(t-a+r,x)(s)ds)dr\Big) da \\
&\quad + \int_0^t b\Big(t-a, \int_0^\infty p(t-a,s)\eta_2(t-a,x)(s)ds\Big) \\
&\quad \Big|\exp\Big(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+t,s)\eta_1(t-a+r,x)(s)ds)dr\Big) \\
&\quad -\exp\Big(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\eta_2(t-a+r,x)(s)ds)dr\Big)\Big| da \\
&\quad + \int_t^\infty x(a-t)|\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta_1(r,x)(s)ds)dr\Big) \\
&\quad -\exp\Big(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta_2(r,x)(s)ds)dr\Big)\Big| da
\end{aligned}$$

$$
\begin{aligned}
&\leqslant\bar{b}\int_0^t e^{-\mu_{\min}a}\int_0^\infty p(t-a,s)\left|\eta_1(t-a,x)(s)-\eta_2(t-a,x)(s)\right|dsda\\
&+\int_0^t b_{\max}\int_0^a\Big|\mu\Big(t-a+r,r,\int_0^\infty q(r,s)\eta_1(r,x)(s)ds\Big)\\
&-\mu\Big(t-a+r,r,\int_0^\infty q(r,s)\eta_2(r,x)(s)ds\Big)\Big|drda\\
&+\int_t^\infty x(a-t)\int_0^t\Big|\mu\Big(r,a-t+r,\int_0^\infty q(r,s)\eta_1(r,x)(s)ds\Big)\\
&-\mu\Big(r,a-t+r,\int_0^\infty q(r,s)\eta_2(r,x)(s)ds\Big)\Big|drda\\
&\leqslant\bar{b}\int_0^t e^{-\mu_{\min}a}p_{\sup}\|\eta_1-\eta_2\|da+b_{\max}\int_0^t\int_0^a q_{\sup}\bar{\mu}\|\eta_1-\eta_2\|drda\\
&+\int_t^\infty x(a-t)\int_0^t q_{\sup}\bar{\mu}\|\eta_1-\eta_2\|drda\\
&\leqslant p_{\sup}\bar{b}\frac{1-e^{-\mu_{\min}t}}{\mu_{\min}}\|\eta_1-\eta_2\|+\frac{t^2}{2}q_{\sup}\bar{\mu}b_{\max}\|\eta_1-\eta_2\|+q_{\sup}t\bar{\mu}\|x\|\|\eta_1-\eta_2\|\\
&\leqslant\left(p_{\sup}\bar{b}\frac{1-e^{-\mu_{\min}t}}{\mu_{\min}}+\frac{t^2}{2}q_{\sup}\bar{\mu}b_{\max}+q_{\sup}t\bar{\mu}\|x\|\right)\|\eta_1-\eta_2\|\\
&\leqslant\epsilon M\|\eta_1-\eta_2\|,
\end{aligned}
$$

with some constant $M>0$, $p_{\sup}=\sup\limits_{a\geqslant0,t\geqslant0}\{p(t,a)\}$ and $q_{\sup}=\sup\limits_{a\geqslant0,t\geqslant0}\{q(t,a)\}$. It is noted that, in the above proof, $|e^{-x}-e^{-y}|\leqslant|x-y|$, $\forall x,y>0$ is used.

Thus, Λ is a contraction mapping on $\mathcal{B}$ when ϵ is small enough. The contraction mapping theorem guarantees the existence of a unique fixed point of Λ in $\mathcal{B}$, denoted by χ. In conclusion, $\chi(t,x)$ is the continuous solution to (3.3) on $[0,\epsilon]\times B_0$ with $\chi(0,x)=x$ for any $x\in B_0$. $\square$

We can easily check from the integral form (3.3) that this solution to (3.1) remains nonnegative whenever it exists for any nonnegative initial value $\rho(0,\cdot)$. Hence the following theorem holds.

Theorem 3.2. *Any solution to (3.3) through a non-negative initial value remains non-negative for every* $a \geqslant 0$ *and all* $t \geqslant 0$ *on the interval of existence.*

3.3 DDE model with time dependent delays

In this section, we shall reduce the hyperbolic equation into a system of delay differential equations, for which the tick population dynamics is easier to infer. However, the reduction process involves careful biological justifications. We first assume some age thresholds in order to stratify the tick growth into some discrete age stages, and in this project, we divide the ticks into four stages, including egg, larval, pupal and adult stages. Since the maturation age is determined by weather conditions, and therefore two periodically time-dependent terms are introduced, which are the developmental period and the chronological age. We use $\tau_i(t)$ to denote the time period needed for ticks to develop from the i-th stage ($i = E, L, N$, denoting egg-stage, larval-stage and nymphal-stage respectively) to the $(i+1)$-th stage ($i+1 = L, N, A$, representing larval-stage, nymphal-stage and adult-stage respectively) at time t. In general, $\tau_i(t)$ is determined by ambient environment conditions and can be implicitly considered as a periodic function of time t with the period T. That is, the ticks developing to the $(i+1)$-th stage at time t were entering the i-th stage at time $t - \tau_i(t)$. Likewise, the threshold age for each stage at the instant time t is a periodic function of t with the same period T and we assume the maximum chronological ages at time t are $f_E(t)$, $f_L(t)$ and $f_N(t)$ for egg, larval and nymphal stages respectively, which are in order of increasing maturity (e.g. egg, larval and nymphal stages), that is $f_N(t) \geqslant f_L(t) \geqslant f_E(t)$ for every $t \geqslant 0$. In addition, we assume the maximum chronological age of adult ticks is a constant, $a_{\max}$, rather than infinity as the life span of ticks is between 2 to 4 years [13]. The relationships between time dependent threshold ages and time-varying delays can be formulated as follows:

$$\begin{cases} f_E(t) = \tau_E(t), \\ f_L(t) = \tau_L(t) + \tau_E\left(t - \tau_L(t)\right) = \tau_L(t) + f_E\left(t - \tau_L(t)\right), \\ f_N(t) = \tau_N(t) + \tau_L(t - \tau_N(t)) + \tau_E(t - \tau_N(t) - \tau_L(t - \tau_N(t))) = \tau_N(t) + f_L(t - \tau_N(t)), \\ 1 - f_L'(t) = (1 - \tau_L'(t))(1 - f_E'(t - \tau_L(t))), \\ 1 - f_N'(t) = (1 - \tau_N'(t))(1 - f_L'(t - \tau_N(t))). \end{cases} \tag{3.5}$$

These relationships are illustrated in Figure 3.1 and interested readers can also find another derivation for these relationships in [128].

Moreover, the following arguments guarantee that $\tau_i(t)$ must satisfy $1 - \tau_i'(t) \geqslant 0$ $(i = E, L, N)$. Indeed, this assumption is biologically reasonable since the following relationship holds:

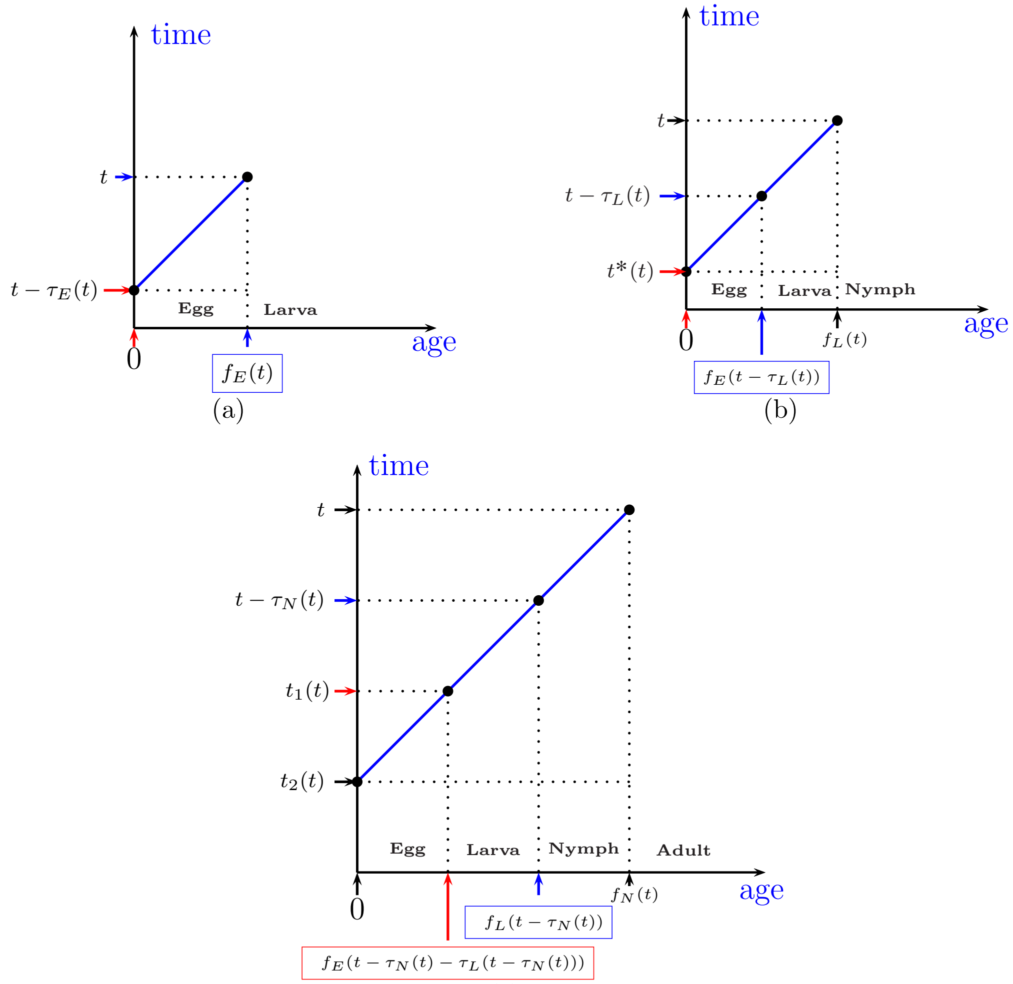
$$\int_{t-\tau_i(t)}^{t} \sigma(r)dr = 1, \quad i = E, L, N,$$

where $\sigma(r)$ is the developmental proportion at time r. After taking the derivative with respect to t, we have

$$1 - \tau_i'(t) = \frac{\sigma(t)}{\sigma(t - \tau_i(t))}, \quad i = E, L, N,$$

which indicates $1 - \tau_i'(t) > 0$. Then, it is easy to check that $1 - f_i'(t) \geqslant 0$ $(i = E, L, N)$. Experimentally, we can measure the developmental proportion to evaluate the development duration by using the above relationship. However, in our model system (3.8) presented later, we will use the chronological age thresholds $f(t)$ through the identities in (3.5).

The population size for each stage can be computed as the accumulative density between two age thresholds, in particular, we have the following mathematical expressions for the numbers of individuals within the egg $(E(t))$, larval $(L(t))$, nymphal



(a) (b) (c)

Figure 3.1: (a) At time t, the ticks reach the threshold age $f_E(t)$ and develop into the larval stage. These newly developed larvae are grown from eggs laid at previous time $t - \tau_E(t)$. Thus, the threshold age at time t is $f_E(t) = t - (t - \tau_E(t)) = \tau_E(t)$. (b) At time t, the ticks reach the threshold age $f_L(t)$ and develop into nymphal stage. These newly developed nymphs are grown from ticks entering larval-stage at previous time $t - \tau_L(t)$ which were developed from eggs laid at earlier time $t^*(t) = t - \tau_L(t) - \tau_E(t - \tau_L(t))$. Thus, the threshold age at time t admits $f_L(t) = t - t^*(t) = \tau_L(t) + \tau_E(t - \tau_L(t)) = \tau_L(t) + f_E(t - \tau_L(t))$. (c) At time t, the ticks reach the threshold age $f_N(t)$ and mature into adults. These newly developed adults are grown from ticks entering nymphal-stage at previous time $t - \tau_N(t)$ which were developed from larvae at earlier time $t_1(t) = t - \tau_N(t) - \tau_L(t - \tau_N(t))$. Likewise, these larvae stem from eggs laid at previous time $t_2(t) = t - \tau_N(t) - \tau_L(t - \tau_N(t)) - \tau_E(t - \tau_N(t) - \tau_L(t - \tau_N(t)))$. Thus, the threshold age at time t is $f_N(t) = t - t_2(t) = \tau_N(t) + \tau_L(t - \tau_N(t)) + \tau_E(t - \tau_N(t) - \tau_L(t - \tau_N(t))) = \tau_N(t) + f_L(t - \tau_N(t))$.

$(N(t))$ and adult stage $(A(t))$:

$$\begin{aligned} E(t) &= \int_0^{f_E(t)} \rho(t,a)da, \quad L(t) = \int_{f_E(t)}^{f_L(t)} \rho(t,a)da, \\ N(t) &= \int_{f_L(t)}^{f_N(t)} \rho(t,a)da, \quad A(t) = \int_{f_N(t)}^{a_{\max}} \rho(t,a)da. \end{aligned} \tag{3.6}$$

Since the solution of equation (3.1) is in $L_+(0,\infty)$ based on Theorem 3.1 and 3.2, the above terms are all well-defined and remain nonnegative when it exists for all nonnegative initial values.

Next, we propose natural biological assumptions for the birth and death rates in the hyperbolic equation (3.1). Since only adults give birth, $b\left(t, \int_0^{a_{\max}} p(t,s)\rho(t,s)ds\right)$ can be rewritten as $b(t,A)$, a periodic function in t. This can be done by choosing an appropriate weight function $p(t,a)$ in the general model (3.1) as follows.

$$p(t,a) = \begin{cases} 1, & \text{if } f_N(t) < a < a_{\max}, \\ 0, & \text{otherwise.} \end{cases}$$

For individuals in each stage, they are subject to a natural death rate $\mu_i(t)$ and a possible density dependent death rate (except eggs) $D_i(t, i(t))i(t)$ $(i = L,\ N,\ A)$ due to intra-specific stage competition [75]. This assumption can be formulated in the general PDE equation by choosing an appropriate kernel function $\mu\left(t, a, \int_0^{a_{\max}} q(t,s)\rho(t,s)ds\right)$, that is

$$q(t,a) = \begin{cases} q_E(t,a), & \text{if } 0 \leqslant a \leqslant f_E(t), \\ q_L(t,a), & \text{if } f_E(t) < a \leqslant f_L(t), \\ q_N(t,a), & \text{if } f_L(t) < a \leqslant f_N(t), \\ q_A(t,a), & \text{if } f_N(t) < a < a_{\max}. \end{cases}$$

The value of q_i ($i = E,\ L,\ N,\ A$ represent egg, larval, nymphal and adult stages respectively) is 1 if the ticks develop into the $i-th$ stage, otherwise the value takes

0. Furthermore, we choose the function $\mu\left(t, a, \int_0^{a_{\max}} q(t,s)\rho(t,s)ds\right)$ as the following form:

$$\mu(t,a,\int_0^{a_{\max}} q(t,s)\rho(t,s)ds) = \begin{cases} \mu_E(t), & \text{if} \quad 0 \leqslant a \leqslant f_E(t), \\ \mu_L(t) + D_L(t, L(t))L(t), & \text{if} \quad f_E(t) < a \leqslant f_L(t), \\ \mu_N(t) + D_N(t, N(t))N(t), & \text{if} \quad f_L(t) < a \leqslant f_N(t), \\ \mu_A(t) + D_A(t, A(t))A(t), & \text{if} \quad f_N(t) < a < a_{\max}. \end{cases}$$

Differentiating the equations in system (3.6) with respect to time t on both sides yields

$$\begin{aligned} \frac{dE(t)}{dt} =& \int_0^{f_E(t)} \frac{\partial \rho(t,a)}{\partial t} da + \rho(t, f_E(t))f_E'(t) \\ =& \rho(t,0) - \rho(t, f_E(t)) - \mu_E(t)E(t) + \rho(t, f_E(t))f_E'(t) \\ =& b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))\rho(t, f_E(t)), \\ \frac{dL(t)}{dt} =& \int_{f_E(t)}^{f_L(t)} \frac{\partial \rho(t,a)}{\partial t} da + \rho(t, f_L(t))f_L'(t) - \rho(t, f_E(t))f_E'(t) \\ =& \rho(t, f_E(t)) - \rho(t, f_L(t)) - \mu_L(t)L(t) - D_L(t, L(t))L^2(t) \\ & + \rho(t, f_L(t))f_L'(t) - \rho(t, f_E(t))f_E'(t) \\ =& (1 - f_E'(t))\rho(t, f_E(t)) - \mu_L(t)L(t) - D_L(t, L(t))L^2(t) \\ & - (1 - f_L'(t))\rho(t, f_L(t)), \end{aligned}$$

$$
\begin{aligned}
\frac{dN(t)}{dt} =& \int_{f_L(t)}^{f_N(t)} \frac{\partial \rho(t,a)}{\partial t} da + \rho(t, f_N(t)) f_N'(t) - \rho(t, f_L(t)) f_L'(t) \\
=& \rho(t, f_L(t)) - \rho(t, f_N(t)) - \mu_N(t) N(t) - D_N(t, N(t)) N^2(t) \\
& + \rho(t, f_N(t)) f_N'(t) - \rho(t, f_L(t)) f_L'(t) \\
=& (1 - f_L'(t)) \rho(t, f_L(t)) - \mu_N(t) N(t) - D_N(t, N(t)) N^2(t) \\
& - (1 - f_N'(t)) \rho(t, f_N(t)), \\
\frac{dA(t)}{dt} =& \int_{f_N(t)}^{a_{\max}} \frac{\partial \rho(t,a)}{\partial t} da - \rho(t, f_N(t)) f_N'(t) \\
=& \rho(t, f_N(t)) - \mu_A(t) A(t) - D_A(t, A(t)) A^2(t) - \rho(t, f_N(t)) f_N'(t) \\
=& (1 - f_N'(t)) \rho(t, f_N(t)) - \mu_A(t) A(t) - D_A(t, A(t)) A^2(t).
\end{aligned}
$$

To get the closed form of the above system, $\rho(t, f_i(t))$ (for $i = E, L, N$) is evaluated by method of integration along characteristics. Setting $t = t_0 + h$, $a = a_0 + h$ and $V(h) = \rho(t_0 + h, a_0 + h)$. Then,

$$
\begin{aligned}
\frac{dV(h)}{dh} &= \left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right) \rho(t,a) \\
&= -\mu\Big(t_0 + h, a_0 + h, \int_0^{a_{\max}} q(t_0 + h, s) \rho(t_0 + h, s) ds\Big) \rho(t_0 + h, a_0 + h) \quad (3.7) \\
&= -\mu\Big(t_0 + h, a_0 + h, \int_0^{a_{\max}} q(t_0 + h, s) \rho(t_0 + h, s) ds\Big) V(h).
\end{aligned}
$$

Integrating equation (3.7) from h_1 to h_2, yields,

$$
V(h_2) = V(h_1) e^{-\int_{h_1}^{h_2} \mu\left(t_0 + r, a_0 + r, \int_0^{a_{\max}} q(t_0 + r, s) \rho(t_0 + r, s) ds\right) dr}.
$$

For $t \geqslant f_i(t)$, setting $t_0 = t - f_i(t)$, $h = f_i(t)$ and $a_0 = 0$, for $i = E, L, N$, we have

$$
\begin{aligned}
\rho(t, f_i(t)) &= \rho(t - f_i(t), 0) e^{-\int_0^{f_i(t)} \mu\left(t - f_i(t) + r, r, \int_0^{a_{\max}} q(t - f_i(t) + r, s) \rho(t - f_i(t) + r, s) ds\right) dr} \\
&= b(t - f_i(t), A(t - f_i(t))) e^{-\int_0^{f_i(t)} \mu\left(t - f_i(t) + r, r, \int_0^{a_{\max}} q(t - f_i(t) + r, s) \rho(t - f_i(t) + r, s) ds\right) dr}.
\end{aligned}
$$

Since we focus on the long-term behavior of population dynamics, the closed form of the model for $t \geqslant f_N(t)$ is obtained as follows.

$$
\begin{aligned}
\frac{dE(t)}{dt} =& b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))b(t - f_E(t), A(t - f_E(t))) \\
& \times \exp\Big(- \int_0^{f_E(t)} \mu\Big(t - f_E(t) + r, r, \int_0^{a_{\max}} q(t - f_E(t) + r, s)\rho(t - f_E(t) + r, s)ds\Big)dr\Big) \\
=& b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))b(t - f_E(t), A(t - f_E(t))) \\
& \exp\Big(- \int_0^{f_E(t)} \mu_E(t - f_E(t) + r)dr\Big) \\
=& b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))b(t - f_E(t), A(t - f_E(t))) \\
& \exp\Big(- \int_{t-f_E(t)}^{t} \mu_E(r)dr\Big),
\end{aligned}
$$

$$
\begin{aligned}
&\frac{dL(t)}{dt}\\
=&(1-f_E'(t))b(t-f_E(t),A(t-f_E(t)))\exp\Big(-\int_{t-f_E(t)}^{t}\mu_E(r)dr\Big)\\
&-\mu_L(t)L(t)-D_L(t,L(t))L^2(t)-(1-f_L'(t))b(t-f_L(t),A(t-f_L(t)))\\
&\exp\Big(-\int_0^{f_L(t)}\mu\Big(t-f_L(t)+r,r,\int_0^{a_{\max}}q(t-f_L(t)+r,s)\rho(t-f_L(t)+r,s)ds\Big)dr\Big)\\
=&(1-f_E'(t))b(t-f_E(t),A(t-f_E(t)))\exp\Big(-\int_{t-f_E(t)}^{t}\mu_E(r)dr\Big)\\
&-\mu_L(t)L(t)-D_L(t,L(t))L^2(t)-(1-f_L'(t))b(t-f_L(t),A(t-f_L(t)))\\
&\exp\Big(-\int_{t-f_L(t)}^{t}\mu\Big(r,r-(t-\tau_L(t)),\int_0^{a_{\max}}q(r,s)\rho(r,s)ds\Big)dr\Big)\\
=&(1-f_E'(t))b(t-f_E(t),A(t-f_E(t)))\exp\Big(-\int_{t-f_E(t)}^{t}\mu_E(r)dr\Big)\\
&-\mu_L(t)L(t)-D_L(t,L(t))L^2(t)-(1-f_L'(t))b(t-f_L(t),A(t-f_L(t)))\\
&\exp\Big(-\int_{t-\tau_L(t)}^{t}(\mu_L(r)+D_L(r,L(r))L(r))dr-\int_{t-f_L(t)}^{t-\tau_L(t)}\mu_E(r)dr\Big)\\
=&(1-f_E'(t))b(t-f_E(t),A(t-f_E(t)))\exp\Big(-\int_{t-f_E(t)}^{t}\mu_E(r)dr\Big)\\
&-\mu_L(t)L(t)-D_L(t,L(t))L^2(t)-(1-f_L'(t))b(t-f_L(t),A(t-f_L(t)))\\
&\exp\Big(-\int_{t-\tau_L(t)}^{t}\mu_L(r)dr-\int_{t-f_L(t)}^{t-\tau_L(t)}\mu_E(r)dr\Big)\exp\Big(-\int_{t-\tau_L(t)}^{t}D_L(r,L(r))L(r)dr\Big),
\end{aligned}
$$

$$
\begin{aligned}
&\frac{dN(t)}{dt}\\
=&(1-f_L'(t))b(t-f_L(t),A(t-f_L(t)))\\
&\times\exp\Big(-\int_{t-\tau_L(t)}^{t}\mu_L(r)dr-\int_{t-f_L(t)}^{t-\tau_L(t)}\mu_E(r)dr\Big)\exp\Big(-\int_{t-\tau_L(t)}^{t}D_L(r,L(r))L(r)dr\Big)\\
&-\mu_N(t)N(t)-D_N(t,N(t))N^2(t)-(1-f_N'(t))b(t-f_N(t),A(t-f_N(t)))\\
&\times\exp\Big(-\int_{0}^{f_N(t)}\mu\Big(t-f_N(t)+r,r,\int_{0}^{a_{\max}}q(t-f_N(t)+r,s)\rho(t-f_N(t)+r,s)ds\Big)dr\Big)\\
=&(1-f_L'(t))b(t-f_L(t),A(t-f_L(t)))\exp\Big(-\int_{t-\tau_L(t)}^{t}\mu_L(r)dr-\int_{t-f_L(t)}^{t-\tau_L(t)}\mu_E(r)dr\Big)\\
&\times\exp\Big(-\int_{t-\tau_L(t)}^{t}D_L(r,L(r))L(r)dr\Big)-\mu_N(t)N(t)-D_N(t,N(t))N^2(t)\\
&-(1-f_N'(t))b(t-f_N(t),A(t-f_N(t)))\exp\Big(-\int_{t-\tau_N(t)}^{t}(\mu_N(r)+D_N(r,N(r))N(r))dr\\
&-\int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)}(\mu_L(r)+D_L(r,L(r))L(r))dr-\int_{t-f_N(t)}^{t-\tau_N(t)-\tau_L(t-\tau_N(t))}\mu_E(r)dr\Big)\\
=&(1-f_L'(t))b(t-f_L(t),A(t-f_L(t)))\exp\Big(-\int_{t-\tau_L(t)}^{t}\mu_L(r)dr-\int_{t-f_L(t)}^{t-\tau_L(t)}\mu_E(r)dr\Big)\\
&\times\exp\Big(-\int_{t-\tau_L(t)}^{t}D_L(r,L(r))L(r)dr\Big)-\mu_N(t)N(t)-D_N(t,N(t))N^2(t)\\
&-(1-f_N'(t))b(t-f_N(t),A(t-f_N(t)))\exp\Big(-\int_{t-\tau_N(t)}^{t}\mu_N(r)dr\\
&-\int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)}\mu_L(r)dr-\int_{t-f_N(t)}^{t-\tau_N(t)-\tau_L(t-\tau_N(t))}\mu_E(r)dr\Big)\\
&\times\exp\Big(-\int_{t-\tau_N(t)}^{t}D_N(r,N(r))N(r)dr-\int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)}D_L(r,L(r))L(r)dr\Big),
\end{aligned}
$$

$$
\begin{aligned}
\frac{dA(t)}{dt} &= (1-f_N'(t))b(t-f_N(t),A(t-f_N(t)))\exp\Big(-\int_{t-\tau_N(t)}^{t}\mu_N(r)dr \\
&\quad -\int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)}\mu_L(r)dr-\int_{t-f_N(t)}^{t-\tau_N(t)-\tau_L(t-\tau_N(t))}\mu_E(r)dr\Big) \\
&\quad \exp\Big(-\int_{t-\tau_N(t)}^{t}D_N(r,N(r))N(r)dr-\int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)}D_L(r,L(r))L(r)dr\Big) \\
&\quad -\mu_A(t)A(t)-D_A(t,A(t))A^2(t).
\end{aligned}
$$

There are two different expressions for $\rho(t,f_i(t))$ for $t>f_i(t)$ and $t\leqslant f_i(t)$ respectively. Since we focus on the long-term behavior of population dynamics, without loss of generality, we study the case when $t\geqslant f_i(t)(i=E,L,N)$, which is feasible due to the boundedness of $f_i(t)$. It follows from the integral form of the solution 3.3 that when $t\geqslant f_N(t)$ (note that $f_N(t)\geqslant f_L(t)\geqslant f_E(t)$), we have:

$$
\rho(t,f_i(t))=b(t-f_i(t),A(t-f_i(t)))e^{-\int_0^{f_i(t)}\mu\Big(t-f_i(t)+r,r,\int_0^{a_{\max}}q(t-f_i(t)+r,s)\rho(t-f_i(t)+r,s)ds\Big)dr}.
$$

Therefore, we can obtain a closed form, in terms of delay differential equations, to describe the tick population growth when $t\geqslant f_N(t)$:

$$
\begin{aligned}
\frac{dE(t)}{dt} =& b(t,A(t))-\mu_E(t)E(t)-(1-f_E'(t))h_1(t)b(t-f_E(t),A(t-f_E(t))), \\
\frac{dL(t)}{dt} =& (1-f_E'(t))h_1(t)b(t-f_E(t),A(t-f_E(t)))-\mu_L(t)L(t)-D_L(t,L(t))L^2(t) \\
& -(1-f_L'(t))h_2(t)g_1(t,L(t))b(t-f_L(t),A(t-f_L(t))), \\
\frac{dN(t)}{dt} =& (1-f_L'(t))h_2(t)g_1(t,L(t))b(t-f_L(t),A(t-f_L(t)))-D_N(t,N(t))N^2(t) \\
& -\mu_N(t)N(t)-(1-f_N'(t))h_3(t)g_2(t,L(t),N(t))b(t-f_N(t),A(t-f_N(t))), \\
\frac{dA(t)}{dt} =& (1-f_N'(t))h_3(t)g_2(t,L(t),N(t))b(t-f_N(t),A(t-f_N(t))) \\
& -\mu_A(t)A(t)-D_A(t,A(t))A^2(t),
\end{aligned}
\tag{3.8}
$$

where

$$
\begin{aligned}
h_1(t) &= \exp\Big(-\int_{t-f_E(t)}^{t} \mu_E(r)dr\Big),\\
h_2(t) &= \exp\Big(-\int_{t-\tau_L(t)}^{t} \mu_L(r)dr - \int_{t-f_L(t)}^{t-\tau_L(t)} \mu_E(r)dr\Big),\\
h_3(t) &= \exp\Big(-\int_{t-\tau_N(t)}^{t} \mu_N(r)dr - \int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)} \mu_L(r)dr\\
&\qquad - \int_{t-f_N(t)}^{t-\tau_N(t)-\tau_L(t-\tau_N(t))} \mu_E(r)dr\Big),
\end{aligned}
$$

are probabilities surviving through natural death during development while

$$
\begin{aligned}
g_1(t, L(t)) &= \exp\Big(-\int_{t-\tau_L(t)}^{t} D_L(r, L(r))L(r)dr\Big),\\
g_2(t, L(t), N(t)) &= \exp\Big(-\int_{t-\tau_N(t)}^{t} D_N(r, N(r))N(r)dr\\
&\qquad - \int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)} D_L(r, L(r))L(r)dr\Big),
\end{aligned}
$$

represent the probabilities surviving through additional death due to competition.

Alternatively, $E(t)$, $L(t)$, $N(t)$ and $A(t)$ can be expressed into integral forms. Note that $\tau_E(t)$ is the developmental time for eggs at time t. Hence, the eggs at time t consist of all eggs laid at previous time ξ with $\xi \in (t - \tau_E(t), t)$ and survived to time t. We have

$$
\begin{aligned}
E(t) &= \int_{t-\tau_E(t)}^{t} \exp\Big(-\int_{\xi}^{t} \mu\Big(r, a, \int_0^{a_{\max}} q(t,s)\rho(t,s)ds\Big)dr\Big) b(\xi, A(\xi))d\xi\\
&= \int_{t-\tau_E(t)}^{t} \exp\Big(-\int_{\xi}^{t} \mu_E(r)dr\Big) b(\xi, A(\xi))d\xi.
\end{aligned}
\tag{3.9}
$$

All the larvae at time t are developed from eggs laid at previous time $(\xi - f_E(\xi))$ with $\xi \in (t - \tau_L(t), t)$ and successfully survived in the egg stage for $\tau_E(\xi)$ (i.e. $f_E(\xi)$) time period, then matured into larvae with a “maturation rate” $(1 - \tau_E'(\xi))$ at time

ξ and remain alive in the larval stage until time t. Thus, the number of larvae at time t can be expressed as follows.

$$\begin{aligned} L(t) =& \int_{t-\tau_L(t)}^{t} \exp\Big(- \int_{\xi - f_E(\xi)}^{t} \mu\Big(r, a, \int_0^{a_{\max}} q(t,s)\rho(t,s)ds\Big)dr\Big) \\ & b(\xi - f_E(\xi), A(\xi - f_E(\xi)))(1 - \tau_E'(\xi))d\xi \\ =& \int_{t-\tau_L(t)}^{t} \exp\Big(- \int_{\xi}^{t} (\mu_L(r) + D_L(r, L(r))L(r))dr - \int_{\xi - f_E(\xi)}^{\xi} \mu_E(r)dr\Big) \\ & b(\xi - f_E(\xi), A(\xi - f_E(\xi)))(1 - f_E'(\xi))d\xi. \end{aligned} \tag{3.10}$$

Similarly, nymphs at time t contain all newly developed nymphs at previous time ξ with $\xi \in (t - \tau_N(t), t)$ and survived to time t. These newly developed nymphs are grown from larvae produced at time $(\xi - \tau_L(\xi))$, which developed through $\tau_L(\xi)$ time period in the larval stage and matured into nymphs at time ξ with "maturation rate" $(1 - \tau_L'(\xi))$. Likewise, the larvae produced at time $(\xi - \tau_L(\xi))$ come from the eggs laid at time $(\xi - \tau_L(\xi) - \tau_E(\xi - \tau_L(\xi)))$, i.e. $(\xi - f_L(\xi))$, which experience through $(\tau_E(\xi - \tau_L(\xi)))$ time period and matured into larvae at time $(\xi - \tau_L(\xi))$ with "maturation rate" $(1 - \tau_E'(\xi - \tau_L(\xi)))$. Therefore, the total number of nymphs at time t is given as follows.

$$\begin{aligned} N(t) =& \int_{t-\tau_N(t)}^{t} \exp\Big(- \int_{\xi - f_L(\xi)}^{t} \mu\Big(r, a, \int_0^{a_{\max}} q(r,s)\rho(t,s)ds\Big)dr\Big) \\ & b(\xi - f_L(\xi), A(\xi - f_L(\xi)))(1 - \tau_L'(\xi))(1 - \tau_E'(\xi - \tau_L(\xi)))d\xi \\ =& \int_{t-\tau_N(t)}^{t} \exp\Big(- \int_{\xi}^{t} (\mu_N(r) + D_N(r, N(r))N(r))dr - \int_{\xi - \tau_L(\xi)}^{\xi} (\mu_L(r) \\ & + D_L(r, L(r))L(r))dr - \int_{\xi - f_L(\xi)}^{\xi - \tau_L(\xi)} \mu_E(r)dr\Big) b(\xi - f_L(\xi), A(\xi - f_L(\xi)))(1 - f_L'(\xi))d\xi. \end{aligned} \tag{3.11}$$

While for adult ticks, the total number $A(t)$ can be computed in the following integral form:

$$\begin{aligned}A(t) = &\exp\Big(-\int_0^t (\mu_A(\xi) + D_A(\xi, A(\xi))A(\xi))d\xi\Big)\Big[\int_0^t (1 - f_N'(\xi))b(\xi - f_N(\xi), A(\xi - f_N(\xi)))\\
&\times \exp\Big(-\int_{\xi-\tau_N(\xi)}^{\xi} (\mu_N(r) + D_N(r, N(r))N(r))dr\\
&-\int_{\xi-\tau_N(\xi)-\tau_L(\xi-\tau_N(\xi))}^{\xi-\tau_N(\xi)} (\mu_L(r) + D_L(r, L(r))L(r))dr\\
&-\int_{\xi-f_N(\xi)}^{\xi-\tau_N(\xi)-\tau_L(\xi-\tau_N(\xi))} \mu_E(r)dr\Big)\exp\Big(\int_0^{\xi} \mu_A(r) + D_A(r, A(r))A(r))dr\Big)d\xi + A_0\Big],\end{aligned} \tag{3.12}$$

where $A_0 = A(0)$ is the initial value of $A(t)$.

Combining with the relationships between $f_i(t)$ and $\tau_i(t)$ $(i = E, L, N)$ shown in (3.5), it is easy to check by differentiation that the system of integration-differential equations consists of (3.9), (3.10), (3.11) and (3.12) is equivalent to the system (3.8).

We would like to draw readers' attention the fact that a similar model system was formulated in project [128]. The main focus of the current project is on the mathematical analysis of this kind of model system to get the global properties of solutions. Moreover, we will link the relationships between the basic reproduction number and the population dynamics of ticks. Here, we reformulate the model system for readers' convenience. In the subsequent section, we will first investigate the dynamics of a special case for (3.8) when the immature intra-specific competition is not considered.

3.4 Global dynamics without immature intraspecific competition

We will establish the global stability in terms of the basic reproduction number for a special case when there is no intra-specific competition in the immature stages, which means the density dependent death coefficients $D_i(t,i)$ $(i = L, N)$ take 0. Indeed, this assumption makes sense in biology when the host community, which includes a group of small mammals such as deers, white-footed mice, chipmunks and shrews [92], is very rich. If the host density is very high, the intra-specific competition during immature stages can be ignored and system (3.8) can be reduced into the following one:

$$\begin{aligned}
\frac{dE(t)}{dt} &= b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))h_1(t)b(t - f_E(t), A(t - f_E(t))),\\
\frac{dL(t)}{dt} &= (1 - f_E'(t))h_1(t)b(t - f_E(t), A(t - f_E(t))) - \mu_L(t)L(t)\\
&\quad - (1 - f_L'(t))h_2(t)b(t - f_L(t), A(t - f_L(t))),\\
\frac{dN(t)}{dt} &= (1 - f_L'(t))h_2(t)b(t - f_L(t), A(t - f_L(t))) - \mu_N(t)N(t)\\
&\quad - (1 - f_N'(t))h_3(t)b(t - f_N(t), A(t - f_N(t))),\\
\frac{dA(t)}{dt} &= (1 - f_N'(t))h_3(t)b(t - f_N(t), A(t - f_N(t))) - \mu_A(t)A(t) - D_A(t, A(t))A^2(t).
\end{aligned} \tag{3.13}$$

Since variables E, L and N in system (3.13) do not appear in equation related to A, it suffices to study the decoupled system:

$$\frac{dA(t)}{dt} = (1 - f_N'(t))h_3(t)b(t - f_N(t), A(t - f_N(t))) - \mu_A(t)A(t) - D_A(t, A(t))A^2(t). \tag{3.14}$$

To investigate the long-term dynamics of system (3.14), we make the following assumptions:

(H1) The birth rate $b(t, A)$ satisfies:

(i) $b(t, 0) \equiv 0$, $\dfrac{\partial b(t,0)}{\partial A} = \beta(t) > 0$ for all $t \in \mathbb{R}$, where $\beta(t)$ is a T-periodic continuous function;

(ii) $b(t, A)$ is increasing with respect to A for all $A > 0$ and $b(t, A) \leqslant \dfrac{\partial b(t, 0)}{\partial A} A = \beta(t) A$ for all $(t, A) \in \mathbb{R} \times \mathbb{R}_+$.

(H2) The per-capita natural death rate $\mu_A(t)$ and density dependent death coefficient $D_A(t, A)$ are non-negative T-periodic continuous functions with respect to time t. In addition, $D_A(t, A)$ is non-decreasing with respect to A.

(H3) There exist positive constants $D_{\min}$ and A^* such that $b(t, A) < \hat{\beta} A$ and $D_A(t, A) > D_{\min}$ hold for all $t \in \mathbb{R}$ when $A > A^*$, where $\hat{\beta} = \max\limits_{t \in [0,T]} \beta(t)$.

Let $\hat{f} = \max_{t\in[0,T]} f_N(t)$, define $X := C([-\hat{f}, 0], \mathbb{R})$ with the norm $\|\psi\|_X = \max\limits_{\theta \in [-\hat{f}, 0]} \|\psi(\theta)\|_{\mathbb{R}}$. Then X is a Banach space. Let $X^+ = C([-\hat{f}, 0], \mathbb{R}^+)$, then (X, X^+) is a strongly ordered space. Given a function $w(t) : [-\hat{f}, \sigma) \to \mathbb{R}$ for $\sigma > 0$, define $w_t \in X$ by $w_t(\theta) = w(t + \theta)$ for all $\theta \in [-\hat{f}, 0]$ and $t \in [0, \sigma)$. We firstly verify the global existence of the solution to system (3.14).

Lemma 3.1. *A unique solution $A(t)$ of system (3.14) exists globally on $[0, \infty)$ with the initial data $\psi(\theta) \in X^+$. Moreover, system (3.14) generates a T-periodic semiflow $\Psi_t : X^+ \to X^+$, i.e. $\Psi_t(\psi)(\theta) = A(t + \theta; \psi)$, $\forall \psi \in X^+$, $t \geqslant 0$, $\theta \in [-\hat{f}, 0]$.*

Proof. Set $A^{**} = \max\{\dfrac{\hat{\beta}}{D_{\min}} \hat{\gamma}_N, A^*\}$, where $\hat{\gamma}_N = \max\limits_{t \in [0,T]} (1 - f_N'(t))$. Based on assumptions (H1) and (H3), we can show that $[0, \rho A^{**}]$ is positively invariant for system (3.14) with any given $\rho \geqslant 1$, that is, the unique solution $A(t)$ with $0 \leqslant A(\theta) \leqslant \rho A^{**}$ satisfies $0 \leqslant A(t) \leqslant \rho A^{**}$ for all $t \geqslant 0$ and for any $\theta \in [-\hat{f}, 0]$. It easily follows from Theorem 3.2 that $A(t)$ is nonnegative. We claim $A(t) \leqslant \rho A^{**}$ by argument of contradiction. Assume the contrary, there exists t_0 such that $A(t) < \rho A^{**}$ when

$t < t_0$, while $A(t_0) = \rho A^{**}$ and $\left.\dfrac{dA(t)}{dt}\right|_{t_0} > 0$. However, it follows from assumptions (H1) and (H3) that

$$\begin{aligned}\left.\frac{dA(t)}{dt}\right|_{t_0} &\leqslant (1 - f_N'(t_0))b(t_0 - f_N(t_0), A(t_0 - f_N(t_0))) - D_A(t_0, A(t_0))A^2(t_0) \\ &\leqslant \hat{\gamma}_N \hat{\beta} \rho A^{**} - D_{\min}(\rho A^{**})^2 < 0.\end{aligned}$$

Therefore, $A(t) \in [0, \rho A^{**}]$ for all t provided that $0 \leqslant A(\theta) \leqslant \rho A^{**}$ for any $\theta \in [-\hat{f}, 0]$. Due to the arbitrariness of ρ (can be as large as you wish), the non-negativity and boundedness of solutions of system (3.14) hold in $[0, \infty)$. Thus, a unique solution $A(t)$ of system (3.14) exists globally on $[0, \infty)$ with the initial data $\psi(\theta) \in X^+$.

Define the solution map of system (3.14) as

$$\Psi_t(\psi) = A(t + \theta; \psi), \forall t \geqslant 0, \theta \in [-\hat{f}, 0], \psi \in X^+,$$

where $A(t; \psi)$ is the solution of system (3.14) with the initial data $\psi(\theta)$ for all $\theta \in [-\hat{f}, 0]$. Due to the periodicity of the variable coefficients, it easily follows that Ψ_t is a T-periodic semiflow on X^+. □

3.4.1 The basic reproduction number, $\mathcal{R}_0$

It follows from the assumption (H1) that system (3.14) has the extinction equilibrium 0. The linearized system of system (3.14) at the population extinction equilibrium is shown as follows:

$$\frac{dA(t)}{dt} = (1 - f_N'(t))h_3(t)\beta(t - f_N(t))A(t - f_N(t)) - \mu_A(t)A(t). \tag{3.15}$$

Since all time-dependent coefficients are non-negative T-periodic functions, both systems (3.14) and (3.15) are T-periodic. Let C_T be the ordered Banach space of all T-periodic continuous functions from $\mathbb{R}$ to $\mathbb{R}$, which is equipped with the maximum norm $\|\cdot\|$ and the positive cone

$$C_T^+ := \{\phi \in C_T : \phi(t) \geqslant 0, \quad \forall t \in \mathbb{R}\}.$$

Let $F(t)(\phi) = (1 - f'_N(t))h_3(t)\beta(t - f_N(t))\phi(-f_N(t))$ and $V(t) = \mu_A(t)$, then the next generation operator $\mathcal{L} : C_T \to C_T$ is defined as

$$\begin{aligned} [\mathcal{L}\phi](t) &= \int_0^{\infty} e^{-\int_{t-s}^{t} V(r)dr} F(t-s)\phi(t-s+\cdot)ds \\ &= \int_0^{\infty} e^{-\int_{t-s}^{t} \mu_A(r)dr}(1 - f'_N(t-s))h_3(t-s) \\ &\quad \beta(t-s-f_N(t-s))\phi(t-s-f_N(t-s))ds. \end{aligned}$$

We then define the basic reproduction number as the spectral radius of $\mathcal{L}$, i.e. $\mathcal{R}_0 = r(\mathcal{L})$. Let $\mathcal{P}(t)$ be the solution maps of the linear periodic equation (3.15) on X, that is, $\mathcal{P}(t)\phi = w_t(\phi)$, $t \geqslant 0$, where $w_t(\phi)(\theta) = w(t+\theta, \phi)$, $\forall \theta \in [-\hat{f}, 0]$, is the unique solution semiflow of (3.15) satisfying $w_0 = \phi \in X$. Hence, $P := \mathcal{P}(T)$ is the Poincaré map associated with system (3.15). Let $r(P)$ be the spectral radius of P. The following Lemma shows that the system admits a special solution, which is the key technique for investigating the long-term dynamics in later proofs. The argument below is motivated by the treatment in [130].

Lemma 3.2. *There exists a positive T-periodic function $v(t)$ such that $w(t) = e^{\mu t}v(t)$ is a positive solution of (3.15), where $\mu = \dfrac{\ln r(P)}{T}$.*

Proof. Since $(1 - f'_N(t))h_3(t)\beta(t - f_N(t)) > 0$, then P is a positive operator on X. It then follows from Krein-Rutman theorem [47, Theorem 3.1] that $r(P)$ is an eigenvalue of P with a positive eigenfunction ψ^*. In addition, it is easy to check that the linear operator P is strongly monotone when $t > 2\hat{f}$. Therefore, there exists an integer n, such that $nT > 2\hat{f}$, guaranteeing that P^n is strongly positive and compact. Applying Krein-Rutman theorem again, we can get the spectral radius of P^n, $r(P^n)$, is a simple eigenvalue of P^n with a strongly positive eigenfunction ψ_n^*. It is noted that $P^n\psi^* = r(P^n)\psi^* = (r(P))^n\psi^* = P^n\psi_n^*$. Then, we have $\psi^* = s_0\psi_n^* \gg 0$ for some positive constant s_0. Thus, it can be concluded that $\psi^* \gg 0$.

Let $\mu = \dfrac{\ln r(P)}{T}$. Suppose $w(t)$ is the particular solution of (3.15) through ψ^*, that is $w(\theta) = \psi^*(\theta)$ and $w(T+\theta) = P(\psi^*)(\theta) = r(P)\psi^*(\theta)$ for all $\theta \in [-\hat{f}, 0]$. Let $v(t) = e^{-\mu t}w(t)$, then $v(\theta) = e^{-\mu\theta}w(\theta) = e^{-\mu\theta}\psi^*(\theta)$ for all $\theta \in [-\hat{f}, 0]$. Furthermore, for all $\theta \in [-\hat{f}, 0]$ we have

$$v(T+\theta) = e^{-\mu(T+\theta)}w(T+\theta) = e^{-\mu(T+\theta)}r(P)\psi^*(\theta) = e^{-\mu\theta}\psi^*(\theta) = v(\theta).$$

Based on the uniqueness of solutions, we know $v(t)$ is periodic and $w(t) = e^{\mu t}v(t)$. $\square$

3.4.2 Global dynamics in terms of $\mathcal{R}_0$

We will show the main focus of this section, that is, the positive periodic solution is globally attractive when $\mathcal{R}_0 > 1$. To do this, we will employ the theory of monotone and subhomogeneous semiflows [135, Section 2.3]. To employ this result, the key idea is to show that the periodic semiflow of the decoupled system (3.14) is (eventually) strongly monotone in a suitable phase space. However, in the natural space $X := C([-\hat{f}, 0], \mathbb{R})$, the periodic semiflow is monotone but not strongly monotone. As a matter of fact, a solution periodic semiflow $\tilde{\Phi}_t$ can also be defined through a new phase $Y := C([-f_N(0), 0], \mathbb{R})$ with maximum norm $\|\cdot\|$ and positive cone $Y^+ := \{\phi \in C([-f_N(0), 0], \mathbb{R}) : \phi(\theta) \geqslant 0\}$, see [77]. Then we can show that the periodic semiflow $\tilde{\Phi}_t$ is strongly monotone and strictly subhomogeneous. Now we have two phase spaces for (3.14), X and Y with the following observation for the solution in these two phase spaces [77, Lemma 3.3 and 3.5]:

$$A(t,\phi) = A(t,\psi), \forall \psi \in X, \ \forall \phi \in Y, \ \text{ provided that } \phi(\theta) = \psi(\theta), \ \forall \theta \in [-f_N(0), 0].$$

However, since different phase spaces are used, $\mathcal{R}_0$ may not determine the stability of the linear periodic system of (3.14) on Y. It is necessary to prove the equivalence of stability properties for the linear periodic system of (3.14) in two different spaces. Recall that $P(t)$ is already defined as the solution map of linear periodic system

(3.15) on X in the above proof. We denote $\mathcal{Q}(t)$ as the solution map of the linear periodic system of (3.14) on Y. Let $\tilde{Q} := \mathcal{Q}(T)$ be the Poincaré map related to system (3.15) on Y. Its spectral radius is denote by $r(\tilde{Q})$. The following lemma reveals the equivalence of stability properties for the linear periodic system in these two spaces, which can be obtained by an argument similar to that in [77].

Lemma 3.3. *Poincaré map P and $\tilde{Q}$ has the same spectral radius, that is, $r(P) = r(\tilde{Q})$.*

The subsequent two theorems show that $\tilde{\Phi}_t$ is a strongly monotone and strictly subhomogeneous periodic semiflow in Y.

Theorem 3.3. *For any ϕ_1 and ϕ_2 in Y^+ with $\phi_1 > \phi_2$ (that is, $\phi_1 \geqslant \phi_2$ but $\phi_1 \neq \phi_2$), the solutions $u_1(t)$ and $u_2(t)$ of system (3.14) with $u_1(\cdot) = \phi_1$ and $u_2(\cdot) = \phi_2$, respectively, satisfy $u_1(t) > u_2(t)$ for all $t > \hat{f}$, and hence $\tilde{\Phi}_t(\phi_1) \gg \tilde{\Phi}_t(\phi_2)$ in Y for all $t \geqslant 2\hat{f}$.*

Proof. It is easy to prove $u_1(t) \geqslant u_2(t)$ for all $t \geqslant 0$ by a repeated comparison argument on each interval $[nf_N(0), (n+1)f_N(0)]$, $n \in \mathbb{N}$. Since $u_i(t)$ $(i = 1, 2)$ is bounded on $[0, \infty)$, then $u_i(t)$ $(i = 1, 2)$ can be restricted in an order interval $[0, h]$ for all $t \geqslant 0$, where h is a positive real number. Hence, we can construct a function $g(t, A) = -\mu_A(t)A - D_A(t, A)A^2 + HA$, where $H > 0$ is a large number to guarantee g is increasing with respect to A when $A \in [0, h]$. It is noted that $u_i(t)$ $(i = 1, 2)$ for all $t \geqslant 0$ satisfies the integral equation:

$$\begin{aligned} A(t) =& e^{-Ht}A(0) + \int_0^t e^{-H(t-s)}g(s, A(s))ds \\ &+ \int_0^t e^{-H(t-s)}(1 - f_N'(s))h_3(s)b(s - f_N(s), A(s - f_N(s)))ds. \end{aligned} \tag{3.16}$$

It is apparent that $[-f_N(0), 0] \subset m_A([0, \hat{f}])$, where $m_A(t) := t - f_N(t)$ is increasing with respect to $t \in \mathbb{R}$. Since $\phi_1 > \phi_2$, there exists an $\eta \in [-f_N(0), 0]$ such that

$u_1(\eta) > u_2(\eta)$. It follows from equation (3.16) and the comparison theorem [105, Theorem 5.1.1] that $u_1(t) > u_2(t)$ for all $t > \hat{f}$. Thus, the solution map $\tilde{\Phi}_t$ is strongly monotone if $t > 2\hat{f}$. □

Before conducting the proof of strictly subhomogeneous, we need to make some assumption about the birth rate $b(t, A)$, that is,

(S1) The birth rate $b(t, A)$ can be expressed as follows,

$$b(t, A) = B(t, A)A,$$

where $B(t, A)$ is the per-capita birth rate and nonincreasing in A for all $t \in \mathbb{R}$.

This assumption is reasonable for ticks according to [89], as the per-capita birth rate for ticks is decreasing with respect to the number of adults due to host grooming or host resistance. With this assumption, we can show that $\tilde{\Phi}$ is strictly subhomogeneous by the following theorem.

Theorem 3.4. *For any $\psi \gg 0$ in Y and any $r \in (0, 1)$, the following two results hold, that is,*

(i) $u(t, r\psi) > ru(t, \psi)$ for all $t > \hat{f}$;

(ii) $\tilde{\Phi}_T^n(r\psi) \gg r\tilde{\Phi}_T^n(\psi)$ in Y, where the integer n satisfies that $nT > 2\hat{f}$.

Proof. Let $u(t, \psi)$ be the unique solution of system (3.14) with $u_0 = \psi \gg 0$ in Y. For notational simplification, we use $w(t) = u(t, r\psi)$ and $v(t) = ru(t, \psi)$. It then follows from Theorem 3.2 that $u(t) > 0$ and $v(t) > 0$ for all $t \geqslant 0$ and $w(\theta) = r\psi(\theta) = v(\theta)$ for all $\theta \in [-f_N(0), 0]$.

Note that

$$
\begin{aligned}
\frac{dv}{dt}\Big|_{t=0} =& r(1-f_N'(0))h_3(0)B(0-f_N(0),u(0-f_N(0)))u(0-f_N(0)) - \mu_A(0)v(0) \\
& - \frac{D_A(0,u(0))}{r}v^2(0) \\
<& (1-f_N'(0))h_3(0)B(-f_N(0),ru(-f_N(0)))v(-f_N(0)) - \mu_A(0)v(0) \\
& - D_A(0,u(0))v^2(0) \\
\leqslant& (1-f_N'(0))h_3(0)B(-f_N(0),ru(-f_N(0)))v(-f_N(0)) - \mu_A(0)v(0) \\
& - D_A(0,ru(0))v^2(0) \\
=& (1-f_N'(0))h_3(0)b(-f_N(0),w(-f_N(0))) - \mu_A(0)w(0) - D_A(0,v(0))w^2(0) \\
=& \frac{dw}{dt}\Big|_{t=0}.
\end{aligned}
$$

It follows from $w(0) = v(0) > 0$ that there must be an $\xi \in (0, \hat{f})$ such that $w(t) > v(t) > 0$ holds for all $t \in (0, \xi)$. We can further conclude that $w(t) > v(t)$ holds for all $0 < t \leqslant f_N(0)$. If we assume the contrary, then there is a $\tilde{t} \in (0, f_N(0)]$ such that $w(t) > v(t)$ for all $t \in (0, \tilde{t})$ and $w(\tilde{t}) = v(\tilde{t})$, which indicates $\frac{dv}{dt}\Big|_{t=\tilde{t}} \geqslant \frac{dw}{dt}\Big|_{t=\tilde{t}}$.

However,

$$\begin{aligned}\left.\frac{dv}{dt}\right|_{t=\tilde{t}} =& r(1-f_N'(\tilde{t}))h_3(\tilde{t})B(\tilde{t}-f_N(\tilde{t}),u(\tilde{t}-f_N(\tilde{t})))u(\tilde{t}-f_N(\tilde{t}))-\mu_A(\tilde{t})v(\tilde{t})\\ &-\frac{D_A(\tilde{t},u(\tilde{t}))}{r}v^2(\tilde{t})\\ <&(1-f_N'(\tilde{t}))h_3(\tilde{t})B(\tilde{t}-f_N(\tilde{t}),u(\tilde{t}-f_N(\tilde{t})))v(\tilde{t}-f_N(\tilde{t}))-\mu_A(\tilde{t})v(\tilde{t})\\ &-D_A(\tilde{t},u(\tilde{t}))v^2(\tilde{t})\\ \leqslant&(1-f_N'(\tilde{t}))h_3(\tilde{t})B(\tilde{t}-f_N(\tilde{t}),ru(\tilde{t}-f_N(\tilde{t})))v(\tilde{t}-f_N(\tilde{t}))-\mu_A(\tilde{t})v(\tilde{t})\\ &-D_A(\tilde{t},ru(\tilde{t}))v^2(\tilde{t})\\ =&(1-f_N'(\tilde{t}))h_3(\tilde{t})b(\tilde{t}-f_N(\tilde{t}),w(\tilde{t}-f_N(\tilde{t})))-\mu_A(\tilde{t})w(\tilde{t})-D_A(\tilde{t},w(\tilde{t}))w^2(\tilde{t})\\ =&\left.\frac{dw}{dt}\right|_{t=\tilde{t}},\end{aligned}$$

which is a contradiction. Similarly, we can repeat this procedure to prove $w(t) > v(t)$ for all $t \in (nf_N(0),(n+1)f_N(0)]$, where n can be any integer. Note that $t-f_N(t) > 0$ when $t > \hat{f}$. Thus, $u(t,r\psi) > ru(t,\psi)$ for all $t > \hat{f}$ and $\tilde{\Phi}_T^n(r\psi) = \tilde{\Phi}_{nT}(r\psi) \gg r\tilde{\Phi}_{nT}(\psi) = r\tilde{\Phi}_T^n(\psi)$ in Y, where the integer n satisfies that $nT > 2\hat{f}$. $\square$

We now prove the global stability of system (3.14) when $\mathcal{R}_0 > 1$ bu focusing on the positive cone $Y^+ := \{\phi \in C([-f_N(0),0],\mathbb{R}) : \phi(\theta) \geqslant 0\}$.

Theorem 3.5. *If $\mathcal{R}_0 > 1$, then system (3.14) has a unique positive T-periodic solution $A^*(t)$, which is globally asymptotically stable in $Y^+\backslash\{0\}$.*

Proof. Note that $\tilde{\Phi}_t$ can be regarded as an n_0T-periodic semiflow in Y^+ if we choose proper integer n_0 such that $n_0T > 2\hat{f}$. It follows from Theorems 5.2 and 3.4 that $\tilde{\Phi}_{n_0T}$ is a strongly monotone and strictly subhomogeneous map on Y^+. It is shown that the sign of R_0-1 is the same as $r(D\tilde{\Phi}_{n_0T}(0))-1$ [134], where $r(D\tilde{\Phi}_{n_0T}(0)) = r(\mathcal{Q}(n_0T)) = (r(\tilde{Q}))^{n_0}$. Based on [135, Theorem 2.3.4] for periodic maps, if $r(D\tilde{\Phi}_{n_0T}(0)) > 1$, system (3.14) admits a unique positive n_0T-periodic solution $A^*(t)$, which is globally asymptotically stable for system (3.14) in $Y^+\backslash\{0\}$. In addition, $A^*(t)$ is T-periodic. This is true since

$$\tilde{\Phi}_T^{n_0}(\tilde{\Phi}_T\psi^*) = \tilde{\Phi}_T(\tilde{\Phi}_T^{n_0}\psi^*) = \tilde{\Phi}_T(\tilde{\Phi}_{n_0T}\psi^*) = \tilde{\Phi}_T(\psi^*),$$

where $\psi^* = A_0^* \in Y$ guarantees $\tilde{\Phi}_{n_0T}\psi^* = \psi^*$. It follows from the uniqueness of positive fixed point of $\tilde{\Phi}_T^{n_0} = \tilde{\Phi}_{n_0T}$ that $\tilde{\Phi}_T\psi^* = \psi^*$ holds. Thus, $A^*(t)$ is a T-periodic solution of system (3.14). $\square$

Based on the information about the undecoupled equation (3.14) for $A(t)$, we can also deduce the solution property for other variables $E(t)$, $L(t)$ and $N(t)$ by their integral expressions:

$$\begin{aligned}
E(t) &= \int_{t-\tau_E(t)}^{t} \exp\Big(-\int_{\xi}^{t}\mu_E(r)dr\Big)b(\xi, A(\xi))d\xi,\\
L(t) &= \int_{t-\tau_L(t)}^{t} (1-f_E'(\xi))\exp\Big(-\int_{\xi}^{t}\mu_L(r)dr - \int_{\xi-f_E(\xi)}^{\xi}\mu_E(r)dr\Big)\\
&\quad b(\xi - f_E(\xi), A(\xi - f_E(\xi)))d\xi,\\
N(t) &= \int_{t-\tau_N(t)}^{t} (1-f_L'(\xi))\exp\Big(-\int_{\xi}^{t}\mu_N(r)dr - \int_{\xi-\tau_L(\xi)}^{\xi}\mu_L(r)dr - \int_{\xi-f_L(\xi)}^{\xi-\tau_L(\xi)}\mu_E(r)dr\Big)\\
&\quad b(\xi - f_L(\xi), A(\xi - f_L(\xi)))d\xi.
\end{aligned}$$

It easily follows from the global stability of $A(t)$ that

$$\lim_{t\to\infty}[E(t) - E^*(t)] = 0,\ \lim_{t\to\infty}[L(t) - L^*(t)] = 0,\ \text{and}\ \lim_{t\to\infty}[N(t) - N^*(t)] = 0,$$

where

$$E^*(t) = \int_{t-\tau_E(t)}^{t} \exp\Big(- \int_{\xi}^{t} \mu_E(r)dr\Big) b(\xi, A^*(\xi))d\xi,$$

$$L^*(t) = \int_{t-\tau_L(t)}^{t} (1 - f_E'(\xi)) \exp\Big(- \int_{\xi}^{t} \mu_L(r)dr - \int_{\xi - f_E(\xi)}^{\xi} \mu_E(r)dr\Big)$$

$$b(\xi - f_E(\xi), A^*(\xi - f_E(\xi)))d\xi,$$

$$N^*(t) = \int_{t-\tau_N(t)}^{t} (1 - f_L'(\xi)) \exp\Big(- \int_{\xi}^{t} \mu_N(r)dr - \int_{\xi-\tau_L(\xi)}^{\xi} \mu_L(r)dr - \int_{\xi - f_L(\xi)}^{\xi-\tau_L(\xi)} \mu_E(r)dr\Big)$$

$$b(\xi - f_L(\xi), A^*(\xi - f_L(\xi)))d\xi,$$

are all positive T-periodic functions. Thus, the global attractivity of the full system (3.13) can be obtained.

Theorem 3.6. *If $\mathcal{R}_0 > 1$, then system (3.13) has a unique positive T-periodic solution $(E^*(t),\ L^*(t),\ N^*(t),\ A^*(t))$, which is globally attractive for all nontrivial solutions.*

3.5 Dynamics under immature intraspecific competition

Under the consideration of competitions among immature individuals, the model (3.8) is composed of four coupled delay differential equations with time-dependent delays. We will conduct a series of rigorous analysis including the well-posedness and threshold dynamics in terms of the basic reproduction number, which constitutes the main focus of our project. To investigate the long-term dynamics of system (3.8), we make the additional assumptions for the immature mortality rates based on the assumptions made in last section:

(C1) All the mortality rates including per-capita natural death rates $\mu_i(t)$ ($i = E, L, N$) and density dependent death coefficients $D_i(t, i)$ ($i = L, N$) are nonnegative T-periodic continuous functions with respect to time t. In addition, $D_i(t,i)$ is non-decreasing with respect to i for $i = L, N$.

Define $C_{\hat{f}} := C([-\hat{f},0],\mathbb{R}^4)$ with the norm $\|\phi\|_{C_{\hat{f}}} = \max\limits_{\theta\in[-\hat{f},0]} \|\phi(\theta)\|_{\mathbb{R}}^4$. Then $C_{\hat{f}}$ is a Banach space. Let $C_{\hat{f}}^+ = C([-\hat{f},0],\mathbb{R}_+^4)$, then $(C_{\hat{f}}, C_{\hat{f}}^+)$ is a strongly ordered space. Given a function $u(t) : [-\hat{f},\sigma) \to \mathbb{R}^4$ for $\sigma > 0$, define $u_t \in C_{\hat{f}}$ by $u_t(\theta) = u(t+\theta)$ for all $\theta \in [-\hat{f},0]$ and $t \in [0,\sigma)$. Before exploring the long-term dynamics, we firstly verify the global existence of the solution to (3.8) defined on.

Lemma 3.4. *A unique solution $(E(t), L(t), N(t), A(t))$ of system (3.8) exists globally on $[0,\infty)$ with the initial data $\phi(\theta) \in C_{\hat{f}}^+$. Moreover, system (3.8) generates a T-periodic semiflow $\Phi_t : C_{\hat{f}}^+ \to C_{\hat{f}}^+$, i.e. $\Phi_t(\phi)(\theta) = (E(t+\theta;\phi), L(t+\theta;\phi), N(t+\theta;\phi), A(t+\theta;\phi))$, $\forall \phi \in C_{\hat{f}}^+$, $t \geqslant 0$, $\theta \in [-\hat{f},0]$.*

Proof. Based on assumptions (H1) and (H3), we can show that $[0, \rho A^{**}]$ is positively invariant for the last equation of system (3.8) with any given $\rho \geqslant 1$, which is analogous to the proof of Lemma 3.1 in the previous section.

Likewise, $E(t)$, $L(t)$ and $N(t)$ are bounded since

$$\begin{aligned}
E(t) &\leqslant \int_{t-\tau_E(t)}^{t} b(\xi, A(\xi))d\xi \leqslant \int_{t-\tau_E(t)}^{t} \beta(\xi)A(\xi)d\xi \leqslant \rho\hat{\tau}_E\hat{\beta}A^{**},\\
L(t) &\leqslant \int_{t-\tau_L(t)}^{t} (1 - f_E'(\xi))b(\xi - f_E(\xi), A(\xi - f_E(\xi)))d\xi\\
&\leqslant \int_{t-\tau_L(t)}^{t} (1 - f_E'(\xi))\beta(\xi - f_E(\xi))A(\xi - f_E(\xi))d\xi \leqslant \rho\hat{\tau}_L\hat{\gamma}_E\hat{\beta}A^{**},\\
N(t) &\leqslant \int_{t-\tau_N(t)}^{t} (1 - f_L'(\xi))b(\xi - f_L(\xi), A(\xi - f_L(\xi)))d\xi\\
&\leqslant \int_{t-\tau_N(t)}^{t} (1 - f_L'(\xi))\beta(\xi - f_L(\xi))A(\xi - f_L(\xi))d\xi \leqslant \rho\hat{\tau}_N\hat{\gamma}_L\hat{\beta}A^{**},
\end{aligned}$$

where $\hat{\tau}_E = \max\limits_{t\in[0,T]} \tau_E(t)$, $\hat{\tau}_L = \max\limits_{t\in[0,T]} \tau_L(t)$, $\hat{\tau}_N = \max\limits_{t\in[0,T]} \tau_N(t)$, $\hat{\gamma}_E = \max\limits_{t\in[0,T]} (1 - f'_E(t))$ and $\hat{\gamma}_L = \max\limits_{t\in[0,T]} (1 - f'_L(t))$. Hence,

$$S := C([-\hat{f}, 0], [0, \rho\hat{\tau}_E\hat{\beta}A^{**}] \times [0, \rho\hat{\tau}_L\hat{\gamma}_E\hat{\beta}A^{**}] \times [0, \rho\hat{\tau}_N\hat{\gamma}_L\hat{\beta}A^{**}] \times [0, \rho A^{**}]),$$

is positively invariant for system (3.8). Due to the arbitrariness of ρ (can be as large as you wish), the non-negativity and boundedness of solutions of system (3.8) hold in $[0, \infty)$. Thus, a unique solution $(E(t), L(t), N(t), A(t))$ of system (3.8) exists globally on $[0, \infty)$ with the initial data $\phi(\theta) \in C^+_{\hat{f}}$.

Define the solution map of system (3.8) as

$$\Phi_t(\phi) = (E(t+\theta;\phi), L(t+\theta;\phi), N(t+\theta;\phi), A(t+\theta;\phi)), \forall t \geqslant 0, \theta \in [-\hat{f}, 0], \phi \in C^+_{\hat{f}},$$

where $(E(t;\phi), L(t;\phi), N(t;\phi), A(t;\phi))$ is the solution of system (3.8) with the initial data $\phi(\theta)$ for all $\theta \in [-\hat{f}, 0]$. Due to the periodicity of the variable coefficients, it easily follows that Φ_t is a $T-$ periodic semiflow on $C^+_{\hat{f}}$. □

It follows from the assumption (H1) that system (3.8) has the extinction equilibrium $(0, 0, 0, 0)$. The linearized system of system (3.8) at the population extinction equilibrium is shown as follows:

$$\begin{aligned}
\frac{dE(t)}{dt} &= \beta(t)A(t) - \mu_E(t)E(t) - (1 - f'_E(t))h_1(t)\beta(t - f_E(t))A(t - f_E(t)),\\
\frac{dL(t)}{dt} &= (1 - f'_E(t))h_1(t)\beta(t - f_E(t))A(t - f_E(t)) - \mu_L(t)L(t)\\
&\quad - (1 - f'_L(t))h_2(t)\beta(t - f_L(t))A(t - f_L(t)),\\
\frac{dN(t)}{dt} &= (1 - f'_L(t))h_2(t)\beta(t - f_L(t))A(t - f_L(t)) - \mu_N(t)N(t)\\
&\quad - (1 - f'_N(t))h_3(t)\beta(t - f_N(t))A(t - f_N(t)),\\
\frac{dA(t)}{dt} &= (1 - f'_N(t))h_3(t)\beta(t - f_N(t))A(t - f_N(t)) - \mu_A(t)A(t).
\end{aligned} \tag{3.17}$$

The last equation in (3.17) is decoupled, giving a linear scalar delay differential equation as below:

$$\frac{dA(t)}{dt} = (1 - f'_N(t))h_3(t)\beta(t - f_N(t))A(t - f_N(t)) - \mu_A(t)A(t).$$

Note that the linearized system for system (3.8) at the population extinction equilibrium is precisely (3.15). Therefore, the formulation of the basic reproduction number, $\mathcal{R}_0$, serving as a threshold parameter, and the related theoretical results involving Lemma 3.2 in the previous section remain valid.

3.5.1 Extinction and persistence

The following theorem deals with extinction and uniform persistence in terms of $\mathcal{R}_0$. Let

$$M_0 := \{\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in C_{\hat{f}} : \phi_i(0) > 0, \forall i \in \{1, 2, 3, 4\}\},$$

and

$$\partial M_0 := C_{\hat{f}} \backslash M_0 = \{\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in C_{\hat{f}}, \phi_i(0) = 0, \text{for some } i \in \{1, 2, 3, 4\}\}.$$

Theorem 3.7. *Let* $(H1 - H3)$ *and* $(C1)$ *hold. Then the following statements are valid:*

(1) If $\mathcal{R}_0 < 1$*, then the population extinction equilibrium* $(0, 0, 0, 0)$ *is globally attractive for system (3.8) on* $C_{\hat{f}}$*.*

(2) If $\mathcal{R}_0 > 1$*, then system (3.8) admits a positive* T*-periodic solution* $(E^*(t), L^*(t), N^*(t), A^*(t))$ *in* M_0 *and there exists a real number* $\eta > 0$ *such that the solution* $(E(t), L(t), N(t), A(t))$ *with* $\phi \in M_0$ *satisfies* $\liminf_{t\to\infty} i(t) \geqslant \eta$ *for* $i = E, L, N, A$*.*

Proof. In the case where $\mathcal{R}_0 < 1$, we have $r(P) < 1$ since $sign(\mathcal{R}_0 - 1) = sign(r(P) - 1)$ in light of [134, Theorem 2.1]. Based on Lemma 3.2, there is a positive T-periodic function $v(t)$ such that $w(t) = e^{\mu t}v(t)$ is a positive solution of (3.15), where $\mu = \dfrac{\ln r(P)}{T} < 0$. Then, the positivity of $A(t)$ and assumption (H1) indicate that

$$\begin{aligned}\frac{dA(t)}{dt} &\leqslant (1-f_N'(t))h_3(t)b(t-f_N(t), A(t-f_N(t))) - \mu_A(t)A(t)\\ &\leqslant (1-f_N'(t))h_3(t)\beta(t-f_N(t))A(t-f_N(t)) - \mu_A(t)A(t),\end{aligned}$$

since

$$h_3(t)\exp\Big(-\int_{t-\tau_N(t)}^{t} D_N(r,N(r))N(r)dr - \int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)} D_L(r,L(r))L(r)dr\Big) \leqslant h_3(t).$$

Hence, the comparison theorem [105, Theorem 5.1.1] implies that there exists a constant $K > 0$ such that $A(\theta) \leqslant Ke^{\mu\theta}v(\theta)$ for all $-\hat{f} \leqslant \theta \leqslant 0$ guaranteeing that

$$A(t) \leqslant Kw(t) = Ke^{\mu t}v(t),$$

and further, $\lim\limits_{t\to\infty} A(t) = 0$.

Besides, based on equation (3.9), (3.10) and (3.11), it follows from assumption (H3) that

$$\begin{aligned}E(t) &\leqslant \int_{t-\tau_E(t)}^{t} b(\xi, A(\xi))d\xi \leqslant \int_{t-\tau_E(t)}^{t} \beta(\xi)A(\xi)d\xi,\\ L(t) &\leqslant \int_{t-\tau_L(t)}^{t} (1-f_E'(\xi))b(\xi-f_E(\xi), A(\xi-f_E(\xi)))d\xi\\ &\leqslant \int_{t-\tau_L(t)}^{t} \hat{\gamma}_E\beta(\xi-f_E(\xi))A(\xi-f_E(\xi))d\xi,\\ N(t) &\leqslant \int_{t-\tau_N(t)}^{t} (1-f_L'(\xi))b(\xi-f_L(\xi), A(\xi-f_L(\xi)))d\xi\\ &\leqslant \int_{t-\tau_N(t)}^{t} \hat{\gamma}_L\beta(\xi-f_L(\xi))A(\xi-f_L(\xi))d\xi.\end{aligned}$$

Thus, when $\mathcal{R}_0 < 1$,

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

In the case where $\mathcal{R}_0 > 1$, we have $r(P) > 1$. Then, there exists a sufficiently small $\epsilon > 0$, such that r_ϵ, the spectral radius of the Poincaré map corresponding to

$$u'(t) = (1 - f_N'(t))h_3(t)(\beta(t - f_N(t)) - \epsilon)u(t - f_N(t)) - (\mu_A(t) + \epsilon)u(t), \quad (3.18)$$

satisfies $r_\epsilon > 1$. Similarly, there is a positive T-periodic function $v^\epsilon(t)$ such that $u(t) = e^{\lambda t}v^\epsilon(t)$ is a positive solution of equation (3.18) with $\lambda = \dfrac{\ln r_\epsilon}{T} > 0$.

Based on the continuity of $g_2(t, \cdot, \cdot)$ and differentiability of $b(t, \cdot)$, for any $\epsilon > 0$, we can choose a sufficiently small number $\eta_1 > 0$ such that for all $i \in [0, \eta_1]$ $(i = L, N, A)$

$$g_2(t, L, N)b(t, A) \geqslant (g_2(t, 0, 0)\frac{\partial b(t, 0)}{\partial A} - \epsilon)A = (\beta(t) - \epsilon)A,$$

and $D_A(t, A)A < D_A(t, \eta_1)\eta_1 < \epsilon$ hold according to assumption (H2).

Recall that the solution semiflow $\Phi_t(\phi)$ (defined in Lemma 3.4) tends to 0 uniformly for all $t \in [0, T]$ when ϕ approaches to 0, then there exists $\eta_0 > 0$ such that for any $\|\phi\| \leqslant \eta_0$, we have

$$\|\Phi_t(\phi)\| \leqslant \eta_1, \ \forall t \in [0, T].$$

Furthermore, we can prove the following claim to obtain weak persistence when $\mathcal{R}_0 > 1$.

Claim: There exists $\eta_0 > 0$ such that $\limsup_{n\to\infty} \|\Phi_{nT}(\phi)\| \geqslant \eta_0$ for all $\phi \in M_0$.

Suppose the claim is false, then $\limsup_{n\to\infty} \|\Phi_{nT}(\phi)\| < \eta_0$ for some $\phi \in M_0$. Hence, there exists a positive integer N_1, such that $\|\Phi_{nT}(\phi)\| < \eta_0$ when $n \geqslant N_1$. Thus, for any $t = nT + t_1$ with $n \geqslant N_1$ and $t_1 \in [0, T]$, we have $\|\Phi_t(\phi)\| = \|\Phi_{t_1}(\Phi_{nT}(\phi))\| \leqslant \eta_1$ and

$$\frac{dA(t)}{dt} \geqslant (1 - f_N'(t))h_3(t)(\beta(t - f_N(t)) - \epsilon)A(t - f_N(t)) - (\mu_A(t) + \epsilon)A(t).$$

Again, by the comparison theorem [105, Theorem 5.1.1], we can conclude that there exists a constant $L > 0$ such that $A(\theta) \geqslant Le^{\lambda\theta}v^\epsilon(\theta)$ for all $-\hat{f} \leqslant \theta \leqslant 0$, which implies that

$$A(t) \geqslant Lu(t) = Le^{\lambda t} v^{\epsilon}(t).$$

However $\lim\limits_{t\to\infty} e^{\lambda t} v^{\epsilon}(t) = \infty$ holds, which contradicts to the uniform boundedness of $A(t)$.

Define $\tilde{\mathcal{P}}(t)$ as the solution map for the linear periodic system of (3.8) on $C_{\hat{f}}$, that is, $\tilde{\mathcal{P}}(t)\phi = w_t(\phi)$, $t \geqslant 0$, where $w_t(\phi)(\theta) = w(t+\theta;\phi)$, $\forall \theta \in [-\hat{f}, 0]$ is the unique solution of system (3.17). Denote $\tilde{P} := \tilde{\mathcal{P}}(T)$ as the Poincaré map associated with system (3.17). Let $M_1 = (0,0,0,0)$. It then follows from the above claim that M_1 is a isolated invariant set for $\tilde{P}$ on $C_{\hat{f}}$ and $W^s(M_1) \cap M_0 = \varnothing$, where $W^s(M_1)$ is the stable set of M_1 for $\tilde{P}$. Define

$$M_{\partial} := \{\phi \in \partial M_0 : P^n(\phi) \in \partial M_0, \forall n \geqslant 0\}.$$

Then $\cup_{\phi \in M_{\partial}} \omega(\phi) = M_1$. In addition, it is easy to see that no subset of M_1 forms a cycle in M_{∂}, which also holds in ∂M_0. According to the acyclicity theorem on uniform persistence for maps in [135], we have $\tilde{P} : C_{\hat{f}} \to C_{\hat{f}}$ is uniformly persistent with respect to M_0. Thus, Theorem 3.1.1 of [135] implies that the semiflow $\Phi_t : C_{\hat{f}} \to C_{\hat{f}}$ is also uniformly persistent with respect to M_0. Based on [133, Theorem 3.1], it can be concluded that system (3.8) admits a T-periodic solution $(E^*(t), L^*(t), N^*(t), A^*(t))$ with $(E^*(\theta), L^*(\theta), N^*(\theta), A^*(\theta)) \in M_0$.

In order to obtain the practical uniform persistence, we define a continuous function $p : C_{\hat{f}} \to \mathbb{R}_+$ by

$$p(\phi) = \min(\phi_1(0), \phi_2(0), \phi_3(0), \phi_4(0)), \qquad \forall \phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in C_{\hat{f}},$$

with maximum norm $\| \cdot \|$. By applying similar arguments with the proof of [76, Theorem 3.2], we can obtain the existence of a positive T-periodic solution and the practical uniform persistence, that is, there exists $\eta > 0$ such that

$$\liminf_{t\to\infty} \min(E(t,\phi), L(t,\phi), N(t,\phi), A(t,\phi)) = \liminf_{t\to\infty} p(\Phi_t(\phi)) \geqslant \eta \text{ for all } \phi \in M_0.$$

This completes the proof. □

3.6 Discussion

This chapter started from a periodic version of McKendrick-von Foerster equation with periodic coefficients to describe the population growth with seasonal effects. Using the equivalent integral equation obtained by the method of integration along characteristics, we presented a detailed proof of the uniqueness and existence of the solution in the light of contraction mapping theorem. It is worth noting that the age-dependent models can also be studied by using the semigroup theory [94] and similar models have been extensively studied in [122]. Our approach is highly motivated by [18, 122]. Then the hyperbolic equation was reduced to a periodic differential system with periodic delays through rigorous biological and mathematical arguments, with the tick population growth as our motivating example. The derived age-structured model with time-dependent periodic delays is quite different from previous time-independent delay system.

When the host community for immature ticks is very rich, the intra-specific competition between immature stages of ticks is negligible. In this scenario, the basic reproduction number $\mathcal{R}_0$ is defined as the spectral radius of the next generation operator following the work [134]. We should mention that the study [128] has also used the approach in [7] to define and derive the basic reproduction number for tick population dynamics, with some numerics for the model parameterized by the blacklegged ticks. The formulation of the basic reproduction number for models with periodic coefficients has been extensively studied and interesting readers can find more details from [9, 10, 58, 121] and references therein. Even though the specific form of $\mathcal{R}_0$ is not known, it is shown that $\mathcal{R}_0$ is a threshold value for the stability of zero solution of the corresponding linear equation [134, Theorem 2.1]. Given this, we further obtain the global stability of the positive periodic solution with the following two steps. Firstly, we investigate the global attractivity on this decoupled scalar subsystem when $\mathcal{R}_0 > 1$ by applying the theory of monotone systems. We showed that the solution semiflow is strongly monotone and strictly subhomogeneous in a novel space $Y := \{C[-f_N(0), 0], \mathbb{R}\}$, different from the usual space $X := \{C[-\hat{f}, 0], \mathbb{R}\}$. Then, we extended the result to the full system as the other variables can be represented by the decoupled variable for adult size. However, the introduction of novel phase space introduces new challenges and we need to argue the following facts: (1) show that the solution can define a periodic semiflow; (2) the basic reproduction number $\mathcal{R}_0$ can not only determine the stability of the system on Y, but also determined the stability in X; and (3) the periodic semilfow is (eventually) strongly monotone and strictly subhomogeneous. When the immature competition is included, we proved the global existence and uniqueness of the solution, and found that the basic reproduction number in this case is the same as in the previous case. The extinction and uniform persistence of tick population was further shown in terms of $\mathcal{R}_0$.

Chapter 4

A nonlocal reaction-diffusion growth model with periodic delay and competition

4.1 Background

The environment that organisms inhabit in the natural world is heterogeneously distributed. Many physiological factors such as climates and food resources may differ from place to place, which drive the organisms to keep drifting or dispersing. Spatial effects affecting population dynamics and the structures of the communities are of particular interest to scientists. Different kinds of models can be formulated to incorporate spatial effects explicitly. The patchy framework [46, 69, 108] involving a system of ordinary or delay differential equations describes the movement in a discontinuous spatial region consisting of multiple patches. Alternatively, spatial effects can be treated as a continuum and described appropriately by a reaction-diffusion model [21, 46], which is the main tool we are going to employ in this chapter.

Different reaction diffusion models with age-structure and nonlocal terms have been derived and investigated theoretically in the bounded or unbounded domain [44, 108, 114, 131]. For example, a stage structured nonlocal reaction diffusion model was proposed in [129], where the threshold dynamics and global attractivity of the positive steady state were investigated through the decoupled equation for adult variable as the immature intra-specific competition was ignored. By generalizing the model in [129] to a nonautonomous version, authors in [61] established the existence of the asymptotic speed of spread in an unbounded domain and a threshold result on the global attractivity of either zero or a positive periodic solution in a bounded domain. Authors in [131] studied the global dynamics of a class of age-structured reaction diffusion models with a fixed temporal delay and a nonlocal term in an unbounded domain.

In order to simplify the analysis, two significant factors regulating population growth were ignored in these stage structured nonlocal reaction diffusion models. One factor is the immature intra-specific competition, which enables these models to be reduced into only one equation for mature variable. However, the intra-specific competition within one stage, especially the immature stage, will generate a series of variations in successive stages and greatly influences the dynamics of organisms with complex life cycles [6]. For example, the body size and longevity of adult mosquitoes are to a large extent affected by the larval competition [4, 96]. The alteration of susceptibility of adult mosquitoes to dengue virus may be induced by the competition among larval mosquitoes [5]. The density-dependent acquired host resistance to ticks leads to the increased deaths of feeding and developing ticks [24, 123, 124]. Models incorporating density dependent death terms for immature individuals are more realistic to describe complex population dynamics of some species experiencing intra-specific competition. In this study, we assume that immature (mature) individuals only compete with all other individuals in the same stage and there is no competition between immature and mature stages. This assumption is biologically reasonable since the intra-specific competition within one stage rather than between stages can be commonly founded in species such as some insects and amphibious animals, which immature and mature individuals live in different environments and have quite different requirements for food or resources [38].

The other negligible factor is the time varying maturation period, which serves as a developmental index measuring the developmental progression and addresses the timing of the transition from the previous life stage [87]. In this chapter, we assume the maturation duration for juveniles is dependent on time, which is particular suitable for insects subject to climatic factors. For instance, the maturation periods of mosquitoes [100] and ticks [89] greatly rely on the temperature, which varies with time. Time-dependent maturation durations were considered in [45], where the authors derived a size structured delay differential equation (DDE) model with state-dependent delays to describe the population growth of a single species experiencing larval competition. To investigate the population growth influenced by seasonality, authors in [128] also took into account intra-specific competition and time varying development durations within each developmental stage of ticks and developed a stage-structured DDE model with periodic delays by building a link between time dependent age thresholds and developmental durations. Based on a similar model, authors in [72] provided a rigorous analysis involving the well posedness of the solution and threshold dynamics for tick populations subject to seasonal effects.

For these aforementioned models involving time-varying maturation period, spatial movement of individuals is not considered, which motivates us to formulate an age structured nonlocal reaction diffusion growth model with consideration of immature intra-specific competition and time dependent maturation duration simultaneously. In addition, it is well known that the annual trends of population dynamics are greatly affected by the seasonal changes in rainfall, temperature and accessible food or resources. This is particular true for some insect species such as ticks, the primary vector transmitting tick-borne diseases, the distribution and abundance of which are very sensitive to the climate conditions as they need relatively high humidity and moderate temperature to survive during their prolonged nonparasitic stages [89]. Incorporating seasonal effects in the model would be a sensible choice to better investigate the population dynamics, with all the time-dependent parameter functions in our model being periodic with the same period T. The main focus of this chapter is to provide a rigorous and detailed theoretical analysis on a delayed nonlocal reaction diffusion population model with age structure and time dependent delays from the perspective of periodic dynamical systems.

In the next section, a closed system related to the densities of immatures $I(t,x)$ and adults $M(t,x)$ is formulated in terms of a system involving time-periodic delays due to the seasonal juvenile maturation period. The time-dependent periodic delay in our model brings novel challenges to the theoretical analysis. Section 4.3 conducts theoretical analysis on the model ignoring juvenile intra-specific competition, making the model reducible to one equation for $M(t,x)$, based on which, the well posedness of the system and the existence of the global attractor are established. In addition, the basic reproduction number $\mathcal{R}_0$ is formulated and the global stability of one equation in terms of $\mathcal{R}_0$ is obtained by employing the theory of monotone and subhomogeneous semiflows. In section 4.4, we investigate the threshold dynamics for the obtained model under the consideration of immature intra-specific competition when the immature individuals have limited dispersal ability. It is impossible to decouple the equation for the matured population density $M(t,x)$ from the model system as usual due to the existence of the intra-specific juvenile competition. A discussion session in the final part concludes this chapter.

4.2 Model formulation

We start with a well-accepted age-structured framework proposed in [85] and generalize it into the following spatial model with periodic coefficients to study the interactive effects of the age structure and spatial dispersal on population growth subject to seasonal effects:

$$(\tfrac{\partial}{\partial t}+\tfrac{\partial}{\partial a})\rho(t,a,x)=D(a)\tfrac{\partial^2}{\partial x^2}\rho(t,a,x)-\mu\left(t,a,\textstyle\int_0^\infty q(t,s)\rho(t,s,x)ds\right)\rho(t,a,x), \tag{4.1}$$

where $\rho(t,a,x)$ is the population density of one species at time t, age a ($\geqslant 0$) and location x in a bounded spatial domain Ω with smooth boundary $\partial\Omega$, $D(a)$ ($\geqslant 0$) is the age-dependent diffusion rate, $\mu\left(t,a,\int_0^\infty q(t,s)\rho(t,s,x)ds\right)$ ($\geqslant 0$) represents the per-capita death rate, which varies with the time t, age a and a weighted population density with kernel $q(t,a)$ ($\geqslant 0$).

By choosing appropriate weight functions as in [72], the specific form of the per-capita death rates $\mu\left(t,a,\int_0^\infty q(t,s)\rho(t,s,x)ds\right)$ for immature and mature stages are assumed to be:

$$\mu\left(t,a,\int_0^\infty q(t,s)\rho(t,s,x)ds\right)$$
$$=\begin{cases}\mu_I(t)+f(I(t,x)), & t>-\tau(0),\ 0<a\leqslant\tau(t),\ x\in\Omega,\\ \mu_M(t)+g(M(t,x)), & t>-\tau(0),\ a>\tau(t),\ x\in\Omega.\end{cases} \quad ll$$

In this formula, $\mu_I(t)$ and $\mu_M(t)$ are density-independent per capita death rates for immature and mature individuals respectively, while $f(\cdot)$ and $g(\cdot)$ are density-dependent death rates, which represent the intra-specific competition between individuals within the immature and mature stages respectively.

Let $\tau(t)$ denote the juvenile maturation period at time t, that is, a newly matured individual at time t is developed from an immature individual born at time $t-\tau(t)$.

That is, the age threshold classifying the population into immature and mature stages at time t is $\tau(t)$. In other words, the chronological age at time t for adults should be greater than $\tau(t)$. Thus, the densities of individuals within the immature stage $I(t,x)$ and mature stage $M(t,x)$ at time t and location x can be represented as follows:

$$I(t,x) = \textstyle\int_0^{\tau(t)} \rho(t,a,x)da \quad \text{and} \quad M(t,x) = \textstyle\int_{\tau(t)}^{\infty} \rho(t,a,x)da. \tag{4.2}$$

Provided that the developmental proportion during juvenile stage at day t is $\sigma(t)$, the immature individuals attain maturity when the corresponding accumulative developmental proportion during the interval $[t-\tau(t), t]$ is unity, that is

$$\int_{t-\tau(t)}^{t} \sigma(r)dr = 1.$$

By taking the derivative with respect to t, it follows that

$$1 - \tau'(t) = \frac{\sigma(t)}{\sigma(t-\tau(t))}.$$

This indicates $1-\tau'(t) > 0$, which guarantees that developmental processes proceed according to the chronological order and never develop back to the previous stage.

Based on (4.1), the population model incorporating both seasonal effects and spatial movements is presented as the following reaction diffusion equations with no flux boundary condition:

$$\begin{cases} (\dfrac{\partial}{\partial t}+\dfrac{\partial}{\partial a})\rho(t,a,x) = D_1\Delta\rho(t,a,x) - (\mu_I(t)+f(I(t,x)))\rho(t,a,x), \\ \hfill t > -\tau(0),\ 0 < a \leqslant \tau(t),\ x \in \Omega, \\ (\dfrac{\partial}{\partial t}+\dfrac{\partial}{\partial a})\rho(t,a,x) = D_2\Delta\rho(t,a,x) - (\mu_M(t)+g(M(t,x)))\rho(t,a,x), \\ \hfill t > -\tau(0),\ a > \tau(t),\ x \in \Omega, \\ \rho(t,0,x) = b\left(t, M(t,x)\right), \hfill t \geqslant -\tau(0),\ x \in \Omega, \\ \rho(-\tau(0),a,x) = \phi(a,x), \hfill a \geqslant 0,\ x \in \Omega, \\ \dfrac{\partial\rho(t,a,x)}{\partial n} = 0, \hfill t > -\tau(0),\ x \in \partial\Omega, \end{cases} \tag{4.3}$$

where Δ is the laplacian operator, n is the outward normal vector on $\partial\Omega$, D_1 (> 0 or $= 0$) and D_2 (> 0) denote the diffusion coefficients for immature and mature individuals respectively, $b\left(t, M(t,x)\right)$ is the birth rate, which is dependent on the density of matured individuals, $\phi(a,x)$ is the initial distribution. Note that all above functions are non-negative. Due to the seasonal factors regulating the population growth, we assume that $\tau(t)$, $b(t,M)$, $\mu_I(t)$ and $\mu_M(t)$ are periodic in time t with the same period T. Moreover, the inherent relationships between boundary and initial condition must be satisfied in order to keep the system consistent, that is,

$$\rho(-\tau(0),0,x) = b\left(-\tau(0), M(-\tau(0),x)\right) = \phi(0,x).$$

In addition, for the sake of clarity, we introduce the following notations:

$$\hat{\tau} = \max_{t\in[0,T]}\{\tau(t)\}, \quad \overline{\tau} = \min_{t\in[0,T]}\{\tau(t)\}. \tag{4.4}$$

The basic assumptions for the coefficients are made as below, with the birth and death functions illustrated in Figure 5.3.

(A1) The birth rate $b(t, M)$ is Hölder continuous on $\mathbb{R} \times \mathbb{R}$, periodic in time t with the period $T > 0$, and increasing with respect to $M \geqslant 0$. Moreover, $b(t, 0) \equiv 0$, $b(t, M) > 0$ when $M > 0$, $\frac{\partial b(t,0)}{\partial M} = \beta(t) > 0$ for all $t \in \mathbb{R}$ and $b(t, M) \leqslant \beta(t)M$ for all $t \in \mathbb{R}$ and $M > 0$, where $\beta(t)$ is a T-periodic continuous function. Furthermore, there exists a number $\widetilde{M} \geqslant 0$ such that for all $H > \widetilde{M}$, $(1 - \tau'(t))b(t - \tau(t), H) - (\mu_M(t) + g(H))H < 0$.

(A2) All the per-capita death rates including natural death rates $\mu_I(t)$ and $\mu_M(t)$ and density dependent death rates $f(I)$ and $g(M)$ are Hölder continuous. In particular, $\mu_I(t)$ and $\mu_M(t)$ are positive functions and periodic in time t with the same period $T > 0$. Function $g(M)$ is non-decreasing with respect to M. In addition, $f(0) = 0$, $g(0) = 0$, $f(I) \geqslant 0$ and $g(M) > 0$ when $I > 0$ and $M > 0$ respectively.

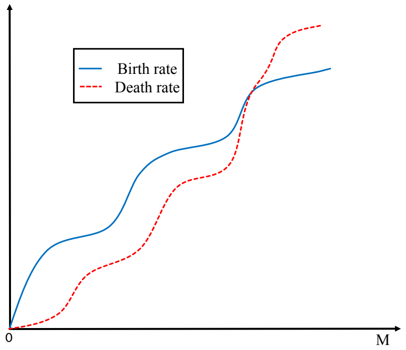


Figure 4.1: Model assumption for the birth rate $b(t, M)$ and death function $(\mu_M(t) + g(M))M$ for fixed time instant t.

By differentiating (4.2) with respect to time t and combining with (4.3), we obtain the following system:

$$
\begin{aligned}
&\frac{\partial I(t,x)}{\partial t}\\
=&\int_0^{\tau(t)} \frac{\partial \rho(t,a,x)}{\partial t} da + \tau'(t)\rho(t,\tau(t),x)\\
=&\int_0^{\tau(t)} \left(-\frac{\partial \rho(t,a,x)}{\partial a} + D_1 \Delta \rho(t,a,x) - (\mu_I(t) + f(I(t,x)))\rho(t,a,x) \right) da + \tau'(t)\rho(t,\tau(t),x)\\
=&D_1 \Delta I(t,x) + \rho(t,0,x) - \rho(t,\tau(t),x) - (\mu_I(t) + f(I(t,x)))I(t,x) + \tau'(t)\rho(t,\tau(t),x)\\
=&D_1 \Delta I(t,x) + b(t,M(t,x)) - (\mu_I(t) + f(I(t,x)))I(t,x) - (1-\tau'(t))\rho(t,\tau(t),x),
\end{aligned}
$$

and

$$
\begin{aligned}
&\frac{\partial M(t,x)}{\partial t}\\
=&\int_{\tau(t)}^{\infty} \frac{\partial \rho(t,a,x)}{\partial t} da - \tau'(t)\rho(t,\tau(t),x)\\
=&\int_{\tau(t)}^{\infty} \left(-\frac{\partial \rho(t,a,x)}{\partial a} + D_2 \Delta \rho(t,a,x) - (\mu_M(t) + g(M(t,x)))\rho(t,a,x) \right) da - \tau'(t)\rho(t,\tau(t),x)\\
=&D_2 \Delta M(t,x) + \rho(t,\tau(t),x) - \rho(t,\infty,x) - (\mu_M(t) + g(M(t,x)))M(t,x) - \tau'(t)\rho(t,\tau(t),x)\\
=&D_2 \Delta M(t,x) + (1-\tau'(t))\rho(t,\tau(t),x) - (\mu_M(t) + g(M(t,x)))M(t,x),
\end{aligned}
$$

where the reasonable biological assumption guarantees that $\rho(t,\infty,x)$ is zero since no individual can survive forever.

To get the closed form of the above system, we need to determine $\rho(t,\tau(t),x)$ by integrating along characteristics. For any $\xi \geqslant -\tau(0)$, let $v(\xi,x) = \rho(t_0+\xi, a_0+\xi, x)$, where t_0 and a_0 are fixed. Then, when $0 < a_0 + \xi \leqslant \tau(t)$, we have,

$$\begin{cases} \dfrac{\partial}{\partial \xi} v(\xi, x) = \left(\dfrac{\partial}{\partial t} + \dfrac{\partial}{\partial a} \right) \rho(t_0 + \xi, a_0 + \xi, x) \\ \qquad\qquad = D_1 \Delta \rho(t_0 + \xi, a_0 + \xi, x) - \left(\mu_I(t_0 + \xi) + f(I(t_0 + \xi, x)) \right) \rho(t_0 + \xi, a_0 + \xi, x) \\ \qquad\qquad = D_1 \Delta v(\xi, x) - \left(\mu_I(t_0 + \xi) + f(I(t_0 + \xi, x)) \right) v(\xi, x), \\ v(-\tau(0), x) = \rho(t_0 - \tau(0), a_0 - \tau(0), x). \end{cases} \tag{4.5}$$

Clearly, the expression of the solutions $v(\xi, x)$ of (4.5) depends on coefficients D_1 and $f(I)$. More precisely, the fundamental solution corresponding to the partial differential operator $L :\equiv [\partial_t - D_1 \Delta - \mu_I(t) - f(I(t, \cdot))]$ involves D_1 and $f(I)$. Especially, when $D_1 > 0$ and $f(I) > 0$, it is very challenging for us to show such fundamental solution (see [41]). At what follows, we study the equation (4.5) in terms of D_1 and $f(I)$ with three cases: (I) $D_1 > 0, f(I) \equiv 0$ for $I > 0$; (II) $D_1 = 0, f(I) \equiv 0$ for $I > 0$; (III) $D_1 = 0, f(I) > 0$ for $I > 0$, and then we show the closed form of the system on I and M. As a matter of fact, the fundamental solution based on (II) is a special case of it involved with (I) due to $f(I) \equiv 0$. Hence, we mainly concern cases (I) and (III).

Case I: $D_1 > 0$ **and** $f(I) \equiv 0$**.** For some species such as mammals [42] and raptor [83], the juvenile individuals have the ability to disperse, which alleviates the intra-specific competition within immature stages [86]. Consequently, the juvenile intra-specific competition can be ignored when immature individuals can move or disperse efficiently, that is, $f(I) \equiv 0$ when $D_1 > 0$. In view of (4.5), we have

$$\begin{aligned} v(\xi, x) &= \int_\Omega \Gamma(t_0 + \xi, t_0 - \tau(0), x, y, D_1) v(-\tau(0), y) dy \\ &= \int_\Omega \Gamma\left(t_0 + \xi, t_0 - \tau(0), x, y, D_1\right) \rho(t_0 - \tau(0), a_0 - \tau(0), y) dy, \end{aligned}$$

where $\Gamma(t, s, x, y, D_1)$ represents the fundamental solution corresponding to the partial differential operator $L :\equiv [\partial_t - D_1\Delta - \mu_I(t)]$ (see [41, Chapter 1]). For all $t \geqslant 0$, let $t_0 = t + \tau(0) - \tau(t)$, $\xi = \tau(t) - \tau(0)$ and $a_0 = \tau(0)$, then $\xi \geqslant -\tau(0)$ and $\xi + a_0 = \tau(t)$. In this case,

$$\begin{aligned} &\rho(t, \tau(t), x) = v(\tau(t) - \tau(0), x) \\ =&\int_\Omega \Gamma(t, t-\tau(t), x, y, D_1)\rho(t-\tau(t), 0, y)dy, \\ =&\int_\Omega \Gamma\left(t, t-\tau(t), x, y, D_1\right) b(t-\tau(t), M(t-\tau(t), y))dy. \end{aligned}$$

Therefore, the closed form of the system describing the population growth when $t \geqslant 0$ can be written as:

$$\begin{cases} \dfrac{\partial I(t,x)}{\partial t} =& D_1\Delta I(t,x) + b(t, M(t,x)) - \mu_I(t)I(t,x) \\ & -(1-\tau'(t))\displaystyle\int_\Omega \Gamma\left(t, t-\tau(t), x, y, D_1\right) b(t-\tau(t), M(t-\tau(t), y))dy, \\ & \qquad\qquad\qquad\qquad\qquad\qquad t > 0,\ x \in \Omega, \\ \dfrac{\partial M(t,x)}{\partial t} =& D_2\Delta M(t,x) - (\mu_M(t) + g(M(t,x)))M(t,x) \\ & +(1-\tau'(t))\displaystyle\int_\Omega \Gamma\left(t, t-\tau(t), x, y, D_1\right) b(t-\tau(t), M(t-\tau(t), y))dy, \\ & \qquad\qquad\qquad\qquad\qquad\qquad t > 0,\ x \in \Omega, \\ \dfrac{\partial I(t,x)}{\partial n} =& \dfrac{\partial M(t,x)}{\partial n} = 0, \quad t > 0,\ x \in \partial\Omega, \end{cases} \tag{4.6}$$

When $D_1 = 0$ and $f(I) \equiv 0$, the fundamental solution operator $\Gamma\left(t, t-\tau(t), x, y, D_1\right)$ is reduced to

$$\Gamma\left(t, t-\tau(t), x, y, D_1\right) = e^{\int_{t-\tau(t)}^{t} \mu_I(s)ds},$$

and hence, we have the following system:

$$\begin{cases} \dfrac{\partial I(t,x)}{\partial t} =& D_1\Delta I(t,x) + b(t, M(t,x)) - \mu_I(t)I(t,x) \\ & - (1-\tau'(t))e^{\int_{t-\tau(t)}^{t}\mu_I(s)ds} b(t-\tau(t), M(t-\tau(t),y)), \quad t>0,\ x \in \Omega, \\ \dfrac{\partial M(t,x)}{\partial t} =& D_2\Delta M(t,x) - (\mu_M(t) + g(M(t,x)))M(t,x) \\ & + (1-\tau'(t))e^{\int_{t-\tau(t)}^{t}\mu_I(s)ds} b(t-\tau(t), M(t-\tau(t),y)), \quad t>0,\ x \in \Omega, \\ \dfrac{\partial I(t,x)}{\partial n} =& \dfrac{\partial M(t,x)}{\partial n} = 0, \quad t>0,\ x \in \partial\Omega, \end{cases} \tag{4.7}$$

Case III: $D_1 = 0$, $f(I) > 0$. For some species such as mosquitoes [66] or frogs [35], the immature individuals are often restricted in a limited area due to inefficient dispersal ability, which would intensify the competition for food and resources among immature individuals. In this scenario, the diffusion rate for immature individuals is negligible (i.e. $D_1 \equiv 0$) while the immature intra-specific competition is taken into consideration, that is, $f(I) > 0$ for $I > 0$. Then, the fundamental solution corresponding to the differential operator $L = [\partial_t - \mu_I(t) - f(I(t,\cdot))]$ is given by $\exp\left(\int_{t-\tau(t)}^{t} (\mu_I(s) + f(I(s,\cdot)))\,ds\right)$. Similar to the former arguments, we obtain that

$$\begin{aligned} &\rho(t,\tau(t),x) = v(\tau(t)-\tau(0),x) \\ =& \exp\left(\int_{t-\tau(t)}^{t} (\mu_I(s) + f(I(s,\cdot)))\,ds\right)\rho(t-\tau(t),0,y), \\ =& \exp\left(\int_{t-\tau(t)}^{t} (\mu_I(s) + f(I(s,\cdot)))\,ds\right)b(t-\tau(t),M(t-\tau(t),y)). \end{aligned}$$

Consequently, the closed form of the system describing the population growth when

$t \geqslant 0$ can be written as:

$$\begin{cases} \dfrac{\partial I(t,x)}{\partial t} =& b(t,M(t,x)) - (\mu_I(t) + f(I(t,x)))I(t,x) - (1-\tau'(t)) \\ & \times \exp\left(-\displaystyle\int_{t-\tau(t)}^{t} (\mu_I(s) + f(I(s,x)))ds\right) b(t-\tau(t), M(t-\tau(t),x)), \\ & \qquad t > 0,\ x \in \Omega, \\ \dfrac{\partial M(t,x)}{\partial t} =& D_2 \Delta M(t,x) - (\mu_M(t) + g(M(t,x)))M(t,x) + (1-\tau'(t)) \\ & \times \exp\left(-\displaystyle\int_{t-\tau(t)}^{t} (\mu_I(s) + f(I(s,x)))ds\right) b(t-\tau(t), M(t-\tau(t),x)), \\ & \qquad t > 0,\ x \in \Omega, \\ \dfrac{\partial I(t,x)}{\partial n} =& \dfrac{\partial M(t,x)}{\partial n} = 0, \quad t > 0,\ x \in \partial\Omega. \end{cases} \tag{4.8}$$

Notice that during derivation of the above system, it is not difficult to see that

$$\rho(t,a,x) = \exp\left(-\int_{t-a}^{t} (\mu_I(r) + f(I(r,x)))dr\right) b(t-a, M(t-a,x))$$

for $t \geqslant \tau(t) \geqslant a$, while

$$\begin{aligned} I(t,x) &= \int_0^{\tau(t)} \rho(t,a,x)da \\ &= \int_0^{\tau(t)} \exp\left(-\int_{t-a}^{t} (\mu_I(r) + f(I(r,x)))dr\right) b(t-a, M(t-a,x))da \\ &= \int_{t-\tau(t)}^{t} \exp\left(-\int_{s}^{t} (\mu_I(r) + f(I(r,x)))dr\right) b(s, M(s,x))ds \end{aligned}$$

for $t \geqslant \tau(t) \geqslant a$. Letting $t = 0$ in the above equation for I, we obtain the following constraint:

$$I(0,x) = \int_{-\tau(0)}^{0} \exp\left(-\int_{s}^{0} (\mu_I(r) + f(I(r,x)))dr\right) b(s, M(s,x))ds. \tag{4.9}$$

When the competition among immature individuals is non-negligible, that is, $f(I) > 0$ provided $I > 0$, the model (4.8) consists of two coupled equations which is not reducible to a single equation. The model structure of (4.8) is quiet different from systems (4.6) and (4.7). A series of rigorous analysis including the well-posedness and threshold dynamics in terms of the basic reproduction number will be conducted, which constitutes the main focus of our chapter. In the subsequent section, we will first investigate systems (4.6) and (4.7) where the immature intra-specific competition is negligible.

4.3 Dynamics for the model without immature intra-specific competition

In this section, we establish the global dynamics for (4.6) via the basic reproduction number. It is easy to check that the system is reducible to one single equation for $M(t,x)$. In fact, since the M equation in (4.6) is independent of I, it suffices to study the decoupled system:

$$\begin{cases} \dfrac{\partial M(t,x)}{\partial t} = D_2\Delta M(t,x) - (\mu_M(t) + g(M(t,x)))M(t,x) \\ \qquad\qquad + (1-\tau'(t))\displaystyle\int_\Omega \Gamma\left(t, t-\tau(t), x, y, D_1\right) b(t-\tau(t), M(t-\tau(t), y))dy, \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad t > 0,\ x \in \Omega, \\ \dfrac{\partial M(t,x)}{\partial n} = 0, \quad t > 0,\ x \in \partial\Omega. \end{cases} \tag{4.10}$$

4.3.1 Global existence and uniqueness of solutions

Without loss of generality, we choose the initial timing as the global maximum point of $\tau(t)$ in $[0, T]$, that is, $\tau(0) = \max_{t\in[0,T]}\{\tau(t)\} = \hat{\tau}$, which is feasible with solution evolution. Let $\mathbf{Y} := C(\overline{\Omega}, \mathbb{R})$ be the Banach space of continuous functions with the supremum norm $\|\cdot\|_{\mathbf{Y}}$. Define $\mathcal{C} = C([-\tau(0), 0], \mathbf{Y})$. For any $\psi \in \mathcal{C}$, define the norm $\|\psi\| = \max_{\theta\in[-\tau(0),0]} \|\psi(\theta)\|_{\mathbf{Y}}$. Then, $\mathcal{C}$ is a Banach space. Let $\mathbf{Y}^+ := C(\overline{\Omega}, \mathbb{R}^+)$ and $\mathcal{C}^+ = C([-\tau(0), 0], \mathbf{Y}^+)$, then $(\mathbf{Y}, \mathbf{Y}^+)$ and $(\mathcal{C}, \mathcal{C}^+)$ are both strongly ordered spaces. Given a function $u(t) : [-\tau(0), \sigma) \to \mathbf{Y}$ for $\sigma > 0$, define $u_t \in \mathcal{C}$ by $u_t(\theta, x) = u(t + \theta, x)$, for all $\theta \in [-\tau(0), 0]$, $x \in \overline{\Omega}$ and $t \in [0, \sigma)$.

Define the linear operator $\mathcal{A}$ by

$$
\begin{aligned}
&D(\mathcal{A}(t)) = \{\psi \in C^2(\overline{\Omega}) : \frac{\partial \psi}{\partial n} = 0 \text{ on } \partial\Omega\}, \\
&\mathcal{A}(t)\psi = D_2\Delta\psi - \mu_M(t)\psi, \quad \forall \psi \in D(\mathcal{A}(t)).
\end{aligned}
$$

Define the nonlinear operator $\mathcal{F} : \mathbb{R} \times \mathcal{C}^+ \to \mathbf{Y}$ by

$$
\mathcal{F}(t, \psi) = -g(\psi(0, \cdot))\psi(0, \cdot) + (1 - \tau'(t)) \int_\Omega \Gamma\left(t, t - \tau(t), \cdot, y, D_1\right) b(t - \tau(t), \psi(-\tau(t), y))dy,
$$

for $t \geqslant 0$ and $\psi \in \mathcal{C}^+$.

Then, system (4.10) can be reformulated as the following abstract functional differential equation:

$$
\begin{cases}
\frac{\partial M(t,\cdot)}{\partial t} = \mathcal{A}(t)M(t, \cdot) + \mathcal{F}(t, M_t), & t > 0,\ x \in \Omega, \\
M(\theta, x) = \psi(\theta, x), & \theta \in [-\tau(0), 0],\ x \in \Omega.
\end{cases}
\tag{4.11}
$$

Let $W(t, s)$ be the evolution operator determined by the following linear reaction-diffusion equation

$$
\begin{cases}
\frac{\partial M(t,x)}{\partial t} = D_2\Delta M(t, x) - \mu_M(t)M(t, x), & t > 0,\ x \in \Omega, \\
\frac{\partial M(t,x)}{\partial n} = 0, & t > 0,\ x \in \partial\Omega.
\end{cases}
\tag{4.12}
$$

The equivalent integral form of system (4.11) is shown as follows:

$$
M(t; \psi) = W(t, 0)\psi(0) + \int_0^t W(t, s)\mathcal{F}(s, M_s)ds, \quad t \geqslant 0,\ \psi \in \mathcal{C}^+,
$$

and the solution of which is a mild solution of (4.10).

Clearly, $\mathcal{F}(t,\cdot)$ is locally Lipschitz continuous on $\mathcal{C}^+$, and hence for any $\psi \in \mathcal{C}^+$, system (4.10) admits a unique non-continuable mild solution $M(t;\psi)$ such that $M_t(\psi) \in \mathcal{C}$ for all t in its maximal interval of existence $[0,\sigma_\psi)$ for $\sigma_\psi > 0$. Since $W(t,s)$ is compact and analytic for $t > s, t, s \in \mathbb{R}$, $M(t;\psi)$ is compact and a classical solution of (4.11) for $t > \hat{\tau}$. In view of assumption (A1), it easily follows that for any $H \geqslant \widetilde{M}$, $\Sigma_H := \{\psi \in \mathcal{C}^+ : 0 \leqslant \psi \leqslant H\}$ is a positively invariant set for (4.11) (see, e.g. [82] and [125]). Thus, for any $\psi \in \mathcal{C}^+$, $M(t;\psi)$ globally exists on $[0,\infty)$, and hence the equation (4.10) can define a periodic semiflow $\Psi_t : \mathcal{C}^+ \to \mathcal{C}^+$ by

$$\Psi_t(\psi)(s,x) = M(t+s,x;\psi), \quad \forall s \in [-\tau(0),0],\ x \in \overline{\Omega}.$$

Consider the following time-periodic and delayed differential equation:

$$\begin{cases} \dot{v}(t) = -(\mu_M(t) + g(v(t)))v(t) + (1-\tau'(t))b(t-\tau(t), v(t-\tau(t))) \\ v(s) = \varphi(s) \in C([-\tau(0),0],\mathbb{R}^+), \quad \forall s \in [-\tau(0),0]. \end{cases} \tag{4.13}$$

Note that the function $b(t,\cdot)$ is Lipschitz in any bounded subset of $\mathbb{R}^+$ as defined in Assumption (A1). Consequently, for any $\varphi \in C([-\tau(0),0],\mathbb{R}^+)$, the equation (4.13) admits a unique bounded solution $v(t;\varphi)$ with $v(s;\varphi) = \varphi(s)$, $\forall s \in [-\tau(0),0]$, which globally exists on $[0,\infty)$. In the following, we state a comparison theorem associated with the solutions of equations (4.10) and (4.13).

Lemma 4.1. *For any given $\xi \in \mathcal{C}^+$, let $\widehat{H}(s) = \max\{\xi(s,x), x \in \overline{\Omega}\}$, $\forall s \in [-\tau(0),0]$. Let $v(t;\widehat{H})$ be the solution of the following differential equation:*

$$\begin{cases} \dot{v}(t) = -(\mu_M(t) + g(v(t)))v(t) + (1-\tau'(t))b(t-\tau(t), v(t-\tau(t))), \\ v(s) = \widehat{H}(s) \in C([-\tau(0),0],\mathbb{R}^+), \quad \forall s \in [-\tau(0),0]. \end{cases}$$

Then the solution $M(t,x;\xi)$ of (4.10) with $M_0 = \xi$ satisfies $M(t,x;\xi) \leqslant v(t;\widehat{H})$ for all $(t,x) \in (0,\infty) \times \overline{\Omega}$.

Proof. Let $g_\alpha(t,u) = \alpha u - (\mu_M(t) + g(u))u$, where α is a sufficiently large number that makes $g_\alpha(t,u)$ increasing with respect to all $u \in [0,H]$. Note that,

$$\dot{v}(t) = -\alpha v(t) + g_\alpha(t,v) + (1-\tau'(t))b(t-\tau(t), v(t-\tau(t))),$$

and

$$\begin{aligned}\frac{\partial M(t,x)}{\partial t} =& D_2\Delta M(t,x) - \alpha M(t,x) + g_\alpha(t, M(t,x)) \\ &+ (1-\tau'(t))\int_\Omega \Gamma\left(t, t-\tau(t), x, y, D_1\right) b(t-\tau(t), M(t-\tau(t), y))dy,\end{aligned}$$

Let $\mathcal{Q}(t)$ $(t \geqslant 0)$ be the strongly continuous semigroups generated by $D_2\Delta$ and the Neumann boundary condition. Thus,

$$v(t) = e^{-\alpha(t-s)}v(s) + \int_s^t e^{-\alpha(t-r)}\left[g_\alpha(r, v(r)) + (1-\tau'(r))b(r-\tau(r), v(r-\tau(r)))\right]dr$$

and

$$\begin{aligned}M(t,x) =& e^{-\alpha(t-s)}\mathcal{Q}(t-s)M(s,x) + \int_s^t e^{-\alpha(t-r)}\mathcal{Q}(t-r)\Bigg[g_\alpha(r, M(r)) + (1-\tau'(r)) \\ &\int_\Omega \Gamma_0\left(r, r-\tau(r), x, y, D_1\right) b(r-\tau(r), M(r-\tau(r), y))dy\Bigg](x)dr.\end{aligned}$$

Set $w(t,x) = M(t,x;\xi) - v(t;\widehat{H})$ for any $(t,x) \in [0,\overline{\tau}] \times \overline{\Omega}$. Then, we have

$$w(t,x) \leqslant e^{-\alpha(t-s)}\mathcal{Q}(t-s)w(s,x) + \int_s^t e^{-\alpha(t-r)}\mathcal{Q}(t-r)(g_\alpha(r, M(r)) - g_\alpha(r, v(r)))(x)dr, \tag{4.14}$$

for $0 \leqslant s < t \leqslant \overline{\tau}$, where $\overline{\tau}$ is defined as in (4.4). Let $\hat{w}(t) = \sup\limits_{x\in\overline{\Omega}} w(t,x)$ for $t \in [-\tau(0), \overline{\tau}]$. It is obvious that $\hat{w}(t) \leqslant 0$ for $t \in [-\tau(0), 0]$. We first prove $\hat{w}(t) \leqslant 0$ for any $t \in (0, \tilde{t}]$, where $\tilde{t} = \min\{\overline{\tau}, \frac{1}{\rho}\}$ with $\rho > 0$ being a constant determined later.

Suppose, by contradiction, that there exist a positive number δ and a $t_0 \in (0, \tilde{t}]$ such that $0 < \hat{w}(t_0) < \delta$ and $\hat{w}(t_0) \geqslant \hat{w}(t)$ for $t \in (0, t_0]$. By the definition of $g_\alpha(t, u)$, there is a $\rho > 0$ such that $0 \leqslant \frac{\partial g_\alpha}{\partial u}(t, u) \leqslant \rho$ for $t \geqslant 0$ and $u \in [0, H]$. Thus,

$$\begin{aligned} g_\alpha(t, M(r, x)) - g_\alpha(t, v(r)) =& \frac{\partial g_\alpha}{\partial u}(t, \zeta(r, x))(M(r, x) - v(r)) \\ \leqslant& \frac{\partial g_\alpha}{\partial u}(t, \zeta(r, x))\hat{w}(t_0) \leqslant \rho\hat{w}(t_0), \end{aligned}$$

for any $r \in (0, t_0]$ and $x \in \overline{\Omega}$, where $\zeta(r, x)$ is between $u(r, x)$ and $v(r)$. It then follows from (4.14) that

$$\begin{aligned} \hat{w}(t_0) \leqslant& \sup_{x \in \overline{\Omega}} e^{-\alpha t_0} \mathcal{Q}(t_0) w(0)(x) + \sup_{x \in \overline{\Omega}} \int_0^{t_0} e^{-\alpha(t_0 - r)} (g_\alpha(r, M(r)) - g_\alpha(r, v(r)))(x) dr \\ \leqslant& e^{-\alpha t_0} \hat{w}(0) + \rho\hat{w}(t_0) \int_0^{t_0} e^{-\alpha(t_0 - r)} dr \\ \leqslant& \rho\hat{w}(t_0) \int_0^{t_0} e^{-\alpha(t_0 - r)} dr \\ \leqslant& \rho t_0 \hat{w}(t_0) \\ <& \hat{w}(t_0), \end{aligned}$$

which is a contradiction, and hence, $\hat{w}(t) \leqslant 0$ for any $t \in (0, \tilde{t}]$. By repeating the above arguments for finite times, we can prove that $\hat{w}(t) \leqslant 0$ for any $(t, x) \in [0, \hat{\tau}] \times \overline{\Omega}$. This means that

$$M(t, x) \leqslant v(t) \text{ for } (t, x) \in [0, \hat{\tau}] \times \overline{\Omega}.$$

Now we prove that $M(t, x; \xi) \leqslant v(t, \widehat{H})$ holds for $t \in (\hat{\tau}, \infty)$. In this situation, $M(t, x; \xi)$ is a classical solution of (4.10). Let $w(t, x) = M(t, x; \xi) - v(t; \widehat{H})$. Then we have

$$\begin{cases} \dfrac{\partial}{\partial t}w(t,x) - D_2\Delta w(t,x) + \mu_M(t)w(t,x) + h(t,x)w(t,x) \\ = \dfrac{\partial}{\partial t}w(t,x) - D_2\Delta w(t,x) + \mu_M(t)w(t,x) + (g(M)M - g(v)v) \leqslant 0, \ \forall x \in \Omega, \\ \dfrac{\partial}{\partial n}w(t,x) = 0, \quad \forall x \in \partial\Omega, \end{cases}$$

for $t \in (\hat{\tau}, \hat{\tau} + \overline{\tau})$, where $h(t,x) = G'(M(t,x) + \varrho[v(t) - M(t,x)]), \varrho \in (0,1)$, is bounded and $G(u) = g(u)u$. Thus, the parabolic maximum principle implies that $w(t,x) \leqslant 0$, and hence, $M(t,x;\xi) \leqslant v(t;\widehat{H})$ for any $t \in (\hat{\tau}, \hat{\tau} + \overline{\tau}]$. Continuing this procedure on $t \in [\hat{\tau} + n\overline{\tau}, \hat{\tau} + (n+1)\overline{\tau}]$, $n = 1, \ldots, \infty$, respectively, we can obtain that $M(t,x;\xi) \leqslant v(t;\widehat{H})$ holds for $t \in (\hat{\tau}, \infty)$.

□

Remark 4.1. *Note that $v(t,x) = v(t,\widehat{H})$ for all $x \in \overline{\Omega}$ also satisfies the reaction-diffusion equation* (4.10) *and the comparison principle for reaction-diffusion systems with time delays [82] can also be used to establish this result. Here we use a basic approach for reader's interest.*

On the basis of the above discussion and Lemma 4.1, we show the following results on the existence of a global attractor of $\Psi_T : \mathcal{C}^+ \to \mathcal{C}^+$.

Theorem 4.1. *For each $\psi \in \mathcal{C}^+$, the equation* (4.10) *admits a unique solution $M(t,x;\psi)$ on $[0,\infty) \times \overline{\Omega}$ with $M_0 = \psi$. Moreover, equation* (4.10) *generates a T-periodic semiflow $\Psi_t = M_t(\cdot) : \mathcal{C}^+ \to \mathcal{C}^+$, i.e. $\Psi_t(\psi)(\theta,x) = M(t+\theta,x;\psi)$, $\forall \psi \in \mathcal{C}^+$, $t \geqslant 0$, $\theta \in [-\tau(0),0]$, $x \in \Omega$, and $\Psi_T : \mathcal{C}^+ \to \mathcal{C}^+$ has a global compact attractor in $\mathcal{C}^+$.*

Proof. Here we only prove the existence of a global attractor as the global existence of solutions was argued earlier. To do that, we first show the solutions of (4.10) are eventually uniformly bounded.

Note that the equation (4.13) admits a unique bounded solution $v(t;\varphi)$ with $v(s;\varphi) = \varphi(s)$, $\forall s \in [-\tau(0), 0]$, which globally exists on $[0, \infty)$. Therefore, for any $\varphi \in C([-\tau(0), 0], \mathbb{R}^+)$, the omega limit set $\omega(\varphi)$ of the positive orbit $\gamma^+(\varphi) = \{v_t(\varphi) : t \geqslant 0\}$ is nonempty, compact and invariant. Let $G := \{\psi(s) : \psi \in \omega(\varphi), s \in [-\tau(0), 0]\}$. On the basis of the compactness of $\omega(\varphi)$, it follows that G is compact. As a result, there exist $s_0 \in [-\tau(0), 0]$ and $\psi \in \omega(\varphi)$ such that $\psi(s_0) = \max\{G\} := H_G$. For any $t \in [0, \hat{\tau}]$, since $t - \tau(t)$ is increasing with respect to t, we have

$$-\tau(0) = 0 - \tau(0) \leqslant t - \tau(t) \leqslant \hat{\tau} - \tau(\hat{\tau}) \text{ while } \hat{\tau} - \tau(\hat{\tau}) \geqslant \hat{\tau} - \hat{\tau} = 0.$$

Hence there exists $t_0 \in [0, \hat{\tau}]$ such that $t_0 = \tau(t_0)$. By means of the invariance of $\omega(\varphi)$, there exists $\psi^* \in \omega(\varphi)$ such that $v_{t_0}(\psi^*) = \psi$, i.e. $v(t_0 + s; \psi^*) = \psi(s)$, $\forall s \in [-\tau(0), 0]$. Without loss of generality, we assume that $\psi(0) = H_G$. Assume that $H_G > \widetilde{M}$, it then follows from assumption (A1) that

$$\begin{aligned} \dot{v}(t_0; \psi^*) \leqslant & -(\mu_M(t_0) + g(v(t_0; \psi^*)))v(t_0; \psi^*) + (1 - \tau'(t_0))b(0, v(0; \psi^*)) \\ \leqslant & -(\mu_M(t_0) + g(H_G))H_G + (1 - \tau'(t_0))b(0, H_G) < 0. \end{aligned}$$

Hence, there exists some $s \in [-\tau(0), 0)$ such that $\psi(s) > \psi(0) = H_G$, a contradiction. Thus,

$$\limsup_{t\to\infty} v(t;\varphi) \leqslant \widetilde{M}, \quad \forall \varphi \in C([-\tau(0), 0], \mathbb{R}^+).$$

For any given $\phi \in \mathcal{C}^+$, let $\widehat{\phi}(\theta) := \max\{\phi(\theta, x) : x \in \overline{\Omega}\}$, $\forall \theta \in [-\tau(0), 0]$. Then, $\limsup_{t\to\infty} v(t; \widehat{\phi}) \leqslant \widetilde{M}$. By Lemma 4.1, we have $\limsup_{t\to\infty} M(t, x; \phi) \leqslant \limsup_{t\to\infty} v(t; \widehat{\phi}) \leqslant \widetilde{M}$, $\forall x \in \overline{\Omega}$, which means that $\Psi_t : \mathcal{C}^+ \to \mathcal{C}^+$ is point dissipative. According to [132, Lemma 4.1] and [135, Section 3.5], $\Psi_T : \mathcal{C}^+ \to \mathcal{C}^+$ is κ-contraction and hence asymptotically smooth. Therefore, it follows from [135, Theorem 1.1.2] that $\Psi_T : \mathcal{C}^+ \to \mathcal{C}^+$ has a global compact attractor. $\square$

We further show that the periodic semiflow $\Psi_t : \mathcal{C}^+ \to \mathcal{C}^+$ is strongly monotone and strictly subhomogeneous in $\mathcal{C}^+$.

Lemma 4.2. *For any ϕ and ψ in $\mathcal{C}^+$ with $\phi > \psi$ (that is, $\phi \geqslant \psi$ but $\phi \neq \psi$), the solutions $u(t,x;\phi)$ and $v(t,x;\psi)$ of system (4.10) with $u(\theta,x) = \phi(\theta,x)$ and $v(\theta,x) = \psi(\theta,x)$, for all $\theta \in [-\tau(0),0]$ and $x \in \overline{\Omega}$ respectively, satisfy that $u(t,x;\phi) > v(t,x;\psi)$ for all $t > \hat{\tau}$, and hence $\Psi_t(\phi) \gg \Psi_t(\psi)$ in $\mathcal{C}$ for all $t > 2\hat{\tau}$.*

Proof. By a comparison argument on each interval $[n\tau(0),(n+1)\tau(0)]$, $\forall n \in \mathbb{N}$ as in the proof of Lemma 4.1, it is not difficult to show that $u(t,x;\phi) \geqslant v(t,x;\psi)$ for all $t \geqslant 0$. Note that u_t and v_t satisfy the following integral equation for all $t \geqslant 0$:

$$\begin{aligned} M(t)(x) =& e^{-\alpha t}\mathcal{Q}(t)M(0)(x) + \int_0^t e^{-\alpha(t-s)}\mathcal{Q}(t-s)\Big[g_\alpha(s,M(s)) + (1-\tau'(s)) \\ & \int_\Omega \Gamma_0\left(s,s-\tau(s),x,y,D_1\right) b(s-\tau(s),M(s-\tau(s),y))dy\Big](x)ds, \end{aligned} \tag{4.15}$$

where $g_\alpha(t,u)$ and $\mathcal{Q}(t)$ are defined as in the proof of Lemma 4.1. Then for any ϕ and ψ in $\mathcal{C}^+$ with $\phi > \psi$, it follows from (4.15) and the strong positivity of $\mathcal{Q}(t), t > 0$ that

$$w(t,x) := u(t,x;\phi) - v(t,x;\psi) \geqslant e^{-\alpha t}\mathcal{Q}(t)\left(\phi(0,\cdot) - \psi(0,\cdot)\right) > 0, \qquad t > 0$$

provided that $\phi(0,\cdot) \not\equiv \psi(0,\cdot)$.

In the following, we show that for any ϕ and ψ in $\mathcal{C}^+$ with $\phi > \psi$ and $\phi(0,\cdot) = \psi(0,\cdot)$, there exists $t_0 \in [0,\hat{\tau}]$ such that $w(t_0,\cdot) > 0$. Suppose, by contradiction, that for a pair of initial values ϕ, $\psi \in \mathcal{C}^+$ with $\phi > \psi$ and $\phi(0,\cdot) = \psi(0,\cdot)$, there holds

$w(t,\cdot) \equiv 0$ for $t \in [0, \hat{\tau}]$. In view of (4.15), we have that

$$0 = w(t)(x) = \int_0^t e^{-\alpha(t-s)} \mathcal{Q}(t-s) \left[g_\alpha(s, u(s,\cdot;\phi) - g_\alpha(s, v(s,\cdot;\psi)) \right](x) ds$$

$$+ \int_0^t e^{-\alpha(t-s)} \mathcal{Q}(t-s)(1-\tau'(s)) \int_\Omega \Gamma\left(s, s-\tau(s), x, y, D_1\right)$$

$$\Big[b(s-\tau(s), u(s-\tau(s),y)) - b(s-\tau(s), v(s-\tau(s),y)) \Big](x) dyds$$

for $t \in [0, \hat{\tau}]$. Since $e^{-\alpha(t-s)}\mathcal{Q}(t-s)$ is strongly positive for $t > s \geqslant 0$, and both $g_\alpha(t,u)$ and $b(t,u)$ are increasing functions with respect to the variable u, we must have

$$b(s-\tau(s), u(s-\tau(s),y)) - b(s-\tau(s), v(s-\tau(s),y)) \equiv 0$$

for any $s \in [0,\hat{\tau}]$ and $y \in \overline{\Omega}$, which implies that $u(s-\tau(s),y) = v(s-\tau(s),y)$ for any $s \in [0,\hat{\tau}]$ and $y \in \overline{\Omega}$. This contradicts to $\phi > \psi$. Consequently, we have $w(t_0,\cdot) > 0$ for some $t_0 \in [0,\hat{\tau}]$. Applying the strong positivity of $e^{-\alpha(t-s)}\mathcal{Q}(t-s)$ for $t > s \geqslant 0$ and (4.15) again, for any $t > t_0$, we see that

$$w(t,x) \geqslant e^{-\alpha(t-t_0)}\mathcal{Q}(t-t_0)\left(u(t_0,\cdot,\phi) - v(t_0,\cdot,\psi)\right) = e^{-\alpha(t-t_0)}\mathcal{Q}(t-t_0)w(t_0,\cdot) > 0, \qquad t > t_0.$$

Therefore, for any ϕ and ψ in $\mathcal{C}^+$ with $\phi > \psi$, there holds $u(t,x;\phi) > v(t,x;\psi)$ for all $t > \hat{\tau}$ and $x \in \overline{\Omega}$, which further implies that Ψ_t is strongly monotone whenever $t > 2\hat{\tau}$. □

In order to show the periodic semiflow is strictly subhomogeneous, a further assumption about the birth rate $b(t,M)$ should be imposed:

(A3) The birth rate $b(t,M)$ is strictly subhomogeneous in M in the sense that for any $k \in (0,1)$, $b(t,kM) > kb(t,M)$ for all $M > 0$ and $t \geqslant 0$.

Based on this assumption, we can show Ψ_t is strictly subhomogeneous through the following lemma.

Lemma 4.3. *For each $t > 2\hat{\tau}$, $\Psi_t : \mathcal{C}^+ \to \mathcal{C}^+$ is strictly subhomogeneous.*

Proof. For any $\psi \in \mathcal{C}^+$ with $\psi \not\equiv 0$, let $u(t, x; \psi)$ be the solution of system (4.10) with $u(\theta, x) = \psi(\theta, x)$ for all $\theta \in [-\tau(0), 0]$ and $x \in \overline{\Omega}$. For a fixed $k \in (0, 1)$, by (A2) and (A3), we have

$$\begin{aligned}\frac{\partial(ku(t,x))}{\partial t} =& D_2\Delta(ku(t,x)) - (\mu_M(t) + g(u(t,x)))(ku(t,x)) \\ &+ k(1-\tau'(t))\int_\Omega \Gamma\left(t, t-\tau(t), x, y, D_1\right) b(t-\tau(t), u(t-\tau(t), y))dy \\ \leqslant& D_2\Delta(ku(t,x)) - \mu_M(t)(ku(t,x)) - g(ku(t,x))(ku(t,x)) \\ &+ (1-\tau'(t))\int_\Omega \Gamma\left(t, t-\tau(t), x, y, D_1\right) b(t-\tau(t), ku(t-\tau(t), y))dy.\end{aligned}$$

By a similar comparison argument to the proof of Lemma 4.1, it is not difficult to see from the above inequality that $ku(t, x; \psi) \leqslant u(t, x; k\psi)$ for $t \geqslant 0$, where $u(t, x; k\psi)$ is the solution of (4.10) with $u(\theta, x; k\psi) = k\psi(\theta, x)$ for $(\theta, x) \in [-\tau(0), 0] \times \overline{\Omega}$.

Let $w(t, x) = u(t, x; k\psi) - ku(t, x; \psi)$. Then $w(\theta, x) = 0$ for $(\theta, x) \in [-\tau(0), 0] \times \overline{\Omega}$ and $w(\theta, x) \geqslant 0$ for $(\theta, x) \in [-\tau(0), \infty) \times \overline{\Omega}$. In the following, we show that $w(t, x) > 0$ for all $t > \hat{\tau}$, $x \in \overline{\Omega}$. Let

$$\begin{aligned}&\mathbf{P}(t, u(t,x), u(t-\tau(t), x)) \\ =& -g(u(t,x))u(t,x) + (1-\tau'(t))\int_\Omega \Gamma(t, t-\tau(t), x, y, D_1) b(t-\tau(t), u(t-\tau(t), y))dy.\end{aligned}$$

Then we have

$$\begin{aligned}
&\frac{\partial w(t,x)}{\partial t}\\
=&\frac{\partial u(t,x;k\psi)}{\partial t}-k\frac{\partial u(t,x;\psi)}{\partial t}\\
=&D_2\Delta u(t,x;k\psi)-\mu_M(t)u(t,x;k\psi)+\mathbf{P}(t,u(t,x;k\psi),u(t-\tau(t),x;k\psi))\\
&-k[D_2\Delta u(t,x;\psi)-\mu_M(t)u(t,x;\psi)+\mathbf{P}(t,u(t,x;\psi),u(t-\tau(t),x;\psi))]\\
=&D_2\Delta w(t,x)-\mu_M(t)w(t,x)-g(u(t,x;k\psi))u(t,x;k\psi)+kg(ku(t,x;\psi))u(t,x;\psi)\\
&+R(t,x)+(1-\tau'(t))\int_\Omega\Gamma(t,t-\tau(t),x,y,D_1)\Big[b(t-\tau(t),u(t-\tau(t),y;k\psi))\\
&-b(t-\tau(t),ku(t-\tau(t),y;\psi))\Big]dy\\
\geqslant&D_2\Delta w(t,x)-\mu_M(t)w(t,x)-g(u(t,x;k\psi))u(t,x;k\psi)+kg(ku(t,x;\psi))u(t,x;\psi)+R(t,x)
\end{aligned}$$

where

$$R(t,x)=\mathbf{P}(t,ku(t,x;\psi),ku(t-\tau(t),x;\psi))-k\mathbf{P}(t,u(t,x;\psi),u(t-\tau(t),x;\psi)).$$

Note that

$$\begin{aligned}
&g(ku(t,x;\psi))(ku(t,x;\psi))-g(u(t,x;k\psi))u(t,x;k\psi)\\
&=-G'(ku(t,x;\psi)+\varrho[u(t,x;k\psi)-ku(t,x;\psi)])w(t,x),\quad \varrho\in(0,1),
\end{aligned}$$

where $G(\zeta)=g(\zeta)\zeta$, and $G'(\zeta)$ is bounded, that is, there exists a positive number $l>0$ such that $-l\leqslant G'(\zeta)\leqslant l$. Consequently, we have

$$\frac{\partial w(t,x)}{\partial t}\geqslant D_2\Delta w(t,x)-\mu_M(t)w(t,x)-lw(t,x)+R(t,x).$$

In view of the assumption (A3), we have $R(t,x)>0$ for $t>\hat{\tau}$ and $x\in\overline{\Omega}$. Consider the following equation

$$\begin{cases}\frac{\partial\breve{w}(t,x)}{\partial t}=D_2\Delta\breve{w}(t,x)-\mu_M(t)\breve{w}(t,x)-h(t,x)\breve{w}(t,x)+R(t,x), & t>0,\\ \breve{w}(0,x)=0, & x\in\overline{\Omega},\end{cases}\tag{4.16}$$

which can be rewritten as

$$\breve{w}(t, \cdot; \psi) = \int_0^t U(t, s) R(s, \cdot) ds, \quad t \geqslant 0,$$

where $U(t, s), 0 \leqslant s \leqslant t$ is the evolution operator generated by

$$\begin{cases} \frac{\partial \breve{w}(t,x)}{\partial t} = D_2 \Delta \breve{w}(t, x) - \mu_M(t) \breve{w}(t, x) - h(t, x) \breve{w}(t, x), & t > 0, \\ \frac{\partial \breve{w}(t,x)}{\partial n} = 0, & t > 0, \, x \in \partial\Omega. \end{cases}$$

Since $R(t, x) > 0$, $\forall t > \hat{\tau}$, $x \in \overline{\Omega}$, we can conclude from the strong positivity of $U(t, s)$, $0 \leqslant s < t$ that the solution of (4.16) satisfies $\breve{w}(t, x) > 0$ for all $t > \hat{\tau}$ and $x \in \overline{\Omega}$. It then follows from the comparison principle that $w(t, x) \geqslant \breve{w}(t, x) > 0$ for all $t > \hat{\tau}$ and $x \in \overline{\Omega}$. Therefore, $u(t, x; k\psi) > ku(t, x; \psi)$ for all $t > \hat{\tau}$, $x \in \overline{\Omega}$, and hence, $\Psi_t(k\psi) > k\Psi_t(\psi)$ for all $t > \hat{\tau}$, which implies that for each $t > 2\hat{\tau}$, Ψ_t is strictly subhomogeneous. □

4.3.2 Basic reproduction number

Set the ordered Banach space consisting of all T-periodic continuous functions from $\mathbb{R}$ to $\mathbf{Y}$ as $C_T(\mathbb{R}, \mathbf{Y})$, where $\|\phi\|_{C_T(\mathbb{R},\mathbf{Y})} := \max_{\theta \in [0,T]} \|\phi\|_{\mathbf{Y}}$ for any $\phi \in C_T(\mathbb{R}, \mathbf{Y})$. The positive cone of $C_T(\mathbb{R}, \mathbf{Y})$ is defined as follows:

$$C_T^+(\mathbb{R}, \mathbf{Y}) := \{\phi \in C_T(\mathbb{R}, \mathbf{Y}) : \ \phi(t)(x) \geqslant 0, \ \forall t \in \mathbb{R}, \ x \in \overline{\Omega}\}.$$

The linearized system for (4.10) at the population extinction equilibrium $M = 0$

is shown as follows:

$$\begin{cases} \dfrac{\partial w(t,x)}{\partial t} =& D_2\Delta w(t,x) - \mu_M(t)w(t,x) \\ & + (1-\tau'(t))\displaystyle\int_\Omega \Gamma\left(t, t-\tau(t), x, y, D_1\right)\beta(t-\tau(t))w(t-\tau(t),y)dy, \\ & t>0,\ x\in\Omega, \\ \dfrac{\partial w(t,x)}{\partial n} =& 0, \quad t>0,\ x\in\partial\Omega, \\ w(\theta,x) =& \varphi(\theta,x), \quad \varphi\in\mathcal{C},\ \theta\in[-\tau(0),0],\ x\in\Omega. \end{cases} \tag{4.17}$$

Similar to the previous subsection, we know that (4.17) has a unique mild solution $w(t,x;\varphi)$ with $w_0(\cdot,\cdot;\varphi)=\varphi$ and $w_t(\cdot,\cdot;\varphi)\in\mathcal{C}^+$ for all $t\geqslant 0$. Moreover, $w(t,x;\varphi)$ is a classical solution when $t>\hat{\tau}$, and $w_t(\cdot,\cdot;\varphi)$ is strongly positive and compact on $\mathcal{C}^+$ for all $t>2\hat{\tau}$. Define $P:\mathcal{C}\to\mathcal{C}$ by $P(\varphi)=w_T(\varphi)$ for all $\varphi\in\mathcal{C}$, where $w_T(\varphi)(\theta,x)=w(T+\theta,x;\varphi)$ for all $(\theta,x)\in[-\tau(0),0]\times\overline{\Omega}$, and w_t is the solution map of (4.17). Thus, we have $P^{n_0}=w_{n_0T}$ is compact and strongly positive, where $n_0:=\min\{n\in\mathbb{N}: nT>2\hat{\tau}\}$. Let $r(P)$ be the spectral radius of P. By virtue of [71, Lemma 3.1] that $r(P)$ is a simple eigenvalue of P having a strongly positive eigenvector $\bar{\varphi}$, and the modulus of any other eigenvalue is less than $r(P)$. Let $w(t,x;\bar{\varphi})$ be the solution of (4.17) with $w(s,x;\bar{\varphi})=\bar{\varphi}(s,x)$ for all $s\in[-\tau(0),0], x\in\Omega$. By the strong positivity of $\bar{\varphi}$, we have $w(\cdot,\cdot;\bar{\varphi})\gg 0$. Inspired by [130, Proposition 2.1], we can prove the following observation, which indicates the existence of a special solution of system (4.17).

Lemma 4.4. *There exists a positive T-periodic function $v^*(t,x)$ such that $e^{\mu t}v^*(t,x)$ is a solution of (4.17), where $\mu=\frac{\ln r(P)}{T}$.*

Proof. Since $\bar{\varphi}$ is the eigenvector of P, we have $P\bar{\varphi}=r(P)\bar{\varphi}$. That is

$$w(s+T,x;\bar{\varphi})=r(P)\bar{\varphi}(s)(x), \quad \forall s\in[-\tau(0),0].$$

Let $\mu = \frac{\ln r(P)}{T}$ and $v^*(t,x) = e^{-\mu t} w(t,x;\bar{\varphi})$ for all $t \geqslant -\tau(0), x \in \Omega$. Then $r(P) = e^{\mu T}$. By a following simple calculation, we can see that $v^*(t,x)$ is periodic. In fact, for all $s \in [-\tau(0), 0]$, we have

$$w(s+T, x; \bar{\varphi}) = P\bar{\varphi}(s)(x) = r(P)\bar{\varphi}(s)(x).$$

Then, for all $t \geqslant 0$,

$$w(t+T, x; \bar{\varphi}) = r(P) w(t, x; \bar{\varphi}).$$

This indicates that

$$v^*(t+T,x) = e^{-\mu(t+T)} w(t+T,x;\bar{\varphi}) = e^{-\mu t} e^{-\mu T} r(P) w(t,x;\bar{\varphi}) = e^{-\mu t} w(t,x;\bar{\varphi}) = v^*(t,x).$$

Thus, the equation (4.17) admits a positive solution $e^{-\mu t} v^*(t,x)$ with $v^*(t,x)$ being periodic in t.

$\square$

Let $\phi(s,x) = \phi(s)(x) \in C_T(\mathbb{R}, \mathbf{Y}^+)$ be the initial distribution of adult individuals at time $s \in \mathbb{R}$ and the spatial location $x \in \overline{\Omega}$. Define an operator $C(t) : \mathbf{Y} \to \mathbf{Y}$ as follows:

$$(C(t)\varphi)(x) := (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t-\tau(t), x, y, D_1) \beta(t - \tau(t)) \varphi(y) dy, \quad \forall \varphi \in \mathbf{Y}.$$

Recall that $W(t,s)$ is the evolution operator determined by the following linear reaction-diffusion equation:

$$\begin{cases} \frac{\partial w(t,x)}{\partial t} = D_2 \Delta w(t,x) - \mu_M(t) w(t,x), & t > 0,\ x \in \Omega, \\ \frac{\partial w(t,x)}{\partial n} = 0, & t > 0,\ x \in \partial\Omega. \end{cases}$$

Then, $W(t-\tau(t), s)\phi(s)(x)$ represents the density distribution of the individuals who matured into adults at previous time s ($s < t - \tau(t)$) and survived to time $t - \tau(t)$ at location x. Hence, $\int_{-\infty}^{t-\tau(t)} W(t-\tau(t), s)\phi(s)(x) ds$ denotes the density distribution of the accumulative individuals who matured into adults at all previous time $s < t - \tau(t)$ and survived to time $t - \tau(t)$ at location x. Thus, the distribution of new-born individuals at location x and time t can be represented as follows:

$$
\begin{aligned}
&(1-\tau'(t))\int_{\Omega}\Gamma(t,t-\tau(t),x,y,D_1)\beta(t-\tau(t))\Big(\int_{-\infty}^{t-\tau(t)}W(t-\tau(t),s)\phi(s)(y)ds\Big)dy\\
=&(1-\tau'(t))\int_{\Omega}\Gamma(t,t-\tau(t),x,y,D_1)\beta(t-\tau(t))\Big(\int_{\tau(t)}^{\infty}W(t-\tau(t),t-s)\phi(t-s)(y)ds\Big)dy\\
=&\int_{\tau(t)}^{\infty}(1-\tau'(t))\int_{\Omega}\Gamma(t,t-\tau(t),x,y,D_1)\beta(t-\tau(t))W(t-\tau(t),t-s)\phi(t-s)(y)dyds\\
=&\int_{\tau(t)}^{\infty}\Big[C(t)(W(t-\tau(t),t-s)\phi(t-s))\Big](x)ds\\
=&\int_{0}^{\infty}\Big[H(t,s)\phi(t-s)\Big](x)ds,
\end{aligned}
$$

where $H(t,s)$, $t \in \mathbb{R}$, $s \geqslant 0$ is defined as follows:

$$
H(t,s) := \begin{cases} C(t)W(t-\tau(t),t-s), & s > \tau(t),\\ 0, & s \in [0,\tau(t)]. \end{cases}
$$

Thus, the next generation operator $\mathcal{L}$ can be defined as

$$
\mathcal{L}(\phi)(t) := \int_{0}^{\infty} H(t,s)\phi(t-s)ds, \quad \forall t \in \mathbb{R},\ \phi \in C_T(\mathbb{R},\mathbf{Y}).
$$

It easily follows that $\mathcal{L}$ is a positive and bounded linear operator on $C_T(\mathbb{R},\mathbf{Y})$. The basic reproduction number can be defined as the spectral radius of $\mathcal{L}$, that is,

$$
\mathcal{R}_0 := r(\mathcal{L}).
$$

In the light of [132, Theorem 3.4] and [134, Remark 2.1], we obtain the subsequent result, which implies that $\mathcal{R}_0$ serves as a threshold value for the stability of the zero solution for system (4.17).

Lemma 4.5. *$\mathcal{R}_0 - 1$ has the same sign as $r(P) - 1$.*

4.3.3 Global dynamics

The main focus of this section is to show the global attractivity of the system (4.10) in terms of $\mathcal{R}_0$ by employing the theory of monotone and subhomogeneous semiflows [135, Section 2.3]. Since the strong monotonicity and strict sub-homogeneity of the periodic semiflow Ψ_t has been proven (see Lemmas 4.2 and 4.3), it is time to show the global stability of system (4.10) when $\mathcal{R}_0 > 1$ in $\mathcal{C}^+$.

Theorem 4.2. *If $\mathcal{R}_0 > 1$, then system (4.10) admits a unique positive T-periodic solution $M^*(t,x)$, which is globally asymptotically stable in $\mathcal{C}^+\backslash\{0\}$.*

Proof. We can fix an integer n_0 such that $n_0T > 2\hat{\tau}$, then Ψ_t can be regarded as an n_0T-periodic semiflow on $\mathcal{C}^+$. Furthermore, Ψ_{n_0T} is a strongly monotone and strictly subhomogeneous map on $\mathcal{C}^+$ as a consequence of Lemma 4.2 and 4.3. It follows from [135, Theorem 2.3.4] that system (4.10) admits a unique positive n_0T-periodic and globally asymptotically stable solution $M^*(t,x)$ when $r(D\Psi_{n_0T}(0)) > 1$. Note that $r(D\Psi_{n_0T}(0)) = r(P(n_0T)) = (r(P(T)))^{n_0}$. It then follows from Lemma 4.5 that $sign(\mathcal{R}_0 - 1) = sign(r(D\Psi_{n_0T}(0)) - 1)$. Hence, it suffices to show the existence of the unique T-periodic positive solution $M^*(t,x)$ when $\mathcal{R}_0 > 1$. This is true since

$$\Psi_T^{n_0}(\Psi_T\psi^*) = \Psi_T(\Psi_T^{n_0}\psi^*) = \Psi_T(\Psi_{n_0T}\psi^*) = \Psi_T(\psi^*),$$

where $\psi^*(s,\cdot) = M^*(s,\cdot)$ for all $s \in [-\tau(0), 0]$ guaranteeing that $\Psi_{n_0T}\psi^* = \psi^*$. Therefore, the uniqueness of the positive fixed point of $\Psi_T^{n_0} = \Psi_{n_0T}$ implies that $\Psi_T\psi^* = \psi^*$ holds, which indicates that $M^*(t,x)$ is a T-periodic solution of system (4.10). □

By implying [135, Theorem 2.3.4] and a similar argument as in the previous proof, we can establish the following result:

Theorem 4.3. *If $\mathcal{R}_0 \leqslant 1$, then the zero equilibrium 0 is globally attractive for all solutions of system (4.10).*

It can be easily checked that $I(t,x)$ can be represented by the following equivalent integral form:

$$I(t,x) = \int_{t-\tau(t)}^{t} \int_{\Omega} \Gamma(t,s,x,y,D_1) b(s, M(s,y)) dy ds, \quad t > 0, \ x \in \Omega.$$

When $\mathcal{R}_0 > 1$, as a consequence of the global stability of $M(t,x)$, we can obtain the property of the solution for the other variable $I(t,x)$ as well by using its integral form:

$$\lim_{t \to \infty} \Big[I(t,x) - I^*(t,x) \Big] = 0,$$

where

$$I^*(t,x) = \int_{t-\tau(t)}^{t} \int_{\Omega} \Gamma(t,s,x,y,D_1) b(s, M^*(s,y)) dy ds$$

is a positive T-periodic function. The scenario when $\mathcal{R}_0 \leqslant 1$ can be discussed in a similar way. Thus, the global attractivity of the full system (4.6) can be obtained and summarized in the following theorem.

Theorem 4.4. *If* $\mathcal{R}_0 > 1$*, then system (4.6) admits a unique positive* T*-periodic solution* $(I^*(t,x), M^*(t,x))$*, which is globally attractive to all nontrivial solutions. If* $\mathcal{R}_0 \leqslant 1$*, then the population extinction equilibrium* $(0,0)$ *is globally attractive for all solutions.*

Remark 4.2. *The main analytic methodologies for the system* (4.6) *are also applicable to* (4.7)*. In fact, due to the absence of the intra-specific competition* ($f(I) \equiv 0$)*, the* I *equation can be decoupled from* (4.7)*.*

In the next section, we will establish the well-posedness and threshold dynamics for the model when the intra-specific competition is included and the immature dispersal ability is negligible.

4.4 Dynamics under immature intra-specific competition

In this section, we devoted to dynamics for system (4.8) with the constraint (4.9), namely, intra-specific competition is taken into account. As the beginning of this section, we introduce several notations. Let $\mathbf{X} := C(\overline{\Omega}, \mathbb{R}^2)$ be the Banach space of continuous functions with the supremum norm $\|\cdot\|_{\mathbf{X}}$. Define $\mathcal{E} = C([-\tau(0), 0], \mathbf{X})$. For any $\phi \in \mathcal{E}$, define the norm $\|\phi\| = \max_{\theta \in [-\tau(0),0]} \|\phi(\theta)\|_{\mathbf{X}}$. Then, $\mathcal{E}$ is a Banach space. Let $\mathbf{X}^+ := C(\overline{\Omega}, \mathbb{R}^2_+)$ and $\mathcal{E}^+ = C([-\tau(0), 0], \mathbf{X}^+)$, then $(\mathbf{X}, \mathbf{X}^+)$ and $(\mathcal{E}, \mathcal{E}^+)$ are both strongly ordered spaces. Given a function $\mathbf{u}(t) : [-\tau(0), \sigma) \to \mathbf{X}$ for $\sigma > 0$, define $\mathbf{u}_t \in \mathcal{E}$ by $\mathbf{u}_t(\theta, x) = \mathbf{u}(t + \theta, x)$, for all $\theta \in [-\tau(0), 0]$, $x \in \overline{\Omega}$ and $t \in [0, \sigma)$.

Define the linear operator $\mathbf{A} = (\mathbf{A}_1, \mathbf{A}_2)$ by

$$\begin{aligned} &D(\mathbf{A}_1(t)) = \{\phi \in C^2(\overline{\Omega}) : \frac{\partial \phi}{\partial n} = 0 \text{ on } \partial\Omega\}, \\ &\mathbf{A}_1(t)\phi = -\mu_I(t)\phi, \quad \forall \phi \in D(\mathbf{A}_1(t)), \end{aligned}$$

and

$$\begin{aligned} &D(\mathbf{A}_2(t)) = \{\phi \in C^2(\overline{\Omega}) : \frac{\partial \phi}{\partial n} = 0 \text{ on } \partial\Omega\}, \\ &\mathbf{A}_2(t)\phi = D_2\Delta\phi - \mu_M(t)\phi, \quad \forall \phi \in D(\mathbf{A}_2(t)). \end{aligned}$$

respectively. Define the nonlinear operator $\mathbf{F}(t, \cdot) = (\mathbf{F}_1(t, \cdot), \mathbf{F}_2(t, \cdot)) : \mathcal{E}^+ \to \mathbf{X}$ by

$$\begin{aligned} \mathbf{F}_1(t, \phi) =& b(t, \phi_2(0, \cdot)) - f(\phi_1(0, \cdot))\phi_1(0, \cdot) - (1 - \tau'(t)) \\ & \times \exp\left(-\int_{t-\tau(t)}^{t} (\mu_I(s) + f(\phi_1(s, x)))ds\right) b(t - \tau(t), \phi_2(-\tau(t), x)), \\ \mathbf{F}_2(t, \phi) =& -g(\phi_2(0, \cdot))\phi_2(0, \cdot) + (1 - \tau'(t)) \exp\left(-\int_{t-\tau(t)}^{t} (\mu_I(s) + f(\phi_1(s, x)))ds\right) \\ & \times b(t - \tau(t), \phi_2(-\tau(t), x)), \end{aligned}$$

for $t \geqslant 0$, $x \in \overline{\Omega}$ and $\phi = (\phi_1, \phi_2) \in \mathcal{E}^+$.

Then, system (4.8) can be reformulated as the following abstract functional differential equations:

$$\begin{cases} \frac{\partial \mathbf{u}(t,\cdot)}{\partial t} = \mathbf{A}(t)\mathbf{u}(t,\cdot) + \mathbf{F}(t,\mathbf{u}_t), & t > 0, \ x \in \Omega, \\ \mathbf{u}(\theta,x) = \phi(\theta,x), & \theta \in [-\tau(0),0], \ x \in \Omega. \end{cases} \tag{4.18}$$

Let $V(t,s)$ be the evolution operators determined by the following linear reaction-diffusion equations

$$\begin{cases} \frac{\partial I(t,x)}{\partial t} = -\mu_I(t)I(t,x), & t > 0, \ x \in \Omega, \\ \frac{\partial I(t,x)}{\partial n} = 0, & t > 0, \ x \in \partial\Omega. \end{cases}$$

Then, an evolution operator on $\mathbf{X}$ for $(t,s) \in \mathbb{R}^2$ with $t \geqslant s$ can be defined as $\mathbf{U}(t,s) := \begin{pmatrix} V(t,s) & 0 \\ 0 & W(t,s) \end{pmatrix}$, where $W(t,s)$ is the same as defined in (4.12). Hence, the integral form of system (4.18) is shown as follows:

$$\mathbf{u}(t,\phi) = \mathbf{U}(t,0)\phi(0) + \int_0^t \mathbf{U}(t,s)\mathbf{F}(s,\mathbf{u}_s)ds, \quad t \geqslant 0, \ \phi \in \mathcal{E}^+,$$

and the solution of which is a mild solution of (4.18).

Clearly, $\mathbf{F}(t,\cdot)$ is locally Lipschitz continuous on $\mathcal{E}^+$, and hence for any $\phi \in \mathcal{E}^+$, system (4.8) admits a unique non-continuable mild solution $\mathbf{u}(t;\phi)$ such that $\mathbf{u}_t(\phi) \in \mathcal{E}$ for all t in its maximal interval of existence $[0,\sigma_\phi)$ for $\sigma_\phi > 0$ (see [125]).

It is obvious that the constraint (4.9) is equivalent to

$$\phi_1(0,x) = \int_{-\tau(0)}^0 \exp\left(-\int_s^0 (\mu_I(r) + f(\phi_1(r,x)))dr\right) b(s,\phi_2(s,x))ds. \tag{4.19}$$

Denote $\mathcal{X}$ as the set of all $\phi \in \mathcal{E}^+$ such that (4.19) holds. It follows that $\mathcal{X}$ is a nonempty and closed subset of $\mathcal{E}$. Let $\mathbf{u}(t,\phi)(x) = (I(t,x), M(t,x))$ for $\phi \in \mathcal{X}$, and define

$$w(t,x) = \int_{t-\tau(t)}^t \exp\left(-\int_s^t (\mu_I(r) + f(I(r,x)))dr\right) b(s,M(s,x))ds, \quad \forall t \in [0,\sigma_\phi).$$

Thus,

$$\begin{aligned}\frac{\partial w(t,x)}{\partial t} =& b(t,M(t,x)) - (\mu_I(t) + f(I(t,x)))I(t,x) - (1-\tau'(t)) \\ & \times \exp\left(-\int_{t-\tau(t)}^{t} (\mu_I(s) + f(I(s,x)))ds\right) b(t-\tau(t), M(t-\tau(t),x)),\end{aligned}$$

and hence,

$$\frac{\partial (I(t,x)-w(t,x))}{\partial t} = -(\mu_I(t) + f(I(t,x)))(I(t,x)-w(t,x)), \quad \forall t \in [0,\sigma_\phi).$$

Since $I(0,\cdot) = w(0,\cdot)$, we have

$$I(t,\cdot) - w(t,\cdot) = V(t,0)(I(0,\cdot) - w(0,\cdot)) = 0, \quad \forall t \in [0,\sigma_\phi),$$

which implies that for any $\phi \in \mathcal{X}$, the solution $\mathbf{u}(t,x,\phi)$ satisfies

$$I(t,x) = \int_{t-\tau(t)}^{t} \exp\left(-\int_{s}^{t} (\mu_I(r) + f(I(r,x)))dr\right) b(s, M(s,x))ds, \quad \forall t \in [0,\sigma_\phi).$$

By virtue of the maximum principle (see [55, Proposition 13.1]), it follows from (4.8) that $M(t,x)$ is nonnegative. Thus, the above integral equation on I indicates that $I(t,x)$ is also nonnegative, and hence, $\mathbf{u}_t(\phi) \in \mathcal{E}^+$ for all $t \in [0,\sigma_\phi)$.

Recall that a family of operators $\{Q_t\}_{t\geqslant 0}$ is an T-periodic semiflow on a metric space $(\mathbf{Z},\rho)$ with the metric ρ, provided that $\{Q_t\}_{t\geqslant 0}$ satisfies: (i) $Q_0(v) = v, \forall v \in \mathbf{Z}$; (ii) $Q_t(Q_T(v)) = Q_{t+T}(v), \forall t \geqslant 0, \forall v \in \mathbf{Z}$; (iii) $Q_t(v)$ is continuous in (t,v) on $[0,\infty) \times \mathbf{Z}$.

The following results asserts the existence of global solutions of system (4.8).

Theorem 4.5. *Let (A1) and (A2) hold. For each $\phi \in \mathcal{X}$, the system* (4.8) *admits a unique solution $\mathbf{u}(t,x;\phi)$ on $[0,\infty)\times\overline{\Omega}$ with $\mathbf{u}_0 = \phi$. Moreover, system* (4.8) *generates a T-periodic semiflow $\Phi_t = \mathbf{u}_t(\cdot) : \mathcal{X} \to \mathcal{X}$, i.e. $\Phi_t(\phi)(\theta,x) = \mathbf{u}(t+\theta,x;\phi)$, $\forall \phi \in \mathcal{X}$, $t \geqslant T$, $\theta \in [-\tau(0),0]$, $x \in \overline{\Omega}$.*

Proof. For any $\phi \in \mathcal{X}$, let $\mathbf{u}(t,x;\phi) = (I(t,x;\phi), M(t,x;\phi)) = (I(t,\phi)(x), M(t,\phi)(x))$ be the unique solution of (4.8) with (4.9) satisfying $\mathbf{u}_0 = \phi$ with the maximal interval of existence $[0,\sigma_\phi)$ for $\sigma_\phi > 0$. Note that

$$I(t,x;\phi) \geqslant 0,\ M(t,x;\phi) \geqslant 0,\ \forall t \in [0,\sigma_\phi),\ x \in \overline{\Omega}.$$

Since $f(I) > 0$ for $I > 0$, the second equation of system (4.8) gives rise to

$$\begin{cases} \dfrac{\partial M(t,x)}{\partial t} \leqslant & D_2\Delta M(t,x) - (\mu_M(t) + g(M(t,x)))M(t,x) + (1-\tau'(t)) \\ & \times \exp\left(-\displaystyle\int_{t-\tau(t)}^{t} \mu_I(s)ds\right) b(t-\tau(t), M(t-\tau(t),x)), \quad t > 0,\ x \in \Omega, \\ \dfrac{\partial M(t,x)}{\partial n} = & 0, \quad t > 0,\ x \in \partial\Omega. \end{cases}$$

Thus, for any $H > \widetilde{M}$, it follows the parabolic comparison principle and the proof of Theorem 4.1 that $M(t,x)$ satisfies $0 \leqslant M(t,x) \leqslant H$ for all $t \geqslant 0$ and $x \in \overline{\Omega}$ whenever $0 \leqslant M_0(\theta,x) \leqslant H$ for $\theta \in [-\tau(0),0]$ and $x \in \overline{\Omega}$. Moreover, by assumption (A1), we have

$$\begin{aligned} 0 \leqslant I(t,x) &\leqslant \int_{t-\tau(t)}^{t} b(s-\tau(s), M(s-\tau(s),x))ds \\ &\leqslant \int_{t-\tau(t)}^{t} \beta(s-\tau(s))M(s-\tau(s),x)ds \\ &\leqslant \hat{\beta}\hat{\tau}H, \end{aligned}$$

for $t \in (0,\sigma_\phi)$ and $x \in \Omega$, where $\hat{\beta} = \max_{t\in[0,T]} \beta(t)$. Hence,

$$\widetilde{\Sigma}_H := C([-\tau(0),0],[0,H] \times [0,\hat{\beta}\hat{\tau}H]),$$

is positively invariant for system (4.8). Since H can be chosen as large as we can, $\mathbf{u}(t;\phi)$ globally exists on $[0,\infty)$ for any $\phi \in \mathcal{X}$. Hence, (4.8) can define a semiflow $\Phi_t : \mathcal{X} \to \mathcal{X}, t \geqslant T$ by

$$\Phi_t(\phi)(s,x) = \mathbf{u}(t+s,x;\phi), \quad \forall s \in [-\tau(0),0],\ x \in \overline{\Omega}.$$

It easily follows from the periodicity of the variable coefficients that Φ_t is a T-period semiflow. $\square$

Since the first equation in system (4.8) has no diffusion term, the solution semiflow Φ_t is not compact. We impose the following condition on the immature intra-specific competition $f(I)$ in this section:

(A4) $f \in C^1(\mathbb{R}^+, \mathbb{R}^+)$ and $f'(I)$ is bounded on $[0, \infty)$.

Lemma 4.6. *Assume that* (A1), (A2) *and* (A4) *hold. For any* $\phi \in \mathcal{X}$*, let* $(I(t,x;\phi), M(t,x;\phi))$ *be the solutions of system* (4.8) *with initial data* ϕ*. Then there exist positive constants* C *and* C' *such that*

$$\|I(t,\cdot;\phi)\|_{C^\alpha(\overline{\Omega})}, \quad \|M(t,\cdot;\phi)\|_{C^\alpha(\overline{\Omega})} \leqslant C$$

and

$$\left|\frac{\partial I(t,x;\phi)}{\partial t}\right|, \quad \left|\frac{\partial M(t,x;\phi)}{\partial t}\right| \leqslant C'$$

for $t > 2\hat{\tau}, x \in \overline{\Omega}$ *and* $\phi \in \mathcal{X}$, *where* $\alpha \in (0,1)$.

Proof. In view of Theorem 4.1, for any given $\phi = (\phi_1, \phi_2) \in \mathcal{X}$, there exists $\eta > 0$ such that

$$|I(t,x;\phi)| \leqslant \eta, \quad |M(t,x;\phi)| \leqslant \eta, \quad \forall t \geqslant 0,\ x \in \overline{\Omega}.$$

Let $(I(t,x), M(t,x)) = (I(t,x;\phi), M(t,x;\phi))$ for $\forall \phi \in \mathcal{X}, t \geqslant 0, x \in \overline{\Omega}$. By the assumption (A4), it follows that there exists a positive constant C_0 such that $|f'(I)| \leqslant$

C_0 for $I \geqslant 0$. In view of the integral form of I, we have

$$
\begin{aligned}
&|I(t,x)-I(t,y)| \\
&= \left|\int_{t-\tau(t)}^{t} \left[e^{-\int_s^t(\mu_I(r)+f(I(r,x)))dr} b(s,M(s,x)) - e^{-\int_s^t(\mu_I(r)+f(I(r,y)))dr} b(s,M(s,y))\right] ds\right| \\
&= \left|\int_{t-\tau(t)}^{t} \left[e^{-\int_s^t(\mu_I(r)+f(I(r,x)))dr} b(s,M(s,x)) - e^{-\int_s^t(\mu_I(r)+f(I(r,y)))dr} b(s,M(s,x))\right.\right. \\
&\qquad \left.\left. + e^{-\int_s^t(\mu_I(r)+f(I(r,y)))dr} b(s,M(s,x)) - e^{-\int_s^t(\mu_I(r)+f(I(r,y)))dr} b(s,M(s,y))\right] ds\right| \\
&= e^{-\int_s^t \mu_I(r)dr} \int_{t-\tau(t)}^{t} \left|e^{-\int_s^t f(I(r,x))dr} - e^{-\int_s^t f(I(r,y))dr}\right| \left|b(s,M(s,x))\right| ds \\
&\quad + \int_{t-\tau(t)}^{t} e^{-\int_s^t(\mu_I(r)+f(I(r,y)))dr} \left|b(s,M(s,x)) - b(s,M(s,y))\right| ds \\
&\leqslant \int_{t-\tau(t)}^{t} e^{-\int_s^t(\mu_I(r)+f(\theta I(r,x)+(1-\theta)I(r,y)))dr} \left|b(s,M(s,x))\right| \\
&\qquad \times \left|f'(\theta I(r,x)+(1-\theta)I(r,y))\right| \left|I(t,x)-I(t,y)\right| ds \qquad (\theta \in (0,1)) \\
&\quad + \int_{t-\tau(t)}^{t} \left|b(s,M(s,x)) - b(s,M(s,y))\right| ds \\
&\leqslant C_0 \eta \int_{t-\tau(t)}^{t} \left|I(t,x)-I(t,y)\right| ds + \int_{t-\tau(t)}^{t} \left|b(s,M(s,x)) - b(s,M(s,y))\right| ds
\end{aligned}
$$

for $t \geqslant 0, x, y \in \overline{\Omega}$. By virtue of (A1), (A2) and Theorem 4.5, we can conclude from the second equation of system (4.8) and [78, Theorem 5.1.11] that $M(t,\cdot)$ is Hölder continuous on $\overline{\Omega}$ for $t \geqslant 2\tau(0) = 2\hat{\tau}$, that is, there exist a positive constant l and $\alpha \in (0,1)$ such that for any $x, y \in \overline{\Omega}$,

$$
\frac{|M(t,x)-M(t,y)|}{|x-y|^{\alpha}} \leqslant l, \qquad \text{for } t > 2\hat{\tau}.
$$

In addition, there is a positive constant $\tilde{\eta}$ such that $|b(t,M)| \leqslant \tilde{\eta}$ for $t \in \mathbb{R}$ due to

(A1) and the boundedness of M. As a consequence, it follows from the inequality of $|I(t,x)-I(t,y)|$ that

$$\begin{aligned}
&\frac{|I(t,x)-I(t,y)|}{|x-y|^{\alpha}} \\
&\leqslant C_0\eta\int_{t-\tau(t)}^{t}\frac{|I(t,x)-I(t,y)|}{|x-y|^{\alpha}}ds+\int_{t-\tau(t)}^{t}\frac{|b(s,M(s,x))-b(s,M(s,y))|}{|x-y|^{\alpha}}ds \\
&\leqslant C_0\eta\int_{t-\tau(t)}^{t}\frac{|I(t,x)-I(t,y)|}{|x-y|^{\alpha}}ds+l\hat{\tau}
\end{aligned}$$

for $t>2\hat{\tau}, x, y\in\overline{\Omega}$ and $\alpha\in(0,1)$. Then the Gronwall's inequality yields that for any $x,y\in\overline{\Omega}$,

$$\frac{|I(t,x)-I(t,y)|}{|x-y|^{\alpha}}\leqslant l\hat{\tau}e^{\hat{\tau}},$$

for $t>2\hat{\tau}$ and $\alpha\in(0,1)$. Set $C:=\max\{l,l\hat{\tau}e^{\hat{\tau}}\}$. Then we have

$$\|I(t,\cdot;\phi)|_{C^{\alpha}(\overline{\Omega})},\quad \|M(t,\cdot;\phi)|_{C^{\alpha}(\overline{\Omega})}\leqslant C$$

for $t>2\hat{\tau}$ and $\alpha\in(0,1)$.

In view of the I equation of system (4.8) and the boundedness of I and M, we see that there exists a positive constant C_1 such that for any $\phi\in\mathcal{X}$,

$$\left|\frac{\partial I(t,x;\phi)}{\partial t}\right|\leqslant C_1\qquad \text{for t} > 2\hat{\tau},\ \text{x}\in\overline{\Omega}.$$

Additionally, Theorem (4.5) and [78, Theorem 5.1.11] indicate that there exists a $C_2>0$ such that

$$\left|\frac{\partial M(t,x;\phi)}{\partial t}\right|\leqslant C_2\qquad \text{for t} > 2\hat{\tau},\ \text{x}\in\overline{\Omega}$$

due to the diffusion term in M equation of system (4.8). This completes the proof.

□

Recall that the Kuratowski measure of noncompactness (see [29]) κ, is defined by

$$\kappa(B) := \inf\{r : B \text{ has a finite cover of diameter } < r\},$$

for any bounded set. We set $\kappa(B) = \infty$ whenever B is unbounded. It is easy to see that B is precompact (i.e., $\overline{B}$ is compact) if and only if $\kappa(B) = 0$. The following statement is the immediate conclusion of Lemma 4.6.

Corollary 4.1. *Let* (A1), (A2) *and* (A3) *hold. Then the map* Φ_T *is* κ*-contracting in the sense that*

$$\lim_{n\to\infty} \kappa(\Phi_T^n(B)) = 0$$

for any bounded set $B \subset \mathcal{X}$, *where* κ *is the Kuratowski measure of noncompactness.*

Proof. Let B be a given bounded subset in $\mathcal{X}$. Let $(I_n(t,x), M_n(t,x)) = \Phi_t(\phi_n)(x), \forall \phi_n \in B, t \geqslant 2\hat{\tau}, x \in \overline{\Omega}$. By Lemma 4.6, it follows that for any $\phi_n \in B$, there exists a subsequence of $\{(I_n(t_n,\cdot), M_n(t_n,\cdot)\}_{n\geqslant 1}$, which is still labelled as $\{(I_n(t_n,\cdot), M_n(t_n,\cdot)\}_{n\geqslant 1}$, such that it converges in $\mathcal{X}$ as $n \to \infty$. This implies that Φ_t is asymptotically compact on B.

Define the omega limit set of B for the map Φ_T on $\mathcal{X}$:

$$\omega(B) = \{\phi \in \mathcal{E}^+ : \lim_{k\to\infty} \Phi_T^{n_k}(\phi_k) = \phi \text{ for some sequences } \phi_k \in B \text{ and } n_k \to \infty\}.$$

In view of the above discussion, it is easy to see that $\Phi_T^n = \Phi_{nT}$ is asymptotically compact on B in the sense that for any sequences $\phi_k \in B$ and $n_k \to \infty$, there exists a subsequence, which is still labelled as ϕ_k and $n_k \to \infty$, such that $\Phi_T^{n_k}(\phi_k)$ converges in $\mathcal{X}$ as $k \to \infty$. This implies that $\omega(B)$ is a nonempty, compact and invariant set for Φ_T in $\mathcal{X}$, and $\omega(B)$ attracts B (see, e.g., [98, Lemma 23.1(2)]). By [79, Lemma 2.1(b)], we have

$$\kappa(\Phi_T^n(B)) \leqslant \kappa(\omega(B)) + \delta(\Phi_T^n(B), \omega(B)) = \delta(\Phi_T^n(B), \omega(B)) \to 0 \text{ as } n \to \infty.$$

This completes the proof. $\square$

Theorem 4.6. *Let* (A1), (A2) *and* (A4) *hold. The map* Φ_T *admits a global attractor on* $\mathcal{X}$.

Proof. We first show the solutions of (4.8) are eventually uniformly bounded. By modifying the arguments in Lemma 4.1 and Theorem 4.1 slightly, we have

$$\limsup_{t\to\infty} M(t,x;\phi) \leqslant \widetilde{M}, \quad \forall \phi \in \mathcal{X},\ x \in \overline{\Omega},$$

which means there exists a positive number l_0, such that for any $t > l_0 T$, $x \in \overline{\Omega}$ and $\phi \in \mathcal{X}$, $M(t,x;\phi) \leqslant \widetilde{M}$. We further obtain the following inequalities for $I(t,x)$ when $t > l_0 T + \hat{\tau}$ and $x \in \overline{\Omega}$:

$$\begin{aligned} I(t,x) &\leqslant \int_{t-\tau(t)}^{t} b(s-\tau(s), M(s-\tau(s),x))ds \\ &\leqslant \int_{t-\tau(t)}^{t} \beta(s-\tau(s)) M(s-\tau(s),x)ds \\ &\leqslant \hat{\beta}\hat{\tau}\widetilde{M}. \end{aligned}$$

Thus, $\Phi_t : \mathcal{X} \to \mathcal{X}$ is point dissipative. Moreover, the positive orbits of bounded subsets of $\mathcal{X}$ for Φ_T are bounded, and Φ_T is κ-contracting on $\mathcal{X}$ (see Lemma 4.1). Therefore, it follows from [79, Theorem 2.6], Φ_T has a global attractor which attracts each bounded set in $\mathcal{X}$. $\square$

4.4.1 Basic reproduction number

Based on assumption (A1), it is easy to check that system (4.8) has a population extinction equilibrium $E_0 = (0,0)$. Linearizing system (4.8) at the extinction equilibrium E_0, we obtain the following linear system for adults:

$$\begin{cases} \dfrac{\partial v(t,x)}{\partial t} = D_2\Delta v(t,x) - \mu_M(t)v(t,x) + (1-\tau'(t)) \\ \qquad\qquad \times \exp\Big(-\displaystyle\int_{t-\tau(t)}^{t}\mu_I(s)ds\Big)\beta(t-\tau(t))v(t-\tau(t),x), \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad t>0,\ x\in\Omega, \\ \dfrac{\partial v(t,x)}{\partial n} = 0, \quad t>0,\ x\in\partial\Omega, \end{cases} \tag{4.20}$$

It easily follows that (4.20) has a unique mild solution $v(t,x;\varphi)$ with $v_0(\cdot,\cdot;\varphi)=\varphi$ and $v_t(\cdot,\cdot;\varphi)\in\mathcal{C}^+$ for all $t\geqslant 0$, and when $t>\hat{\tau}$, $v(t,x;\varphi)$ is a classical solution and $v_t(\cdot,\cdot;\varphi)$ is strongly positive and compact on $\mathcal{C}^+$ for all $t>2\hat{\tau}$. Define $\widetilde{P}:\mathcal{C}\to\mathcal{C}$ by $\widetilde{P}(\varphi)=v_T(\varphi)$ for all $\varphi\in\mathcal{C}$, where $v_T(\varphi)(\theta,x)=v(T+\theta,x;\varphi)$ for all $(\theta,x)\in[-\tau(0),0]\times\overline{\Omega}$, and v_t is the solution map of (4.20). Thus, we have $\widetilde{P}^{n_0}=v_{n_0T}$ is compact and strongly positive, where $n_0:=\min\{n\in\mathbb{N}: nT>2\hat{\tau}\}$. Let $r(\widetilde{P})$ be the spectral radius of $\widetilde{P}$. In view of [71, Lemma 3.1] that $r(\widetilde{P})$ is a simple eigenvalue of $\widetilde{P}$ having a strongly positive eigenvector $\tilde{\varphi}$, which means the modulus of any other eigenvalue is less than $r(\widetilde{P})$. Let $v(t,x;\tilde{\varphi})$ be the solution of (4.20) with $v(s,x;\tilde{\varphi})=\tilde{\varphi}(s,x)$ for all $s\in[-\tau(0),0], x\in\Omega$. The strong positivity of $\tilde{\varphi}$ implies that $v(\cdot,\cdot;\tilde{\varphi})\gg 0$. Thus, we can apply analogous arguments as in Lemma 4.4 to prove the following observation, which indicates the existence of a special solution of system (4.20).

Lemma 4.7. *There exists a positive T-periodic function $\tilde{v}(t,x)$ such that $e^{\tilde{\mu}t}\tilde{v}(t,x)$ is a solution of (4.20), where $\tilde{\mu}=\frac{\ln r(\widetilde{P})}{T}$.*

Denote the initial distribution of adult individuals at time $s\in\mathbb{R}$ and the spatial location $x\in\overline{\Omega}$ by $\phi(s,x)=\phi(s)(x)\in C_T(\mathbb{R},\mathbf{Y}^+)$. Define an operator $\widetilde{C}(t):\mathbf{Y}\to\mathbf{Y}$

as follows:

$$(\widetilde{C}(t)\varphi)(x) := (1-\tau'(t))\exp\Big(-\int_{t-\tau(t)}^{t}\mu_I(s)ds\Big)\beta(t-\tau(t))\varphi(x), \quad \forall \varphi \in \mathbf{Y}.$$

Recall the arguments in section 4.3.2, we know that $\int_{-\infty}^{t-\tau(t)} W(t-\tau(t),s)\phi(s)(x)ds$ denotes the density distribution of the accumulative individuals who matured into adults at all previous time $s < t-\tau(t)$ and survived to time $t-\tau(t)$ at location x. Hence, the distribution of new-born individuals at location x and time t can be represented as follows:

$$\begin{aligned}
&(1-\tau'(t))\exp\Big(-\int_{t-\tau(t)}^{t}\mu_I(s)ds\Big)\beta(t-\tau(t))\Big(\int_{-\infty}^{t-\tau(t)} W(t-\tau(t),s)\phi(s)(x)ds\Big)\\
=&(1-\tau'(t))\exp\Big(-\int_{t-\tau(t)}^{t}\mu_I(s)ds\Big)\beta(t-\tau(t))\Big(\int_{\tau(t)}^{\infty} W(t-\tau(t),t-s)\phi(t-s)(x)ds\Big)\\
=&\int_{\tau(t)}^{\infty}(1-\tau'(t))\exp\Big(-\int_{t-\tau(t)}^{t}\mu_I(s)ds\Big)\beta(t-\tau(t))W(t-\tau(t),t-s)\phi(t-s)(x)ds\\
=&\int_{\tau(t)}^{\infty}\Big[\widetilde{C}(t)(W(t-\tau(t),t-s)\phi(t-s))\Big](x)ds\\
=&\int_{0}^{\infty}\Big[\widetilde{H}(t,s)\phi(t-s)\Big](x)ds,
\end{aligned}$$

where $\widetilde{H}(t,s)$, $t \in \mathbb{R}$, $s \geqslant 0$ is defined as follows:

$$\widetilde{H}(t,s) := \begin{cases} \widetilde{C}(t)W(t-\tau(t),t-s), & s > \tau(t),\\ 0, & s \in [0,\tau(t)]. \end{cases}$$

The next generation operator $\tilde{\mathcal{L}}$ in this case can be defined as

$$\tilde{\mathcal{L}}(\phi)(t) := \int_0^{\infty}\widetilde{H}(t,s)\phi(t-s)ds, \quad \forall t \in \mathbb{R},\ \phi \in C_T(\mathbb{R},\mathbf{Y}).$$

It can be easily shown that $\tilde{\mathcal{L}}$ is a positive and bounded linear operator on $C_T(\mathbb{R},\mathbf{Y})$. We can define the basic reproduction number as the spectral radius of $\tilde{\mathcal{L}}$, that is,

$$\widetilde{\mathcal{R}}_0 := r(\tilde{\mathcal{L}}).$$

Based on [132, Theorem 3.4] and [134, Remark 2.1], we can also obtain the following similar result as in the previous section, which indicates that $\widetilde{\mathcal{R}}_0$ serves as a threshold value for the stability of the zero solution for system (4.17).

Lemma 4.8. $\widetilde{\mathcal{R}}_0 - 1$ *has the same sign as* $r(\widetilde{P}) - 1$.

In what follows, we establish the threshold dynamics of system (4.8) in terms of the basic reproduction number $\widetilde{\mathcal{R}}_0$. Let

$$W_0 = \{\phi \in \mathcal{X} : \phi_2(0, \cdot) \not\equiv 0, \ \forall i = 1, 2\},$$

and

$$\partial W_0 = \mathcal{E}^+ \backslash W_0 = \{\phi \in \mathcal{X} : \phi_2(0, \cdot) \equiv 0\}.$$

Theorem 4.7. *Let* $\mathbf{u}(t, x; \phi)$ *be the solution of (4.8) with* $\mathbf{u}_0 = \phi \in \mathcal{X}$, *then the following statements are valid:*

(1) If $\widetilde{\mathcal{R}}_0 < 1$, *the population extinction equilibrium* $E_0 = (0, 0)$ *is globally attractive in* $\mathcal{X}$*;*

(2) If $\widetilde{\mathcal{R}}_0 > 1$, *there exists an* $\eta > 0$ *such that for any* $\phi \in W_0$ *guaranteeing that*

$$\liminf_{t \to \infty} u_i(t, x; \phi) \geqslant \eta, \quad \forall i = 1, 2$$

holds uniformly for all $x \in \overline{\Omega}$.

Proof. (1) In the case of $\widetilde{\mathcal{R}}_0 < 1$, we have $\tilde{\mu} = \frac{\ln r(\tilde{P})}{T} < 0$. Note that the second equation of (4.8) for $M(t,x)$ is dominated by (4.20), that is, $M(t,x)$ satisfies

$$\begin{cases} \dfrac{\partial M(t,x)}{\partial t} \leqslant D_2 \Delta M(t,x) - \mu_M(t) M(t,x) \\ \qquad\qquad + (1-\tau'(t)) \exp\left(-\displaystyle\int_{t-\tau(t)}^{t} \mu_I(s)ds\right) b(t-\tau(t), M(t-\tau(t),x)), \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad t > 0,\ x \in \Omega, \\ \dfrac{\partial M(t,x)}{\partial n} = 0, \quad t > 0,\ x \in \partial\Omega. \end{cases} \tag{4.21}$$

It follows from Lemma 4.7 that there exists a positive T-periodic function $\tilde{v}(t,x)$ such that $w(t,x) = e^{\tilde{\mu}t}\tilde{v}(t,x)$ is a positive solution of (4.20). In view of the comparison principle for (4.21), we have

$$M(t,x) \leqslant Kw(t,x) = Ke^{\tilde{\mu}t}\tilde{v}(t,x),$$

with a constant $K > 0$ satisfying $M_0(\theta,x) \leqslant Ke^{\tilde{\mu}\theta}v_0(\theta,x)$ for all $\theta \in [-\tau(0),0]$. Thus, it follows that

$$\lim_{t\to\infty} M(t,x) = 0, \quad \forall x \in \overline{\Omega}.$$

Recall the integral form of $I(t,x)$, we have

$$I(t,x) \leqslant \int_{t-\tau(t)}^{t} \beta(s)M(s,y)dyds,$$

and therefore $\lim_{t\to\infty} I(t,x) = 0$ holds when $\widetilde{R}_0 \leqslant 1$.

(2) In the case of $\widetilde{\mathcal{R}}_0 > 1$, we have $r(\widetilde{P}) > 1$, which results in $\tilde{\mu} = \frac{\ln r(\widetilde{P})}{T} > 0$. It can be easily shown that the positivity of $\mathbf{u}_i(t,x;\phi)$ $(i = 1,2)$ holds for any $\phi \in W_0$, $t > 0$ and $x \in \overline{\Omega}$, which implies that $\Phi_T^n(W_0) \subseteq W_0$ for any $n \in \mathbb{N}$.

Define $\widetilde{P}_\epsilon : \mathcal{C} \to \mathcal{C}$ as the Poincaré map of the following system with a small positive parameter ϵ:

$$\begin{cases} \dfrac{\partial v(t,x)}{\partial t} = D_2\Delta v(t,x) - (\mu_M(t)+\epsilon)v(t,x) + (1-\tau'(t)) \\ \qquad\qquad \times \left[e^{-\int_{t-\tau(t)}^{t}\mu_I(s)ds}\beta(t-\tau(t)) - \epsilon\right] v(t-\tau(t),x), \quad t>0,\ x\in\Omega, \\ \dfrac{\partial v(t,x)}{\partial n} = 0, \qquad t>0,\ x\in\partial\Omega, \\ v(\theta,x) = \varphi(\theta,x), \quad \varphi\in\mathcal{C},\ \theta\in[-\tau(0),0],\ x\in\Omega. \end{cases} \tag{4.22}$$

Then, $\widetilde{P}_\epsilon(\varphi) = v_T(\varphi)$, where $v_T(\varphi)(\theta,x) = v(T+\theta,x;\varphi)$ for $(\theta,x)\in[-\tau(0),0]\times\overline{\Omega}$, and $v(t,x;\varphi)$ is the solution of (4.22) with $v(\theta,x)=\varphi(\theta,x)$ for all $\theta\in[-\tau(0),0]$, $x\in\overline{\Omega}$. The continuity of the spectral radius indicates that there exists a sufficiently small positive number ϵ_1 such that the spectral radius of $\widetilde{P}_\epsilon$, $r(\widetilde{P}_\epsilon)$, satisfies $r(\widetilde{P}_\epsilon)>1$ for all $\epsilon\in[0,\epsilon_1]$. Based on assumptions (A1) and (A2), we may choose some $\eta_1>0$ such that

$$e^{-\int_{t-\tau(t)}^{t}(\mu_I(s)+f(I(s,x)))ds}b(t,M(t,x)) \geqslant (e^{-\int_{t-\tau(t)}^{t}\mu_I(s)ds}\beta(t)-\epsilon)M(t,x),$$

and $g(M)<g(\eta_1)<\epsilon_1$ hold for all $I\leqslant\eta_1$ and $M\leqslant\eta_1$. Moreover, according to the continuous dependence of solutions on the initial value, there exists $\eta_0\in(0,\epsilon_1)$ such that for any $|\phi(s,x)|<\eta_0, s\in[-\tau(0),0], x\in\overline{\Omega}$,

$$|(I(t,x;\phi),M(t,x;\phi))|\leqslant\eta_1, \quad \forall t\in[0,T],\ x\in\overline{\Omega}.$$

Next, we prove the weak persistence when $\widetilde{\mathcal{R}}_0>1$ through the following claim:

Claim: $\limsup_{n\to\infty}\|\Phi_T^n(\phi)\|\geqslant\eta_0$ **for all** $\phi\in W_0$**.**

Suppose the claim is false, there exists some $\phi_0\in W_0$ such that

$$\limsup_{n\to\infty}\|\Phi_T^n(\phi)\|<\eta_0.$$

Hence, there exists a positive integer n_1, such that $\|u_i(nT+\theta,x;\phi_0)\| < \eta_0$ for all $n \geqslant n_1$, $i = 1,2$, $\theta \in [-\tau(0),0]$ and $x \in \overline{\Omega}$. Then for $\phi_0 \in W_0$, we have

$$0 < u_i(t,x;\phi_0) < \eta_1, \quad \forall t > n_1T,\ x \in \overline{\Omega},\ i = 1,2. \tag{4.23}$$

Then, $M(t,x;\phi_0)$ satisfies

$$\begin{cases} \dfrac{\partial M(t,x)}{\partial t} \geqslant & D_2\Delta M(t,x) - (\mu_M(t)+\epsilon_1)M(t,x) + (1-\tau'(t)) \\ & \times \left[e^{-\int_{t-\tau(t)}^{t}\mu_I(s)ds}\beta(t-\tau(t)) - \epsilon_1\right] M(t-\tau(t),x), \quad t > (n_1+1)T,\ x \in \Omega, \\ \dfrac{\partial M(t,x)}{\partial n} = & 0, \qquad t > (n_1+1)T,\ x \in \partial\Omega. \end{cases} \tag{4.24}$$

Let ψ^* be the positive eigenfunction of $\widetilde{P}_{\epsilon_1}$ corresponding to $r(\widetilde{P}_{\epsilon_1})$. For all $t > \hat{\tau}$ and $x \in \overline{\Omega}$, the positivity of $M(t,x;\phi_0)$ gives rise the existence of a constant $\varsigma > 0$ such that

$$M((n_1+1)T+\theta,x;\phi_0) \geqslant \varsigma\psi^*, \quad \forall\theta \in [-\tau(0),0],\ x \in \overline{\Omega}.$$

Then, based on the comparison principle for (4.24), we have

$$M(t,x;\phi_0) \geqslant \varsigma v(t-(n_1+1)T,x;\psi^*) = \varsigma r(\widetilde{P}_{\epsilon_1})^{t-(n_1+1)T}\psi^*(0,x), \quad \forall t \geqslant (n_1+1)T,\ x \in \overline{\Omega},$$

where $v(t,x;\psi^*)$ is a solution for (4.22) with $v(\theta,x) = \psi^*(\theta,x)$ for all $\theta \in [-\tau(0),0]$ and $x \in \overline{\Omega}$. Thus, it follows that

$$\lim_{t\to\infty} M(t,x;\phi_0) = \infty,$$

a contradiction to (4.23).

Let $\mathbf{M} = (0,0)$. The above claim shows that $\mathbf{M}$ is a weaker repeller for W_0 and the stable set of $\mathbf{M}$, $W^s(M)$ satisfies that $W^s(\mathbf{M}) \cap W_0 = \varnothing$. Moreover, $\mathbf{M}$ is an isolated invariant set for Φ_T in $\mathcal{E}^+$. Define

$$M_\partial := \{\phi \in \partial W_0 : \Phi_T^n(\phi) \in \partial W_0,\ \forall n \in \mathbb{N}\},$$

and $\omega(\phi)$ be the omega limit set of the positive orbit $\gamma^+(\phi) := \{\Phi_T^n(\phi) : \forall n \in \mathbb{N}\}$. It then follows from Theorem 4.1 that

$$M_\partial := \{\phi \in \partial W_0 : \phi_2 \equiv 0\},$$

and hence

$$\bigcup_{\psi \in M_\partial} \omega(\psi) = \{(0,0)\}.$$

In the light of the acyclicity theorem on uniform persistence for maps [135, Theorem 1.3.1 and Remark 1.3.1], we obtain the uniform persistence for $\Phi_T : \mathcal{X} \to \mathcal{X}$ with respect to $(W_0, \partial W_0)$ due to Corollary 4.1, that is, there exists an $\hat{\eta} > 0$ such that

$$\liminf_{n\to\infty} d(\Phi_T^n(\phi), \partial W_0) \geqslant \hat{\eta}, \quad \forall \phi \in W_0.$$

Define a continuous function $p : \mathcal{X} \to [0, \infty)$ by

$$p(\phi) := \min_{x \in \overline{\Omega}} \phi_2(0, x), \quad \forall \phi = (\phi_1, \phi_2) \in \mathcal{X}.$$

It follows from $\mathcal{A} = \Phi_T(\mathcal{A})$ that $\phi > 0$ for all $\phi \in \mathcal{A}$. We further obtain $\lim\limits_{n\to\infty} d(\Phi_T^n(\phi), \mathcal{A}) = 0$. The compactness of $\mathcal{A}$ implies that $\min\limits_{\phi \in \mathcal{A}} p(\phi) > 0$, which further indicates that there exists an $\hat{\eta} > 0$ such that

$$\liminf_{n\to\infty} \ (I(nT, x; \phi), M(nT, x; \phi)) \geqslant (\hat{\eta}, \hat{\eta}), \quad \forall \phi \in W_0, \ i = 1, 2.$$

This indicates that there exists $n_1 \in \mathbb{N}^+$ such that for any $n \geqslant n_1$,

$$(I(nT, x; \phi), M(nT, x; \phi)) \geqslant (\hat{\eta}, \hat{\eta}), \quad \forall \phi \in W_0, \ i = 1, 2. \tag{4.25}$$

Note that

$$\begin{cases} \frac{\partial M(t,x)}{\partial t} \geqslant D_2 \Delta M(t, x) - (\hat{\mu}_M + g(H)) M(t, x), \quad t \geqslant n_1 T, \ x \in \Omega, \\ \frac{\partial M(t,x)}{\partial n} = 0, \quad t \geqslant n_1 T, \ x \in \partial\Omega, \end{cases}$$

where $\hat{\mu}_M := \max_{t\in[0,T]} \mu_M(t)$ and H is defined in Theorem 4.5. Then the parabolic comparison principle and (4.25) imply that

$$M(t,x) \geqslant \hat{\eta} e^{-(\hat{\mu}_M + g(H))(t-n_1T)} \geqslant \eta_1' > 0, \qquad t \geqslant n_1T,\ x \in \overline{\Omega},$$

where η_1 is a positive constant. Furthermore, on the basis of the integral form I, it is easy to see that there exists an $\eta_2' > 0$ such that

$$I(t,x;\phi) \geqslant \eta_2', \qquad \forall t \geqslant n_1T,\ x \in \overline{\Omega},\ \phi \in W_0.$$

Set $\eta := \min\{\eta_1', \eta_2'\}$. Then we can obtain the practical uniform persistence stated in the theorem. □

4.5 Discussion

In this chapter, a reaction-diffusion population model with the consideration of seasonal effects, intra-specific competition, age structure and seasonal maturation duration based on a generalized age-structured modeling framework was formulated. By applying the method of integration along characteristics, the full system related to the population densities of juveniles $I(t,x)$ and adults $M(t,x)$ at time t and location x was obtained with two nonlocal periodic reaction diffusion equations involving periodic delays and no flux boundary condition. The introduction of juvenile intra-specific competition and periodic delays, making the system non-cooperative and irreducible, bring more challenges to the theoretical analysis of our model.

It is worth mentioning that our model involves time-varying delays $\tau(t)$. An appropriate space for theoretical analysis should be introduced to analyze it. In this chapter, without loss of generality, the initial timing was chosen as the maximum point of $\tau(t)$ in $[0,T]$, that is, $\tau(0) = \max_{t\in[0,T]}\{\tau(t)\} = \hat{\tau}$, which is feasible by considering the evolution of solutions. If the initial timing instant $t_0 = 0$ does not satisfies $\tau(t_0) = \hat{\tau}$, by applying similar arguments in [72, 77], we may need to introduce two spaces. One is $C([-\hat{\tau}, 0], \mathbf{Y})$ to show the existence and uniqueness of the solution. To verify the global attractivity of the positive periodic solution, the other space $C([-\tau(0), 0], \mathbf{Y})$ is needed, on which we can show the solution semiflow is eventually strongly monotone and strictly homogeneous. Besides that, we need to confirm that the solution can define a periodic semiflow on the new space $C([-\tau(0), 0], \mathbf{Y})$ and $\mathcal{R}_0$ can determine the stability of the system on both phase spaces.

Chapter 5

Modeling diapause in population growth

5.1 Background

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 [111]. 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 include temperate zone insects or some tropical species occasionally and their arthropod relatives [30, 63], such as mosquitoes [3], ticks [12], ladybirds [56], dragonflies [95] and silkworms [54]. Recent extensive studies on different aspects of diapause contributed to understanding how inherent mechanisms regulate organisms surviving through diapause [30, 32, 33, 51, 97] and the critical roles of diapause stage on linking the favourable and adverse seasons, and synchronising the life cycle of organisms with seasonal environmental variations [3, 31, 110, 111].

Mathematical models are believed to be efficient and indispensable tools for better understanding of population dynamics [17, 85]. However, few population models focus on exploring the impact of diapause on population persistence. In this chapter, 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 [103]. 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.

Our literature review indicates that there were two possible ways employed to incorporate the diapause effects into the population model. One way was using piecewise parameter functions to differ either the survival or the development rates between the normal growth and diapause periods. Gong et al. developed two discrete difference models with a piecewise death rate function characterising the impact of adult mosquito diapause to investigate the temporal dynamics of *Culex* mosquito populations [43]. A stage-structure, climate-driven population model of ordinary differential equations (ODE) with a piecewise egg production rate function describing diapause-induced differences was formulated in [116] to simulate *Culex* mosquito population abundance in the Northeastern US. Another temperature-dependent, delay differential equation (DDE) model with piecewise developmental rate functions accounting for the effects of diapause was proposed to demonstrate the sensitivity of seasonal mosquito patterns to annual changes in temperature [36]. However, considerable observational studies suggest that not only the developmental rate but also the reproduction and mortality rates are altered simultaneously when organisms enter into diapause [31, 52, 101]. Consequently, the other fairly reasonable way was to regard the diapause period as an independent dynamic process, during which the population dynamics are completely different from that in the normal growth period. Cailly et al. [20] built two different stage-structured temperature-driven ODE models to predict seasonal mosquito abundance during favourable and unfavourable periods respectively. Based on the above two models, two new fine-tuned ODE models were constructed in [60] to explore the relationships between major climatic variables and diapause related parameters. Following this point of view, we aim to propose a novel and comprehensive framework for modelling diapause in the population growth.

The occurrence of diapause is caused by the advent of adverse environmental conditions such as winter seasons in temperate zones and dry seasons in tropical zones. As such, the organisms surviving through diapause must experience a fixed period of latency before their normal growth resumes [31]. In addition, several observations [31, 63, 64] 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. Since mosquito diapause is restricted to a single stage for most species, on either immature (mostly egg) or adult stage [19, 31], 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 mature classes to explicitly describe different diapausing life stages. In view of the developmental delays induced by the maturation and diapausing time period respectively, it seems the stage-structured DDE framework is more suitable and reasonable. Two distinct DDE models with two different delays 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 separately, by assuming different diapause-related parameters. Although the motivative example of this work is the mosquito species, our modelling framework can be applied to other species including ticks [12], silkworms [54] and flesh flies [40], which are capable of diapause to survive through unfavourable seasons.

The formulations of three DDE models are derived elaborately in Section 5.2. Theoretical analysis on the unified model including the well-posedness of the solutions and global stability of the trivial and positive periodic solutions in terms of an index $\mathcal{R}$ is presented in Section 5.3. Numerical simulations are performed in Section 5.4 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.

5.2 Model formulation

We first derive the formulation describing the growth of population with only one diapausing stage, either adult or immature diapause. 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 integrations:

$$I(t) = \textstyle\int_0^\tau u(a,t)da, \quad M(t) = \textstyle\int_\tau^\infty u(a,t)da. \tag{5.1}$$

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, to derive the closed system, the post-diapause period is set to be 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 $\tau_d > \tau$ [31, 100]. 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 chapter, 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., [26, 48, 77] and the references therein):

$$\begin{cases} \left(\dfrac{\partial}{\partial a} + \dfrac{\partial}{\partial t}\right) u(a,t) &= -\mu(a)u(a,t), \\ u(0,t) &= b(M(t)), \\ u(a,0) &= u_0(a). \end{cases} \tag{5.2}$$

The birth rate function is $b(M(t))$, 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 $a \geqslant \tau$. In view of (5.2), differentiating the integral equations in (5.1) with respect to time t on both sides yields

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

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 [104]).

To proceed, let $\xi^s(t) = u(t-s,t)$, then for $t - s \leqslant \tau$, 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 $s = t - \tau$ ($\geqslant 0$), we have the following expression for $u(\tau,t)$ when $t \geqslant \tau$,

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

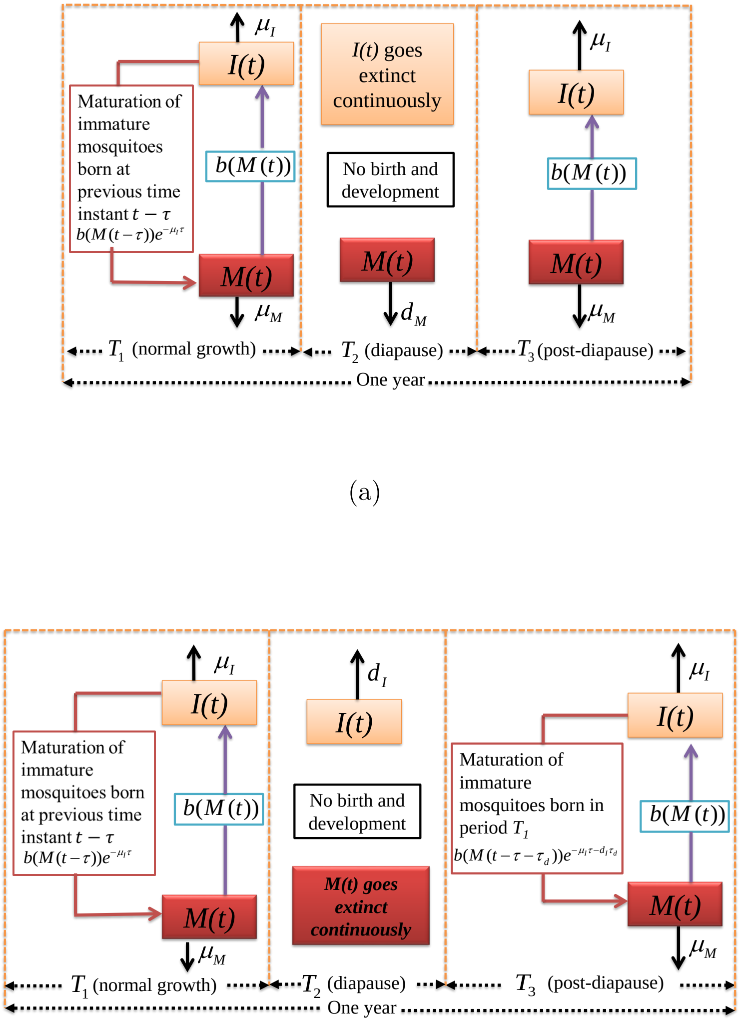
The following system describes the population dynamics taking into consideration of seasonal effects during the normal growth period, i.e. when $n \leqslant t \leqslant n + T_1 = n + 1 - \tau - \tau_d$, here n ($\geqslant 0$) is an integer representing the n-th year:

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

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

5.2.1 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 [109]. Consequently, we assume that the number of immatures $I(t)$ decreases to zero continuously during the diapause period, i.e. when $n + 1 - \tau - \tau_d \leqslant t \leqslant n + 1 - \tau$, moreover, $I(t) \equiv 0$ when $t \in [n + 1 - 2\tau, n + 1 - \tau]$. During the post-diapause period, i.e. when $n+1-\tau \leqslant t \leqslant n+1$, 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. 5.1(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).



(a)

(b)

Figure 5.1: Diagrams depicting the annual growth of mosquito populations with single diapausing stage. (a) Diagram for adult diapause; (b) Diagram for immature 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 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 $t \in [n, n+1-\tau-\tau_d]$:

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

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:

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

5.2.2 Immature diapause

In the case that immature individuals diapause, the annual growth of mosquito population is illustrated in Fig. 5.1(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 [67, 115]. Therefore, we assume that $M(t)$ decreases to zero continuously during the diapause period, i.e. when $n+1-\tau-\tau_d \leqslant t \leqslant n+1-\tau$, and $M(t) \equiv 0$ 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:

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

5.2.3 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. 5.2.

1) During the normal growth period T_1, i.e. when $n \leqslant t \leqslant n + T_1 = n+1-\tau-\tau_d$, the population dynamics are described by the following system, which are the

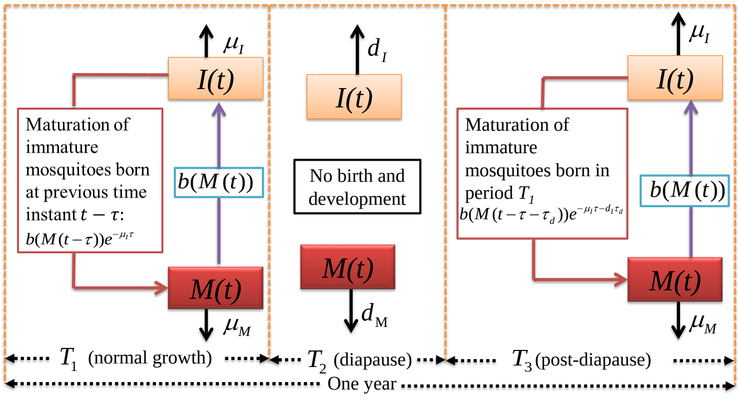


Figure 5.2: Diagram illustrating the annual growth for the mosquito population when both immatures and adults can survive through diapause. The one year period is divided into three intervals with different growth rates for immatures $I(t)$ and adults $M(t)$ on different intervals. Moreover, the lengths of these three different intervals T_1, T_2, T_3 are $1-\tau_d-\tau$, τ_d and τ respectively.

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 $n+1-\tau_d-\tau \leqslant t \leqslant n+1-\tau$) 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 $n+1-\tau \leqslant t \leqslant n+1$, 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) in terms of a threshold, which approximates to (A3). Similarly, when immatures diapause, the dynamics of system (I) can be approximated by those of system (U) with the assumption of $d_M \gg 1$. 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) in the next section, where the detailed proofs for the well-posedness of the solutions and global stability of the trivial and positive periodic solutions in terms of a threshold parameter $\mathcal{R}$ 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.

5.3 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:

$$\begin{cases} \dfrac{dM(t)}{dt} = b(M(t-\tau))e^{-\mu_I \tau} - \mu_M M(t), & t \in [n, n+1-\tau-\tau_d], \\ \dfrac{dM(t)}{dt} = -d_M M(t), & t \in [n+1-\tau-\tau_d, n+1-\tau], \\ \dfrac{dM(t)}{dt} = b(M(t-\tau-\tau_d))e^{-\mu_I \tau - d_I \tau_d} - \mu_M M(t), & t \in [n+1-\tau, n+1], \end{cases} \tag{5.3}$$

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 the existing literature [76]:

(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 assumptions for the birth rate function can be deduced from Fig. 5.3. 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 [31]. 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 [100]. 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).

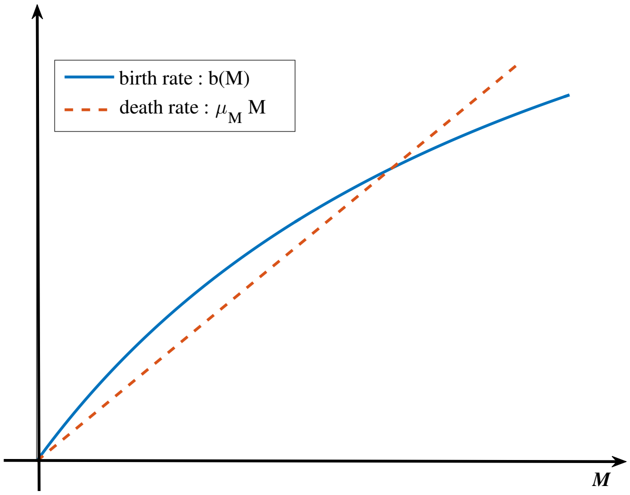


Figure 5.3: A schematic illustration of the birth rate function that satisfies assumption (H1).

5.3.1 The well-posedness

Based on the variation of constant formulae, system (5.3) can be written as the following equivalent integral form:

$$M(t) = e^{-\mu_M(t-n)}\left[\int_n^t b(M(s-\tau))e^{-\mu_I\tau}e^{\mu_M(s-n)}ds + M(n)\right], \quad t \in [n, n+1-\tau_d-\tau], \tag{5.4a}$$

$$M(t) = e^{-d_M(t-(n+1-\tau-\tau_d))}M(n+1-\tau-\tau_d), \qquad t \in [n+1-\tau-\tau_d, n+1-\tau], \tag{5.4b}$$

$$\begin{aligned} M(t) =& e^{-\mu_M(t-(n+1-\tau))}\Big[\int_{n+1-\tau}^t b(M(s-(\tau+\tau_d)))e^{-\mu_I\tau-d_I\tau_d}e^{\mu_M(s-(n+1-\tau))}ds \\ & + M(n+1-\tau)\Big], \qquad t \in [n+1-\tau, n+1]. \end{aligned} \tag{5.4c}$$

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 $u_t(\theta) = u(t + \theta)$, $\forall \theta \in [-\tau, 0], t \geqslant 0$. In what follows, the well-posedness of system (5.3) is established.

Theorem 5.1. *Suppose that assumptions (H1) and (H2) hold, then for any* $\phi \in Y$*, system (5.3) 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 $\rho \geqslant 1$ and any $\phi \in Y$ satisfying $0 \leqslant \phi \leqslant \rho\overline{M}$, where $\overline{M}$ is defined in the assumption (H1), system (5.3) 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 (5.3) admits a unique solution on its maximal interval of existence. It can be easily checked by differentiation that (5.4a) with $n = 0$ satisfies system (5.3) on $[0, \tau]$. Moreover, it follows from the assumption (H1) that the following holds for $t \in [0, \tau]$:

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

Hence, system (5.3) 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 similar approach.

For $t \in [1-\tau-\tau_d, 1-\tau]$, the solution of system (5.3) can be determined uniquely by the initial-value problem for the following linear ODE:

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

which implies that (5.4b) with $n = 0$ is the solution of system (5.3) on $[1-\tau-\tau_d, 1-\tau]$. In view of (5.4b) with $n = 0$, we have the solution $0 \leqslant u(t) \leqslant \rho\overline{M}$. It then follows that system (5.3) 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 (5.3) must satisfy the initial-value problem for the following ODE:

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

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 (5.3). It is easy to verify by differentiation that (5.4c) with $n = 0$ satisfies system (5.3) on $[1-\tau, 1]$. Furthermore, based on assumption (H1), for all $t \in [1-\tau, 1]$, we have

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

Thus, system (5.3) admits a unique solution $u(t, \phi)$ on $[0, 1]$.

Next, we can show the existence of a unique solution $0 \leqslant u(t, \phi) \leqslant \rho\overline{M}$ with $0 \leqslant u_0 = \phi \leqslant \rho\overline{M}$ for all $t \geqslant 0$ by applying the method of steps on each interval $[n, n+1]$. Since ρ can be chosen sufficiently large, it then follows that system (5.3) admits a unique solution $u(t, \phi)$ with $u_0 = \phi \in Y$ on $[0, \infty)$. □

Define Φ_t as the solution semiflow for system (5.3) on Y, that is, $\Phi_t(\phi)(\theta) = u_t(\theta, \phi) = u(t + \theta, \phi)$ for $t \geqslant 0$, $\theta \in [-\tau, 0]$, where $u(t, \phi)$ is the unique solution of system (5.3) on $[0, \infty)$ with $u_0 = \phi \in Y$. The following lemma implies that Φ_t is a 1-periodic semiflow on Y.

Lemma 5.1. *Φ_t is a 1-periodic map on Y, that is, (i) $\Phi_0 = I$, where I is the identity map; (ii) $\Phi_{t+1} = \Phi_t \circ \Phi_1$, $\forall t \geqslant 0$; (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 [81, Theorem 8.5.2]. Now, we show that property (ii) holds. For any $\phi \in Y$ and all $t \geqslant 0$, 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 $t \in [n + 1 - \tau - \tau_d, n + 1 - \tau]$:

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

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

5.3.2 Threshold dynamics

In order to investigate the global dynamics of system (5.3), we employ the theory of strongly monotone and sub-homogeneous semiflows (see [135, Section 2.3]). The next two lemmas show that the periodic semiflow Φ_t is eventually strongly monotone and strictly subhomogeneous on Y.

Lemma 5.2. *For any ϕ and ψ in Y with $\phi > \psi$ (that is, $\phi(s) \geqslant \psi(s)$ for $s \in [-\tau, 0]$ with $\phi \not\equiv \psi$), there are two solutions $u(t, \phi)$ and $v(t, \psi)$ of system (5.3) 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 $u(t) \geqslant v(t)$ for all $t \geqslant 0$ by applying the comparison argument [106, Theorem 5.1.1] on each interval $[n, n+1]$ for all $n \in \mathbb{N}$. In view of (5.4a) 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 solutions, 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,

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

which is a contradiction. For $t \in [1-\tau-\tau_d, 1-\tau]$, it follows from (5.4b) 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 (5.4c), we have

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

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 $1 \leqslant n \in \mathbb{N}$. 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 subhomogeneity 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 5.3. *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 (5.3) 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 5.1 implies that $v(t) > 0$ and $w(t) > 0$ hold for all $t \geqslant 0$. In consideration of assumption (H3), it follows that $v(t)$ satisfies the following system of differential equations:

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

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

$$\begin{cases} v(t) = e^{-\mu_M (t-n)} \left[\displaystyle\int_n^t B\Big(\frac{1}{\lambda} v(s-\tau)\Big) v(s-\tau) e^{-\mu_I \tau} e^{\mu_M (s-n)} ds + v(n) \right], \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad t \in [n, n+1-\tau-\tau_d], \\ v(t) = e^{-d_M (t-(n+1-\tau-\tau_d))} v(n+1-\tau-\tau_d), \quad t \in [n+1-\tau-\tau_d, n+1-\tau], \\ v(t) = e^{-\mu_M (t-(n+1-\tau))} \left[\displaystyle\int_{n+1-\tau}^t B\Big(\frac{1}{\lambda} v(s-(\tau+\tau_d))\Big) v(s-(\tau+\tau_d)) \right. \\ \qquad \left. \times\, e^{-\mu_I \tau - d_I \tau_d} e^{\mu_M (s-(n+1-\tau))} ds + v(n+1-\tau) \right], \ t \in [n+1-\tau, n+1]. \end{cases} \tag{5.5}$$

For all $t \in (0, \tau]$, it follows from assumption (H3) and the first equation of (5.5) that

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

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,

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

which is a contradiction. For all $t \in [1-\tau-\tau_d, 1-\tau]$, in view of the second equation of (5.5), 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 (5.5) imply that

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

Similarly on each interval $(n, n+1]$, we have $0 < v(t) < w(t)$ for all $t \in (n, n+1]$ with $n(\geqslant 0) \in \mathbb{N}$. 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 [135] (or those in [136]) for strongly monotone and strictly sub-homogeneous semiflows, we investigate the global dynamics for system (5.3) in the rest of this section. Based on assumption (H1), it is easy to verify that system (5.3) has a population extinction equilibrium 0. Then, the corresponding linearised system is

$$\begin{cases} \dfrac{dM(t)}{dt} = b'(0)e^{-\mu_I\tau}M(t-\tau) - \mu_M M(t), & t \in [n, n+1-\tau-\tau_d], \\ \dfrac{dM(t)}{dt} = -d_M M(t), & t \in [n+1-\tau-\tau_d, n+1-\tau], \\ \dfrac{dM(t)}{dt} = b'(0)e^{-\mu_I\tau - d_I\tau_d}M(t-(\tau+\tau_d)) - \mu_M M(t), & t \in [n+1-\tau, n+1], \end{cases} \tag{5.6}$$

where $n \in \mathbb{N}$. For any given $t \geqslant 0$, let $P(t)$ be the solution map of the linear system (5.6) on Y. Then, $P(1)$ is the Poincaré map associated with system (5.6) with its spectral radius denoted as $\mathcal{R}$.

We now prove the main result of this section, that is, the global stability of system (5.3) in terms of $\mathcal{R}$.

Theorem 5.2. *The following statements hold for system (5.3):*

(i) If $\mathcal{R} \leqslant 1$, 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 $Y \backslash \{0\}$.

Proof. For a fixed integer n_1 satisfying $n_1 > 2(\tau + \tau_d)$, it follows from Lemma 5.1 that Φ_t can be a n_1-periodic semiflow on Y. In view of Lemmas 5.2 and 5.3, 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 [135], we have:

(i) If $r(D\Phi_{n_1}(0)) \leqslant 1$, then 0 is globally asymptotically stable for system (5.3) in Y.

(ii) If $r(D\Phi_{n_1}(0)) > 1$, then system (5.3) admits a unique positive n_1-periodic solution $M^*(t)$, which is globally asymptotically stable in $Y\backslash\{0\}$.

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 $Y\backslash\{0\}$, 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 (5.3) with $M^*(0) = \phi^*$. $\square$

5.4 Numerical simulations

In this section, some numerical simulations are carried out to show how the mosquito population fluctuates with the diapause-related parameters. In this work, 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 [119]. The other is *Culex pipiens*, only the adults of which undergo diapause to maintain viability in response to harsh environmental conditions [119]. 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* are distributed in similar latitudes [80], 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 at the same values. 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 is 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 environmental conditions is enhanced [53, 97]. 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-dependence in 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 [14] and insects [65]. In this work, the birth rate function is constructed as a special case of Beverton-Holt function, that is, $b(M) = pM/(q + M^r)$, 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 $r = 0.5$. The detailed descriptions of parameters are provided in Table 5.1.

5.4.1 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 as in Table 5.1. The patterns of the periodic solutions are illustrated as red dashed curves in the top four

Table 5.1: 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	[100]
τ_d	Diapause period for immature (mature) mosquitoes (month)	$2.5 \sim 5$	3	[31]
μ_I	Mortality rate for immature mosquitoes during normal growth period (month^{-1})	$0.3 \sim 1.8$	0.6	[25, 28, 93]
μ_M	Mortality rate for mature mosquitoes during normal growth period (month^{-1})	$0.6 \sim 2.1$	0.7	[25, 28, 93]
d_I	Mortality rate for immature mosquitoes during diapause period (month^{-1})	$\geqslant 0.8$	Diapause: 0.8 Otherwise: 6	Assumed
d_M	Mortality rate for mature mosquitoes during diapause period (month^{-1})	$\geqslant 0.9$	Diapause: 0.9 Otherwise: 7	Assumed

figures of Fig. 5.4. Moreover, we plot the curves of the periodic solutions (illustrated as blue dotted lines in Fig. 5.4) to the other two models (A) and (I) since further check is needed to verify whether our unified model can characterise them. The curves of the periodic solutions to the unified model (U) overlap with those simulated by the other two models, which validates that our unified model (U) is reasonable to characterise the dynamics of population experiencing immature and mature diapause respectively, by using different mortality rates in the diapause period. In what follows, all the mentioning simulations are carried out on the unified model (U). Fig. 5.4 also 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 dynamics during only one period containing 12 months in our simulations (Fig. 5.4(e) and 5.4(f)). The number of both immature and adult *Culex pipiens* 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 post-diapause period ends (shown in Fig. 5.4(e)). For *Aedes albopictus*, the population size of immatures and adults both undergo similar decline, different from *Culex pipiens*, the number of juveniles and adults both bounce back immediately after diapause (shown in Fig. 5.4(f)). Different diapausing stages may 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 T_3), the number of adults starts to increase as the new-born immatures attain maturity and mature 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 can be demonstrated intuitively by two phase portraits of systems with respect to immature and adult diapause cases. The phase portraits sketched in Fig. 5.5, 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. 5.5. The stable periodic orbit in Fig. 5.5(b) passing the bottom boundary of the axis related to adult population size implies that adult *Aedes albopictus* die while immatures enter diapause, whereas, for *Culex pipiens* experiencing adult diapause, this periodic orbit may reach the leftmost boundary of the axis referring to the extinction of immatures (shown in Fig. 5.5(a)).

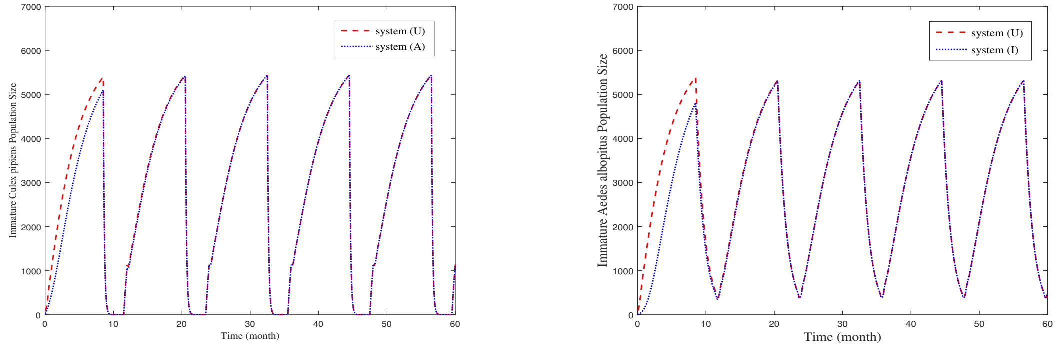
These simulations are as expected and consistent with our theoretical analysis, which further demonstrate that the modelling framework is valid to capture the dynamic behaviour of diapausing species. In the next subsection, sensitivity analysis reveals how the mosquito population dynamics changes due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

5.4.2 Sensitivity analysis

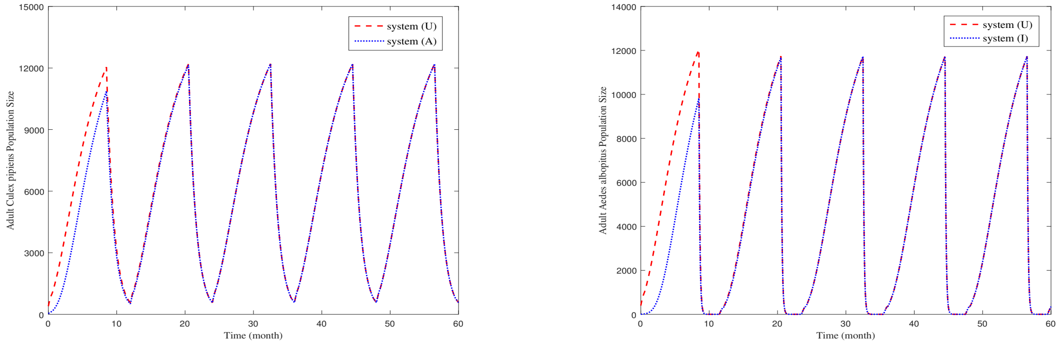
The survivability of mosquitoes under adverse environmental conditions is believed to be the vital factor preserving the population size and maintaining the succeeding normal development [97]. The sensitivity analysis mainly investigates the impacts of the mortality rates during diapause period and the length of diapause duration, which are strongly relevant to the diapausing survivability. To evaluate effects of the variations of diapause-related parameters on population dynamics, four indexes characterising mosquito population abundance are mainly concerned, which involve the maximum population abundance, the minimum population abundance, the time of mosquito population attaining its maximum and minimum values during one period.

(1) Effects of the death rates during the diapause period

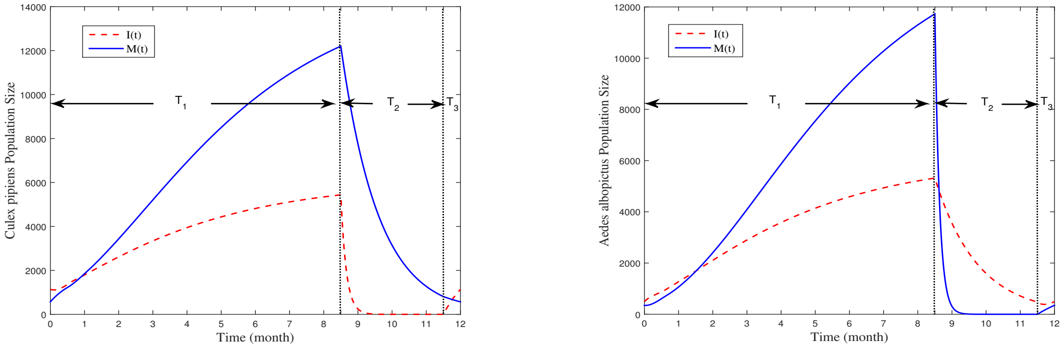
For adult diapause case, all immature *Culex pipiens* die at the end of the diapause period while some adults can survive through diapause. In this case, the survivability of diapausing adults other than immatures during the diapause period is crucial for subsequent population growth. We first examine how the population dynamics change when we vary the diapausing adult death rate and fix the immatures dying



(a) Adult diapause (b) Immature diapause

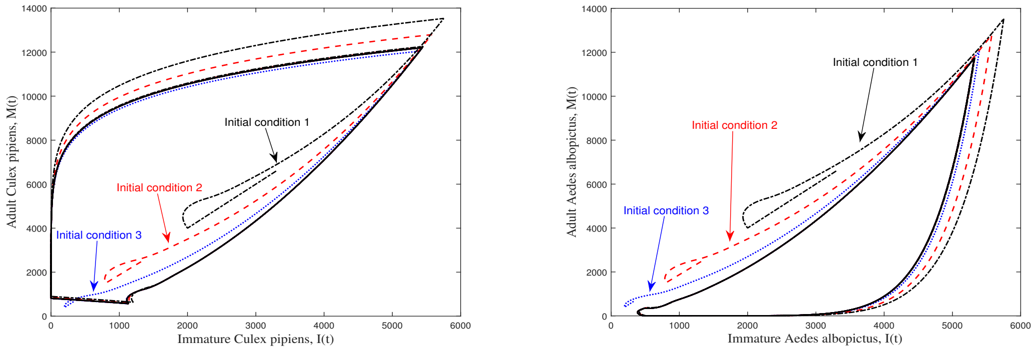


(c) Adult diapause (d) Immature diapause



(e) Adult diapause (f) Immature diapause

Figure 5.4: Simulated mosquito population abundance. (a) and (c): Immature and adult *Culex pipiens* population dynamics, simulated by systems (A) and (U). $d_I = 6$, $d_M = 0.9$. (b) and (d): Immature and adult *Aedes albopictus* population dynamics, simulated by systems (I) and (U). $d_I = 0.8$, $d_M = 7$. (e): *Culex pipiens* population dynamics in one period with adult diapause. (f): *Aedes albopictus* population dynamics in one period with immature diapause. T_1, T_2 and T_3 represent the normal growth period, diapause period and post-diapause period respectively. Here, the values of all other parameters are following Table 5.1.



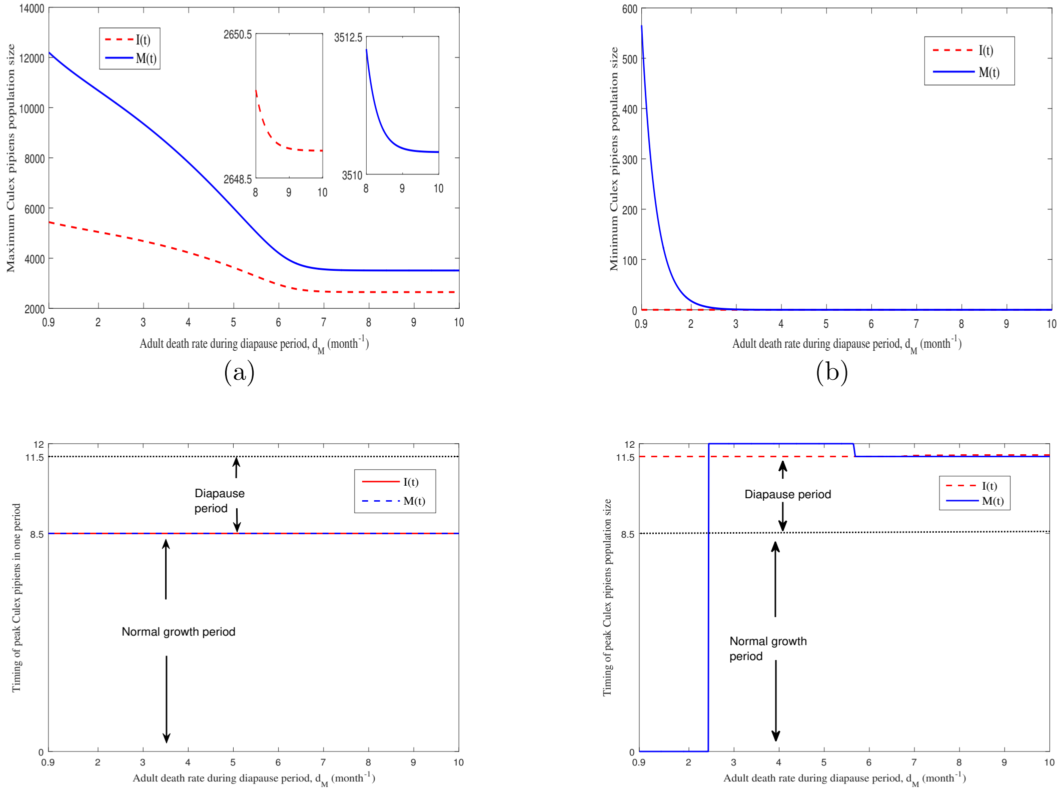
(a) Adult diapause

(b) Immature diapause

Figure 5.5: 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 the 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 the solutions with three different positive initial conditions. Here, $d_I = 6$, $d_M = 0.9$. The values of all other parameters are following Table 5.1. For these two cases, all solutions with different initial conditions converge to a positive periodic solution (shown as the solid closed curve).

at a speed of non-diapausing rate, i.e., $d_I = 6$. The consequences of varying adult mortality rate d_M during diapause period are shown in Fig. 5.6. The curves clearly show that increasing the survivability of diapausing mature mosquitoes during diapause period may benefit the succeeding normal growth, which is embodied in the larger maximum (Fig. 5.6(a)) and minimum population abundance (Fig. 5.6(b)) with lower diapausing adult mortality rate. The decreasing trend of the maximum and minimum population abundance will slow down when d_M is greater than some threshold value. The possible reason may be that d_M only determines the survivability of adults during the diapause period. Once the adult 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. Compared to the peak of immature population, the wider range of the variations in the peak adult population abundance suggests that it is more sensitive to changes in adult death rate d_M as shown in Fig. 5.6(a). Along with the increasing diapausing adult death rate, the difference between the immature and adult peak population sizes is diminishing. Fig. 5.6(c) shows that the peak population sizes for both immatures and adults are always attained at the end of the normal growth period, which is completely irrespective of the diapausing adult death rate. In view of the monotonicity of the unified model (U), this result is as expected since the immature and adult population sizes will both keep increasing until the normal growth stops. Due to the fact that the immatures fail to survive through diapause, the minimum immature population size always appears at the end of the diapause period (Fig. 5.6(d)). However, the timing of the minimum adult population size is shifted forward from the end of the post-diapause period to the end of the diapause period when the adult death rate is larger than some threshold value (Fig. 5.6(d)), which further extends the results on the timing of minimum adult size in Fig. 5.4(f). The cause of this phenomenon may be that the enlarged adult death rate during diapause period accelerates the decreasing speed of the adult population size, which in turn increases the density-dependent per capita adult recruitment rate to be greater than the density-independent per-capita death rate.

In the case of immature *Aedes albopictus* entering diapause, the ability of the immatures surviving though diapause becomes the major concern. In order to explore the influences of immature mortality rates during diapause period on mosquito population dynamics, we vary the diapausing immature death rate by fixing the adult death rate of $d_M = 7$ during the diapause period. Compared with the adult diapausing case, the curves in Fig. 5.7 suggest that the diapausing immature death rate influences the population dynamics in similar ways. Increasing the survivability by lowering the immature death rate d_I during diapause period can raise the maximum (see Fig. 5.7(a)) and minimum population sizes (see Fig. 5.7(b)) for both immatures and adults. The varying diapausing immature death rate has no effects on the timing of the peak immature and adult population sizes, as shown in Fig. 5.7(c). Adult peak population size is more influenced than the immature peak population



(a) (b)

(c) (d)

Figure 5.6: In the case of adult diapause for *Culex pipiens*, four summary statistics characterising mosquito population abundance vary with the adult death rates during adult diapause period. (a) Maximum *Culex pipiens* population size varies with changing d_M. (b) Minimum *Culex pipiens* population size changes with varying d_M. (c) The timing of maximum *Culex pipiens* population size varies with changing d_M. (d) The timing of minimum *Culex pipiens* population size changes with varying d_M. Here, we fix $d_I = 6$, the values of all other parameters are following Table 5.1.

size by the diapausing immature death rate d_I. The minimum mature population size always appears at the end of the diapause period since all adults fail to survive through diapause, while the timing of minimum immature population size is shifted earlier when the diapausing immature death rate is enlarged (Fig. 5.7(d)).

(2) Effects of the length of the diapause period

In addition to the diapausing death rates, the length of the diapause duration τ_d also plays an important role on the survivability. To evaluate the impacts, we change the values of τ_d to see how the length of diapause period affects the mosquito population

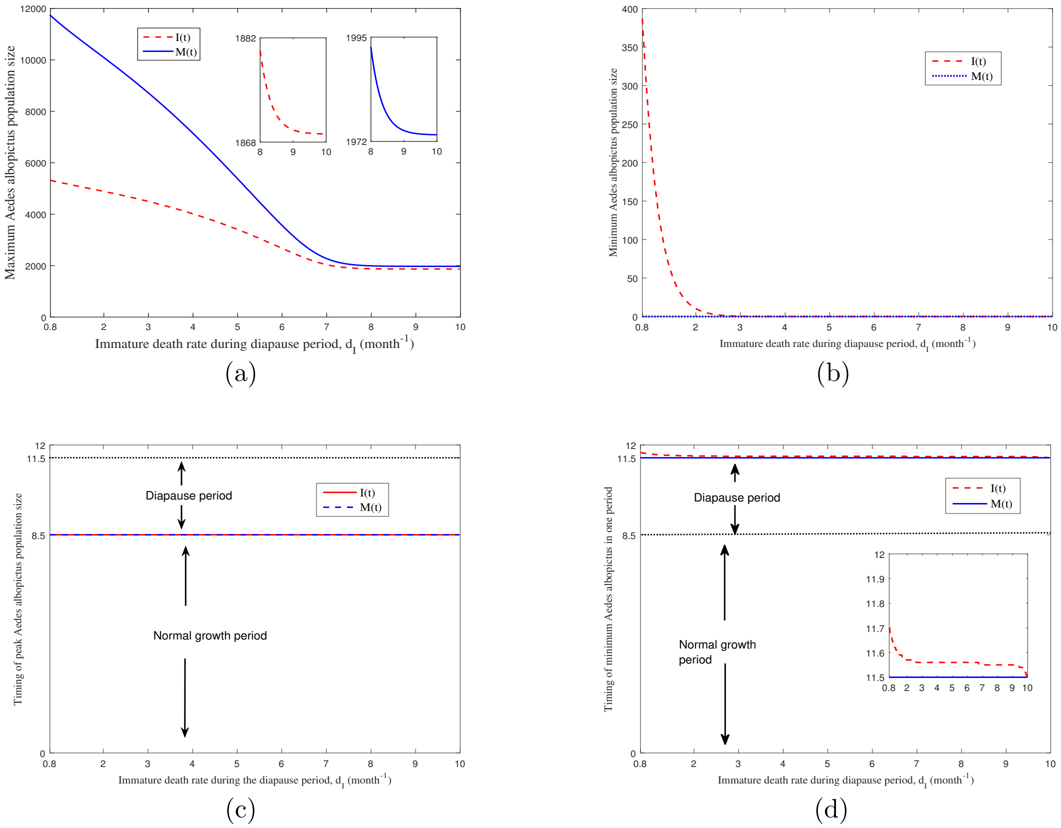
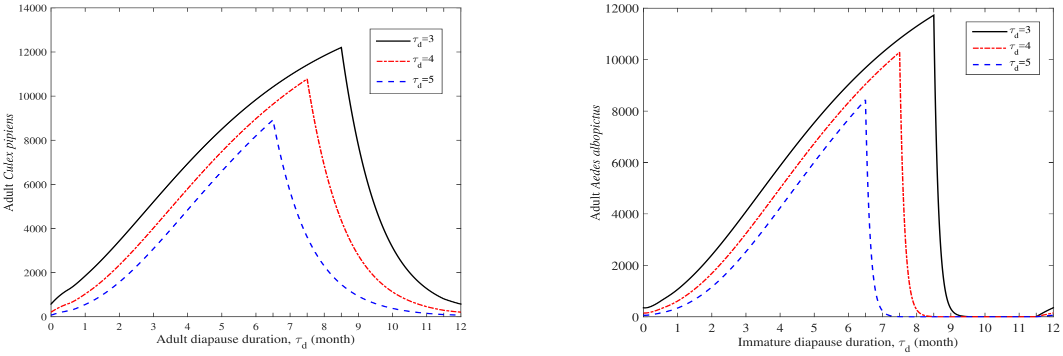
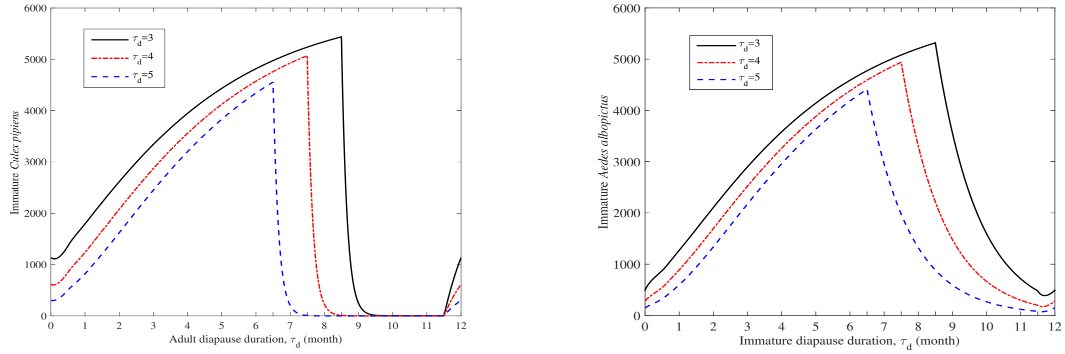


Figure 5.7: In the case of immature diapause for *Aedes albopictus*, the statistics of mosquito population abundance vary with the immature death rates during adult diapause period. (a) Maximum *Aedes albopictus* population size varies with changing d_I. (b) Minimum *Aedes albopictus* population size changes with varying d_I. (c) The timing of peak *Aedes albopictus* population size varies with changing d_I. (d) The timing of minimum *Aedes albopictus* population size changes with varying d_I. Here, we fix $d_M = 7$, the values of all other parameters are following Table 5.1.

dynamics. The curves in Fig. 5.8 describe the fluctuations of the population dynamics during one period with three different values of τ_d. There is little difference in the effects of varying diapause durations on the population dynamics of these two species. For each species, the lengthened diapause period lowers the peak and bottom population abundances and brings forward the peak time of each stage. Adult peak population abundance is more sensitive to the variations of diapause durations in comparison to immature peak. The possible reason is that longer diapause duration results in relatively low survivability during diapause period and shortening normal development time for mosquito population to rebounce.



(a) Adult diapause (b) Immature diapause



(c) Adult diapause (d) Immature diapause

Figure 5.8: The mosquito population abundance in one period with three different diapausing durations. (a) Population dynamics of adult *Culex pipiens*, which can survive through diapause. Here, $d_I = 6$ and $d_M = 0.9$. (b) Population dynamics of adult *Aedes albopitus*, which fail to survive during diapause period. Here, $d_I = 0.8$ and $d_M = 7$. (c) Population dynamics of immature *Culex pipiens* population, which cannot survive during diapause period. Here, $d_I = 6$ and $d_M = 0.9$. (d) Population dynamics of immature *Aedes albopitus*, which can survive through diapause. 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 Fig. 5.6(a) and Fig. 5.7(a)) 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 cause the extinction of the population. Once the environment conditions become suitable for development, the mosquito population will resume growing rapidly as long as there are few mosquitoes surviving through diapause. On account of the short developmental durations for mosquitoes, the normal growth period is long enough for mosquitoes to rebounce 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.

5.4.3 Controlling adult mosquito population

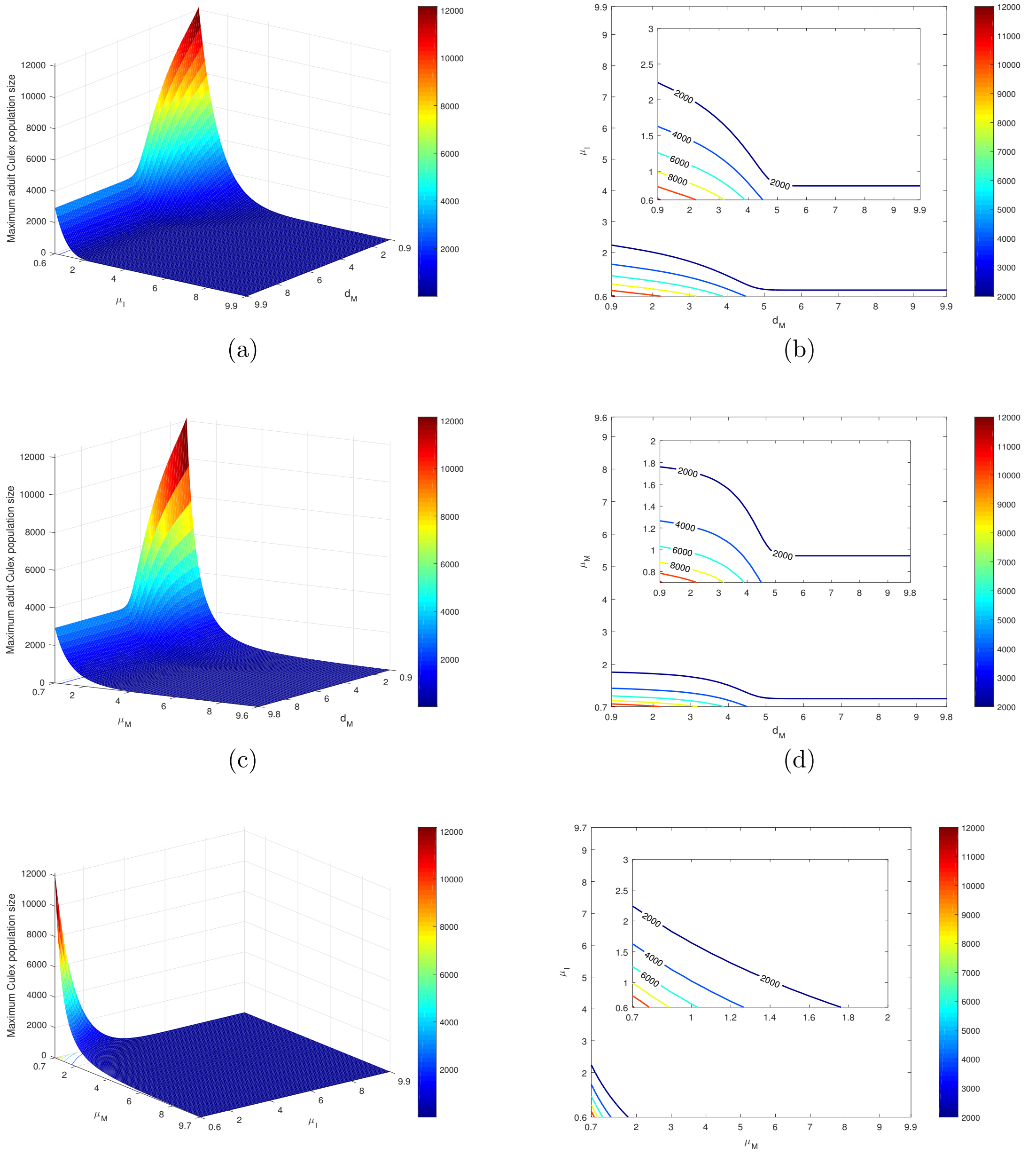
Since all mosquito-borne pathogens such as dengue, West Nile, Japanese encephalitis, Zika and chikunguya viruses are transmitted by adult mosquitoes [103], controlling or reducing the adult mosquito population size is an indispensable tool to fight against the transmission of the mosquito-borne diseases. Based on the sensitivity analysis in the 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 take consideration of the effects of eliminating mosquitoes in the normal growth period. To verify this conjecture, we perform a series of numerical simulations to investigate the integrated affects of the natural death rate and the diapausing death rate on the peak and average adult population sizes.

(1) Controlling peak adult population size

In this subsection, we mainly investigate how the peak adult population sizes of these two species changes with the simultaneous variations of normal and diapausing death rate. The surfaces illustrated in Figs. 5.9 and 5.10 depict the fluctuations of peak adult *Culex pipiens* and *Aedes albopictus* population size 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 (Fig. 5.9(b) and 5.9(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. 5.9(b), 5.9(d), 5.10(b) and 5.10(d)), which indicate 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 Fig. 5.9(f) and 5.10(f) suggest that increasing the adult death rate other than immature death rate during the normal growth period is relatively 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 a relatively larger effects on the peak of adult *Aedes albopictus* (see Fig. 5.9 and 5.10). 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 normal adult death rate.

(2) Controlling average adult population size

In this subsection, the investigation involves the effects of varying normal and diapausing death rates on the average adult population sizes of both species during one period. For each species, the average adult population size is decreasing with respect to the normal and diapausing death rates respectively, which can be seen from the surfaces in Fig. 5.11 and 5.12. By comparing with the effects of diapausing



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

Figure 5.9: The surfaces and contour plots depicting the variations of peak adult *Culex pipiens* population size with varying death rates. (a) The peak varies with changing μ_I and d_M. (b) The contour map of the surface in (a). (c) The peak varies with changing μ_M and d_M. (d) The contour map of the surface in (c). (e) The peak varies with changing μ_I and μ_M. In this case, we fix $d_M = 0.9$. (f) The contour map of the surface in (e). Here, $d_I = 6$, the values of all other parameters are following Table 5.1.

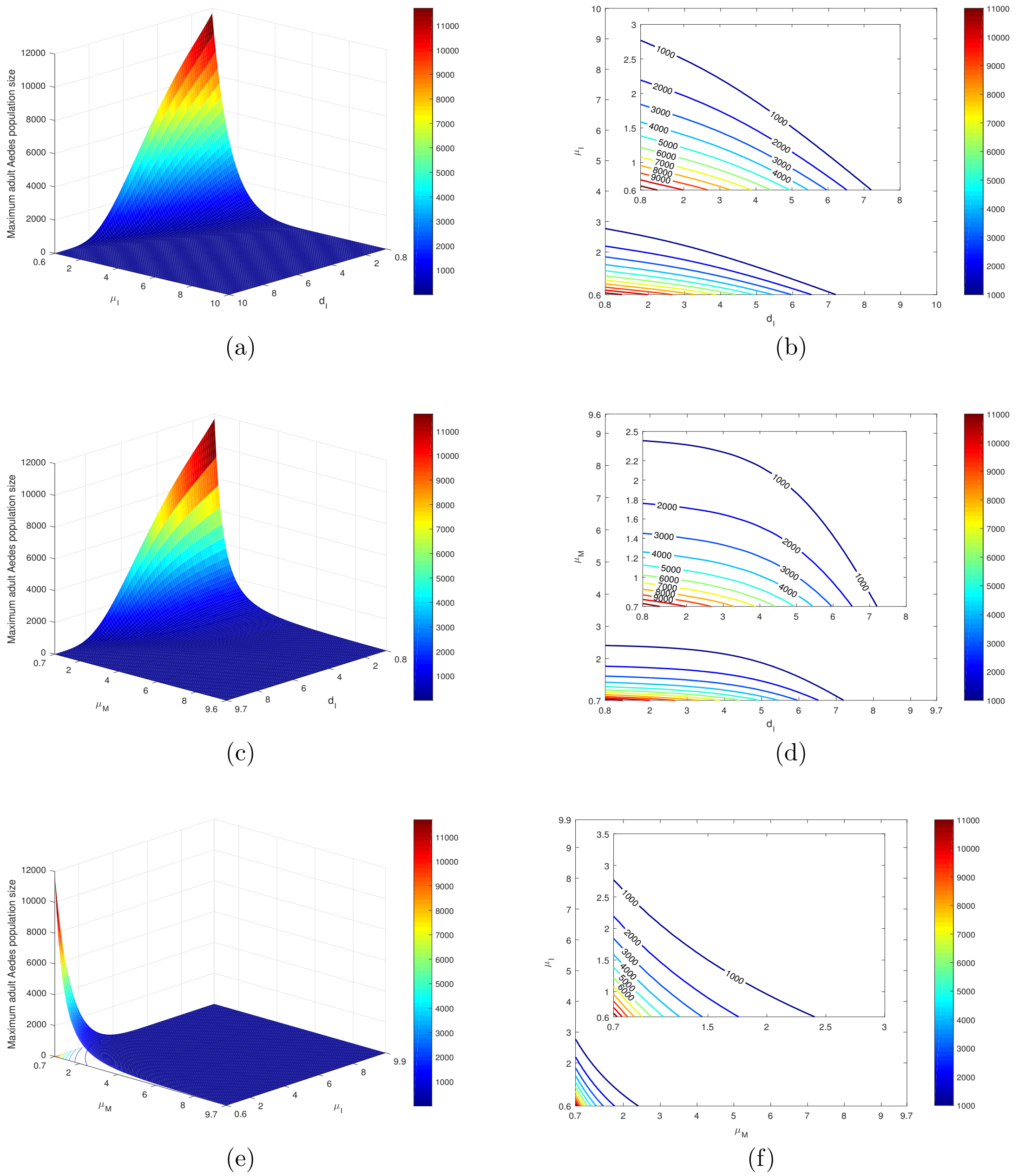


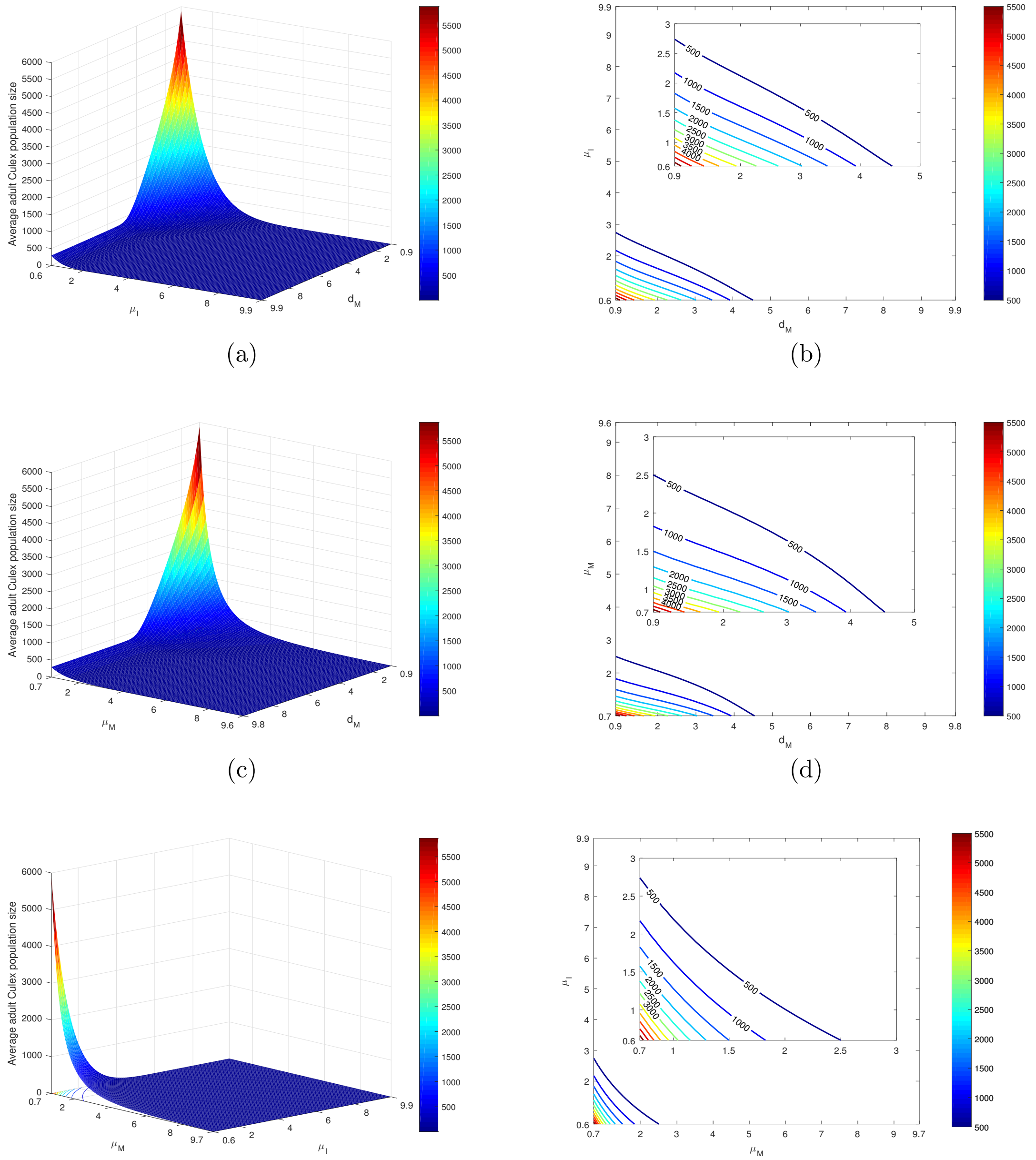
Figure 5.10: The surfaces and contour maps describing the fluctuations of peak adult *Aedes albopictus* population size with varying death rates. (a) The peak varies with changing μ_I and d_I. (b) The contour map of the surface in (a). (c) The peak varies with changing μ_M and d_I. (d) The contour map of the surface in (c). (e) The peak varies with changing μ_I and μ_M. In this case, we fix $d_I = 0.8$. (f) The contour map of the surface in (e). Here, $d_M = 7$, the values of all other parameters are following Table 5.1.

death rate on the peak in previous analysis, it is apparent that the influences of the diapausing death rate especially the diapausing adult death rate d_M on reducing the average adult population is stronger. Similarly, the corresponding contour plots show that less efforts is needed if we focus on controlling the average population size by increasing the death rate during the normal growth period.

5.5 Discussion

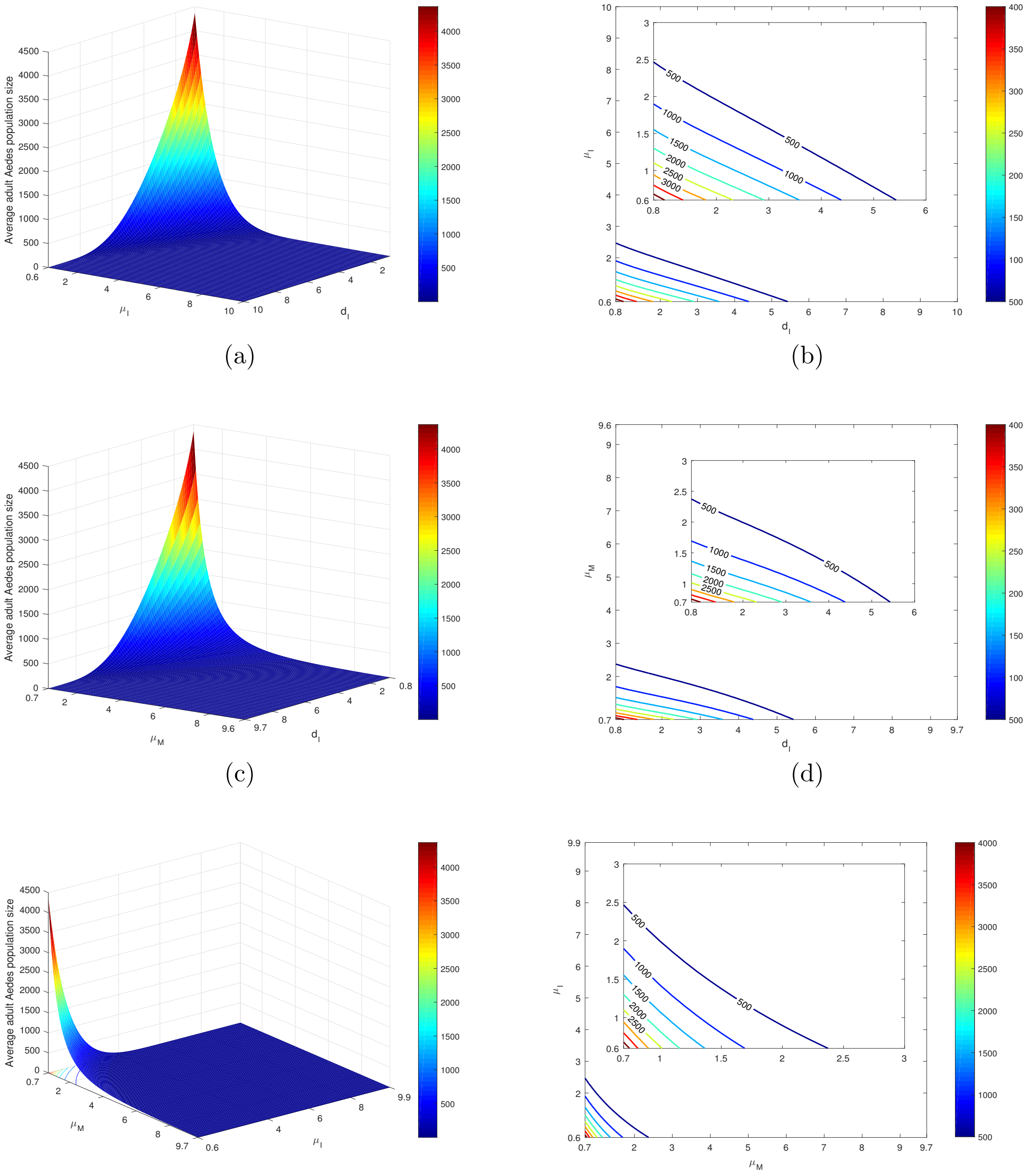
Diapause acting as a survival strategy in response to the adverse environment conditions is believed to play significant roles in preserving population size and maintaining the population growth. The effects of this survival mechanisms on species persistence remain unclear so far. In this project, we attempted to explore how diapause influences the population dynamics by constructing mathematically tractable models. Our results indicated 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 was 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 source 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 and average adult population sizes for these two species. These results indicate that the more effective approach to lower the peak of these two species is to reduce the death rate during the normal growth period especially the normal adult death rate rather than the diapausing death rate. However, the diapausing death rate tends to



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

Figure 5.11: The surfaces and contour plots depicting the variations of average adult *Culex pipiens* population size with varying death rates. (a) The average varies with changing μ_I and d_M. (b) The contour map of the surface in (a). (c) The average varies with changing μ_M and d_M. (d) The contour map of the surface in (c). (e) The average varies with changing μ_I and μ_M. In this case, we fix $d_M = 0.9$. (f) The contour map of the surface in (e). Here, $d_I = 6$, the values of all other parameters are following Table 5.1.



(a) (b)

(c) (d)

(e) (f)

Figure 5.12: The surfaces and contour maps describing the fluctuations of average adult *Aedes albopictus* population size with changing death rates. (a) The average varies with changing μ_I and d_I. (b) The contour map of the surface in (a). (c) The average varies with changing μ_M and d_I. (d) The contour map of the surface in (c). (e) The average varies with changing μ_I and μ_M. In this case, we fix $d_I = 0.8$. (f) The contour map of the surface in (e). Here, $d_M = 7$, the values of all other parameters are following Table 5.1.

have a stronger negative effects on the average adult population size compared with the effects on the peak. As an assistant intervention, killing mosquitoes during the diapause period to decrease the survivability of diapausing mosquitoes is feasible to lower the peak and average adult population sizes, which can prevent the massive outbreaks of mosquitoes to some extent.

Based on our unified model, future stochastic simulations with true climatic data may contribute to understanding the crucial ecological roles that diapause plays in response to spatiotemporal climatic changes [16]. Beyond the aspect of controlling mosquitoes, our modelling framework may shed light on the mechanisms for the differences in temporal or geographic distributions of different mosquito species due to diapause-related variations in seasonal abundance, which will further help us predict the spread of mosquito-borne diseases [15, 31].

Chapter 6

Conclusions and Future Work

In this chapter, we give some conclusions of this thesis and list a few interesting and challengeable research topics for future work.

6.1 Research summary

Even though various continuous age-structured models have been proposed to investigate the population dynamics for single species, few models take into consideration of other factors regulating population growth such as seasonal effects, spatial movement, intra-specific competition and diapause. In particular, the time-varying developmental durations or chronological age thresholds are rarely considered in modelling and analysing age-structured population growth as the induced time-dependent delays would challenge the model derivation and theoretical analysis. In this thesis, we analysed the age-structured population growth subject to the factors mentioned above through three different projects.

The first project (as shown in Chapter 3) was devoted to the analysis of an age-structured model subject to seasonal effects and time-dependent maturation period, with the application of tick population. We started from a generalised McKendrick-von Foerster equation with periodic age and time dependent coefficients to describe the population growth subject to seasonal effects. By employing the method of integration along characteristics, we obtained the equivalent integral equation, based on which we presented a detailed proof of the uniqueness and existence of the solution by applying contraction mapping theorem. With some reasonable biological assumptions and the tick population growth as our motivating example, we reduced the hyperbolic equation to a periodic age-structured model of four coupled delay differential equations with periodic delays, which was quite distinct from previous constant delay systems. For the long-term dynamics, we first analysed a special case, that is, the immature intra-specific competition is negligible due to abundant hosts for immature ticks. In this case, the pervious DDE model can be simplified into a new DDE model, the adult system of which can be decoupled. Based on this decoupled scalar subsystem, we defined the basic reproduction number $\mathcal{R}_0$ as the spectral radius of the next generation operator. To obtain the global attractivity of the positive periodic solution, we showed the solution semiflow is strongly monotone and strictly subhomogeneous in a novel space. Since other variables can be described by the integral form of the decoupled adult variable, the above result can be further extended to the full DDE system. In the case of considering immature intra-specific competition, the DDE model is challenging to conduct global analysis as it consists of a system of four coupled delay differential equations. Nevertheless, we obtained the global existence and uniqueness of the solution and showed the extinction and uniform persistence of tick population in terms of $\mathcal{R}_0$. Other than that, we acquired the existence of at least one positive periodic solution.

The second project (as shown in Chapter 4) mainly involved the analysis of a generalised age-structured model in the first project with the consideration of spatial movements regulating population growth. As a start, a simple case when the immature competition can be ignored due to dispersal capability of immature individuals, reduces the model to one equation for the density of matured individuals. For this single equation, the global existence, uniqueness of the solution and the existence of a global attractor were first shown. Inspired by the work [132, 134], the basic reproduction number $\mathcal{R}_0$ as the spectral radius of the next generation operator was defined and the global attractivity of the single equation in terms of $\mathcal{R}_0$ was established by exploring the theory of monotone and subhomogeneous semiflows. When immature competition exists, the analysis becomes somewhat tough as it is impossible to decouple two equations. In this case, we assumed the immature diffusion rate is negligible, which is justified biologically as follows: For some species such as mosquitoes and frogs experiencing the immature intra-specific competition, their juveniles have to compete food and resources with conspecifics in a restricted area due to inefficient mobility. Consequently, the new model consists of a delay differential equation coupled with a delayed reaction diffusion equation with periodic delays. We obtained the global existence, uniqueness of the solution and the existence of a global attractor. Moreover, the extinction and uniform persistence of the population were proved in terms of the newly defined basic reproduction number $\widetilde{\mathcal{R}}_0$.

In the last project (as shown in Chapter 5), we proposed a novel modelling framework to explore how diapause influences the age-structured population growth subject to seasonal effects. 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 was divided into three different intervals, with respective sets of equations in each interval. To explicitly describe population growth with different diapausing stage, we constructed three different models with an emphasis on mosquitoes, which are 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 the immature and adult diapause cases respectively. This project dealt with discontinuous growth rate of age-structured populations due to the occurrence of diapause, which is slightly different from the first two projects. In addition to the theoretical analysis, the numerical simulations were carried out on our unified model (U). We used 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 supported 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 four statistics characterising mosquito population dynamics were mainly concerned. Our results indicated 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 was 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. We further investigated the integrated effects of the diapausing and natural death rates on the peak and average adult population sizes for these two species. These results indicated that the more effective approach to lower the peak of these two species is to reduce the death rate during the normal growth period especially the normal adult death rate rather than the diapausing death rate. However, the diapausing death rate tends to have a stronger negative effects on the average adult population size compared with the effects on the peak.

6.2 Future Work

In this section, we list several interesting and challenging topics related to the projects in this thesis for future work.

In the first project, the basic reproduction number $\mathcal{R}_0$ is defined through a scalar periodic delay system. However, we can not conclude that its value is equal to the coefficient-averaged system as that for a periodic ordinary differential equation in [121, Lemma 2.2] since a delay is involved. This remains a future question. This project is focused on the mathematical analysis of the model and simulations have not been presented. Interesting simulations can also be performed for the model system to study the effects of seasonal weather variations and global warming on the population growth, as done in [91, 126]. Furthermore, in the current study, the global stability of the positive periodic solution is obtained when $\mathcal{R}_0 > 1$, under the condition that the intra-specific competition for immature ticks is negligible due to the sufficient availability of immature tick hosts. When the competition exists, we only show the uniform persistence of the system and existence of positive periodic solution in this scenario. The number of the positive periodic solutions is an interesting question to address in the future.

The diffusion coefficients of the model in the second project are assumed to be constant. In reality, the spatial dispersion and diffusion are greatly influence by the seasonal variations in biotic or abiotic factors such as resources and climate [132]. Organisms have a high mobility with warmer temperature and tend to keep motionless for the sake of saving energy to survive in colder days. Due to the heterogeneity of resource distribution in spatial scale, nonlinear diffusion or spatial dependent coefficients can also be incorporated in the system. Moreover, in various stages of some species, one stage, such as the immature stage of mosquitoes, is immobile and the diffusion rate can be negligible. Incorporating these biological factors in model formulation and analyzing the resultant models would be good topics for further studies. Furthermore, we focused on the mathematical analysis of the model in the case of $D_1 \cdot f(I) \equiv 0$ and did not consider the case of $D_1 \cdot f(I) > 0$, which will be another interesting problem for future investigation.

In the last project, we ignored the intra-specific competition among immatures during the normal population growth although the density-dependent self-regulation is accounted by assuming that the per-capita birth rate is a decreasing function of the adult density. In mosquitoes, intra-specific competition often occurs during the immature stage [117]. One feasible way to incorporate the immature intra-specific competition is to change the death term in system (5.2) 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 [38]. 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 rate, $\mu(a,t)$, lengths of maturation period, $\tau(t)$, and the diapause period, $\tau_d(t)$, which are strongly related 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 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.

Bibliography

[1] L. M. Abia, O. Angulo, and J. C. López-Marcos. Age-structured population models and their numerical solution. *Ecol. Modell.*, 188(1):112–136, 2005.

[2] W. G. Aiello and H. I. Freedman. A time-delay model of single-species growth with stage structure. *Math. Biosci.*, 101(2):139–153, 1990.

[3] V. R. Alekseev, B. De Stasio, and J. J. Gilbert. *Diapause in Aquatic Invertebrates: Theory and Human Use*, volume 84. Springer, 2007.

[4] B. W. Alto, L. P. Lounibos, S. Higgs, and S. A. Juliano. Larval competition differentially affects arbovirus infection in Aedes mosquitoes. *Ecology*, 86(12):3279–3288, 2005.

[5] B. W. Alto, L. P. Lounibos, C. N. Mores, and M. H. Reiskind. Larval competition alters susceptibility of adult Aedes mosquitoes to dengue infection. *Proc. R. Soc. B*, 275(1633):463–471, 2008.

[6] R. Altwegg. Trait-mediated indirect effects and complex life-cycles in two European frogs. *Evol. Ecol. Res.*, 4(4):519–536, 2002.

[7] N. Bacaër. Approximation of the basic reproduction number R_0 for vector-borne diseases with a periodic vector population. *Bull. Math. Biol.*, 69(3):1067–1091, 2007.

[8] N. Bacaër. *A Short History of Mathematical Population Dynamics.* Springer Science & Business Media, 2011.

[9] N. Bacaër and E. H. Ait Dads. On the biological interpretation of a definition for the parameter R_0 in periodic population models. *J. Math. Biol.*, 65(4):601–621, 2012.

[10] N. Bacaër and S. Guernaoui. The epidemic threshold of vector-borne diseases with seasonality: The case of cutaneous leishmaniasis in Chichaoua, Morocco. *J. Math. Biol.*, 53(3):421–436, 2006.

[11] R. E. Bellman and K. L. Cooke. *Differential-Difference Equations.* Rand Corporation, 1963.

[12] V. N. Belozerov. Diapause and biological rhythms in ticks. In *Physiology of Ticks: Current Themes in Tropical Science. Edited by Frederick D. Obenchain, Rachel Galun*, pages 469–500. Pergamon Press, Oxford, 1982.

[13] V. N. Belozerov and R. L. Naumov. Nymphal diapause and its photoperiodic control in the tick *Ixodes scapularis* (Acari: Ixodidae). *Folia Parasitol.*, 49(4):314–318, 2002.

[14] R. J. Beverton and S. J. Holt. *On the Dynamics of Exploited Fish Populations*, volume 11. Springer Science & Business Media, 2012.

[15] M. E. Bradshaw and C. M. Holzapfel. Resource limitation, habitat segregation, and species interactions of British tree-hole mosquitoes in nature. *Oecologia*, 90(2):227–237, 1992.

[16] W. E. Bradshaw. Geography of photoperiodic response in diapausing mosquito. *Nature*, 262(5567):384–386, 1976.

[17] F. Brauer and C. Castillo-Chavez. *Mathematical Models in Population Biology and Epidemiology*, volume 40. Springer, 2001.

[18] C. J. Browne and S. S. Pilyugin. Global analysis of age-structured within-host virus model. *Discrete Contin. Dyn. Syst. Ser. B*, 18(8):1999–2017, 2013.

[19] J. L. Buth, R. A. Brust, and R. A. Ellis. Development time, oviposition activity and onset of diapause in *Culex tarsalis*, *Culex restuans* and *Culiseta inornata* in southern Manitoba. *J. Am. Mosq. Control Assoc.*, 6(1):55–63, 1990.

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

[21] R. S. Cantrell and C. Cosner. *Spatial Ecology via Reaction-Diffusion Equations.* John Wiley & Sons, 2004.

[22] B. Charlesworth. *Evolution in age-structured populations*, volume 2. Cambridge University Press, 1994.

[23] J. E. Cohen. Human population: The next half century. *Science*, 302(5648):1172–1175, 2003.

[24] L. E. Craig, D. E. Norris, M. L. Sanders, G. E. Glass, and B. S. Schwartz. Acquired resistance and antibody response of raccoons (*Procyon lotor*) to sequential feedings of *Ixodes scapularis* (Acari: Ixodidae). *Vet. Parasitol.*, 63(3-4):291–301, 1996.

[25] G. Cruz-Pacheco, L. Esteva, J. A. Montaõ-Hirose, and C. Vargas. Modelling the dynamics of West Nile virus. *Bull. Math. Biol.*, 67(6):1157, 2005.

[26] J. M. Cushing. *An Introduction to Structured Population Dynamics*, volume 71. SIAM, Philadelphia, 1998.

[27] F. Dantas-Torres, B. B. Chomel, and D. Otranto. Ticks and tick-borne diseases: A one health perspective. *Trends Parasitol.*, 28(10):437–446, 2012.

[28] P. Daszak, A. A. Cunningham, and A. D. Hyatt. Emerging infectious diseases of wildlife–threats to biodiversity and human health. *Science*, 287(5452):443, 2000.

[29] K. Deimling. *Nonlinear Functional Analysis.* Springer, Berlin, 2010.

[30] D. L. Denlinger. Regulation of diapause. *Annu. Rev. Entomol.*, 47(1):93–122, 2002.

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

[32] D. L. Denlinger and R. E. Lee Jr. *Low Temperature Biology of Insects.* Cambridge University Press, 2010.

[33] D. L. Denlinger, G. D. Yocum, J. P. Rinehart, and L. I. Gilbert. Hormonal control of diapause. In *Insect Endocrinology. Edited by L. I. Gilbert*, pages 430–463. San Diego, CA: Academic, 2004.

[34] O. Diekmann, H. J. A. P. Heesterbeek, and J. A. J. Metz. On the definition and the computation of the basic reproduction ratio R_0 in models for infectious diseases in heterogeneous populations. *J. Math. Biol.*, 28(4):365–382, 1990.

[35] M. A. Dziminski. Intraspecific competition in the larvae of quacking frogs (Crinia georgiana). *Copeia*, 2009(4):724–726, 2009.

[36] D. A. Ewing, C. A. Cobbold, B. V. Purse, M. A. Nunn, and S. M. White. Modelling the effect of temperature on the seasonal population dynamics of temperate mosquitoes. *J. Theor. Biol.*, 400:65–79, 2016.

[37] G. Fan, H. R. Thieme, and H. Zhu. Delay differential systems for tick population dynamics. *J. Math. Biol.*, 71(5):1017–1048, 2015.

[38] J. Fang, S. A. Gourley, and Y. Lou. Stage-structured models of intra-and interspecific competition within age classes. *J. Differ. Equ.*, 260(2):1918–1953, 2016.

[39] W. Feller. On the integral equation of renewal theory. In *Mathematical Demography*, pages 131–156. Springer, 1977.

[40] R. D. Flannagan, S. P. Tammariello, K. H. Joplin, R. A. Cikra-Ireland, G. D. Yocum, and D. L. Denlinger. Diapause-specific gene expression in pupae of the flesh fly *Sarcophaga crassipalpis*. *Proc. Natl. Acad. Sci. U. S. A.*, 95(10):5616–5620, 1998.

[41] A. Friedman. *Partial Differential Equations of Parabolic Type.* Courier Dover Publications, 2008.

[42] M. S. Gaines and L. R. McClenaghan Jr. Dispersal in small mammals. *Ann. Rev. EcoL Syst.*, 11(1):163–196, 1980.

[43] H. Gong, A. T. DeGaetano, and L. C. Harrington. Climate-based models for West Nile Culex mosquito vectors in the Northeastern US. *Int. J. Biometeorol.*, 55(3):435–446, 2011.

[44] S. A. Gourley and Y. Kuang. Wavefronts and global stability in a time-delayed population model with stage structure. *Proc. R. Soc. Lond. A*, 459(2034):1563–1579, 2003.

[45] S. A. Gourley, R. Liu, and Y. Lou. Intra-specific competition and insect larval development: A model with time-dependent delay. *P. Roy. Soc. Edinb. A*, 147(2):353–369, 2017.

[46] S. A. Gourley, R. Liu, and J. Wu. Spatiotemporal patterns of disease spread: Interaction of physiological structure, spatial movements, disease progression and human intervention. In *Structured Population Models in Biology and Epidemiology*, volume 1936, pages 165–208. Springer, Berlin, 2008.

[47] S. A. Gourley, R. Liu, and J. Wu. Spatiotemporal distributions of migratory birds: patchy models with delay. *SIAM J. Appl. Dyn. Syst.*, 9(2):589–610, 2010.

[48] S. A. Gourley and J. Wu. Delayed non-local diffusive systems in biological invasion and disease spread. In *Nonlinear Dynamics and Evolution Equations*, pages 137–200. American Mathematical Society, 2006.

[49] W. S. C. Gurney, R. M. Nisbet, and J. H. Lawton. The systematic formulation of tractable single-species population models incorporating age structure. *J. Anim. Ecol.*, 52(2):479–495, 1983.

[50] M. E. Gurtin and R. C. MacCamy. Non-linear age-dependent population dynamics. *Arch. Ration. Mech. Anal.*, 54(3):281–300, 1974.

[51] D. A. Hahn and D. L. Denlinger. Energetics of insect diapause. *Annu. Rev. Entomol.*, 56:103–121, 2011.

[52] S. M. Hanson. Field overwinter survivorship of *Aedes albopictus* eggs in Japan. *J. Am. Mosq. Control Assoc.*, 11(3):354–357, 1995.

[53] S. M. Hanson and G. B. Craig Jr. Cold acclimation, diapause, and geographic origin affect cold hardiness in eggs of *Aedes albopictus* (Diptera: Culicidae). *J. Med. Entomol.*, 31(2):192–201, 1994.

[54] K. Hasegawa. The diapause hormone of the silkworm, *Bombyx mori*. *Nature*, 179(4573):1300–1301, 1957.

[55] P. Hess. *Periodic-Parabolic Boundary Value Problems and Positivity.* Longman Scientific & Technical, 1991.

[56] I. Hodek, H. F. van Emden, and A. Honek. *Ecology and Behaviour of the Ladybird Beetles (Coccinellidae).* John Wiley & Sons, 2012.

[57] M. Iannelli. *Mathematical Theory of Age-Structured Population Dynamics.* Giardini Editori e Stampatori in Pisa, 1995.

[58] H. Inaba. On a new perspective of the basic reproduction number in heterogeneous environments. *J. Math. Biol.*, 65(2):309–348, 2012.

[59] H. Inaba. *Age-Structured Population Dynamics in Demography and Epidemiology.* Springer, 2017.

[60] P. Jia, L. Lu, X. Chen, J. Chen, L. Guo, X. Yu, and Q. Liu. A climate-driven mechanistic population model of *Aedes albopictus* with diapause. *Parasit. Vectors*, 9(1):175, 2016.

[61] Y. Jin and X.-Q. Zhao. Spatial dynamics of a nonlocal periodic reaction-diffusion model with stage structure. *SIAM J. Math. Anal.*, 40(6):2496–2516, 2009.

[62] S. Kingsland. Alfred J. Lotka and the origins of theoretical population ecology. *Proc. Natl. Acad. Sci. U. S. A.*, 112(31):9493–9495, 2015.

[63] V. Košťál. Eco-physiological phases of insect diapause. *J. Insect Physiol.*, 52(2):113–127, 2006.

[64] J. E. Laing and J. E. Corrigan. Diapause induction and post-diapause emergence in *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae): The role of host species, temperature, and photoperiod. *Can. entomol.*, 127(1):103–110, 1995.

[65] M. Lakovic, H.-J. Poethke, and T. Hovestadt. Dispersal timing: Emigration of insects living in patchy environments. *PloS One*, 10(7):e0128672, 2015.

[66] M. Legros, A. L. Lloyd, Y. Huang, and F. Gould. Density-dependent intraspecific competition in the larval stage of Aedes aegypti (Diptera: Culicidae): revisiting the current paradigm. *J. Med. Entomol.*, 46(3):409–419, 2009.

[67] P. T. Leisnham, L. M. Sala, and S. A. Juliano. Geographic variation in adult survival and reproductive tactics of the mosquito *Aedes albopictus*. *J. Med. Entomol.*, 45(2):210–221, 2008.

[68] P. H. Leslie. On the use of matrices in certain population mathematics. *Biometrika*, 33(3):183–212, 1945.

[69] S. A. Levin. Dispersion and population interactions. *Am. Nat.*, 108(960):207–228, 1974.

[70] J. Li and F. Brauer. Continuous-time age-structured models in population dynamics and epidemiology. In *Mathematical Epidemiology*, pages 205–227. Springer, 2008.

[71] X. Liang and X.-Q. Zhao. Asymptotic speeds of spread and traveling waves for monotone semiflows with applications. *Commun. Pure Appl. Math.*, 60(1):1–40, 2007.

[72] K. Liu, Y. Lou, and J. Wu. Analysis of an age structured model for tick populations subject to seasonal effects. *J. Differ. Equ.*, 263(4):2078–2112, 2017.

[73] A. J. Lotka. The stability of the normal age distribution. *Proc. Natl. Acad. Sci. U. S. A.*, 8(11):339–345, 1922.

[74] A. J. Lotka. On an integral equation in population analysis. *Ann. Math. Stat.*, 10(2):144–161, 1939.

[75] Y. Lou, J. Wu, and X. Wu. Impact of biodiversity and seasonality on Lyme-pathogen transmission. *Theor. Biol. Med. Model.*, 11(1):50, 2014.

[76] Y. Lou and X.-Q. Zhao. A climate-based malaria transmission model with structured vector population. *SIAM J. Appl. Math.*, 70(6):2023–2044, 2010.

[77] Y. Lou and X.-Q. Zhao. A theoretical approach to understanding population dynamics with seasonal developmental durations. *J. Nonlinear Sci.*, 27(2):573–603, 2017.

[78] A. Lunardi. *Analytic Semigroups and Optimal Regularity in Parabolic Problems*. Springer Science & Business Media, 2012.

[79] P. Magal and X.-Q. Zhao. Global attractors and steady states for uniformly persistent dynamical systems. *SIAM J. Math. Anal.*, 37(1):251–275, 2005.

[80] G. Marini, G. Guzzetta, F. Baldacchino, D. Arnoldi, F. Montarsi, G. Capelli, A. Rizzoli, S. Merler, and R. Rosà. The effect of interspecific competition on the temporal dynamics of *Aedes albopictus* and *Culex pipiens*. *Parasit. Vectors*, 10(1):102, 2017.

[81] R. H. Martin. *Nonlinear Operators and Differential Equations in Banach Spaces*. Wiley, New York, 1976.

[82] R. H. Martin and H. L. Smith. Abstract functional-differential equations and reaction-diffusion systems. *Trans. Am. Math. Soc.*, 321(1):1–44, 1990.

[83] M. J. Mcgrady, M. Ueta, E. R. Potapov, I. Utekhina, V. Masterov, A. Ladyguine, V. Zykov, J. Cibor, M. Fuller, and W. S. Seegar. Movements by juvenile and immature Steller's Sea Eagles Haliaeetus pelagicus tracked by satellite. *Ibis*, 145(2):318–328, 2003.

[84] A. G. McKendrick. Applications of mathematics to medical problems. *Proc. Edinburgh Math. Soc.*, 44:98–130, 1926.

[85] J. A. J. Metz and O. Diekmann. *The Dynamics of Physiologically Structured Populations*. Springer-Verlag, Berlin Heidelberg, 1986.

[86] H. Mooney. Invasion Dynamics: From Invasion Biology to Invasion Science, 2017.

[87] R. M. Nisbet. Delay-differential equations for structured populations. In *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems*, pages 89–118. Springer, 1997.

[88] R. M. Nisbet and W. S. C. Gurney. The systematic formulation of population models for insects with dynamically varying instar duration. *Theor. Popul. Biol.*, 23(1):114–135, 1983.

[89] N. H. Ogden, M. Bigras-Poulin, C. J. O'callaghan, I. K. Barker, L. R. Lindsay, A. Maarouf, K. E. Smoyer-Tomic, D. Waltner-Toews, and D. Charron. A dynamic population model to investigate effects of climate on geographic range and seasonality of the tick *Ixodes scapularis*. *Int. J. Parasitol.*, 35(4):375–389, 2005.

[90] N. H. Ogden, L. R. Lindsay, G. Beauchamp, D. Charron, A. Maarouf, C. J. O'Callaghan, D. Waltner-Toews, and I. K. Barker. Investigation of relationships between temperature and developmental rates of tick *Ixodes scapularis* (Acari: Ixodidae) in the laboratory and field. *J. Med. Entomol.*, 41(4):622–633, 2004.

[91] N. H. Ogden, M. Radojevic, X. Wu, V. R. Duvvuri, P. A. Leighton, and J. Wu. Estimated effects of projected climate change on the basic reproductive number of the Lyme disease vector *Ixodes scapularis*. *Environ. Health Perspect.*, 122(6):631, 2014.

[92] R. S. Ostfeld. *Lyme Disease: The Ecology of a Complex System.* Oxford University Press, New York, 2010.

[93] K. A. Pawelek, P. Niehaus, C. Salmeron, E. J. Hager, and G. J. Hunt. Modeling dynamics of *Culex pipiens* complex populations and assessing abatement strategies for West Nile Virus. *PloS One*, 9(9):e108452, 2014.

[94] A. Pazy. *Semigroups of Linear Operators and Applications to Partial Differential Equations*, volume 44. Springer-Verlag, New York, 1983.

[95] G. Pritchard. The roles of temperature and diapause in the life history of a temperate-zone dragonfly: *Argia vivida* (Odonata: Coenagrionidae). *Ecol. Entomol.*, 14(1):99–108, 1989.

[96] M. H. Reiskind and L. P. Lounibos. Effects of intraspecific larval competition on adult longevity in the mosquitoes *Aedes aegypti* and *Aedes albopictus*. *Med. Vet. Entomol.*, 23(1):62–68, 2009.

[97] J. P. Rinehart, R. M. Robich, and D. L. Denlinger. Enhanced cold and desiccation tolerance in diapausing adults of *Culex pipiens*, and a role for *Hsp70* in response to cold shock but not as a component of the diapause program. *J. Med. Entomol.*, 43(4):713–722, 2006.

[98] G. R. Sell and Y. You. *Dynamics of Evolutionary Equations*, volume 143. Springer Science & Business Media, 2013.

[99] F. R. Sharpe and A. J. Lotka. A problem in age-distribution. *Lond. Edinb. Dubl. Phil. Mag.*, 21(124):435–438, 1911.

[100] J. B. Silver. *Mosquito Ecology: Field Sampling Methods.* Springer Science & Business Media, 2007.

[101] C. Sim and D. L. Denlinger. Insulin signaling and FOXO regulate the overwintering diapause of the mosquito *Culex pipiens*. *Proc. Natl. Acad. Sci. U. S. A.*, 105(18):6777–6781, 2008.

[102] D. Smith and N. Keyfitz. *Mathematical Demography: Selected Papers*, volume 6. Springer Science & Business Media, 2012.

[103] D. L. Smith, T. A. Perkins, R. C. Reiner Jr, C. M. Barker, T. Niu, L. F. Chaves, A. M. Ellis, D. B. George, A. Le Menach, J. Pulliam, et al. Recasting the theory of mosquito-borne pathogen transmission dynamics and control. *Trans. R. Soc. Trop. Med. Hyg.*, 108(4):185–197, 2014.

[104] H. L. Smith. Reduction of structured population models to threshold-type delay equations and functional differential equations: A case study. *Math. Biosci.*, 113(1):1–23, 1993.

[105] H. L. Smith. *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems. Mathematical Surveys and Monographs*, volume 41. American Mathematical Society, 1995.

[106] H. L. Smith. *An Introduction to Delay Differential Equations with Applications to the Life Sciences*, volume 57. Springer, New York, 2010.

[107] H. L. Smith and X.-Q. Zhao. Robust persistence for semidynamical systems. *Nonlinear Anal. Theory Methods Appl.*, 47(9):6169–6179, 2001.

[108] J. W.-H. So, J. Wu, and X. Zou. Structured population on two patches: Modelling dispersal and delay. *J. Math. Biol.*, 43(1):37–51, 2001.

[109] A. Spielman. Structure and seasonality of nearctic *Culex pipiens* populations. *Ann. N. Y. Acad. Sci.*, 951(1):220–234, 2001.

[110] M. J. Tauber and C. A. Tauber. Insect seasonality: Diapause maintenance, termination, and postdiapause development. *Annu. Rev. Entomol.*, 21(1):81–107, 1976.

[111] M. J. Tauber, C. A. Tauber, and S. Masaki. *Seasonal Adaptations of Insects.* Oxford University Press on Demand, 1986.

[112] R. A. Taylor, A. White, and J. A. Sherratt. How do variations in seasonality affect population cycles? *Proc. R. Soc. B*, 280(1754):2012–2714, 2013.

[113] H. R. Thieme. Spectral bound and reproduction number for infinite-dimensional population structure and time heterogeneity. *SIAM J. Appl. Math.*, 70(1):188–211, 2009.

[114] H. R. Thieme and X.-Q. Zhao. Asymptotic speeds of spread and traveling waves for integral equations and delayed reaction–diffusion models. *J. Differ. Equ.*, 195(2):430–470, 2003.

[115] L. Toma, F. Severini, M. Di Luca, A. Bella, and R. Romi. Seasonal patterns of oviposition and egg hatching rate of *Aedes albopictus* in Rome. *J. Am. Mosq. Control Assoc.*, 19(1):19–22, 2003.

[116] A. Tran, G. L'Ambert, G. Lacour, R. Benoît, M. Demarchi, M. Cros, P. Cailly, M. Aubry-Kientz, T. Balenghien, and P. Ezanno. A rainfall-and temperature-driven abundance model for *Aedes albopictus* populations. *Int. J. Environ. Res. Public Health*, 10(5):1698–1719, 2013.

[117] I. Tsurim, A. Silberbush, O. Ovadia, L. Blaustein, and Y. Margalith. Inter- and intra-specific density-dependent effects on life history and development strategies of larval mosquitoes. *PLoS One*, 8(3):e57875, 2013.

[118] P. van den Driessche and J. Watmough. Reproduction numbers and subthreshold endemic equilibria for compartmental models of disease transmission. *Math. Biosci.*, 180(1):29–48, 2002.

[119] E. B. Vinogradova. Diapause in aquatic insects, with emphasis on mosquitoes. In *Diapause in Aquatic Invertebrates. Edited by: V. R. Alekseev, B. De Stasio, J. J. Gilbert*, pages 83–113. Springer, London, 2007.

[120] H. von Foerster. Some remarks on changing populations. In *The Kinetics of Cellular Proliferation*, pages 382–407. Grune and Stratton, New York, 1959.

[121] W. Wang and X.-Q. Zhao. Threshold dynamics for compartmental epidemic models in periodic environments. *J. Dyn. Differ. Equ.*, 20(3):699–717, 2008.

[122] G. F. Webb. *Theory of Nonlinear Age-Dependent Population Dynamics.* Marcel Dekker, New York, 1985.

[123] P. Willadsen and F. Jongejan. Immunology of the tick–host interaction and the control of ticks and tick-borne diseases. *Parasitol. Today*, 15(7):258–262, 1999.

[124] M. L. Wilson, T. S. Litwin, T. A. Gavin, M. C. Capkanis, D. C. Maclean, and A. Spielman. Host-dependent differences in feeding and reproduction of *Ixodes dammini* (Acari: Ixodidae). *J. Med. Entomol.*, 27(6):945–954, 1990.

[125] J. Wu. *Theory and Applications of Partial Functional Differential Equations*, volume 119. Springer-Verlag, New York, 1996.

[126] X. Wu, V. R. Duvvuri, Y. Lou, N. H. Ogden, Y. Pelcat, and J. Wu. Developing a temperature-driven map of the basic reproductive number of the emerging tick vector of Lyme disease *Ixodes scapularis* in Canada. *J. Theor. Biol.*, 319:50–61, 2013.

[127] X. Wu, V. R. Duvvuri, and J. Wu. Modeling dynamical temperature influence on the *Ixodes scapularis* population. In *2010 International Congress on Environmental Modelling and Software*, pages 2272–2287, 2010.

[128] X. Wu, F. M. G. Magpantay, J. Wu, and X. Zou. Stage-structured population systems with temporally periodic delay. *Math. Methods Appl. Sci.*, 38(16):3464–3481, 2015.

[129] D. Xu and X.-Q. Zhao. A nonlocal reaction-diffusion population model with stage structure. *Canad. Appl. Math. Quart.*, 11(3):303–319, 2003.

[130] D. Xu and X.-Q. Zhao. Dynamics in a periodic competitive model with stage structure. *J. Math. Anal. Appl.*, 311(2):417–438, 2005.

[131] T. Yi and X. Zou. Global dynamics of a delay differential equation with spatial non-locality in an unbounded domain. *J. Differ. Equ.*, 251(9):2598–2611, 2011.

[132] L. Zhang, Z.-C. Wang, and X.-Q. Zhao. Threshold dynamics of a time periodic reaction–diffusion epidemic model with latent period. *J. Differ. Equ.*, 258(9):3011–3036, 2015.

[133] X.-Q. Zhao. Permanence implies the existence of interior periodic solutions for FDEs. *Qual. Theory Differ. Eq. Appl.*, 2:125–137, 2008.

[134] X.-Q. Zhao. Basic reproduction ratios for periodic compartmental models with time delay. *J. Dyn. Differ. Equ.*, 29(1):67–82, 2017.

[135] X.-Q. Zhao. *Dynamical Systems in Population Biology.* Springer-Verlag, New York, 2017.

[136] X.-Q. Zhao and Z.-J. Jing. Global asymptotic behavior in some cooperative systems of functional differential equations. *Can. Appl. Math. Q.*, 4(4):421–444, 1996.