# Global dynamics of periodic infectious disease models with time-dependent delays

by

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# Abstract

Many infectious diseases have seasonal trends and exhibit variable periods of peak seasonality. Understanding the population dynamics due to seasonal changes becomes very important for predicting and controlling disease transmission risks. For some directly transmitted and vector-borne diseases, the length of the incubation period strongly depends on the temperature.

This thesis is devoted to the study of the global dynamics of some periodic epidemic models with periodic incubation periods. We start with a classical SEIRS epidemic model with a time-dependent latent period in Chapter 2. Moreover, vector-borne diseases, such as West Nile virus, bluetongue, and malaria, are always highly dependent on seasonal change, especially the temperature. To investigate the seasonal effects and temperature-dependent delays on West Nile virus, we present a periodic functional differential equations model with the vertical transmission, the periodic maturation delay, and the periodic extrinsic incubation period in Chapter 3. In Chapter 4, we propose a bluetongue model with seasonality and temperature-dependent incubation period, which describes the dynamics of bluetongue transmission via cattle and sheep as hosts and midges as vectors. To explore the effects of the spatial and temporal heterogeneity in hosts and vectors, and only vector movements on the spread of bluetongue, we develop a nonlocal periodic reaction-diffusion model of bluetongue disease with periodic time delays in Chapter 5.

Based on the theory of the basic reproduction ratio, we derive and numerically compute the basic reproduction ratio for our models. By the theory of dynamical systems, we show that the basic reproduction ratio acts as a threshold parameter for the global dynamics for each model. Numerical simulations or case studies are carried out to illustrate the analytic results and help us provide some new findings. At the end of this thesis, we present a brief summary and some interesting future works.

To my dearest family

# Lay summary

The emergence or resurgence of the directly transmitted diseases and vector-borne diseases of humans or animals has brought serious consequences for human and animal health, and economics, and is taking more and more attention in mathematical epidemiology. This thesis focuses on the global dynamics of four periodic disease models with time-dependent delays.

To understand the seasonality of disease, we first considered a periodic SEIRS epidemic model with a periodic time delay. We then derived the basic reproduction ratio and obtained that it acts as a threshold parameter for the uniform persistence and global extinction of the disease. For vector-borne diseases, we considered a periodic West Nile virus model with the vertical transmission, periodic maturation delay and periodic extrinsic incubation period (EIP). We studied its global dynamics and conducted a case study in Orange County, California, USA. We showed that the model-simulated result matches with the reported data well.

Moreover, we presented a bluetongue transmission model accounting for midges with a time-dependent EIP as vectors, and cattle and sheep as hosts. We derived the basic sheep/midges reproduction ratio, the basic reproduction ratio without sheep, and the basic disease reproduction ratio for the whole system, which serve as important threshold parameters for the persistence and extinction of the disease (population). Bluetongue affects the life cycles of two host species very differently. Then uniform disease persistence occurs in two different scenarios, which are distinguished by the basic reproduction ratio without sheep. Further, we incorporated the spatial heterogeneous structure and temperature-dependent EIP into a nonlocal reaction-diffusion model. We established its global dynamics in terms of the basic reproduction ratio. Numerically, we studied the bluetongue transmission in Corsica Island, France, and investigated the impact of some model parameters on the basic reproduction ratio.

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# Statement of contribution

Chapters 2–5 of this thesis consist of the following papers:

Chapter 2: Fuxiang Li and Xiao-Qiang Zhao, A periodic SEIRS epidemic model with a time-dependent latent period, Journal of Mathematical Biology, 78 (2019): 1553–1579.

Chapter 3: Fuxiang Li, Junli Liu and Xiao-Qiang Zhao, A West Nile virus model with vertical transmission and periodic time delays, Journal of Nonlinear Science, 30 (2020): 449–486.

Chapter 4: Fuxiang Li and Xiao-Qiang Zhao, Dynamics of a periodic Bluetongue model with a temperature-dependent incubation period, SIAM Journal on Applied Mathematics, 79 (2019): 2479–2505.

Chapter 5: Fuxiang Li and Xiao-Qiang Zhao, Global dynamics of a nonlocal periodic reaction-diffusion model of Bluetongue disease, Journal of Differential Equations, in review.

The work of the above papers was performed by the author under the supervision of Professor Xiao-Qiang Zhao.

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# Chapter 1

# Preliminaries

In this chapter, we introduce some terminologies and known results which will be used in this thesis. They are involved in chain transitivity, global attractor, uniform persistence, monotone dynamics, and the theory of basic reproduction ratio.

## 1.1 Chain transitivity and global attractor

Let $X$ be a metric space with metric $d$ and $f : X \to X$ a continuous map. For a nonempty invariant set $M$ (i.e., $f(M) = M$), the set $W^s(M) := \{x \in X : \lim_{n\to\infty} d(f^n(x), M) = 0\}$ is called the stable set of $M$. The omega limit set of $x$ is defined as $\omega(x) = \{y \in X : f^{n_k}(x) \to y, \text{ for some } n_k \to +\infty\}$. A negative orbit through $x = x_0$ is a sequence $\gamma^-(x) = \{x_k\}_{-\infty}^{0}$ such that $f(x_{k-1}) = f(x_k)$ for integers $k \leq 0$. If $\gamma^+(x) = \{f_n(x) : n \geq 0\}$ $(\gamma^-(x))$ is precompact (i.e., it is contained in a compact set), then $\omega(x)$ is nonempty, compact, and invariant [151, Section 1.1].

Recall that for any subsets $A, B \subseteq X$, we define $d(x, A) := \inf_{y\in A} d(x, y)$ and $\delta(B, A) := \sup_{x\in B} d(x, A)$. The Kuratowski measure of noncompactness, $\alpha$, is defined by

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

for any bounded set $B$ of $X$. A continuous map $f : X \to X$ is said to be compact (completely continuous) is $f$ maps any bounded set to a precompact set in $X$.

**Lemma 1.1.1.** [151, Lemma 1.1.2] *The following statements are valid:*

(a) *Let* $I \subseteq [0, \infty)$ *be unbounded, and* $\{A_t\}_{t \in I}$ *be a nonincreasing family of nonempty closed subsets (i.e.,* $t \leq s$ *implies* $A_t \subseteq A_s$*). Assume that* $\alpha(A_t) \to 0$ *as* $t \to \infty$*. Then* $A_\infty = \cap_{t \geq 0} A_t$ *is nonempty and compact, and* $\delta(A_t, A_\infty) \to 0$ *as* $t \to \infty$*.*

(b) *For each* $A \subseteq X$ *and* $B \subseteq X$*, we have* $\alpha(B) \leq \alpha(A) + \delta(B, A)$*.*

For a subset $B \subseteq X$, let $\gamma^+(B) := \bigcup_{m \geq 0} f^m(B)$ be the positive orbit of $B$ for $f$, and

$$\omega(B) := \bigcap_{n \geq 0} \overline{\bigcup_{m \geq n} f^m(B)}$$

the omega limit set of $B$. We say that a subset $A \subseteq X$ attracts a subset $B \subseteq X$ for $f$ if $\lim_{n \to \infty} \delta(f^n(B), A) = 0$.

**Definition 1.1.1.** *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* $X$*;* $\alpha$*-condensing (*$\alpha$*-contraction of order* $k$*,* $0 \leq k < 1$*) 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* $B \subseteq X$ *with* $\alpha(B) > 0$*;* $\alpha$*-contracting if* $\lim_{n \to \infty} \alpha(f^n(B)) = 0$ *for any bounded subset* $B \subseteq X$*; asymptotically smooth if for any nonempty closed bounded set* $B \subseteq X$ *for which* $f(B) \subseteq B$*, there is a compact set* $J \subseteq B$ *such that* $J$ *attracts* $B$*.*

**Definition 1.1.2.** *A subset* $A \subseteq X$ *is said to be an attractor for* $f$ *if* $A$ *is nonempty, compact, and invariant, and* $A$ *attracts some open neighborhood* $U$ *of itself; a global attractor for* $f : X \to X$ *is an attractor that attracts every point in* $X$*; and a strong global attractor for* $f$ *if* $A$ *attracts every bounded subset of* $X$*.*

**Definition 1.1.3.** *Let* $A \subseteq X$ *be a nonempty invariant set.* $A$ *is said to be internally chain transitive if for any* $a, b \in A$ *and any* $\epsilon > 0$*, there is a finite sequence* $x_1, \ldots, x_m$ *in* $A$ *with* $x_1 = a$*,* $x_m = b$ *such that* $d(f(x_i), x_{i+1}) < \epsilon$*,* $1 \leq i \leq m - 1$*. The sequence* $\{x_1, \ldots, x_m\}$ *is called an* $\epsilon$*-chain in* $A$ *connecting* $a$ *and* $b$*.*

**Lemma 1.1.2.** [151, Lemma 1.2.1] *Let* $f : X \to X$ *be a continuous map. Then the omega (alpha) limit set of any precompact positive (negative) orbit is internally chain transitive.*

**Definition 1.1.4.** *The process* $\{T_n : X \to X\}$ *is asymptotically autonomous if there exists a continuous map* $S : X \to X$ *such that*

$$n_j \to \infty, x_j \to x \Rightarrow \lim_{j \to \infty} S_{n_j}(x_j) = S(x).$$

*We also say that* $\{T_n\}$ *is asymptotic to* $S$*.*

**Lemma 1.1.3.** [151, Lemma 1.2.2] *Let $T_n : X \to X$, $n \geq 0$, be an asymptotically autonomous discrete process with limit $S : X \to X$. Then the omega limit set of any precompact orbit of $\{T_n\}$ is internally chain transitive for $S$.*

**Theorem 1.1.1.** [151, Theorem 1.2.1] *Let $A$ be an attractor and $C$ a compact internally chain transitive set for $f : X \to X$. If $C \cap W^s(A) \neq \emptyset$, then $C \subseteq A$.*

**Theorem 1.1.2.** [151, Theorem 1.2.2] *Assume that each fixed point of $f$ is an isolated invariant set, that there is no cyclic chain of fixed points, and that every precompact orbit converges to some fixed point of $f$. Then any compact internally chain transitive set is a fixed point of $f$.*

**Theorem 1.1.3.** [151, Theorem 1.1.3] *Let $f : X \to X$ be a continuous map. Assume that $f$ is point dissipative on $X$, and one of the following condition holds:*

- *(i) $f^{n_0}$ is compact for some integer $n_0 \geq 1$, or*
- *(ii) $f$ is asymptotically smooth, and for each bounded set $B \subseteq X$, there exists $k = k(B) \geq 0$ such that the positive orbit $\gamma^+(f^k(B))$ is bounded.*

*Then there is a strong global attractor $A$ for $f$.*

## 1.2 Uniform persistence and coexistence states

Let $f : X \to X$ be a continuous map and $X_0 \subseteq X$ an open set. Define $\partial X_0 := X \setminus X_0$, and $M_\partial := \{x \in \partial X_0 : f^n(x) \in \partial X_0, n \geq 0\}$, which may be empty.

**Theorem 1.2.1.** [151, Theorem 1.3.1 and Remark 1.3.1] *Assume that*

- *(C1) $f(X_0) \subseteq X_0$ and $f$ has a global attractor $A$;*
- *(C2) There exists a finite sequence $\mathcal{M} = \{M_1, \ldots, M_k\}$ of disjoint, compact, and isloated invariant sets in $\partial X_0$ such that*
  - *(a) $\Omega(M_\partial) := \cup_{x \in M_\partial} \omega(x) \subseteq \cup_{i=1}^k M_i$;*
  - *(b) No subset of $\mathcal{M}$ forms a cycle in $\partial X_0$;*
  - *(c) Each $M_i$ is isolated in $X$;*

*(d)* $W^s(M_i) \cap X_0 = \emptyset$ *for each* $1 \le i \le k$.

*Then there exists* $\delta > 0$ *such that for any compact internally chain transitive set* $L$ *with* $L \not\subseteq M_i$ *for all* $1 \le i \le k$*, we have* $\inf_{x \in L} d(x, \partial X_0) > \delta$.

**Definition 1.2.1.** *A function* $f : X \to X$ *is said to be uniformly persistent with respect to* $(X_0, \partial X_0)$ *if there exists* $\eta > 0$ *such that* $\liminf_{n\to\infty} d(f^n(x), \partial X_0) \ge \eta$ *for all* $x \in X_0$*. If* "inf" *in this inequality is replaced with* "sup"*, then* $f$ *is said to be weakly uniformly persistent with respect to* $(X_0, \partial X_0)$*.*

**Theorem 1.2.2.** [151, THEOREM 1.3.3] *Let* $f : X \to X$ *be a continuous map with* $f(X_0) \subseteq X_0$*. Assume that* $f$ *has a global attractor* $A$*. Then weak uniform persistence implies uniform persistence.*

**Theorem 1.2.3.** [151, THEOREM 1.3.6] *Assume that* $f$ *is asymptotically smooth and uniformly persistent with respect to* $(X_0, \partial X_0)$*, and that* $f$ *has a global attractor* $A$*. Then* $f : (X_0, d) \to (X_0, d)$ *has a global attractor* $A_0$*. Moreover, if a subset* $B$ *of* $X_0$ *has the property that* $\gamma^+(f^k(B))$ *is strongly bounded for some* $k \ge 0$*, then* $A_0$ *attracts* $B$ *for* $f$*.*

In order to establish the existence of coexistence steady state (i.e., the fixed point in $X_0$) for uniformly persistent dynamical systems, we always assume that $X$ is a closed subset of a Banach space $E$, and that $X_0$ is a convex and relatively open subset of $X$. Then $\partial X_0 := X \setminus X_0$ is relatively closed in $X$.

**Theorem 1.2.4.** [151, THEOREM 1.3.8] *Assume that* $f$ *is* $\alpha$*-condensing. If* $f : X_0 \to X_0$ *has a global attractor* $A_0$*, then* $f$ *has a fixed point* $x_0 \in A_0$*.*

**Theorem 1.2.5.** [151, THEOREM 1.3.10] *Assume that*

*(1)* $f$ *is point dissipative and uniformly persistent with respect to* $(X_0, \partial X_0)$*;*

*(2) One of the following two conditions holds:*

  *(i)* $f^{n_0}$ *is compact for some integer* $n_0 \ge 1$*, or*

  *(ii) Positive orbits of compact subsets of* $X$ *are bounded;*

*(3)* $f$ *is* $\alpha$*-condensing.*

*Then* $f : X_0 \to X_0$ *admits a global attractor* $A_0$*, and* $f$ *has a fixed point in* $A_0$*.*

**Remark 1.2.1.** *Theorems 1.2.4 and 1.2.5 are still valid if we assume that* $X$ *is an open subset of a Banach space* $E$ *and* $f : X \to X$ *is* $\alpha$*-condensing.*

Let $X$ be a metric space with metric $d$, and let $\omega > 0$. A family of mappings $\Phi(t) : X \to X, t \geq 0$, is called an $\omega$-periodic semiflow on $X$ if it admits the following properties:

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

(ii) $\Phi(t + \omega) = \Phi(t) \circ \Phi(\omega)$, $\forall t \geq 0$;

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

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

**Definition 1.2.2.** *A periodic semiflow* $\Phi(t)$ *is said to be uniformly persistent with respect to* $(X_0, \partial X_0)$ *if there exists* $\eta > 0$ *such that for any* $x \in X_0$*,*

$$\liminf_{t\to\infty} d(\Phi(t)x, \partial X_0) \geq \eta.$$

**Theorem 1.2.6.** [151, THEOREM 3.1.1] *Let* $\Phi(t)$ *be an* $\omega$*-periodic semiflow on* $X$ *with* $\Phi(t)X_0 \subseteq X_0$*,* $t \geq 0$*, and* $\Phi = \Phi(\omega)$*. Assume that* $\Phi : X \to X$ *is asymptotically smooth and has a global attractor. Then uniform persistence of* $\Phi$ *with respect to* $(X_0, \partial X_0)$ *implies that of* $\Phi : X \to X$*. More precisely,* $\Phi(t) : X_0 \to X_0$ *admits a global attractor* $A_0 \subseteq X_0$*, and the compact set* $A_0^* = \bigcup_{0\leq t\leq\omega} \Phi(t)A_0 \subseteq X_0$ *attracts every point in* $X_0$ *for* $\Phi(t)$ *in the sense that* $\liminf_{t\to\infty} d(\Phi(t)x, A_0^*) = 0$ *for any* $x \in X_0$*.*

## 1.3 Monotone dynamics

In this section, we present the comparison principles for ordinary differential equations, delay differential equations and reaction-diffusion equations, and the theories of global attractivity and convergence.

### 1.3.1 The comparison principle

For $x, y \in \mathbb{R}^n$, we write

$$x \leq y \Leftrightarrow x_i \leq y_i \ \ \forall\, i \in N \quad \text{and} \quad x \ll y \Leftrightarrow x_i < y_i \ \forall\, i \in N,$$

where $N = \{1, \ldots, n\}$. The spaces $AC(J)$ and $L(J)$ consist of all functions from $J$ to $\mathbb{R}^n$ that are absolutely continuous or integrable in $J$, respectively. Here and below, $J = [a, b]$, $J_0 = (a, b]$. A measurable set $M \subseteq J$ is said to be dense at $a$ if the set $M \cap [a, a+\epsilon]$ has positive measure for every $\epsilon > 0$. For measurable vector-valued functions $\varphi, \psi$ we write $\varphi \ll \psi$ at $a+$ if the set $\{t \in J : \varphi(t) \ll \psi(t)\}$ is dense at $a$.

Consider the nonlinear equation

$$\frac{\partial u(t)}{\partial t} = f(t, u(t)) \quad \text{a.e. in } J \tag{1.1}$$

and assume for simplilcity that $f(t, x)$ is defined in the strip $S = J \times \mathbb{R}^n$ and satisfies the following conditions: $f(t, \cdot)$ is continuous in $\mathbb{R}^n$ for almost all (fixed) $t \in J$, $f(\cdot, x)$ is measurable in $J$ for all (fixed) $x \in \mathbb{R}^n$, $f(\cdot, 0) \in L(\mathbb{R})$, and for each constant $A > 0$ there is a function $m(\cdot) \in L(J)$ such that

$$|f(t, x) - f(t, y)| \leq m(t)|x - y| \quad \text{for } t \in J \text{ and } |x|, |y| \leq A.$$

The defect $P$ of a function $v \in AC(J)$ with respect to equation (1.1) is defined by

$$(Pv)(t) = v'(t) - f(t, v(t)).$$

The function $f$ is said to be quasimonotone increasing in $x$ if $f_i(t, x)$ is (weakly) increasing in $x_j$ for all $j \neq i$, or equivalently, if

$$x \leq y, x_i = y_i \Rightarrow f_i(t, x) \leq f_i(t, y) \quad \text{a.e. in } J \quad (i = 1, \ldots, n).$$

**Theorem 1.3.1.** *[131, Theorem 4] Assume that the function $f(t, x)$ satisfies the conditions given above and is quasimonotone inceasing in $x$, and let $v, w \in AC(J)$ satisfy*

$$v(a) \leq w(a) \text{ and } Pv \leq Pw \quad \text{a.e. in } J.$$

*Then each of the following conditions is sufficient for the strong inequality $v \ll w$ in $J_0$:*

*(i)* $v(a) \ll w(a)$;

*(ii)* $Pv \ll Pw$ *at* $a+$*;*

*(iii)* *For every pair* $(\alpha, \beta)$ *of nonempty, disjoint index sets with* $\alpha \cup \beta = N$*, there are* $j \in \beta, k \in \alpha$ *such that* $f_j(t,x)$ *is strictly increasing in* $x_k$ *for* $t \in M, x \in U$*, where* $M \subseteq J$ *is dense at* $a$ *and* $U$ *is a neighborhood of* $v(a)$*.*

For a given $\tau > 0$, let $C = C([-\tau, 0], \mathbb{R}^n)$ and $C^+ = C([-\tau, 0], \mathbb{R}^n_+)$. Then $(C, C^+)$ is an order Banach space equipped with the maximum norm $\|\phi\| = \max_{\theta\in[-\tau,0]} \|\phi(\theta)\|_{\mathbb{R}^n}$, $\forall \phi \in C$. For any given continuous function $u : [-\tau, \sigma) \to \mathbb{R}$ with $\sigma > 0$, we define $u_t \in C$ by $u_t(\theta) = u(t+\theta)$, $\forall \theta \in [-\tau, 0]$, for any $t \in [0, \sigma)$.

Consider the nonautonomous equation

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = g(t, u_t), \tag{1.2}$$

where $g : \Omega \to \mathbb{R}^n$ is continuous on $\Omega$, an open subset of $\mathbb{R} \times C$.

Equation (1.2) is a very general type of equation, for example, ordinary differential equations ($\tau = 0$) and delay differential equations

$$x(t) = g(t, x(t), x(t-\tau_1(t)), ..., x(t-\tau_p(t)))$$

with $0 \le \tau_j(t) \le \tau$, $j = 1, 2, ..., p$.

**Definition 1.3.1.** *$g$ is called quasimonotone if for any $\phi \le \psi$ with $\phi_i(0) = \psi_i(0)$ for some integer $i$, then $g_i(t,\phi) \le g_i(t,\psi)$ for all $t$.*

**Theorem 1.3.2.** [116, Theorem 5.1.1] *Let $g, h : \Omega \to \mathbb{R}^n$ be continuous, Lipschitz on each compact subset of $\Omega$, and assume that either $g$ or $h$ satisfies quasimonotone condition. Assume also that $g(t,\phi) \le h(t,\phi)$ for all $(t,\phi) \in \Omega$. If $(t_0, \phi), (t_0, \psi) \in \Omega$ satisfy $\phi \le \psi$, then*

$$u(t, t_0, \phi, g) \le u(t, t_0, \psi, h)$$

*holds for all $t \ge t_0$ for which both are defined.*

Consider a reaction-diffusion system with delays on $\Omega$,

$$\begin{aligned}
&\tfrac{\partial u^i(t,x)}{\partial t} = d_i \Delta u^i(t,x) + g_i(t, x, u^1_t(\cdot,x), ..., u^n_t(\cdot,x)), t > a, x \in \Omega,\\
&\alpha_i(x) u^i(t,x) + k_i \tfrac{\partial u^i(t,x)}{\partial \nu} = \beta_i(t,x), t > a, x \in \partial\Omega,\\
&u^i(a+\theta, x) = \phi^i(\theta, x), -\tau \le \theta \le 0, x \in \Omega,
\end{aligned} \tag{1.3}$$

where $\Omega$ is a bounded domain in $\mathbb{R}^n$ with $\partial\Omega$ smooth, $\Delta$ is the Laplacian operator on $\Omega$, and $\frac{\partial}{\partial\nu}$ is the outward normal derivative on $\partial\Omega$, $a \geq 0$ and $i = 1, ..., n$. It is assumed that the coefficients in system (1.3) satisfy the following:

(a) There is a subset $\sum_0$ of $\{1, ..., n\}$ such that $d_i = 0$ for all $i \in \sum_0$ and $d_i > 0$ for all $i \in \sum_0^c$;
(b) $\alpha_i : \bar{\Omega} \to [0, \infty)$ is $C^1$ and $\beta_i : [0, \infty) \times \bar{\Omega} \to \mathbb{R}$ is $C^2$ for $i = 1, ..., n$;
(c) If $i \in \sum_0^c$ then $k_i = 1$ and if $i \in \sum_0$ then $\alpha_i = 0, d_i \equiv 0,$ and $\beta_i \equiv 0$.

(1.4)

The underlying assumptions on $g$ are as follows:

(a) $g$ is continuous from $[0, \infty) \times \bar{\Omega} \times C^n_\Lambda$ into $\mathbb{R}^n$, where $C^n_\Lambda = \{\phi \in C([-\tau, 0], \mathbb{R}^n) : \phi(\theta) \in \Lambda,$ a closed convex subset of $\mathbb{R}^n, \forall -\tau \leq \theta \leq 0\}$;
(b) For each $R > 0$, there exist $\upsilon = \upsilon(R) \in (0, 1]$ and $L = L(R) \in (0, \infty)$ such that $|g_i(t, x, \phi) - g_i(s, x, \psi)| \leq L(|t - s|^\upsilon + \sum_{j=1}^n |\phi_j - \psi_j|), \forall t, s \in [0, R], x \in \bar{\Omega}$, $\phi, \psi \in C([-\tau, 0], \mathbb{R}^n)$ with $\|\phi\|, \|\psi\| \leq R$, and $i = 1, ..., n$;
(c) $\lim_{k\to 0^+} \frac{1}{k} d(\phi(0) + kg(t, x, \phi); \Lambda) = 0, \forall (t, x, \phi) \in [0, \infty) \times \bar{\Omega} \times C^n_\Lambda$.

(1.5)

Suppose $v^\pm = (v_i^\pm)_1^n$ are continuously differentiable functions from $[a - \tau, c) \times \bar{\Omega}$ into $\Lambda$, where $a < c \leq \infty$, that they are $C^2$ in $x \in \Omega$, $i \in \sum_0^c$, and that

$$v^-(t, x) \leq v^+(t, x), [v^-(t, x), v^+(t, x)] \subseteq \Lambda, \forall (t, x) \in [a - \tau, c) \times \bar{\Omega}.$$

Let $g^\pm = (g_i^\pm)_1^n$ be continuous functions from $[0, \infty) \times \bar{\Omega} \times C([-\tau, 0], \mathbb{R}^n)$ into $\mathbb{R}^n$ and assume the following differential inequalities are satisfied:

$$\begin{aligned} &\tfrac{\partial v_i^+(t,x)}{\partial t} \geq d_i \Delta v_i^+(t, x) + g_i^+(t, x, v_t^+(\cdot, x)), a < t < c, x \in \Omega, \\ &\alpha_i(x) v_i^+(t, x) + \tfrac{\partial v_i^+(t,x)}{\partial \nu} = \beta_i^+(t, x) \geq \beta_i(t, x), a < t < c, x \in \partial\Omega, \\ &v_i^+(a + \theta, x) = \phi_i^+(\theta, x) \geq \phi^i(\theta, x), -\tau \leq \theta \leq 0, x \in \Omega, \end{aligned} \tag{1.6}$$

and

$$\begin{aligned} &\tfrac{\partial v_i^-(t,x)}{\partial t} \leq d_i \Delta v_i^-(t, x) + g_i^-(t, x, v_t^-(\cdot, x)), a < t < c, x \in \Omega, \\ &\alpha_i(x) v_i^-(t, x) + \tfrac{\partial v_i^-(t,x)}{\partial \nu} = \beta_i^-(t, x) \leq \beta_i(t, x), a < t < c, x \in \partial\Omega, \\ &v_i^-(a + \theta, x) = \phi_i^-(\theta, x) \leq \phi^i(\theta, x), -\tau \leq \theta \leq 0, x \in \Omega. \end{aligned} \tag{1.7}$$

**Proposition 1.3.1.** [87, PROPOSITION 1] *Suppose that $v^\pm$ and $f^\pm$ are as in (1.6), (1.7), and that (1.4) and (1.5) are satisfied with (1.5c) replaced by the following: if $k \in \{1, ..., n\}$ and $(t, x, \phi) \in [a, c) \times \bar{\Omega} \times C([-\tau, 0], \mathbb{R}^n)$ with $v^-(t + \theta, x) \leq \phi(\theta) \leq$*

*$v^+(t+\theta, x)$ for all $-\tau \leq \theta \leq 0$, then*
*(a) $\phi_k(0) = v_k^+(t,x)$ implies that $g_k(t,x,\phi) \leq g_k^+(t,x,v_t^+(\cdot,x))$, and*
*(b) $\phi_k(0) = v_k^-(t,x)$ implies that $g_k(t,x,\phi) \geq g_k^-(t,x,v_t^-(\cdot,x))$.*
*Then system (1.3) has a unique noncontinuable mild solution $u$ on $[a,b)$, where $b \geq c$, and this solution satisfies*

$$v^-(t,x) \leq u(x,t) \leq v^+(t,x), \forall (t,x) \in [a,c) \times \bar{\Omega}.$$

### 1.3.2 Global attractivity and convergence

Let $E$ be an ordered Banach space with positive cone $P$ such that $\mathrm{Int}(P) \neq \emptyset$. For any $x, y \in E$, we write $x \geq y$ if $x - y \in P$, $x > y$ if $x - y \in P \setminus \{0\}$, and $x \gg y$ if $x - y \in \mathrm{Int}(P)$. If $a < b$, we define $[a,b]_E := \{x \in E : a \leq x \leq b\}$.

**Definition 1.3.2.** *A linear operator $L : E \to E$ is said to be positive if $L(P) \subseteq P$; strongly positive if $L(P \setminus \{0\}) \subseteq \mathrm{Int}(P)$.*

**Definition 1.3.3.** *Let $E$ be a Banach space, $K \subseteq E$ be a cone with $K \neq \{0\}$, and $L$ be a positive and bounded linear operator. $r(L)$ is called the principal eigenvalue if there exists some $x \in K \backslash \{0\}$ such that $Lx = r(L)x$.*

**Theorem 1.3.3.** (KREIN-RUTMAN THEOREM) [52, THEOREMS 7.1 AND 7.2] *Assume that a compact operator $L : E \to E$ is positive and $r(L)$ is the spectral radius of $L$. If $r(L) > 0$, then $r(L)$ is an eigenvalue of $L$ with an eigenfunction $x > 0$. Moreover, if $L$ is strongly positive, then $r(L) > 0$ and it is an algebraically simple eigenvalue with an eigenfunction $x \gg 0$; there is no other eigenvalue with the associated eigenfunction $x \gg 0$; $|\lambda| < r(L)$ for all eigenvalues $\lambda \neq r(L)$.*

**Theorem 1.3.4.** (WEAK VERSION OF THE GENERALIZED KREIN-RUTMAN THEOREM) [98, COROLLARY 2.2] *Let $E$ be a Banach space with a total cone $K \subseteq E$ (i.e., $E = \overline{K - K}$), and $L$ be a positive and bounded linear operator on $E$. If the essential spectral radius $r_e(L)$ of $L$ is less than the spectral radius $r(L)$ of $L$, then there exists some $x \in K \backslash \{0\}$ such that $Lx = r(L)x$.*

**Theorem 1.3.5.** (GENERALIZED KREIN-RUTMAN THEOREM) [98, 151] *Let $E$ be a Banach space, $K \subseteq E$ be a cone with nonempty interior, and $L : E \to E$ be a strongly positive and bounded linear operator. If $r_e(L) < r(L)$, then $r(L)$ is an algebraically* *simple eigenvalue of* $L$ *with an eigenvector* $v \in \mathrm{Int}(K)$, *and all other eigenvalues of* $L$ *have their absolute values less than* $r(L)$.

**Definition 1.3.4.** *Let* $U$ *be a subset of* $E$, *and* $f : U \to U$ *a continuous map. The map* $f$ *is said to be monotone if* $x \geq y$ *implies that* $f(x) \geq f(y)$; *strictly monotone if* $x > y$ *implies that* $f(x) > f(y)$; *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 $[u, v]_E \in K$ whenever $u, v \in K$ satisfy $u < v$.

**Definition 1.3.5.** *Let* $U \subseteq P$ *be a nonempty, closed and order convex set. A continuous map* $f : U \to U$ *is said to be subhomogeneous if* $f(\lambda x) \geq \lambda f(x)$ *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* $\lambda \in (0, 1)$.

Denote the Fréchet derivative of $f$ at $u = a$ by $Df(a)$ if it exists, and let $r(Df(a))$ be the spectral radius of the linear operator $Df(a) : E \to E$.

**Theorem 1.3.6.** (THRESHOLD DYNAMICS) [151, THEOREM 2.3.4] *Let either* $V = [0, b]_E$ *with* $b \gg 0$ *or* $V = P$. *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 exists threshold dynamics:*

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

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

**Theorem 1.3.7.** [151, Generalized Arzela–Ascoli Theorem] *Let* $a < b$ *be two real numbers and* $X$ *be a complete metric space. Assume that a sequence of functions* $\{f_n\}$ *in* $C([a, b], X)$ *satisfies the following conditions:*

*(1) The family* $\{f_n(s)\}_{n \geq 1}$ *is uniformly bounded on* $[a, b]$*;*

*(2) For each* $s \in [a, b]$*, the set* $\{f_n(s) : n \geq 1\}$ *is precompact in* $X$*;*

*(3) The family* $\{f_n(s)\}_{n \geq 1}$ *is equi-continuous on* $[a, b]$*.*

*Then* $\{f_n\}$ *has a convergent subsequence in* $C([a, b], X)$*, that is, there exists a subsequence of functions* $\{f_{n_k}(s)\}$ *which converges in* $X$ *uniformly for* $s \in [a, b]$*.*

## 1.4 Basic reproduction ratio

The basic reproduction ratio (number) $R_0$ is a very important parameter in population biology. In epidemiology, $R_0$ is the expected number of secondary cases produced, in a completely susceptible population, by a typical infected individual during its entire period of infectiousness [31]. $R_0$ serves as a threshold value to measure the effort needed to control the infectious disease and this threshold criterion states that the disease can invade if $R_0 > 1$, whereas it cannot if $R_0 < 1$. Since then the celebrated works by Diekmann, Heesterbeek and Metz [31] and by van den Driessche and Watmough [129], there have been numerous works on the analysis of $R_0$ for various autonomous infectious disease models. To study the population models in a periodic environment, several works about the theory and applications of $R_0$ for model systems have been proposed (see, e.g., [6–8, 58, 124, 133] and the references therein). Recently, the theory of $R_0$ has been developed for periodic and time-delayed compartmental population models in [150]. And then Liang, Zhang and Zhao [75] extended such a theory to abstract functional differential equations whose solution maps may be noncompact. In this section, we present the theory of $R_0$ for periodic and time-delayed models developed by [75, 150] and the numerical algorithm for the computation of $R_0$.

### 1.4.1 Definition of $R_0$

Let $\tau$ be a nonnegative real number and $m$ be a positive integer, $C = C([-\tau, 0], \mathbb{R}^m)$, and $C^+ = C([-\tau, 0], \mathbb{R}^m_+)$. Then $(C, C^+)$ is an ordered Banach space equipped with the maximum norm and the positive cone $C^+$. Let $F : \mathbb{R} \to \mathcal{L}(C, \mathbb{R}^m)$ 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 $\omega$-periodic in $t$ for some real number $\omega > 0$. For a continuous function $u : [-\tau, \sigma) \to \mathbb{R}^m$ with $\sigma > 0$, define $u_t \in C$ by

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

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

We consider a linear and periodic functional differential system on $C$:

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = F(t)u_t - V(t)u(t), \quad t \geq 0. \tag{1.8}$$

System (1.8) may come from the equations of infectious variables in the linearization of a given $\omega$-periodic and time-delayed compartmental epidemic model at a disease-free $\omega$-periodic solution. As such, $m$ is the total number of the infectious compartments, and the newly infected individuals at time $t$ depend linearly on the infectious individuals over the time interval $[t - \tau, t]$, which is described by $F(t)u_t$. Further, the internal evolution of individuals in the infectious compartments (e.g., natural and disease-induced deaths, and movements among compartments) is governed by the linear ordinary differential system:

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = -V(t)u(t). \tag{1.9}$$

Let $\Phi(t, s), t \geq s$, be the evolution matrices associated with system (1.9), that is, $\Phi(t, s)$ satisfies

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

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

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

We assume that

(H1) Each operator $F(t) : C \to \mathbb{R}^m$ is positive in the sense that $F(t)C^+ \subseteq \mathbb{R}^m_+$.

(H2) Each matrix $-V(t)$ is cooperative, and $\omega(\Phi) < 0$.

We supposed that the $\omega$-periodic function $v(t)$ is the initial distribution of infectious individuals. For any given $s \geq 0$, $F(t-s)v_{t-s}$ is the distribution of newly infected individuals at time $t-s$, which is produced by the infectious individuals who were introduced 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 infected individuals who were newly infected at time $t-s$ and remain in the infected 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 new infections at time $t$ produced by all those infectious individuals introduced at all previous time to $t$. Note that for any given $s \geq 0$, $\Phi(t, t-s)v(t, t-s)$ is the distribution of those infectious individuals at time $t-s$ and remain in the infected compartments at time $t$, and hence $\int_0^\infty \Phi(t, t-s)v(t-s)\mathrm{d}s$ is the distribution of accumulative infectious individuals who were introduced at all previous time to $t$ and remain in the infected compartments at time $t$. Thus, the distribution of newly infected individuals at time $t$ is $F(t)\int_0^\infty \Phi(t+\cdot, t-s+\cdot)v(t-s+\cdot)\mathrm{d}s$.

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

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

and

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

Let $A$ and $B$ be two bounded linear operators on $C_\omega$ defined by

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

It then follows that $L = A \circ B$ and $\hat{L} = B \circ A$, and hence $L$ and $\hat{L}$ have the same spectral radius. Motivated by the concept of next generation operators (see, e.g., [8,31, 124,129,133,150]), we define the spectral radius of $L$ and $\hat{L}$ as the basic reproduction number $\mathcal{R}_0 := r(L) = r(\hat{L})$ for periodic system (1.8).

Let $P$ be the Poincaré map of system (1.8) on $C$, that is, $P\phi = u_\omega(\phi)$, where $u(t,\phi)$ is the unique solution of system (1.8) with $u_0 = \phi$. The following result shows that $R_0$ is a threshold value for the stability of the zero solution for periodic system (1.8).

**Theorem 1.4.1.** [150, THEOREM 2.1] *Let (H1) and (H2) hold. The following statements are valid:*

*(i)* $R_0 = 1$ *if and only if* $r(P) = 1$.

*(ii)* $R_0 > 1$ *if and only if* $r(P) > 1$.

*(iii)* $R_0 < 1$ *if and only if* $r(P) < 1$.

*Thus,* $R_0 - 1$ *has the same sign as* $r(P) - 1$.

In the case where $\tau = 0$, we have the following result for a periodic ordinary differential system.

**Lemma 1.4.1.** [133, LEMMA 2.2] *The following statements are valid:*

*(i) If* $V(t) = diag(V_1(t), ..., V_m(t))$ *and* $F(t) = diag(F_1(t), ..., F_m(t))$, *then* $R_0 = \max_{1\le i\le m}\{\frac{[F_i]}{[V_i]}\}$.

*(ii) If* $V(t) = V$ *and* $F(t) = F$ *are constant matrices, then* $R_0 = \rho(V^{-1}F) = \rho(FV^{-1})$.

The above results in [150] can also be employed for the periodic and time-delayed reaction-diffusion models whose solution maps are eventually compact. If solution maps are noncompact, we need to use the following theory of $R_0$ developed in [75].

Let $X$ be a Banach space with a normal and reproducing cone $X^+$, and $\tilde{X}$ be a Banach space with $\tilde{X} \hookrightarrow X$. Let $\tau \ge 0$ be a given number, and $C = C([-\tau,0],X)$ equipped with the maximum norm $\|\cdot\|_C$ and a positive cone $C^+ = C([-\tau,0],X^+)$.

Let $(V(t))_{0\le t\le w}$ be a family of $\omega$-periodic closed linear operators with the following properties:

(i) $D(V(t)) = \tilde{X}$, $\forall t \in [0,\omega]$.

(ii) There is some $\lambda_0 \in \mathbb{R}$ such that $\{\lambda \in \mathbb{C} : \Re e\lambda \geq \lambda_0\} \subseteq \rho(-V(t))$, $\forall t \in [0,\omega]$ and $\|(\lambda + V(t))^{-1}\|_X \leq \frac{c}{1+|\lambda|}$, $\forall \lambda \in \mathbb{C}$ with $\Re e\lambda \geq \lambda_0$, $\forall t \in [0,\omega]$.

(iii) $V(\cdot) : [0,\omega] \to \mathcal{L}(\tilde{X}, X)$ is Hölder continuous.

Assume that $F(\cdot) : \mathbb{R} \to \mathcal{L}(C, X)$ is $\omega$-periodic, $F(t)\phi$ is continuous jointly in $(t,\phi) \in \mathbb{R} \times C$ and the operator norm of $F(t)$ is uniformly bounded for all $t \in [0,\omega]$.

We consider a linear and $\omega$-periodic functional differential system:

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = F(t)u_t - V(t)u(t), \quad t \geq 0. \tag{1.10}$$

Let $\Phi(t,s), t \geq s$, be the evolution operators associated with the following system

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = -V(t)u(t). \tag{1.11}$$

Let $C_\omega(\mathbb{R}, X)$ be the ordered Banach space of all continuous and $\omega$-periodic functions from $\mathbb{R}$ to $X$, with the maximum norm. Then we define two linear operators on $C_\omega(\mathbb{R}, X)$ by

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

and

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

Similarly, we define the spectral radius of $L$ and $\hat{L}$ as the basic reproduction number $\mathcal{R}_0 := r(L) = r(\hat{L})$ for periodic system (1.10).

Let $\{U(t,s,\lambda) : t \geq s\}$ be the evolution operators on $C$ of the following linear periodic system with $\lambda \in (0, +\infty)$:

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = \frac{1}{\lambda}F(t)u_t - V(t)u(t), \quad t \geq 0. \tag{1.12}$$

Then $U(\omega, 0, 1) = U(\omega, 0)$ be the Poincaré map of system (1.10) on $C$. We present the following assumptions:

(H1) Each operator $F(t) : C \to X$ is positive in the sense that $F(t)C^+ \subseteq X^+$.

(H2) Each operator $-V(t)$ is resolvent positive in the sense that there is $\gamma \in \mathbb{R}$ such that $(\gamma, +\infty) \subseteq \rho(-V(t))$ and $(\lambda + V(t))^{-1}$ is positive $\lambda > \gamma$, and $\omega(\Phi) < 0$.

(H3) The positive linear operator $L$ possesses the principal eigenvalue.

(H4) The positive linear operators $U(\omega, 0, \lambda)$ possesses the isolated principal eigenvalue with finite multiplicity for any $\lambda \in [0, +\infty)$ whenever $r(U(\omega, 0, \lambda)) \geq 1$.

(H5) Either the principal eigenvalue of $L$ is isolated, or there exists an integer $n_0 > 0$ such that $L^{n_0}$ is strongly positive.

(H6) Each operator $\Phi(t, s)$ is compact on $X$ for $t > s$.

Note that under the assumptions (H1) and (H2), (H6) is sufficient for (H3)-(H5) to hold.

**Theorem 1.4.2.** [75, Theorem 3.7] *Let (H1)-(H5) hold. The following statements are valid:*

*(i)* $R_0 = 1$ *if and only if* $r(U(\omega, 0)) = 1$.

*(ii)* $R_0 > 1$ *if and only if* $r(U(\omega, 0)) > 1$.

*(iii)* $R_0 < 1$ *if and only if* $r(U(\omega, 0)) < 1$.

*Thus,* $R_0 - 1$ *has the same sign as* $r(U(\omega, 0)) - 1$.

### 1.4.2 Computation of $R_0$

**Theorem 1.4.3.** [150, Theorem 2.2] and [75, Theorem 3.8] *If* $R_0 > 0$, *then* $\lambda = R_0$ *is the unique solution of* $r(U(\omega, 0, \lambda)) = 1$.

**Lemma 1.4.2.** [75, Lemma 2.5] *Assume that* $(C, C^+)$ *is an ordered Banach space with* $C^+$ *being normal and* $\mathrm{Int}(\mathrm{C}^+) \neq \emptyset$, *which is equipped with the norm* $\|\cdot\|_C$. *Let* $\mathcal{L}$ *be a positive bounded linear operator. Choose* $v_0 \in \mathrm{Int}(\mathrm{C}^+)$ *and define* $a_n = \|\mathcal{L} v_{n-1}\|_C$, $v_n = \frac{\mathcal{L} v_{n-1}}{a_n}$, $\forall n \geq 1$. *If* $\lim_{n\to\infty} a_n$ *exists, then* $r(\mathcal{L}) = \lim_{n\to\infty} a_n$.

For any given $\lambda \in (0, +\infty)$, we choose $v_0 \in \mathrm{Int}(C^+)$ and define

$$a_n = \|U(\omega, 0, \lambda) v_{n-1}\|_C, \; v_n = \frac{U(\omega, 0, \lambda) v_{n-1}}{a_n}, \; \forall n \geq 1.$$

By Lemma 1.4.2, it then follows that if $\lim_{n\to+\infty} a_n$ exists, then $r(U(\omega, 0, \lambda)) = \lim_{n\to+\infty} a_n$. Thus, we can solve $r(U(\omega, 0, \lambda)) = 1$ for $\lambda$ numerically via the bisection method, which is an approximation of $\mathcal{R}_0$.

# Chapter 2

# A periodic SEIRS epidemic model with a time-dependent latent period

## 2.1 Introduction

Mathematical models provide powerful tools to explain and predict the spread of infectious diseases, and to test control strategies. One of the earliest models in epidemiology was introduced in 1937 [65]. Since then, numerous mathematical models for infectious diseases have been described by autonomous systems of differential equations, e.g., the dynamics of SIS, SIR, SIRS, SEI, SEIR and SEIRS epidemic models were intensively investigated in the last few decades (see, e.g., [4,24,39,53,56,66,86,144]).

In fact, many diseases show seasonal behaviors (see, e.g., [3,33,38,46]). From [2,37,46,81,91,101], we have known that Ebola, measles, diphtheria, chickenpox, tuberculosis, influenza, cholera and malaria in humans, bluetongue in cattle and sheep, viral haemorrhagic septicaemia and furunculosis in fish, are recognized as having seasonal trends and show variable periods of peak seasonality. The causes of seasonal patterns for different diseases are complex, such as temperature, humidity, photoperiod, host aggregation, and resource availability. For example, there is a strong relationship between the seasonal outbreaks of meningococcal meningitis disease and climate, e.g., wind speed and low absolute humidity affect respiratory transmission [119]. As mentioned in [34], the seasonal patterns of invasive pneumococcal disease in humans correlate with the photoperiod-dependent variation in host susceptibility and fall aggregation among school children were considered. In [128], a mathematical model of low pathogenic avian influenza dynamics that includes both time-varying environmental effects and seasonal migration. In addition, unlike warm-blooded animals, temperature has a particularly important influence on fish diseases in areas where there is a wide amplitude in daily and seasonal temperature changes because it affects the rate of metabolism, immunologic response, reproduction, amount of oxygen dissolved in water, biological oxygen demand, toxicity of pollutants, and growth of fish pathogens and parasites (see, e.g., [91, 104, 117]).

Annual changes in host and parasite biology can generate outbreaks that occur around the same time each year, and there is the growing awareness that seasonality can cause population fluctuations ranging from annual cycles to multiyear oscillations, and even chaotic dynamics (see, e.g., [1, 3, 5, 47]). It thus becomes natural to model these diseases by incorporating periodic variations into epidemic models. For example, Liu et al. [78] studied the global dynamics of a non-autonomous SEIR system for tuberculosis with seasonality by introducing a possible seasonal variation in pulmonary tuberculosis. Towers et al. [125] proposed an SIR epidemic model with periodic transmission rate to assess the efficacy of control strategies via antiviral drug treatment during an outbreak of pandemic influenza. Zhang and Teng [149] considered a non-autonomous SEIRS epidemic model and established some sufficient conditions for the permanence and extinction of the disease. Later, Nakata and Kuniya [95] improved the results in a periodic environment.

Cooke and Driessche [24] proposed an SEIRS epidemic model with two time delays. Since then, a number of the dynamic behaviors of SEIRS epidemic models with constant delays have been studied (see, e.g., [63, 102, 132, 146, 150]). Meanwhile, many population models with time-dependent delays have been developed (see, e.g., [12,82,100,136,143]). Recently, Lou and Zhao [82] proposed a host-macroparasite model with seasonal developmental durations and time-dependent delays, and studied the global dynamics by introducing a periodic semiflow on a suitably chosen phase space. Wang and Zhao [136] studied the global dynamics of a malaria transmission model with a time-dependent incubation period by using the same theoretical approach as in [82]. Indeed, the latent (or incubation) periods of quite a few diseases are related to seasonal changes. For some vector-borne diseases, there is considerable evidence to show that the extrinsic incubation period of the parasite is always sensitive to temperature. Similarly, for the directly transmitted diseases, the length of the latent period depends not only on the strength of the individual's immune system, but also on the climate changes, especially for the aquatic animal and plant disease epidemics (see, e.g., [48, 57, 85, 91, 100]). For example, the incubation period for fish furunculosis ranges probably from 2 to 4 days. However, at lower temperatures, the incubation period may be extended by several weeks [48]. In [100], Omori and Adams developed a mathematical model with time-dependent delays to analyse the effect of seasonal temperature cycles on koi herpes virus (KHV) in common carp due to the time delays depending on water temperature. Therefore, it is more reasonable to incorporate this seasonally forced latent period into the disease transmission models.

Motivated by the above works, the purpose of this chapter is to develop a class of periodic SEIRS epidemic models that, for the first time, incorporates the time-dependent latent period. We will use the theoretical approach developed in [82] and the theory of uniform persistence for periodic semiflows to study our model system.

The organization of the chapter is as follows. In Section 2.2, we formulate the model and give the underlying assumptions. In Section 2.3, we introduce the basic reproduction ratio $R_0$ for the model system and show that $R_0$ acts as a threshold parameter for the uniform persistence and global extinction of the disease. In Section 2.4, some numerical simulations are presented to illustrate the main results.

## 2.2 Model formulation

In order to formulate the model, we first consider a classical SIRS epidemic model in a population. Let $N(t)$ be the total population number at time t which is divided into three classes: susceptible population, infectious population, and recovered (or removed) population (i.e., who have been infected and then removed from the possibility of infection through the temporary immunity). Let $S(t)$, $I(t)$, and $R(t)$ be the total number of the susceptible, infectious, and recovered (or removed) populations at time $t$, respectively. Anderson and May [4] proposed the following famous SIRS model:

$$\begin{aligned}\tfrac{\mathrm{d}S(t)}{\mathrm{d}t} &= \Lambda - \beta S(t)I(t) - \mu S(t) + \alpha R(t),\\ \tfrac{\mathrm{d}I(t)}{\mathrm{d}t} &= \beta S(t)I(t) - (\mu + d + \gamma)I(t),\\ \tfrac{\mathrm{d}R(t)}{\mathrm{d}t} &= \gamma I(t) - \mu R(t) - \alpha R(t).\end{aligned} \tag{2.1}$$

Here the constant $\Lambda$ is the recruitment rate, $\beta$ is the disease transmission coefficient, $\mu$ is the natural death rate of the population, $d$ is the disease-induced death rate, $\gamma$ is the recovery rate of the infectious population, and $\alpha$ is the lose of immunity rate.

In fact, upon infection, the susceptible individuals become exposed for some diseases (e.g., tuberculosis, influenza, measles, KHV epidemiology), that is, infected but not yet infective. These individuals remain in the exposed class for a certain latent period before becoming infective. Thus it is natural to introduce a latent delay into system (2.1) and consider an SEIRS epidemic model. Let $E(t)$ be the total number of the exposed population at time $t$, and $M(t)$ be the number of newly occurred infectious population per unit time at time $t$. We assume that the latent period of the disease is time-periodic due to the seasonal weather changes, denoted by $\tau(t)$. Motivated by [78, 82, 88, 95, 100, 125, 136, 149], we propose the following evolution system with general incidence rate:

$$\begin{aligned}\tfrac{\mathrm{d}S(t)}{\mathrm{d}t} &= \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t),\\ \tfrac{\mathrm{d}E(t)}{\mathrm{d}t} &= f(t, S(t), I(t)) - \mu(t)E(t) - M(t),\\ \tfrac{\mathrm{d}I(t)}{\mathrm{d}t} &= M(t) - (\mu(t) + d(t) + \gamma(t))I(t),\\ \tfrac{\mathrm{d}R(t)}{\mathrm{d}t} &= \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t),\end{aligned} \tag{2.2}$$

where $\Lambda(t)$, $\mu(t)$, $\alpha(t)$, $d(t)$, and $\gamma(t)$ have the same biological meanings as $\Lambda$, $\mu$, $\alpha$, $d$, and $\gamma$ in system (2.1), respectively. The incidence function $f(t, S, I)$ depends on time $t$ and variables $S$ and $I$. In the following, we will use the same arguments as in [96, 100].

Let $q$ represent the development level of infection such that $q$ increases at a time-dependent rate $\kappa(t)$ (i.e., $\mathrm{d}q/\mathrm{d}t = \kappa(t)$), and assume that $q = q_E = 0$ at the transition from $S$ to $E$, and $q = q_I$ at the transition from $E$ to $I$. The variable $q$ describes how complete the latency stage is. Let $\rho(q, t)$ be the density of individuals with infection development level $q$ at time $t$. Then $M(t) = \kappa(t)\rho(q_I, t)$.

Let $J(q, t)$ be the flux, in the direction of increasing $q$, of individuals with infection development level $q$ at time $t$. Thus, we have the following equation (see, e.g., [68])

$$\frac{\partial \rho(q,t)}{\partial t} = -\frac{\partial J}{\partial q} - \mu(t)\rho.$$

Since $J(q,t)=\kappa(t)\rho(q,t)$, we have

$$\frac{\partial\rho(q,t)}{\partial t}=-\frac{\partial[\kappa(t)\rho(q,t)]}{\partial q}-\mu(t)\rho(q,t). \tag{2.3}$$

For the state $E$, system (2.3) has the boundary condition

$$\rho(q_E,t)=\frac{f(t,S(t),I(t))}{\kappa(t)}.$$

In order to solve system (2.3) with the above boundary condition, we introduce a new variable

$$\eta=h(t):=q_E+\int_0^t\kappa(s)ds.$$

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

$$\hat{\rho}(q,\eta)=\rho(q,h^{-1}(\eta)),\hat{\mu}(\eta)=\mu(h^{-1}(\eta)),\hat{\kappa}(\eta)=\kappa(h^{-1}(\eta)).$$

From system (2.3), we have

$$\frac{\partial\hat{\rho}(q,\eta)}{\partial\eta}=-\frac{\partial\hat{\rho}(q,\eta)}{\partial q}-\frac{\hat{\mu}(\eta)}{\hat{\kappa}(\eta)}\hat{\rho}(q,\eta).$$

Let $V(s)=\hat{\rho}(s+q-\eta,s)$. Then

$$\frac{\mathrm{d}V(s)}{\mathrm{d}s}=-\frac{\hat{\mu}(s)}{\hat{\kappa}(s)}V(s).$$

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

$$V(\eta)=V(\eta-(q-q_E))e^{-\int_{\eta-(q-q_E)}^{\eta}\frac{\hat{\mu}(s)}{\hat{\kappa}(s)}ds}.$$

Then

$$\hat{\rho}(q,\eta)=\hat{\rho}(q_E,\eta-(q-q_E))e^{-\int_{\eta-(q-q_E)}^{\eta}\frac{\hat{\mu}(s)}{\hat{\kappa}(s)}ds}.$$

Let $\tau(q,t)$ be the time taken to grow from infection development level $q_E$ to level $q$ by a individual who arrives at infection development level $q$ at time $t$. Since $\mathrm{d}q/\mathrm{d}t=\kappa(t)$, we have

$$q-q_E=\int_{t-\tau(q,t)}^{t}\kappa(s)ds, \tag{2.4}$$

and hence,

$$h(t-\tau(q,t))=q_E+\int_0^{t-\tau(q,t)}\kappa(s)ds=h(t)-\int_{t-\tau(q,t)}^{t}\kappa(s)ds=h(t)-q+q_E.$$

Letting $s = h(r)$, we then obtain

$$\int_{\eta-(q-q_E)}^{\eta} \frac{\hat{\mu}(s)}{\hat{\kappa}(s)} ds = \int_{t-\tau(q,t)}^{t} \mu(r) dr.$$

It follows that

$$\begin{aligned} \rho(q,t) &= \hat{\rho}(q, h(t)) \\ &= \rho(q_E, t-\tau(q,t)) e^{-\int_{t-\tau(q,t)}^{t} \mu(r)dr} \\ &= \frac{f(t-\tau(q,t), S(t-\tau(q,t)), I(t-\tau(q,t)))}{\kappa(t-\tau(q,t))} e^{-\int_{t-\tau(q,t)}^{t} \mu(r)dr}. \end{aligned}$$

Let $\tau(t) = \tau(q_I, t)$. Then we have

$$\kappa(t)\rho(q_I, t) = f(t-\tau(t), S(t-\tau(t)), I(t-\tau(t))) \frac{\kappa(t)}{\kappa(t-\tau(t))} e^{-\int_{t-\tau(t)}^{t} \mu(r)dr}.$$

Letting $q = q_I$ and $q_E = 0$ in (2.4), we then obtain

$$q_I = \int_{t-\tau(t)}^{t} \kappa(s) ds,$$

where $\kappa(s)$ is $\omega$-periodic in $s$. Clearly, $\tau(t)$ is an implicitly defined function of $t$. The periodicity of $\kappa(s)$ in $s$ implies the periodicity of the delay $\tau(t)$ in time variable $t$. Taking the derivative with respect to $t$, we have

$$1 - \tau'(t) = \frac{\kappa(t)}{\kappa(t-\tau(t))} > 0.$$

Substituting $M(t) = \kappa(t)\rho(q_I, t)$ into system (2.2), we obtain the following system:

$$\begin{aligned} \tfrac{\mathrm{d}S(t)}{\mathrm{d}t} &= \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t), \\ \tfrac{\mathrm{d}E(t)}{\mathrm{d}t} &= f(t, S(t), I(t)) - \mu(t)E(t) \\ &\quad -(1-\tau'(t))e^{-\int_{t-\tau(t)}^{t} \mu(r)dr} f(t-\tau(t), S(t-\tau(t)), I(t-\tau(t))), \\ \tfrac{\mathrm{d}I(t)}{\mathrm{d}t} &= (1-\tau'(t))e^{-\int_{t-\tau(t)}^{t} \mu(r)dr} f(t-\tau(t), S(t-\tau(t)), I(t-\tau(t))) \\ &\quad -(\mu(t) + d(t) + \gamma(t))I(t), \\ \tfrac{\mathrm{d}R(t)}{\mathrm{d}t} &= \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t). \end{aligned} \tag{2.5}$$

We assume that $f(t, S, I)$ and all these time-dependent coefficients are $\omega$-periodic in $t$ for some real number $\omega > 0$. Then it is easy to see that the function

$$a(t) := e^{-\int_{t-\tau(t)}^{t} \mu(r)dr}$$

is also $\omega$-periodic, and hence system (2.5) is an $\omega$-periodic functional differential system.

In view of biological meanings, we should impose the following compatibility condition:

$$E(0) = \int_{-\tau(0)}^{0} e^{-\int_s^0 \mu(r)dr} f(s, S(s), I(s))ds. \tag{2.6}$$

By the uniqueness of solutions, we then have

$$E(t) = \int_{t-\tau(t)}^{t} e^{-\int_s^t \mu(r)dr} f(s, S(s), I(s))ds.$$

To study the evolution dynamics of system (2.5), we make the following assumptions:

(A1) $\Lambda(t)$, $\mu(t)$, $\alpha(t)$, $d(t)$, and $\gamma(t)$ are all non-negative and continuous functions with $\Lambda(t) > 0$, $\int_0^\omega \mu(t)dt > 0$, and $\int_0^\omega \gamma(t)dt > 0$;

(A2) $f(t, S, I)$ is a $C^1$-function with the following properties:

  (i) $f(t, S, 0) \equiv 0$, $f(t, 0, I) \equiv 0$, and $\frac{\partial f(t,S,0)}{\partial I}$ is positive and non-decreasing for all $S > 0$.

  (ii) $\frac{\partial f(t,S,I)}{\partial S} \geq 0$ and $f(t, S, I) \leq \frac{\partial f(t,S,0)}{\partial I} I$ for all $(t, S, I) \in \mathbb{R} \times \mathbb{R}_+^2$.

A prototypical example for incidence function is $f(t, S, I) = \frac{\beta(t)SI}{1+\varepsilon(t)I}$ with $\varepsilon(t) \geq 0$.

## 2.3 Threshold dynamics

In this section, we first introduce the basic reproduction ratio $R_0$ and then study the global dynamics of system (2.5). Since the second equation of system (2.5) is decoupled from the other equations, it suffices to study the following system:

$$\begin{aligned}
\frac{\mathrm{d}S(t)}{\mathrm{d}t} &= \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t), \\
\frac{\mathrm{d}I(t)}{\mathrm{d}t} &= (1 - \tau'(t))e^{-\int_{t-\tau(t)}^t \mu(r)dr} f(t - \tau(t), S(t - \tau(t)), I(t - \tau(t))) \\
&\quad -(\mu(t) + d(t) + \gamma(t))I(t), \\
\frac{\mathrm{d}R(t)}{\mathrm{d}t} &= \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t).
\end{aligned} \tag{2.7}$$

It is easy to see that the scalar linear periodic equation

$$\frac{\mathrm{d}S(t)}{\mathrm{d}t} = \Lambda(t) - \mu(t)S(t) \tag{2.8}$$

has a unique positive $\omega$-periodic solution

$$S^*(t) = \left[ \int_0^t \Lambda(r) e^{\int_0^r \mu(s)ds} dr + \frac{\int_0^\omega \Lambda(r) e^{\int_0^r \mu(s)ds} dr}{e^{\int_0^\omega \mu(s)ds} - 1} \right] e^{-\int_0^t \mu(s)ds},$$

which is globally stable in $\mathbb{R}$.

Linearizing system (2.7) at the disease-free periodic solution $(S^*(t), 0, 0)$, we obtain the following periodic linear equation for the infective variable $I$:

$$\frac{\mathrm{d}I(t)}{\mathrm{d}t} = c(t)I(t - \tau(t)) - b(t)I(t), \tag{2.9}$$

where $c(t) = (1 - \tau'(t))a(t)\frac{\partial f(t-\tau(t), S^*(t-\tau(t)), 0)}{\partial I}$ and $b(t) = \mu(t) + d(t) + \gamma(t)$.

Let $\hat{\tau} = \max_{0 \le t \le \omega} \tau(t)$, $C = C([-\hat{\tau}, 0], \mathbb{R})$, and $C^+ = C([-\hat{\tau}, 0], \mathbb{R}_+)$. Then $(C, C^+)$ is an ordered Banach space equipped with the maximum norm and the positive cone $C^+$. For any given continuous function $v : [-\hat{\tau}, \sigma) \longrightarrow \mathbb{R}$ with $\sigma > 0$, we define $v_t \in C$ by $v_t(\theta) = v(t + \theta)$, $\forall \theta \in [-\hat{\tau}, 0]$, for any $t \in [0, \sigma)$. Let $F : \mathbb{R} \longrightarrow \mathcal{L}(C, \mathbb{R})$ be a map and $V(t)$ be a continuous function on $\mathbb{R}$ defined as follows:

$$F(t)\phi = c(t)\phi(-\tau(t)), \quad V(t) = b(t).$$

Then the linear system (2.9) can be written as

$$\frac{\mathrm{d}v(t)}{\mathrm{d}t} = F(t)v_t - V(t)v(t).$$

Then the internal evolution of infective compartment $I$ is described by the following evolution system

$$\frac{\mathrm{d}v(t)}{\mathrm{d}t} = -V(t)v(t).$$

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

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

It then easily follows that

$$\Phi(t, s) = e^{-\int_s^t b(r)dr}, \forall t \ge s, s \in \mathbb{R}.$$

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

Suppose that $v \in C_\omega$ is the initial distribution of infectious individuals. Then for any given $s \geq 0$, $F(t-s)v_{t-s}$ is the distribution of newly infectious individuals at time $t-s$, which is produced by the infectious individuals who were introduced over the time interval $[t-s-\hat{\tau}, t-s]$. Then $\Phi(t, t-s)F(t-s)v_{t-s}$ is the distribution of those infectious individuals who newly became infectious at time $t-s$ and remain in the infectious 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 new infectious at time $t$ produced by all those infectious individuals introduced at all previous time to $t$.

We define the next generation operator $L : C_\omega \longrightarrow C_\omega$ by

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

Following [150], we define $R_0 = r(L)$, the spectral radius of $L$. For any given $t \geq 0$, let $\hat{P}(t)$ be the solution map of system (2.9), that is, $\hat{P}(t)\psi = u_t(\psi)$, where $u(t, \psi)$ is the unique solution of system (2.9) with $u_0 = \psi \in C$. Then $\hat{P} := \hat{P}(\omega)$ is the Poincaré (period) map associated with linear system (2.9). Let $r(\hat{P})$ be the spectral radius of $\hat{P}$. In view of Theorem 1.4.1, we have the following result.

**Lemma 2.3.1.** *$R_0 - 1$ has the same sign as $r(\hat{P}) - 1$.*

Let $X = C([-\hat{\tau}, 0], \mathbb{R}_+^3)$. Then we have the following result for system (2.7).

**Lemma 2.3.2.** *For any $\varphi \in X$, system (2.7) has a unique nonnegative solution $u(t, \varphi)$ with $u_0 = \varphi$ for all $t \geq 0$, and solutions are also ultimately bounded.*

*Proof.* For any $\varphi = (\varphi_1, \varphi_2, \varphi_3) \in X$, we define

$$\tilde{f}(t, \varphi) = \begin{pmatrix} \Lambda(t) - f(t, \varphi_1(0), \varphi_2(0)) - \mu(t)\varphi_1(0) + \alpha(t)\varphi_3(0) \\ (1-\tau'(t))e^{-\int_{t-\tau(t)}^t \mu(r)dr} f(t-\tau(t), \varphi_1(-\tau(t)), \varphi_2(-\tau(t))) \\ \qquad -(\mu(t) + d(t) + \gamma(t))\varphi_2(0) \\ \gamma(t)\varphi_2(0) - \mu(t)\varphi_3(0) - \alpha(t)\varphi_3(0) \end{pmatrix}.$$

Note that $\tilde{f}(t,\varphi)$ is continuous in $(t,\varphi)\in\mathbb{R}_+\times X$ and $\tilde{f}(t,\varphi)$ is Lipschitz in $\varphi$ on each compact subset of $X$. By [50, Theorems 2.2.1 and 2.2.3], it then follows that system (2.7) has a unique solution $u(t,\varphi)$ on its maximal interval $[0,\sigma_\varphi)$ of existence with $u_0=\varphi$.

Let $\varphi=(\varphi_1,\varphi_2,\varphi_3)\in X$ be given. If $\varphi_i(0)=0$ for some $i\in\{1,2,3\}$, then $\tilde{f}_i(t,\varphi)\geq 0$. By [116, Theorem 5.2.1], it follows that for any $\varphi\in X$, the solution $u(t,\varphi)$ of system (2.7) with $u_0=\varphi$ is nonnegative for all $t\in[0,\sigma_\varphi)$. Define

$$D:=\left\{\psi\in C([-\hat{\tau},0],\mathbb{R}_+^4):\psi_2(0)=\int_{-\tau(0)}^{0}e^{-\int_s^0\mu(r)dr}f(s,\psi_1(s),\psi_3(s))ds\right\}.$$

It then easily follows that for any $\psi\in D$, system (2.5) has a unique nonnegative solution $v(t,\psi)=(S(t),E(t),I(t),R(t))$ satisfying $v_0=\psi$ for all $t\in[0,\sigma_\varphi)$.

Let $N(t)=S(t)+E(t)+I(t)+R(t)$. Then we have

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t}=\Lambda(t)-\mu(t)N(t)-d(t)I(t)\leq\Lambda(t)-\mu(t)N(t),$$

for all $t\in[0,\sigma_\varphi)$. Thus, $S(t)$, $E(t)$, $I(t)$, and $R(t)$ are bounded on $t\in[0,\sigma_\varphi)$. Therefore, [50, Theorem 2.3.1] implies that $\sigma_\varphi=\infty$. It follows that

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t}=\Lambda(t)-\mu(t)N(t)-d(t)I(t)\leq\Lambda(t)-\mu(t)N(t),t\geq 0. \tag{2.10}$$

Then the global attractivity of $S^*(t)$ for system (2.8), together with the comparison argument, implies that solutions of system (2.5) with initial data in $D$, and hence system (2.7) in $X$, exist globally on $[0,\infty)$ and are also ultimately bounded. □

Let

$$Y:=C([-\tau(0),0],\mathbb{R}_+^2)\times\mathbb{R}_+.$$

**Lemma 2.3.3.** *For any $\varphi\in Y$, system (2.7) has a unique nonnegative solution $u(t,\varphi)$ with $u_0=\varphi$ for all $t\geq 0$.*

*Proof.* Let $\bar{\tau}=\min_{t\in[0,\omega]}\tau(t)$. For any $t\in[0,\bar{\tau}]$, since $t-\tau(t)$ is strictly increasing in $t$, we have

$$-\tau(0)=0-\tau(0)\leq t-\tau(t)\leq\bar{\tau}-\tau(\bar{\tau})\leq\bar{\tau}-\bar{\tau}=0,$$

and hence,

$$S(t-\tau(t))=\varphi_1(t-\tau(t))\ \text{ and }\ I(t-\tau(t))=\varphi_2(t-\tau(t)).$$

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

$$\begin{aligned}
\tfrac{\mathrm{d}S(t)}{\mathrm{d}t} &= \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t), \\
\tfrac{\mathrm{d}I(t)}{\mathrm{d}t} &= (1 - \tau'(t))e^{-\int_{t-\tau(t)}^{t} \mu(r)dr} f(t - \tau(t), \varphi_1(t - \tau(t)), \varphi_2(t - \tau(t))) \\
&\quad -(\mu(t) + d(t) + \gamma(t))I(t), \\
\tfrac{\mathrm{d}R(t)}{\mathrm{d}t} &= \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t).
\end{aligned}$$

Given $\varphi \in Y$, the solution $(S(t), I(t), R(t))$ of the above system exists for all $t \in [0, \bar{\tau}]$. In other words, we have obtained the values of $\psi_1(\theta) := S(\theta)$, $\psi_2(\theta) := I(\theta)$ for $\theta \in [-\tau(0), \bar{\tau}]$ and $\psi_3(\theta) := R(\theta)$ for $\theta \in [0, \bar{\tau}]$.

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

$$-\tau(0) = 0 - \tau(0) \leq \bar{\tau} - \tau(\bar{\tau}) \leq t - \tau(t) \leq 2\bar{\tau} - \tau(2\bar{\tau}) \leq 2\bar{\tau} - \bar{\tau} = \bar{\tau},$$

and hence,

$$S(t - \tau(t)) = \psi_1(t - \tau(t)) \quad \text{and} \quad I(t - \tau(t)) = \psi_2(t - \tau(t)).$$

Solving the following ordinary differential equations for $t \in [\bar{\tau}, 2\bar{\tau}]$ with $S(\bar{\tau}) = \psi_1(\bar{\tau})$, $I(\bar{\tau}) = \psi_2(\bar{\tau})$, $R(\bar{\tau}) = \psi_3(\bar{\tau})$,

$$\begin{aligned}
\tfrac{\mathrm{d}S(t)}{\mathrm{d}t} &= \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t), \\
\tfrac{\mathrm{d}I(t)}{\mathrm{d}t} &= (1 - \tau'(t))e^{-\int_{t-\tau(t)}^{t} \mu(r)dr} f(t - \tau(t), \psi_1(t - \tau(t)), \psi_2(t - \tau(t))) \\
&\quad -(\mu(t) + d(t) + \gamma(t))I(t), \\
\tfrac{\mathrm{d}R(t)}{\mathrm{d}t} &= \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t),
\end{aligned}$$

we get the solution $(S(t), I(t), R(t))$ on $[\bar{\tau}, 2\bar{\tau}]$. Repeating this procedure for $t \in [2\bar{\tau}, 3\bar{\tau}]$, $[3\bar{\tau}, 4\bar{\tau}]$,..., it then follows that for any $\varphi \in Y$, system (2.7) has a unique solution $u(t, \varphi)$ with $u_0 = \varphi$ for all $t \geq 0$. $\square$

**Remark 2.3.1.** *By the uniqueness of solutions in Lemmas 2.3.2 and 2.3.3, it follows that for any* $\psi \in X$ *and* $\phi \in Y$ *with* $\psi_1(\theta) = \phi_1(\theta)$, $\psi_2(\theta) = \phi_2(\theta)$, *for all* $\theta \in [-\tau(0), 0]$ *and* $\psi_3 = \phi_3$, *we have* $w(t, \psi) = \nu(t, \phi)$ *for all* $t \geq 0$, *where* $w(t, \psi)$ *and* $\nu(t, \phi)$ *are solutions of system (2.7) satisfying* $w_0 = \psi$ *and* $\nu_0 = \phi$, *respectively.*

Let

$$W = C([-\tau(0), 0], \mathbb{R}), \quad W^+ = C([-\tau(0), 0], \mathbb{R}_+).$$

For any given $t \geq 0$, let $P(t)$ be the solution map of the scalar linear periodic system (2.9) on $W$, that is, $P(t)\phi = v_t(\phi)$, $t \geq 0$, where $v(t, \phi)$ is the unique solution of system (2.9) satisfying $v_0 = \phi \in W$. By similar arguments to those in [82, Lemma 3.5], we have the following result.

**Lemma 2.3.4.** *$P(t)$ is an $\omega$-periodic semiflow on $W$ in the sense that (i) $P(0) = I$; (ii) $P(t+\omega) = P(t) \circ P(\omega)$ for all $t \geq 0$; and (iii) $P(t)\phi$ is continuous in $(t, \phi) \in [0, \infty) \times W$.*

Let $P := P(\omega)$ be the Poincaré map associated with system (2.9) on $W$ and $r(P)$ be its spectral radius. We first prove that the solution map $P(t)$ is monotone for each $t \geq 0$. For any given $\varphi, \psi \in W$ with $\varphi \geq \psi$, let $\bar{v}(t) = v(t, \varphi)$ and $v(t) = v(t, \psi)$ be the unique solution of system (2.9) with $\bar{v}_0 = \varphi$ and $v_0 = \psi$, respectively. Since

$$-\tau(0) = 0 - \tau(0) \leq t - \tau(t) \leq \bar{\tau} - \tau(\bar{\tau}) \leq \bar{\tau} - \bar{\tau} = 0, \forall t \in [0, \bar{\tau}],$$

we have

$$\bar{v}(t - \tau(t)) = \varphi(t - \tau(t)) \;\text{ and }\; v(t - \tau(t)) = \psi(t - \tau(t)), \forall t \in [0, \bar{\tau}].$$

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

$$\begin{aligned} \tfrac{\mathrm{d}I(t)}{\mathrm{d}t} &= c(t)\varphi(t - \tau(t)) - b(t)I(t), \\ \tfrac{\mathrm{d}I(t)}{\mathrm{d}t} &= c(t)\psi(t - \tau(t)) - b(t)I(t). \end{aligned}$$

Given $\varphi, \psi \in W$, the solution $I(t)$ of the above equations exists for all $t \in [0, \bar{\tau}]$. In the view of $\bar{v}(0) = \varphi(0) \geq \psi(0) = v(0)$, the comparison theorem for cooperative ordinary differential systems implies that $\bar{v}(t) \geq v(t)$ for all $t \in [0, \bar{\tau}]$. Repeating this procedure for $t \in [\bar{\tau}, 2\bar{\tau}]$, $[2\bar{\tau}, 3\bar{\tau}]$,..., it follows that $v(t, \varphi) \geq v(t, \psi)$ for all $t \in [0, \infty)$. This implies that the solution map $P(t)$ is monotone for each $t \geq 0$. Now we show that the solution map $P(t)$ is eventually strongly monotone.

**Lemma 2.3.5.** *For any $\varphi$ and $\psi$ in $W$ with $\varphi > \psi$ (that is, $\varphi \geq \psi$, but $\varphi \neq \psi$), the solutions $\bar{v}(t)$ and $v(t)$ of system (2.9) with $\bar{v}_0 = \varphi$ and $v_0 = \psi$, respectively, satisfy $\bar{v}(t) > v(t)$ for all $t \geq \hat{\tau}$, and hence, $P(t)\varphi \gg P(t)\psi$ in $W$ for all $t \geq \hat{\tau} + \tau(0)$.*

*Proof.* We first show that $\bar{v}(t_0) > v(t_0)$ for some $t_0 \in [0, \hat{\tau}]$. Assume, by contradiction, that $\bar{v}(t) = v(t)$ for all $t \in [0, \hat{\tau}]$. Then $\frac{\mathrm{d}\bar{v}(t)}{\mathrm{d}t} = \frac{\mathrm{d}v(t)}{\mathrm{d}t}$ for all $t \in [0, \hat{\tau}]$, and hence,

$$\frac{\mathrm{d}\bar{v}(t)}{\mathrm{d}t} = (1 - \tau'(t))a(t)\frac{\partial f(t - \tau(t), S^*(t - \tau(t)), 0)}{\partial \bar{v}}\bar{v}(t - \tau(t)) - (\mu(t) + d(t) + \gamma(t))\bar{v}(t),$$

$$\frac{\mathrm{d}v(t)}{\mathrm{d}t} = (1 - \tau'(t))a(t)\frac{\partial f(t - \tau(t), S^*(t - \tau(t)), 0)}{\partial v}v(t - \tau(t)) - (\mu(t) + d(t) + \gamma(t))v(t),$$

that is,

$$(1-\tau'(t))a(t)\frac{\partial f(t-\tau(t),S^*(t-\tau(t)),0)}{\partial \bar{v}}[\bar{v}(t-\tau(t))-v(t-\tau(t))]=0,\forall t\in[0,\hat{\tau}].$$

It follows that $\bar{v}(t-\tau(t))=v(t-\tau(t))$ for all $t\in[0,\hat{\tau}]$. Since $-\tau(0)=0-\tau(0)\le t-\tau(t)\le\hat{\tau}-\tau(\hat{\tau}),\forall t\in[0,\hat{\tau}]$, and $\hat{\tau}-\tau(\hat{\tau})\ge 0$, we have $\varphi(\theta)=\psi(\theta)$ for all $\theta\in[-\tau(0),0]$, which is a contradiction to the assumption $\varphi>\psi$ in $W$.

Let

$$g(t,\xi):=(1-\tau'(t))a(t)\frac{\partial f(t-\tau(t),S^*(t-\tau(t)),0)}{\partial v}v(t-\tau(t))-(\mu(t)+d(t)+\gamma(t))\xi.$$

By (A2), $\frac{\partial f(t,S,0)}{\partial I}$ is positive for all $S>0$. It then follows that for all $t\ge t_0$,

$$\begin{aligned}\frac{\mathrm{d}\bar{v}(t)}{\mathrm{d}t}=&(1-\tau'(t))a(t)\frac{\partial f(t-\tau(t),S^*(t-\tau(t)),0)}{\partial \bar{v}}\bar{v}(t-\tau(t))\\&-(\mu(t)+d(t)+\gamma(t))\bar{v}(t)\\\ge&(1-\tau'(t))a(t)\frac{\partial f(t-\tau(t),S^*(t-\tau(t)),0)}{\partial v}v(t-\tau(t))\\&-(\mu(t)+d(t)+\gamma(t))\bar{v}(t)=g(t,\bar{v}(t)),\end{aligned}$$

and hence,

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

Since $\bar{v}(t_0)>v(t_0)$, the comparison theorem for ordinary differential equations (see Theorem 1.3.1) implies that $\bar{v}(t)>v(t)$ for all $t\ge t_0$. Since $t_0\in[0,\hat{\tau}]$, $\bar{v}(t)>v(t)$ for all $t\ge\hat{\tau}$, and hence, $P(t)\varphi\gg P(t)\psi$ for all $t\ge\hat{\tau}+\tau(0)$. □

Let $Q(t)$ be the solution maps of system (2.7) on $Y$, that is, $Q(t)\phi=\nu_t(\phi)$, $t\ge 0$, where $\nu(t,\phi)$ is the unique solution of system (2.7) satisfying $\nu_0=\phi\in Y$. By arguments similar to those in [82, Lemma 3.5], we have the following result.

**Lemma 2.3.6.** *$Q(t)$ is an $\omega$-periodic semiflow on $Y$ in the sense that (i) $Q(0)=I$; (ii) $Q(t+\omega)=Q(t)\circ Q(\omega)$ for all $t\ge 0$; and (iii) $Q(t)\phi$ is continuous in $(t,\phi)\in[0,\infty)\times Y$.*

We also need the following observation in our analysis of system (2.7).

**Lemma 2.3.7.** *Assume that $f(t)$ is a nonnegative continuous and $\omega$-periodic function on $\mathbb{R}_+$ with $\int_0^\omega f(t)dt>0$, and $g(t)$ is a continuous function on $\mathbb{R}_+$. If $\lim_{t\to\infty}g(t)=0$, then any solution $u(t)$ of the linear non-homogeneous equation*

$$u'(t)=-f(t)u(t)+g(t),\ t\ge 0 \tag{2.11}$$

*satisfies $\lim_{t\to\infty}u(t)=0$.*

*Proof.* Let $U(t,s) = e^{-\int_s^t f(r)dr}$ and $M := \frac{1}{\omega}\int_0^\omega f(t)dt$. For any $t \geq s \geq 0$, letting $n = \left[\frac{t-s}{\omega}\right]$, we then have

$$\begin{aligned}\int_s^t f(r)dr =& \int_s^{s+n\omega} f(r)dr + \int_{s+n\omega}^t f(r)dr \\ =& n\int_0^\omega f(r)dr + \int_{s+n\omega}^t f(r)dr \\ =& n\omega M + \int_s^{t-n\omega} f(r)dr.\end{aligned}$$

Let $K := e^{M\omega}$. Since $M > 0$ and $n\omega \leq t-s < (n+1)\omega$, it follows that

$$U(t,s) = e^{-n\omega M}e^{-\int_s^{t-n\omega} f(r)dr} \leq e^{-(t-s-\omega)M} = Ke^{-M(t-s)}, \ \forall t \geq s \geq 0.$$

Let $\varepsilon > 0$ be given. Since $\lim_{t\to\infty} g(t) = 0$, there exists a sufficiently large $t_0 > 0$ such that $|g(t)| < \varepsilon$, $\forall t \geq t_0$. It then follows that the solution $u(t)$ of equation (2.11) satisfies

$$u(t) = U(t,t_0)u(t_0) + \int_{t_0}^t U(t,s)g(s)ds, \ \forall t \geq t_0,$$

and hence,

$$\begin{aligned}|u(t)| \leq& Ke^{-M(t-t_0)}|u(t_0)| + \varepsilon\int_{t_0}^t Ke^{-M(t-s)}ds \\ \leq& Ke^{-M(t-t_0)}|u(t_0)| + \frac{\varepsilon K}{M}(1-e^{-M(t-t_0)}), \ \forall t \geq t_0.\end{aligned}$$

This implies that $\lim_{t\to\infty} u(t) = 0$. □

Now we are ready to prove the main result of this section.

**Theorem 2.3.1.** *Let (A1) and (A2) hold. Then the following statements are valid:*

*(i) If $r(P) < 1$, then the disease-free periodic solution $(S^*(t), 0, 0)$ is globally attractive for system (2.7) in $Y$.*

*(ii) If $r(P) > 1$, then system (2.7) admits a positive $\omega$-periodic solution $(\bar{S}(t), \bar{I}(t), \bar{R}(t))$ and there exists a real number $\eta > 0$ such that for any $\phi \in Y$ with $\phi_2(0) > 0$, the solution $\nu(t,\phi) = (S(t), I(t), R(t))$ satisfies $\liminf_{t\to\infty} I(t) \geq \eta$.*

*Proof.* Our proof is motivated by the arguments in [150, Theorem 3.1]. By [50, Theorem 3.6.1], it follows that for each $t \geq \hat{\tau}$, the linear operator $\hat{P}(t)$ is compact on $C$, and hence $P(t)$ is also compact on $W$ for any $t \geq \hat{\tau}$. In view of Lemma 2.3.5, $P(t)$ is strongly positive on $W$ for any $t \geq \hat{\tau} + \tau(0)$. Thus, for any $t \geq \tilde{\tau} = \hat{\tau} + \tau(0)$, $P(t)$ is compact and strongly positive on $W$. Choose an integer $n_0 > 0$ such that $n_0\omega \geq \tilde{\tau}$. Since $P^{n_0} = P(n_0\omega)$, [74, Lemma 3.1] implies that $r(P)$ is a simple eigenvalue of $P$ having a strongly positive eigenvector, and the modulus of any other eigenvalue is less than $r(P)$. Let $\mu = \frac{\ln r(P)}{\omega}$. By [135, Lemma 1 ], it then follows that there is a positive $\omega$-periodic function $v(t)$ such that $u(t) = e^{\mu t}v(t)$ is a positive solution of linear equation (2.9).

In the case where $r(P) < 1$, let $P_\epsilon(t)$ be the solution maps of the following perturbed linear periodic equation on $W$:

$$\begin{aligned}\frac{\mathrm{d}I(t)}{\mathrm{d}t} =& (1-\tau'(t))a(t)\frac{\partial f(t-\tau(t), S^*(t-\tau(t))+\epsilon, 0)}{\partial I}I(t-\tau(t)) \\ &- (\mu(t)+d(t)+\gamma(t))I(t), \end{aligned} \tag{2.12}$$

and $P_\epsilon := P_\epsilon(\omega)$. Since $\lim_{\epsilon\to 0} r(P_\epsilon) = r(P) < 1$, we can fix a sufficiently small number $\epsilon > 0$ such that $r(P_\epsilon) < 1$. It is easy to verify that $P_\epsilon(t)$ is also compact and strongly monotone on $W$ for each $t \geq \tilde{\tau}$. As discussed above, there is a positive $\omega$-periodic function $v_\epsilon(t)$ such that $u_\epsilon(t) = e^{\mu_\epsilon t}v_\epsilon(t)$ is a positive solution of system (2.12), where $\mu_\epsilon = \frac{\ln r(P_\epsilon)}{\omega} < 0$. Clearly, $\lim_{t\to\infty} u_\epsilon(t) = 0$.

In view of (2.10) and the global attractivity of $S^*(t)$ for system (2.8), there exists a sufficiently large integer $N_1 > 0$ such that $N_1\omega \geq \hat{\tau}$ and $S(t) \leq S^*(t)+\epsilon$, $\forall t \geq N_1\omega - \hat{\tau}$. By assumption (A2), we then have

$$\begin{aligned}\frac{\mathrm{d}I(t)}{\mathrm{d}t} \leq& \left((1-\tau'(t))a(t)\frac{\partial f(t-\tau(t), S^*(t-\tau(t))+\epsilon, 0)}{\partial I}I(t-\tau(t))\right) \\ &- (\mu(t)+d(t)+\gamma(t))I(t),\end{aligned}$$

for all $t \geq N_1\omega$. Choose a sufficiently large number $k > 0$ such that $I(t) \leq ku_\epsilon(t)$, $\forall t \in [N_1\omega, N_1\omega + \hat{\tau}]$. Thus, the comparison theorem for delay differential equations (see Theorem 1.3.2) implies that $I(t) \leq ku_\epsilon(t)$, $\forall t \geq N_1\omega + \hat{\tau}$. Thus, $\lim_{t\to\infty} I(t) = 0$. By Lemma 2.3.7 with $f(t) = \mu(t) + \alpha(t)$ and $g(t) = \gamma(t)I(t)$, as applied to the third equation of system (2.7), it then follows that $\lim_{t\to\infty} R(t) = 0$. Let $w(t) := S(t) - S^*(t)$. In view of (2.7) and (2.8), we have

$$w'(t) = -\mu(t)w(t) + (\alpha(t)R(t) - f(t, S(t), I(t))).$$

Since $\lim_{t\to\infty} I(t) = 0$ and $\lim_{t\to\infty} R(t) = 0$, it follows that

$$\lim_{t\to\infty}(\alpha(t)R(t) - f(t, S(t), I(t))) = 0.$$

Now Lemma 2.3.7 implies that $\lim_{t\to\infty} w(t) = 0$, that is, $\lim_{t\to\infty}(S(t) - S^*(t)) = 0$. This proves statement (i).

In the case where $r(P) > 1$, we will apply the persistence theory for periodic semiflows. Let $Y_0 = \{\phi = (\phi_1, \phi_2, \phi_3) \in Y : \phi_2(0) > 0\}$ and $\partial Y_0 := Y \backslash Y_0 = \{\phi = (\phi_1, \phi_2, \phi_3) \in Y : \phi_2(0) = 0\}$. Let $Q(t)\phi = \nu_t(\phi)$, $\forall \phi \in Y$. Then $Q := Q(\omega)$ is the Poincaré map associated with system (2.7) on $Y$ and $Q^n = Q(n\omega)$, $\forall n \geq 0$.

From the second equation of system (2.7), it is easy to see that $Q(t)Y_0 \subseteq Y_0$ for all $t \geq 0$. By Lemma 2.3.2 and Remark 2.3.1, the discrete-time system $\{Q^n : Y \to Y\}_{n\geq 0}$ is point dissipative. By [50, Theorem 3.6.1] and Remark 2.3.1, for each $t \geq \hat{\tau}$, $Q(t)$ is compact, and hence $Q^n$ is compact for sufficiently large $n$. It then follows from Theorem 1.1.3 that $Q$ admits a strong global attractor in $Y$. Now we prove that $Q$ is uniformly persistent with respect to $(Y_0, \partial Y_0)$.

Let $M_\delta$ be the Poincaré map of the following perturbed linear periodic equation:

$$\begin{aligned}\frac{\mathrm{d}I(t)}{\mathrm{d}t} =&(1-\tau'(t))a(t)\left(\frac{\partial f(t-\tau(t), S^*(t-\tau(t)), 0)}{\partial I} - \delta\right) I(t-\tau(t))\\ &- (\mu(t) + d(t) + \gamma(t))I(t).\end{aligned} \tag{2.13}$$

Since $\lim_{\delta\to 0} r(M_\delta) = r(P) > 1$, we can fix a sufficiently small $\delta$ such that $r(M_\delta) > 1$. It follows that there is a small number $\eta_0 > 0$ such that

$$f(t-\tau(t), S^*(t-\tau(t)) - \eta_0, I) \geq \left(\frac{\partial f(t-\tau(t), S^*(t-\tau(t)), 0)}{\partial I} - \delta\right) I, \forall I \in [0, \eta_0].$$

Let $M_1 = (S_0^*, 0, 0)$, where $S_0^*(\theta) = S^*(\theta)$ for all $\theta \in [-\tau(0), 0]$. Then $Q(t)M_1 = (S_t^*, 0, 0)$, $\forall t \geq 0$, and $Q(M_1) = M_1$. Since $\lim_{\phi\to M_1} \|Q(t)\phi - Q(t)M_1\|$=0 uniformly for $t \in [0, \omega]$, there exists $\eta_1 = \eta_1(\eta_0) > 0$ such that for any $\phi \in Y_0$ with $\|\phi - M_1\| < \eta_1$, we have $\|Q(t)\phi - Q(t)M_1\| < \eta_0$ for all $t \in [0, \omega]$. We further have the following claim.
**Claim.** $\limsup_{n\to\infty} \|Q^n(\phi) - M_1\| \geq \eta_1$ for all $\phi \in Y_0$.

Suppose, by contradiction, that $\limsup_{n\to\infty} \|Q^n(\psi) - M_1\| < \eta_1$ for some $\psi \in Y_0$. Then there exists an integer $N_2 \geq 1$ such that $\|Q^n(\psi) - M_1\| < \eta_1$ for all $n \geq N_2$. For any $t \geq N_2\omega$, we have $t = n\omega + t'$ with $n \geq N_2$ and $t' \in [0, \omega]$, and hence,

$$\|Q(t)\psi - Q(t)M_1\| = \|Q(t')(Q^n(\psi)) - Q(t')M_1\| < \eta_0, \forall t \geq N_2\omega.$$

It follows that $S(t-\tau(t)) > S^*(t-\tau(t)) - \eta_0$ for all $t \geq N_2\omega + \hat{\tau}$. In view of (A2), we see that $f(t, S, I)$ is nondecreasing in $S$. Thus, $\nu(t, \psi) = (S(t), I(t), R(t))$ satisfies

$$\begin{aligned}\frac{\mathrm{d}I(t)}{\mathrm{d}t} =&(1-\tau'(t))a(t)f(t-\tau(t), S(t-\tau(t)), I(t-\tau(t))) - (\mu(t)+d(t)+\gamma(t))I(t)\\ \geq&(1-\tau'(t))a(t)f(t-\tau(t), S^*(t-\tau(t))-\eta_0, I(t-\tau(t)))\\ &-(\mu(t)+d(t)+\gamma(t))I(t)\\ \geq&(1-\tau'(t))a(t)\left(\frac{\partial f(t-\tau(t), S^*(t-\tau(t)), 0)}{\partial I} - \delta\right)I(t-\tau(t))\\ &-(\mu(t)+d(t)+\gamma(t))I(t),\end{aligned}$$

for all $t \geq N_2\omega + \hat{\tau}$. Note that $r(M_\delta) > 1$. As discussed earlier, there is a positive $\omega$-periodic function $v_\delta(t)$ such that $u_\delta(t) = e^{\mu_\delta t}v_\delta(t)$ is a positive solution of system (2.13), where $\mu_\delta = \frac{\ln r(M_\delta)}{\omega} > 0$. Since $Q(t)(Y_0) \subseteq Y_0$, $I(t) > 0$ for all $t \geq 0$. We can choose a sufficiently small $k > 0$ such that $I(t) \geq ku_\delta(t)$, $\forall t \in [N_2\omega+\hat{\tau}, N_2\omega+2\hat{\tau}]$. By the comparison theorem for delay differential equations (see Theorem 1.3.2), it follows that $I(t) \geq ku_\delta(t)$, $\forall t \geq N_2\omega + 2\hat{\tau}$. Clearly, $\lim_{t\to\infty} u_\delta(t) = \infty$. Thus, $\lim_{t\to\infty} I(t) = \infty$, which is a contradiction.

The above claim implies that $M_1$ is an isolated invariant set for $Q$ in $Y$ and $W^S(M_1)\bigcap Y_0 = \emptyset$, where $W^S(M_1)$ is the stable set of $M_1$ for $Q$. Define

$$M_\partial := \{\phi \in \partial Y_0 : Q^n(\phi) \in \partial Y_0, \forall n \geq 0\}.$$

Since

$$\frac{\mathrm{d}I(t)}{\mathrm{d}t} \geq -(\mu(t)+d(t)+\gamma(t))I(t), \forall t \geq 0,$$

it is easy to see that if $I(t_0) > 0$ for some $t_0 \geq 0$, then $I(t) > 0$ for all $t \geq t_0$. This implies that $I(t) = 0$, $\forall t \geq 0$, whenever $\phi \in M_\partial$. It then follows that $\omega(\phi) = M_1$ for any $\phi \in M_\partial$, and $M_1$ cannot form a cycle for $Q$ in $\partial Y_0$. By the acyclicity theorem on uniform persistence for maps (see Theorem 1.2.1 ), $Q : Y \to Y$ is uniformly persistent with respect to $(Y_0, \partial Y_0)$.

Define

$$X_0 = \{\psi = (\psi_1, \psi_2, \psi_3) \in X : \psi_2(0) > 0\},$$

$$\partial X_0 := X\backslash X_0 = \{\psi = (\psi_1, \psi_2, \psi_3) \in X : \psi_2(0) = 0\}.$$

Let $\hat{Q}(t)$ be the solution maps of system (2.7) on $X$, that is, $\hat{Q}(t)\psi = w_t(\psi), \forall t \geq 0$, where $w(t, \psi)$ is the unique solution of system (2.7) satisfying $w_0 = \psi \in X$. Then

$\hat{Q} := \hat{Q}(\omega)$ is the Poincaré map associated with system (2.7) and $\hat{Q}^n := \hat{Q}(n\omega)$, $\forall n \geq 0$.

From [50, Theorem 3.6.1], we know that $\hat{Q}(t)$ is compact on $X$ for each $t \geq \hat{\tau}$, and hence $\hat{Q}^n$ is compact for sufficiently large $n$. By Lemma 2.3.2, solutions $w(t, \psi)$ are ultimately bounded on $[0, \infty)$, and hence, the discrete-time system $\{\hat{Q}^n : X \to X\}_{n \geq 0}$ is point dissipative. By Remark 2.3.1, it follows that $\hat{Q}$ is uniformly persistent with respect to $(X_0, \partial X_0)$.

Note that for any integer $\hat{n}_0$ with $\hat{n}_0\omega \geq \hat{\tau}$, $\hat{Q}^{\hat{n}_0} = \hat{Q}(\hat{n}_0\omega) : X \to X$ is compact. By [151, Theorem 3.5.1], $\hat{Q}(t)$ is an $\alpha$-contraction with respect to an equivalent norm in $C([-\hat{\tau}, 0], \mathbb{R}^3)$ for any $t > 0$. It then follows from Theorem 1.2.5 that there exists a global attractor $A$ for $\hat{Q} : X_0 \to X_0$ and $\hat{Q}$ has a fixed point $\psi^* \in A$, and hence, $w(t, \psi^*) = (\bar{S}(t), \bar{I}(t), \bar{R}(t))$ is an $\omega$-periodic solution of system (2.7) with $\psi^* \in X_0$. By Remark 2.3.1, $\nu(t, \phi^*) = (\bar{S}(t), \bar{I}(t), \bar{R}(t))$ is also an $\omega$-periodic solution of system (2.7) with $\phi^* \in Y_0$, where $\phi_1^*(\theta) = \psi_1^*(\theta)$, $\phi_2^*(\theta) = \psi_2^*(\theta)$, for all $\theta \in [-\tau(0), 0]$ and $\phi_3^* = \psi_3^*$. Then $\bar{S}(t) \geq 0, \bar{I}(t) > 0$ and $\bar{R}(t) \geq 0$.

We claim that there exists some $\bar{t} \in [0, \omega]$ such that $\bar{S}(\bar{t}) > 0$. If not, then $\bar{S}(t) \equiv 0$ for all $t \geq 0$, due to the periodicity of $\bar{S}(t)$. Since $\Lambda(t) > 0$ and $f(t, 0, I) \equiv 0$, we see from the first equation of system (2.7) that $0 = \Lambda(t) + \alpha(t)\bar{R}(t) > 0$, which is a contradiction. Since $\bar{S}(\bar{t}) > 0$ for some $\bar{t} \in [0, \omega]$, and

$$\begin{aligned}\frac{\mathrm{d}\bar{S}(t)}{\mathrm{d}t}\Big|_{\bar{S}(t)=0} &= \Lambda(t) - f(t, \bar{S}(t), \bar{I}(t)) - \mu(t)\bar{S}(t) + \alpha(t)\bar{R}(t) \\ &= \Lambda(t) + \alpha(t)\bar{R}(t) > 0, \forall t \geq \bar{t},\end{aligned}$$

it follows that $\bar{S}(t) > 0$ for all $t \geq \bar{t}$. Now the periodicity of $\bar{S}(t)$ implies that $\bar{S}(t) > 0$ for all $t \geq 0$. We claim that there exists some $\hat{t} \in [0, \omega]$ such that $\bar{R}(\hat{t}) > 0$. If not, then $\bar{R}(t) \equiv 0$ for all $t \geq 0$, due to the periodicity of $\bar{R}(t)$. Since $\gamma(t) \geq 0$ and $\int_0^\omega \gamma(t)dt > 0$, $\gamma(t) \not\equiv 0$, the third equation of system (2.7) implies that $0 = \gamma(t)I(t) \not\equiv 0$ for all $t \geq 0$, which is a contradiction. Since $\bar{R}(\hat{t}) > 0$ for some $\hat{t} \in [0, \omega]$ and

$$\frac{\mathrm{d}\bar{R}(t)}{\mathrm{d}t} \geq -(\mu(t) + \alpha(t))\bar{R}(t),$$

it follows that $\bar{R}(t) > 0$ for all $t \geq \hat{t}$. Now the periodicity of $\bar{R}(t)$ implies that $\bar{R}(t) > 0$ for all $t \geq 0$. Therefore, $\nu(t, \phi^*) = (\bar{S}(t), \bar{I}(t), \bar{R}(t))$ is a positive $\omega$-periodic solution of system (2.7) with $\phi^* \in Y_0$.

By Theorem 1.2.3, it then follows that $Q : Y_0 \to Y_0$ has a global attractor $A_0$. Since $A_0 = Q(A_0) = Q(\omega)A_0$, we have $\phi_2(0) > 0, \forall \phi \in A_0$. Let $B_0 := \bigcup_{t\in[0,\omega]} Q(t)A_0$. Then $\psi_2(0) > 0$ for all $\psi \in B_0$. Moreover, $B_0 \subseteq Y_0$, and Theorem 1.2.6 implies that $\lim_{t\to\infty} d(Q(t)\phi, B_0) = 0$ for all $\phi \in Y_0$. Define a continuous function $p : Y \to \mathbb{R}_+$ by

$$p(\phi) = \phi_2(0), \forall \phi \in Y.$$

Since $B_0$ is a compact subset of $Y_0$, we have $\inf_{\phi\in B_0} p(\phi) = \min_{\phi\in B_0} p(\phi) > 0$. Consequently, there exists $\eta > 0$ such that

$$\liminf_{t\to\infty} I(t, \phi) = \liminf_{t\to\infty} p(Q(t)\phi) \geq \eta, \forall \phi \in Y_0.$$

This completes the proof. □

By the same arguments as in [82, Lemma 3.8], we have $r(P) = r(\hat{P})$. Combining Lemma 2.3.1 and Theorem 2.3.1, we have the following result on the global dynamics of system (2.7).

**Theorem 2.3.2.** *Let (A1) and (A2) hold. Then the following statements are valid for system (2.7):*

*(i) If $R_0 < 1$, then the disease-free periodic solution $(S^*(t), 0, 0)$ is globally attractive for system (2.7) in $Y$.*

*(ii) If $R_0 > 1$, then system (2.7) admits a positive $\omega$-periodic solution $(\bar{S}(t), \bar{I}(t), \bar{R}(t))$ and there exists a real number $\eta > 0$ such that for any $\phi \in Y$ with $\phi_2(0) > 0$, the solution $\nu(t, \phi) = (S(t), I(t), R(t))$ satisfies $\liminf_{t\to\infty} I(t) \geq \eta$.*

In the rest of this section, we derive the asymptotic behavior of the variable $E(t)$ in system (2.5). We have known that

$$E(t) = \int_{t-\tau(t)}^{t} e^{-\int_s^t \mu(r)dr} f(s, S(s), I(s))ds. \tag{2.14}$$

In the case where $R_0 < 1$, we have

$$\lim_{t\to\infty} [(S(t), I(t), R(t)) - (S^*(t), 0, 0)] = 0.$$

It then follows from equation (2.14) that $\lim_{t\to\infty} E(t) = 0$.

In the case where $R_0 > 1$, we have known that system (2.7) admits a positive $\omega$-periodic solution $(\bar{S}(t), \bar{I}(t), \bar{R}(t))$. By using the integral form (2.14), we obtain

$$\bar{E} = \int_{t-\tau(t)}^{t} e^{-\int_s^t \mu(r)dr} f(s, \bar{S}(s), \bar{I}(s))ds$$

is also a positive $\omega$-periodic function. Consequently, we have the following result on the global dynamics of system (2.5).

**Theorem 2.3.3.** *Let (A1) and (A2) hold. Then the following statements are valid for system (2.5):*

*(i) If $R_0 < 1$, then the disease-free periodic solution $(S^*(t), 0, 0, 0)$ is globally attractive for system (2.5) in $D$.*

*(ii) If $R_0 > 1$, then system (2.5) admits a positive $\omega$-periodic solution $(\bar{S}(t), \bar{E}(t), \bar{I}(t), \bar{R}(t))$ and there exists a real number $\eta > 0$ such that for any initial value $\phi \in D$ with $\phi_3(0) > 0$, the solution $(S(t), E(t), I(t), R(t))$ of system (2.5) satisfies*

$$\liminf_{t\to\infty} I(t) \geq \eta.$$

## 2.4 Numerical simulations

To illustrate our results, in this section we apply our results to a special case and reveal the influence of the periodic time delay.

Let us choose $f(t, S, I) = \frac{\beta(t)SI}{1+\varepsilon(t)I}$ and $\omega = 365$ days. Based on the data of [88], we take the following parameter values,

$\Lambda(t) = 1000/25550(1 + 0.2\cos(2\pi t/365))\text{day}^{-1}$,

$\mu(t) = 1/25550(1 + 0.2\cos(2\pi t/365))\text{day}^{-1}$,

$\alpha(t) = 1/7(1 + 0.5\cos(2\pi t/365))\text{day}^{-1}, \gamma(t) = 1/2.2(1 + 0.1\cos(2\pi t/365))\text{day}^{-1}$.

Any periodic function can be expressed as a sum of harmonic terms. For the sake of convenience, we assume that the periodic time delay is $\tau(t) = 23(1+0.8\cos(2\pi t/365))$ day, the disease-induced death rate is $d(t) = 0.00079(1 + 0.2\cos(2\pi t/365))$ day$^{-1}$, the transmission coefficient is $\beta(t) = 0.0015(1+0.2\cos(2\pi t/365))$ day$^{-1}$, and $\varepsilon(t) = 0.011$. It should be pointed out these parameters are chosen for illustrative purpose only, and may not be meaningful biologically.

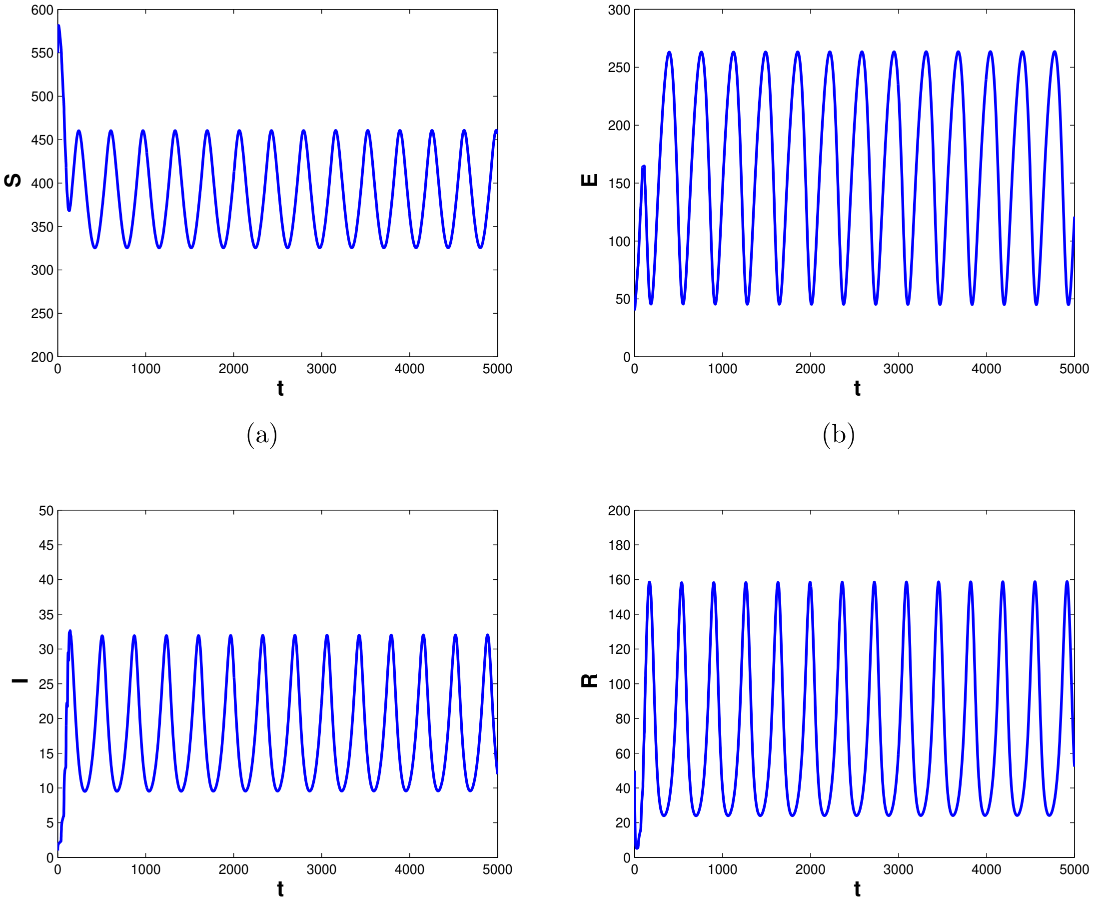
Firstly, to compute the basic reproduction ratio $R_0$ numerically, we apply Lemma 1.4.2. With the above set of parameters, we obtain $R_0 = 3.1263 > 1$. When the initial functions are chosen as $S(\theta) = 550$, $I(\theta) = 1$, $R(0) = 50$ for all $\theta \in [-\hat{\tau}, 0]$, we calculate $E(0) \approx 39.9441$. The model is simulated by using ddesd in MATLAB software. In this case, all compartments fluctuates periodically, which implies that the disease will persist and exhibit periodic fluctuations eventually. Figure 2.1 illustrates the result and is coincident with Theorem 2.3.3 (ii). In order to understand the seasonal patterns of disease risk, we only consider the number of the infectious population in one year. Figure 2.2 shows that the number of infectious individuals is expected to peak between 840th day (April) and 910th day (June). Hence control strategies should aim to lower the number of infections during the course of a pandemic and postpone the timing of the peaks so that people have enough time to take appropriate measures. If we decrease the transmission coefficient to $0.2\beta(t)$, and the initial functions are chosen as $S(\theta) = 550$, $I(\theta) = 73$, $R(0) = 50$ for all $\theta \in [-\hat{\tau}, 0]$, and hence $E(0) \approx 327.0103$, then we calculate $R_0 = 0.6253 < 1$. In this case, from Theorem 2.3.3 (i), the susceptible population exhibits periodic fluctuations (constant as a special case), and the exposed, infectious and recovered populations all converge to zero, which means that the disease will be eliminated. Figure 2.3 illustrates the results above.

Secondly, we explore the influence of the transmission coefficient on $R_0$. Let $\beta(t) = a(1 + b\cos(2\pi t/365))$, $0 \leq b \leq 1$, where $a$ is the mean contact rate and $b$ is the amplitude of fluctuations (or the strength of seasonal forcing). For fixed $b = 0.2$, $R_0$ is strictly increasing with respect to the mean contact $a$ from Figure 2.4. For fixed $a = 0.0015$, $R_0$ is decreasing with respect to the amplitude of fluctuations $b$ from Figure 2.5. That is, the basic reproduction ratio $R_0$ depends not only on the mean contact rate, but also on the amplitude of fluctuations. Then we see that $R_0$ is highly sensitive to $\beta(t)$. This also shows that the transmission rate has an important role in the spread of the disease. Clearly, by taking some control measures such as isolation or vaccination effort, we assume that the control effort is $k$ $(0 \leq k \leq 1)$, that is, the transmission rate becomes $(1-k)\beta(t)$. If we can decrease the transmission coefficient to $0.31\beta(t)$, then $R_0 < 1$, which implies that the disease will die out, see Figure 2.6.

Thirdly, we define the time-averaged latent period as

$$[\tau] := \frac{1}{\omega} \int_0^{\omega} \tau(t)dt.$$

It follows that $[\tau] = 23$ day. Figure 2.7 compares the long-term behavior of the infectious population of system (2.5) with different values of the latent period: the periodic $\tau(t)$ and the constant $[\tau]$. Furthermore, fixed $b = 0.2$ and $a = 0.0015$, Figures 2.8 and 2.9 compare the effect of periodic $\tau(t)$ and constant $[\tau]$ on $R_0$ in these parameter values, respectively. This implies that the use of the time-averaged latent period may underestimate or overestimate the value of $R_0$.



(a) (b)

(c) (d)

Figure 2.1: Long-term behavior of the solution of system (2.5) when $R_0 = 3.1263 > 1$.

## 2.5 Discussion

In this chapter, we have proposed a class of periodic SEIRS epidemic models with general incidence rate by incorporating seasonality into the model so that the parameters are periodic functions and the time-dependent delay describes the latent period.

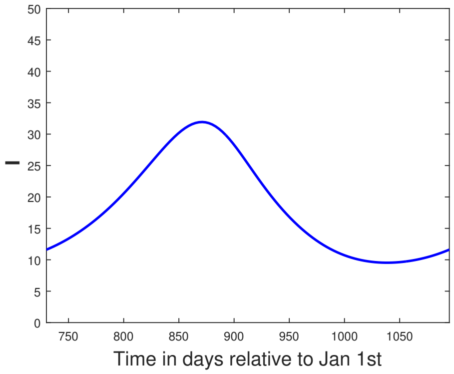
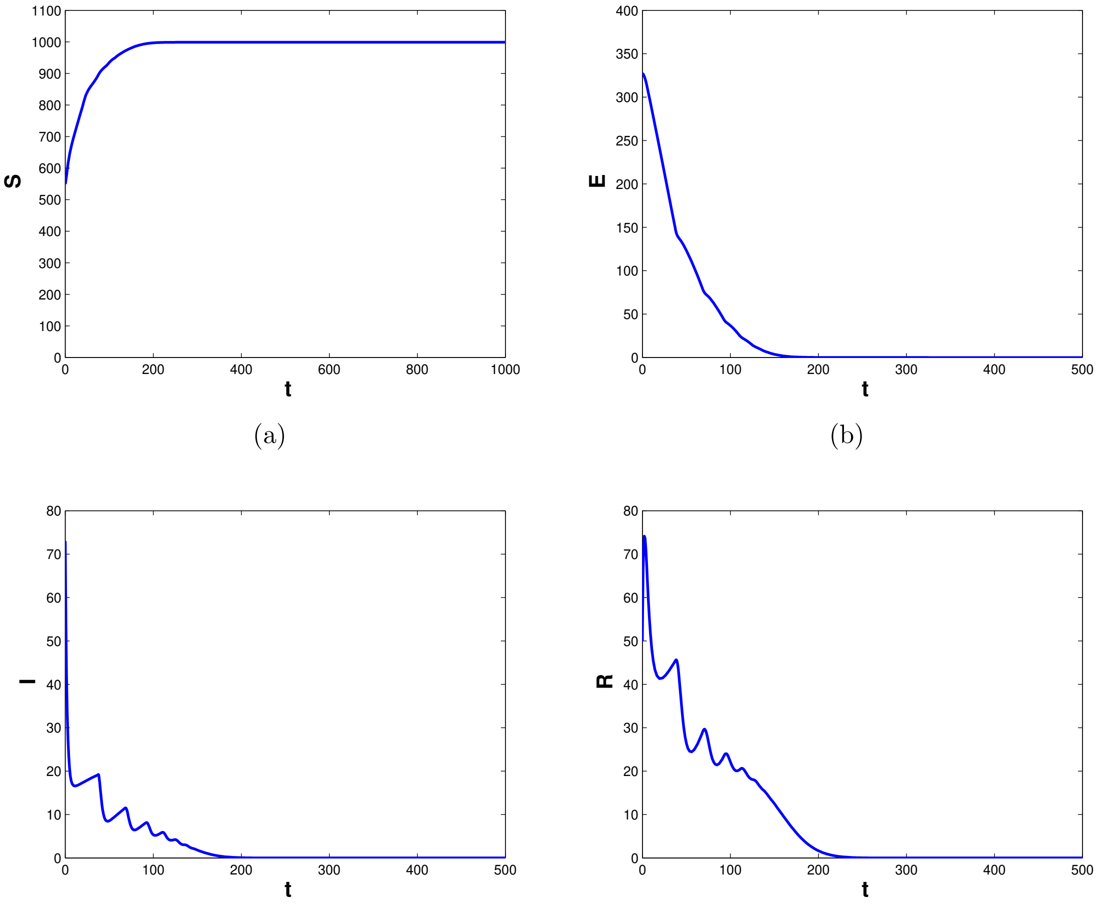


Figure 2.2: The curve of the number of the infectious population of system (2.5) when $R_0 = 3.1263 > 1$ in one year.



(a) (b)

(c) (d)

Figure 2.3: Long-term behavior of the solution of system (2.5) when $R_0 = 0.6253 < 1$.

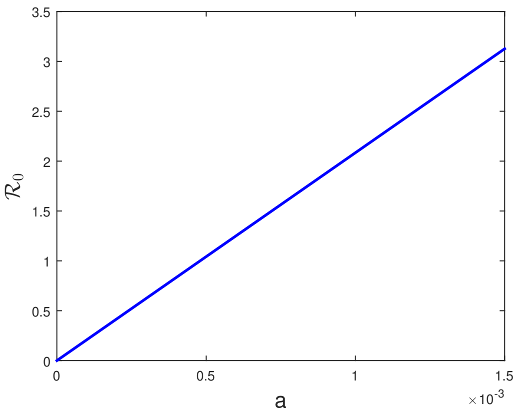


Figure 2.4: $R_0$ as a function of $a$ for system (2.5) fixed $b = 0.2$.

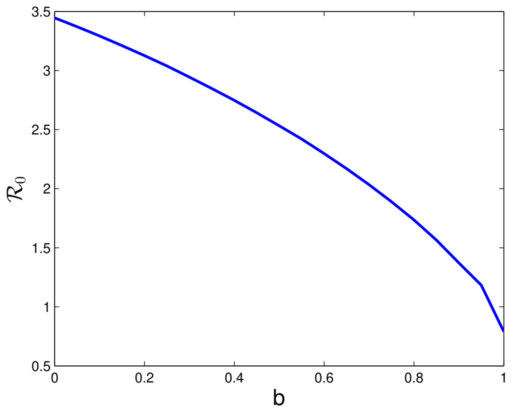


Figure 2.5: $R_0$ as a function of $b$ for system (2.5) fixed $a = 0.0015$.

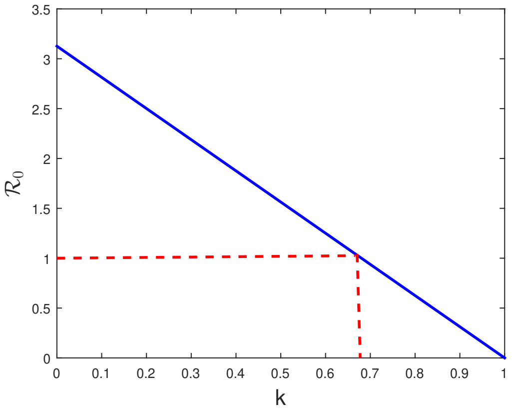


Figure 2.6: $R_0$ as a function of $k$ for system (2.5).

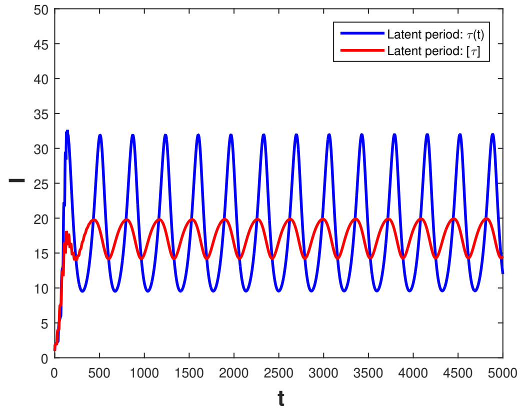


Figure 2.7: Comparison of the long-term behaviors of the infectious population of system (2.5) with different latent periods.

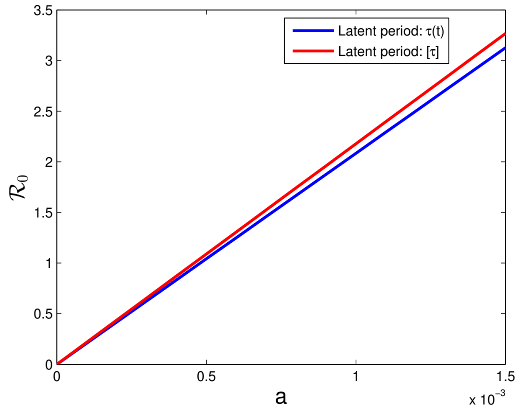


Figure 2.8: $R_0$ as a function of $a$ for system (2.5) with $\tau(t)$ and $[\tau]$ when $b = 0.2$.

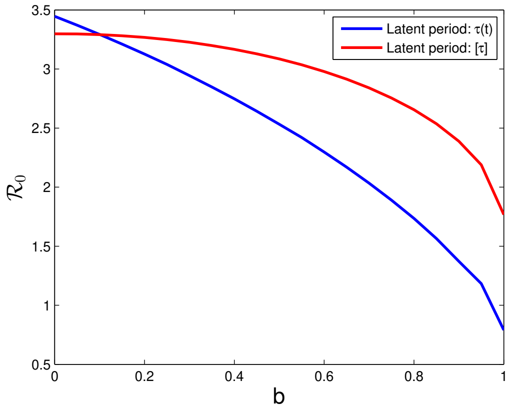


Figure 2.9: $R_0$ as a function of $b$ for system (2.5) with $\tau(t)$ and $[\tau]$ when $a = 0.0015$.

By using the theory developed in [150], we have derived the basic reproduction ratio $R_0$ for our model system. Following the theoretical approach in [82], we define a new phase space on which the periodic linear system (2.9) generates an eventually strongly monotone periodic semiflow. By applying the theorem of uniform persistence for periodic semiflows, we have obtained that the basic reproduction ratio $R_0$ acts as a threshold parameter for the uniform persistence and global extinction of the disease. If $R_0 < 1$, then the disease-free periodic solution is globally attractive and the disease will be eliminated. If $R_0 > 1$, then there is a positive periodic solution, and the disease is uniformly persistent and exhibits seasonal fluctuations.

For periodic models with time-dependent delays, the numerical approximation of $R_0$ is challenging. We have numerically calculated $R_0$ and explored the influences of some key parameters in system (2.5) on $R_0$. The numerical simulations about the long-term behavior of solutions are consistent with the obtained analytic results. We have observed that the increase of the transmission coefficient has a negative impact for disease eradication. Therefore, we should make some measures to control disease through decreasing the transmission coefficient for certain parameters.

Furthermore, we have found that there is a difference of the values of $R_0$ between the use of $\tau(t)$ and its average $[\tau]$. Using the time-averaged latent period may underestimate or overestimate the value of $R_0$. Therefore, in order to find more effective preventive measures during an outbreak of disease, the time-dependent latent delay is important to be considered for some seasonal infectious diseases. Obviously, it is important to acquire some epidemiologically realistic data and to investigate sensitivity studies for the parameters. From the practical viewpoint, our proposed periodic SEIRS epidemic model may be used to understand and predict the outbreak of seasonal infectious diseases.

# Chapter 3

# A West Nile virus model with vertical transmission and periodic time delays

## 3.1 Introduction

West Nile virus (WNV) is a flavivirus of emerging public health relevance. It is transmitted among mosquitoes, birds, humans and other animals. Mosquitoes are the vector of the virus and birds are its natural reservoir, whereas humans and other vertebrates are dead-end hosts, that is, they can be infected by an infectious mosquito, but they do not transmit the disease. Thus, in nature the virus is maintained in enzootic cycles between bird reservoir hosts and mosquitoes [107]. The first WNV case in the United States occurred at the Bronx Zoo, New York, in 1999 [60], and then the virus subsequently spread into many US states and became endemic in few years.

Only the adult female mosquitoes bite humans and animals in order to take blood meals, and the male mosquitoes feed only on plant juices, nectar. Mosquitoes become infected when they feed on infected birds. Infected mosquitoes then spread WNV to humans and other animals by biting them. The WNV can also be passed via vertical transmission from a mosquito to its offspring [10, 121] and this increases the survival of WNV in nature. WNV transmission models involving vertical transmission have also been recently studied in [26, 36, 93, 140].

Compartmental models play an important role in understanding and predicting WNV transmission trend. Much has been done in terms of modeling transmission dynamics of WNV. For example, Bowman et al. [16] formulated a single-season ordinary differential equation model to assess the anti-WNV preventive strategies. Jiang et al. [61, 62] further analyzed this model and gave a complete classification of its global dynamics. Liu et al. [79] also studied the directional dispersal of birds and its impact on the virus spread. To take into account the movement of birds and mosquitoes, Lewis et al. [71] developed a reaction-diffusion model for the spatial spread of WNV, and they proved the existence of traveling waves and calculated the spatial spread rate of infection for a simplified version of the model. Kou et al. [69] also studied the local stability and Hopf bifurcation for a time-delayed WNV model. For other works on the WNV transmission dynamics, we refer to [22, 77, 140] and the references therein. However, the following three biological factors related to WNV transmission seem to have received little attention:

(i) The effect of climate on the transmission of the virus spread. Temperature is a particularly important factor for mosquitoes, as it directly affects rates of immature development, survival of immature stages, adult size, adult longevity, blood feeding, and fecundity of mosquitoes [23]. Although climate and weather strongly influence the biology of vectors in different forms, few papers take into account the seasonality of the species involved in the transmission. In [27], seasonality has been introduced by simply assuming that the total mosquito population follows a sinusoidal fluctuation. In [93], seasonal changes in host and vector densities have been considered, and overwintering of infection is assumed to occur through diapausing mosquito females, with or without vertical transmission.

(ii) Maturation time. The mosquito life cycle is composed of four main life stages: egg, larval, pupa and adult. The first three stages take place in the water, so they are also known as immature stages or aquatic forms while adults (mature mosquitoes) live on land in the air. It usually takes 1-2 weeks from eggs to adults, which is large compared to the average life span (about 3 weeks) of an adult mosquito [36]. So it is important and necessary to consider the maturation time, the length from eggs to adult mosquitoes. Fan et al. [36] considered a delay differential equation model including a constant maturation time of mosquitoes. Increasing temperature is known to decrease the length of time spent in each of the immature stages [80] since the maturation time is sensitive to temperature.

(iii) Extrinsic incubation period (EIP). The EIP is the length of time between an adult vector contracting a pathogen and becoming infectious [51]. Increasing temperature leads to decreases in the EIP of the virus [51], which means that vectors become infectious more quickly than at cooler temperatures. Thus, the EIP is an important parameter in measuring the rate of virus transmission. Recently, researchers have started to introduce the temperature-dependent time delays into delay differential models (see, e.g., [72, 82, 136]).

Motivated by the works of [27, 36, 93], in this chapter we formulate a periodic time-delayed model by taking into account the seasonality. This model contains the maturation time and the EIP in mosquitoes, and both of these delays are periodic in time. Vertical transmission of virus is also incorporated into the model.

The rest of the chapter is organized as follows. In Section 3.2, we derive a WNV transmission model with periodic time delays and study its well-posedness. In Section 3.3, we introduce the reproduction ratio $R_0$ for this model and then establish the threshold dynamics in terms of $R_0$. In Section 3.4, we prove the global attractivity for the model system without seasonality. In Section 3.5, we carry out a case study for WNV transmission in Orange County, California. A brief discussion completes the chapter.

## 3.2 The model

Let $M_s(t)$, $M_L(t)$ and $M_i(t)$ denote the numbers of susceptible, exposed and infectious female adult mosquitoes at time $t$, respectively. The total female adult mosquito population is $M(t) = M_s(t) + M_L(t) + M_i(t)$. Let $B_s(t)$, $B_i(t)$ and $B_r(t)$ be the numbers of susceptible, infectious, and recovered birds at time $t$, respectively. The total bird population is $N_B(t) = B_s(t) + B_i(t) + B_r(t)$. We divide the mosquitoes into two stages: immature and mature, and assume that the maturation time is temperature-dependent. The temperature $T$ can be assumed to vary as a function of time $t$. Let $\tau_A(t)$ be the maturation time at time $t$. For the immature stage, we suppose that the egg, larva, and pupa have the same development rate with the death rate $d_A(t)$ at time $t$, where $d_A(t)$ is determined by the climate profile. Since the

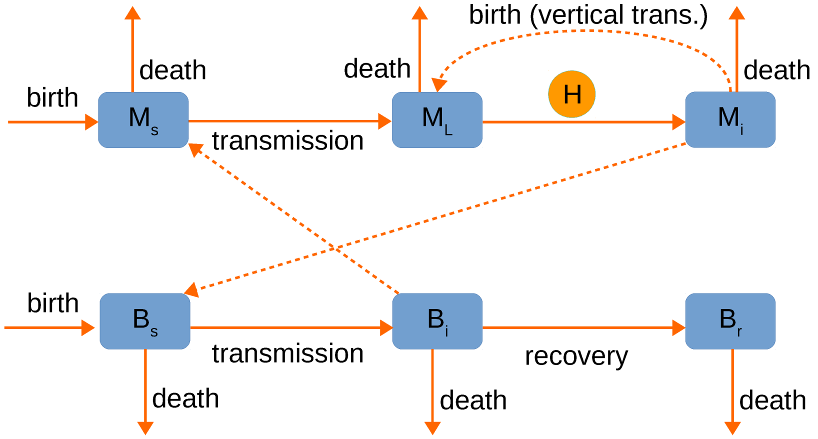


Figure 3.1: Schematic diagram for the WNV transmission among mosquitoes and birds.

development of mosquitoes from eggs to adults is density dependent, a Ricker type function is chosen for the birth rate into adult mosquitoes. This function has been used for example in [83] to model the vector population of West Nile virus disease [36] and malaria disease [84]. By the same idea of model formulation as in [82], we see that the maturation rate function of mosquitoes is $(1-\tau_A'(t))B(t-\tau_A(t), M(t-\tau_A(t)))M(t-\tau_A(t))e^{-\int_{t-\tau_A(t)}^{t} d_A(\xi)d\xi}$ with $1-\tau_A'(t) > 0$, where $B(t, M(t)) = r_m(t)e^{-\alpha(t)M(t)}$, $r_m(t)$ is the per capita mosquito egg production rate at time $t$, and $\alpha(t)$ measures the strength of density dependence for adult mosquitoes at time $t$. Let $d_M(t)$ be the natural mortality rate for adult female mosquitoes at time $t$. Vertical transmission of the virus in the mosquito population is incorporated by a fraction $q \in (0, 1)$. The biting rate $\beta(t)$ of mosquitoes is the number of bites per mosquito per unit time at time $t$. Suppose the transmission probabilities from birds to vectors and from vectors to birds are denoted by $b$ and $c$, respectively. Then the numbers of newly occurred infectious mosquitoes and birds per unit time at time $t$ are given by

$$\frac{b\beta(t)M_s(t)B_i(t)}{N_B(t)} \text{ and } \frac{c\beta(t)M_i(t)B_s(t)}{N_B(t)},$$

respectively. Susceptible mosquitoes move into the exposed class after biting infectious birds. Let $\tau_L(t)$ be the length of the EIP at time $t$, $H(t)$ be the number of newly occurred infectious mosquitoes per unit time at time $t$, $\Lambda(t)$ be the recruitment rate

Table 3.1: Biological interpretations for variables and parameters in system (3.1)

| Parameter | Description |
|---|---|
| $M_s(t)$, $M_L(t)$, $M_i(t)$ | Numbers of susceptible, exposed and infectious female adult mosquitoes at time $t$ |
| $B_s(t)$, $B_i(t)$, $B_r(t)$ | Numbers of susceptible, infectious and recovered birds at time $t$ |
| $M(t) = M_s(t) + M_L(t) + M_i(t)$ | Total number of female adult mosquitoes at time $t$ |
| $N_B(t) = B_s(t) + B_i(t) + B_r(t)$ | Total number of birds at time $t$ |
| $r_m(t)$ | Per capita mosquito egg production rate at time $t$ |
| $\alpha(t)$ | Strength of density dependence for adult mosquitoes at time $t$ ($1/\alpha(t)$ is the size of mosquito population at which egg laying is maximized) |
| $q$ | Vertical transmission fraction in mosquitoes |
| $d_A(t)$, $d_M(t)$ | Per capita mortality rate for immature mosquitoes and adult mosquitoes at time $t$ |
| $b$, $c$ | Probability transmission per bite to mosquitoes and to birds |
| $\beta(t)$ | Per capita biting rate of mosquitoes at time $t$ |
| $\tau_A(t)$ | Duration of the immature stage of mosquitoes at time $t$ |
| $\tau_L(t)$ | Extrinsic incubation period at time $t$ |
| $\Lambda(t)$ | Recruitment rate of birds at time $t$ |
| $d_B(t)$ | Per capita natural death rate of birds at time $t$ |
| $\mu_B(t)$ | Per capita disease-induced mortality rate of birds at time $t$ |
| $\gamma(t)$ | Per capita recovery rate of birds at time $t$ |

of birds at time $t$, and $d_B(t)$ and $\mu_B(t)$ be the natural and disease-induced death rates of birds at time $t$, respectively. We assume that the birds recover at the rate $\gamma(t)$. The features of transmission are illustrated in Figure 3.1. Accordingly, we obtain the following WNV transmission model with periodic time delays:

$$\begin{aligned}
\frac{\mathrm{d}M_s(t)}{\mathrm{d}t} &= (1-\tau_A'(t))B(t-\tau_A(t), M(t-\tau_A(t)))(M_s(t-\tau_A(t)) + M_L(t-\tau_A(t)) \\
&\quad +(1-q)M_i(t-\tau_A(t)))e^{-\int_{t-\tau_A(t)}^{t} d_A(\xi)d\xi} - d_M(t)M_s(t) - \frac{b\beta(t)M_s(t)B_i(t)}{N_B(t)}, \\
\frac{\mathrm{d}M_L(t)}{\mathrm{d}t} &= (1-\tau_A'(t))B(t-\tau_A(t), M(t-\tau_A(t)))qM_i(t-\tau_A(t))e^{-\int_{t-\tau_A(t)}^{t} d_A(\xi)d\xi} \\
&\quad -d_M(t)M_L(t) + \frac{b\beta(t)M_s(t)B_i(t)}{N_B(t)} - H(t), \\
\frac{\mathrm{d}M_i(t)}{\mathrm{d}t} &= H(t) - d_M(t)M_i(t), \\
\frac{\mathrm{d}B_s(t)}{\mathrm{d}t} &= \Lambda(t) - \frac{c\beta(t)M_i(t)B_s(t)}{N_B(t)} - d_B(t)B_s(t), \\
\frac{\mathrm{d}B_i(t)}{\mathrm{d}t} &= \frac{c\beta(t)M_i(t)B_s(t)}{N_B(t)} - (d_B(t) + \mu_B(t) + \gamma(t))B_i(t), \\
\frac{\mathrm{d}B_r(t)}{\mathrm{d}t} &= \gamma(t)B_i(t) - d_B(t)B_r(t).
\end{aligned} \tag{3.1}$$

By arguments similar to those in [72, 136], it follows that

$$H(t) =(1-\tau_L'(t))\Big[(1-\tau_A'(h_L(t)))B(g_A(t),M(g_A(t)))qM_i(g_A(t))e^{-\int_{g_A(t)}^{h_L(t)} d_A(\xi)d\xi} \\ +\frac{b\beta(h_L(t))M_s(h_L(t))B_i(h_L(t))}{N_B(h_L(t))}\Big]e^{-\int_{h_L(t)}^{t} d_M(\xi)d\xi},$$

and $1-\tau_L'(t)>0$, where $h_L(t)=t-\tau_L(t)$, $M_A(t)=t-\tau_A(t)$, $g_A(t)=M_A(h_L(t))=t-\tau_L(t)-\tau_A(t-\tau_L(t))$. We assume that all parameters in system (3.1) are positive and $\omega$-periodic functions with the same period $\omega$ for some real number $\omega>0$. The biological interpretations for all variables and parameters can be found in Table 3.1.

For notational simplicity, we rewrite system (3.1) into

$$\begin{aligned}
\tfrac{\mathrm{d}M_s(t)}{\mathrm{d}t} &= b_1(t)B(t-\tau_A(t),M(t-\tau_A(t)))(M_s(t-\tau_A(t))+M_L(t-\tau_A(t)) \\
&\quad +(1-q)M_i(t-\tau_A(t)))-d_M(t)M_s(t)-\tfrac{b\beta(t)M_s(t)B_i(t)}{N_B(t)}, \\
\tfrac{\mathrm{d}M_L(t)}{\mathrm{d}t} &= b_1(t)B(t-\tau_A(t),M(t-\tau_A(t)))qM_i(t-\tau_A(t))-d_M(t)M_L(t) \\
&\quad +\tfrac{b\beta(t)M_s(t)B_i(t)}{N_B(t)}-H(t), \\
\tfrac{\mathrm{d}M_i(t)}{\mathrm{d}t} &= H(t)-d_M(t)M_i(t), \\
\tfrac{\mathrm{d}B_s(t)}{\mathrm{d}t} &= \Lambda(t)-\tfrac{c\beta(t)M_i(t)B_s(t)}{N_B(t)}-d_B(t)B_s(t), \\
\tfrac{\mathrm{d}B_i(t)}{\mathrm{d}t} &= \tfrac{c\beta(t)M_i(t)B_s(t)}{N_B(t)}-(d_B(t)+\mu_B(t)+\gamma(t))B_i(t), \\
\tfrac{\mathrm{d}B_r(t)}{\mathrm{d}t} &= \gamma(t)B_i(t)-d_B(t)B_r(t),
\end{aligned} \tag{3.2}$$

where

$$H(t)=b_2(t)B(g_A(t),M(g_A(t)))M_i(g_A(t))+b_3(t)\frac{\beta(h_L(t))M_s(h_L(t))B_i(h_L(t))}{N_B(h_L(t))},$$

$$b_1(t)=(1-\tau_A'(t))e^{-\int_{t-\tau_A(t)}^{t} d_A(\xi)d\xi},$$

$$b_2(t)=(1-\tau_L'(t))(1-\tau_A'(h_L(t)))qe^{-\int_{g_A(t)}^{h_L(t)} d_A(\xi)d\xi}e^{-\int_{h_L(t)}^{t} d_M(\xi)d\xi},$$

$$b_3(t)=(1-\tau_L'(t))be^{-\int_{h_L(t)}^{t} d_M(\xi)d\xi}.$$

Clearly, $b_1(t)$, $b_2(t)$ and $b_3(t)$ are all positive $\omega$-periodic functions. For a given continuous $\omega$-periodic function $g(t)$, we define $\hat{g}:=\max_{t\in[0,\omega]}g(t)$ and $\bar{g}:=\min_{t\in[0,\omega]}g(t)$.

To address the well-posedness of system (3.2), we introduce some notations. Let $\hat{\tau}=\max\{\hat{\tau}_A,\hat{\tau}_L,\ \max_{t\in[0,\omega]}\{\tau_L(t)+\tau_A(t-\tau_L(t))\}\}$, $\bar{C}:=C([-\hat{\tau},0],\mathbb{R}^6)$, and $\bar{C}^+:=$

$C([-\hat{\tau}, 0], \mathbb{R}_+^6)$. Then $(\bar{C}, \bar{C}^+)$ is an ordered Banach space equipped with the maximum norm. For any given continuous function $x : [-\hat{\tau}, \sigma) \to \mathbb{R}_+^6$ with $\sigma > 0$, we define $x_t \in \bar{C}$ as $x_t(\theta) = x(t + \theta)$, $\forall \theta \in [-\hat{\tau}, 0]$, for any $t \in [0, \sigma)$.

Define

$$\begin{aligned}\Gamma_\delta :=& \Big\{\varphi \in \bar{C}^+ : \sum_{i=4}^{6} \varphi_i(s) \geq \delta, \forall s \in [-\hat{\tau}, 0], \varphi_2(0) = \int_{h_L(0)}^{0} e^{-\int_\xi^0 d_M(r)dr} [\frac{b\beta(\xi)\varphi_1(\xi)\varphi_5(\xi)}{\sum_{i=4}^6 \varphi_i(\xi)} \\ &+ b_1(\xi)B(\xi - \tau_A(\xi), \sum_{i=1}^{3} \varphi_i(\xi - \tau_A(\xi)))q\varphi_3(\xi - \tau_A(\xi))]d\xi\Big\},\end{aligned}$$

for any given $\delta \in \Big(0, \frac{\bar{\Lambda}}{\hat{d}_B + \hat{\mu}_B}\Big)$.

**Lemma 3.2.1.** *For any $\varphi \in \Gamma_\delta$, system (3.2) has a unique nonnegative solution $u(t, \varphi)$ with $u_0 = \varphi$ such that $u_t(\varphi) \in \Gamma_\delta$ for all $t \geq 0$, and solutions are ultimately bounded and uniformly bounded.*

*Proof.* For any $\varphi \in \Gamma_\delta$, we define $\bar{f}(t, \varphi) = (\bar{f}_1(t, \varphi), \bar{f}_2(t, \varphi), \bar{f}_3(t, \varphi), \bar{f}_4(t, \varphi), \bar{f}_5(t, \varphi), \bar{f}_6(t, \varphi))$ with

$$\begin{aligned}
\bar{f}_1(t, \varphi) =& b_1(t)B(t - \tau_A(t), \sum_{i=1}^{3} \varphi_i(-\tau_A(t)))(\varphi_1(-\tau_A(t)) + \varphi_2(-\tau_A(t)) \\
&+ (1 - q)\varphi_3(-\tau_A(t))) - d_M(t)\varphi_1(0) - \frac{b\beta(t)\varphi_1(0)\varphi_5(0)}{\sum_{i=4}^6 \varphi_i(0)}, \\
\bar{f}_2(t, \varphi) =& b_1(t)B(t - \tau_A(t), \sum_{i=1}^{3} \varphi_i(-\tau_A(t)))q\varphi_3(-\tau_A(t)) - d_M(t)\varphi_2(0) \\
&- b_2(t)B(g_A(t), \sum_{i=1}^{3} \varphi_i(-\tau_L(t) - \tau_A(h_L(t))))\varphi_3(-\tau_L(t) - \tau_A(h_L(t))) \\
&+ \frac{b\beta(t)\varphi_1(0)\varphi_5(0)}{\sum_{i=4}^6 \varphi_i(0)} - \frac{b_3(t)\beta(h_L(t))\varphi_1(-\tau_L(t))\varphi_5(-\tau_L(t))}{\sum_{i=4}^6 \varphi_i(-\tau_L(t))}, \\
\bar{f}_3(t, \varphi) =& b_2(t)B(g_A(t), \sum_{i=1}^{3} \varphi_i(-\tau_L(t) - \tau_A(h_L(t))))\varphi_3(-\tau_L(t) - \tau_A(h_L(t))) \\
&+ \frac{b_3(t)\beta(h_L(t))\varphi_1(-\tau_L(t))\varphi_5(-\tau_L(t))}{\sum_{i=4}^6 \varphi_i(-\tau_L(t))} - d_M(t)\varphi_3(0), \\
\bar{f}_4(t, \varphi) =& \Lambda(t) - \frac{c\beta(t)\varphi_3(0)\varphi_4(0)}{\sum_{i=4}^6 \varphi_i(0)} - d_B(t)\varphi_4(0), \\
\bar{f}_5(t, \varphi) =& \frac{c\beta(t)\varphi_3(0)\varphi_4(0)}{\sum_{i=4}^6 \varphi_i(0)} - (d_B(t) + \mu_B(t) + \gamma(t))\varphi_5(0),
\end{aligned}$$

$$\bar{f}_6(t,\varphi) = \gamma(t)\varphi_5(0) - d_B(t)\varphi_6(0).$$

Since $\bar{f}(t,\varphi)$ is continuous in $(t,\varphi) \in \mathbb{R}_+ \times \Gamma_\delta$ and Lipschitz in $\varphi$ on each compact subset of $\Gamma_\delta$. It follows from [50, Theorems 2.2.1 and 2.2.3] that system (3.2) has a unique solution $u(t,\varphi)$ with $u_0 = \varphi$ on its maximum interval $[0,\sigma_\varphi)$ of existence.

With the compatibility condition on $\varphi_2$ in $\Gamma_\delta$, it follows from the second equation in system (3.2) that

$$\begin{aligned} M_L(t) = \int_{h_L(t)}^{t} & e^{-\int_\xi^t d_M(r)dr} \Big[ b_1(\xi) B(M_A(\xi), M(M_A(\xi))) q M_i(M_A(\xi)) \\ & + \frac{b\beta(\xi) M_s(\xi) B_i(\xi)}{N_B(\xi)} \Big] d\xi. \end{aligned} \tag{3.3}$$

We also observe that $u_2(t) \geq 0$, $\forall t \in [0,t_0]$ whenever $u_i(t) \geq 0$ for all $i \neq 2$ and $t \in [0,t_0] \subseteq [0,\sigma_\varphi)$. Let $\varphi = (\varphi_1,\varphi_2,\varphi_3,\varphi_4,\varphi_5,\varphi_6) \in \Gamma_\delta$ be given. If $\varphi_i(0) = 0$ for some $i \in \{1,3,4,5,6\}$, then $\bar{f}_i(t,\varphi) \geq 0$. By [116, Theorem 5.2.1] and its proof, it follows that for any $\varphi \in \Gamma_\delta$, $u_i(t,\varphi) \geq 0$ for $i = 1,3,4,5,6$, for all $t \in [0,\sigma_\varphi)$. From the integral form (3.3) of $M_L(t)$ and the above observation, we have $M_L(t) \geq 0$ for all $t \in [0,\sigma_\varphi)$. Therefore, it follows that for any $\varphi \in \Gamma_\delta$, the solution $u(t,\varphi)$ of system (3.2) with $u_0 = \varphi$ is nonnegative for all $t \in [0,\sigma_\varphi)$. Clearly, the total number $N_B(t)$ of vectors satisfies

$$\frac{\mathrm{d}N_B(t)}{\mathrm{d}t} \geq \Lambda(t) - (d_B(t) + \mu_B(t))N_B(t) \geq \bar{\Lambda} - (\hat{d}_B + \hat{\mu}_B)N_B(t).$$

Note that the linear equation $\frac{\mathrm{d}y}{\mathrm{d}t} = \bar{\Lambda} - (\hat{d}_B + \hat{\mu}_B)y(t)$ has a globally asymptotically stable equilibrium $\frac{\bar{\Lambda}}{\hat{d}_B+\hat{\mu}_B}$, and for any $0 < \delta < \frac{\bar{\Lambda}}{\hat{d}_B+\hat{\mu}_B}$, $\frac{\mathrm{d}y}{\mathrm{d}t}|_{y=\delta} = \bar{\Lambda} - (\hat{d}_B + \hat{\mu}_B)\delta > 0$. It then follows that if $y(0) \geq \delta$, then $y(t) \geq \delta, \forall t \geq 0$. By the comparison principle, $N_B(t) \geq \delta$ if $N_B(0) = \sum_{i=4}^{6} \varphi_i(0) \geq \delta$. This implies that $u_t(\varphi) \in \Gamma_\delta$ for all $t \in [0,\sigma_\varphi)$. Since the total numbers for vectors and hosts, $M(t)$ and $N_B(t)$, satisfy

$$\begin{aligned} \tfrac{\mathrm{d}M(t)}{\mathrm{d}t} &\leq \tfrac{(1-\tau_A'(t))r_m(t-\tau_A(t))}{\alpha(t-\tau_A(t))} e^{-1} e^{-\int_{t-\tau_A(t)}^{t} d_A(\xi)d\xi} - d_M(t)M(t), \\ \tfrac{\mathrm{d}N_B(t)}{\mathrm{d}t} &= \Lambda(t) - d_B(t)N_B(t) - \mu_B(t)B_i(t) \leq \Lambda(t) - d_B(t)N_B(t) \end{aligned} \tag{3.4}$$

for all $t \in [0,\sigma_\varphi)$, it follows that both $M(t)$ and $N_B(t)$ are bounded on $[0,\sigma_\varphi)$, and hence, [50, Theorem 2.3.1] implies that $\sigma_\varphi = \infty$, and solutions are ultimately bounded.

In view of system (3.4), it is easy to see that $\frac{\mathrm{d}M(t)}{\mathrm{d}t} < 0$ and $\frac{\mathrm{d}N_B(t)}{\mathrm{d}t} < 0$ whenever $M(t) > \max\{\frac{\hat{B}_1}{\bar{d}_M}, \frac{\hat{\Lambda}}{\bar{d}_B}\}$ and $N_B(t) > \max\{\frac{\hat{B}_1}{\bar{d}_M}, \frac{\hat{\Lambda}}{\bar{d}_B}\}$, where $B_1(t) = \frac{(1-\tau_A'(t))r_m(t-\tau_A(t))}{\alpha(t-\tau_A(t))}$ $e^{-1}e^{-\int_{t-\tau_A(t)}^{t} d_A(\xi)d\xi}$. This implies that solutions are uniformly bounded. $\square$

## 3.3 Threshold dynamics

In order to study the dynamics for $M_s(t)$, we consider the scalar delay equation on the total vector population $M(t) = M_s(t) + M_L(t) + M_i(t)$:

$$\begin{aligned}\frac{\mathrm{d}M(t)}{\mathrm{d}t} =&(1-\tau_A'(t))r_m(t-\tau_A(t))e^{-\alpha(t-\tau_A(t))M(t-\tau_A(t))}M(t-\tau_A(t))e^{-\int_{t-\tau_A(t)}^{t} d_A(\xi)d\xi}\\ &-d_M(t)M(t). \end{aligned} \tag{3.5}$$

In Appendix A, it is shown that system (3.5) has a globally attractive positive $\omega$-periodic solution $M^*(t)$ in $C([-\hat{\tau}_A, 0], \mathbb{R}_+) \setminus \{0\}$ under the following conditions:

(C1) $r(\tilde{P}) > 1$, where $r(\tilde{P})$ is the spectral radius of the Frechét derivative $\tilde{P}$ of the Poincaré map associated with system (3.5) on $C([-\hat{\tau}_A, 0], \mathbb{R})$ at zero.

(C2) $\bar{M}^*(t-\tau_A(t)) < \frac{1}{\alpha(t-\tau_A(t))}$ for all $t \in [0, \omega]$, where $\bar{M}^*(t)$ is the unique positive $\omega$-periodic solution of the nonhomogeneous ordinary differential equation:

$$\frac{\mathrm{d}\bar{M}(t)}{\mathrm{d}t} = \frac{(1-\tau_A'(t))r_m(t-\tau_A(t))}{\alpha(t-\tau_A(t))}e^{-1}e^{-\int_{t-\tau_A(t)}^{t} d_A(\xi)d\xi} - d_M(t)\bar{M}(t).$$

Let $N_B^*(t)$ be the globally asymptotically stable positive $\omega$-periodic solution of $\frac{\mathrm{d}B_s(t)}{\mathrm{d}t} = \Lambda(t) - d_B(t)B_s(t)$. It is easy to see that system (3.2) has a unique disease-free periodic solution $(M^*(t), 0, 0, N_B^*(t), 0, 0)$ under the conditions (C1) and (C2). Linearizing system (3.2) at the disease-free periodic solution $(M^*(t), 0, 0, N_B^*(t), 0, 0)$, we then obtain the following periodic linear system for the infective variables $M_i$ and $B_i$:

$$\begin{aligned}\frac{\mathrm{d}M_i(t)}{\mathrm{d}t} &= b_2(t)B(g_A(t), M^*(g_A(t)))M_i(g_A(t)) + b_3(t)\beta(h_L(t))\frac{M^*(h_L(t))}{N_B^*(h_L(t))}B_i(h_L(t))\\ &\quad -d_M(t)M_i(t),\\ \frac{\mathrm{d}B_i(t)}{\mathrm{d}t} &= c\beta(t)M_i(t) - (d_B(t)+\mu_B(t)+\gamma(t))B_i(t). \end{aligned} \tag{3.6}$$

Let $\hat{\tau}_1 = \max_{t\in[0,\omega]}\{\tau_L(t) + \tau_A(t-\tau_L(t))\}$, $\hat{\tau}_0 = \max\{\hat{\tau}_A, \hat{\tau}_1\}$, and $\hat{\tau}_2 = \max\{\hat{\tau}_1, \hat{\tau}_L\}$, $C := C([-\hat{\tau}_2, 0], \mathbb{R}^2)$ and $C^+ := C([-\hat{\tau}_2, 0], \mathbb{R}_+^2)$. Define a map $F : \mathbb{R} \to \mathfrak{L}(C, \mathbb{R}^2)$ and a matrix function $V(t)$ as follows:

$$F(t)\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix} = \begin{pmatrix} b_2(t)B(g_A(t), M^*(g_A(t)))\phi_1(-\tau_L(t)-\tau_A(h_L(t)))\\ +b_3(t)\beta(h_L(t))\frac{M^*(h_L(t))}{N_B^*(h_L(t))}\phi_2(-\tau_L(t))\\ c\beta(t)\phi_1(0)\end{pmatrix}$$

and

$$V(t) = \begin{pmatrix} d_M(t) & 0 \\ 0 & d_B(t) + \mu_B(t) + \gamma(t) \end{pmatrix}.$$

Then the linear system (3.6) can be written as

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = F(t)u_t - V(t)u(t), \forall t \geq 0.$$

The internal evolution of the infective compartments $M_i$ and $B_i$ can be expressed by

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

Let $Z(t,s)$, $t \geq s$, be the evolution matrix of the above linear system, that is, for each $s \in \mathbb{R}$, $Z(t,s)$ satisfies

$$\frac{\partial}{\partial t} Z(t,s) = -V(t)Z(t,s),\ \forall t \geq s, \text{ and } Z(s,s) = I,$$

where $I$ is a 2×2 identity matrix. It then easily follows that

$$Z(t,s) = \begin{pmatrix} e^{-\int_s^t d_M(\xi)d\xi} & 0 \\ 0 & e^{-\int_s^t (d_B(\xi)+\mu_B(\xi)+\gamma(\xi))d\xi} \end{pmatrix}.$$

Let $C_\omega$ be the ordered Banach space of all continuous and $\omega$-periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$, which is equipped with maximum norm $\|\cdot\|_\infty$ and the positive cone $C_\omega^+ = \{v \in C_\omega : v(t) \geq 0, \text{ for any } t \in \mathbb{R}\}$. Suppose $v \in C_\omega$ is the initial distribution of infectious mosquitoes and birds. Then for any given $s \geq 0$, $F(t-s)v_{t-s}$ is the distribution of newly infectious mosquitoes and birds at time $t-s$, which is produced by the infectious mosquitoes and birds who were introduced over the time interval $[t-s-\hat{\tau}_2, t-s]$. Then $Z(t,t-s)F(t-s)v_{t-s}$ is the distribution of those infectious mosquitoes and birds who were newly infected at time $t-s$ and remain in the infectious compartments at time $t$. Hence,

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

is the distribution of accumulative new infections at time $t$ produced by all those infectious mosquitoes and birds introduced at all previous time to $t$. Define a linear operator $\mathcal{L} : C_\omega \to C_\omega$ by

$$[\mathcal{L}v](t) = \int_0^\infty Z(t,t-s)F(t-s)v(t-s+\cdot)ds.$$

According to [150], we define the basic reproduction ratio as $R_0 := r(\mathcal{L})$, the spectral radius of $\mathcal{L}$.

For any given $t \geq 0$, let $\hat{P}(t)$ be the solution map of system (3.6), that is, $\hat{P}(t)\phi = u_t(\phi)$, where $u(t, \phi)$ is the unique solution of system (3.6) with $u_0 = \phi \in C$. Then $\hat{P} := \hat{P}(\omega)$ is the Poincaré map associated with (3.6). Let $r(\hat{P})$ be the spectral radius of $\hat{P}$. By Theorem 1.4.1, we have the following result.

**Lemma 3.3.1.** *$R_0 - 1$ has the same sign as $r(\hat{P}) - 1$.*

Let $\tilde{\tau} = \tau_L(0) + \tau_A(-\tau_L(0))$, and define

$$\Omega := C([-\tilde{\tau}, 0], \mathbb{R}) \times C([-\tau_L(0), 0], \mathbb{R}), \quad \Omega^+ := C([-\tilde{\tau}, 0], \mathbb{R}_+) \times C([-\tau_L(0), 0], \mathbb{R}_+).$$

By the method of steps, we then have the following result.

**Lemma 3.3.2.** *For any $\varphi \in \Omega^+$, system (3.6) has a unique nonnegative solution $v(t, \varphi)$ with $v_0 = \varphi$ for all $t \geq 0$.*

**Remark 3.3.1.** *By the uniqueness of solutions in Lemmas 3.2.1 and 3.3.2, it follows that for any $\psi \in C^+$ and $\phi \in \Omega^+$ with $\psi_1(\theta) = \phi_1(\theta)$ for all $\theta \in [-\tilde{\tau}, 0]$, $\psi_2(\theta) = \phi_2(\theta)$ for all $\theta \in [-\tau_L(0), 0]$, we have $w(t, \psi) = \nu(t, \phi)$ for all $t \geq 0$, where $w(t, \psi)$ and $\nu(t, \phi)$ are solutions of system (3.6) satisfying $w_0 = \psi$ and $\nu_0 = \phi$, respectively.*

For any given $t \geq 0$, let $P(t)$ be the solution map of system (3.6) on $\Omega$. Then $P := P(\omega)$ is the Poincaré map associated with linear system (3.6). Let $r(P)$ be its spectral radius. The following lemma indicates that the periodic semiflow $P(t)$ is eventually strongly positive.

**Lemma 3.3.3.** *For any $\varphi$ and $\psi$ in $\Omega$ with $\varphi > \psi$ (that is, $\varphi \geq \psi$, but $\varphi \neq \psi$), the solutions $\bar{v}(t)$ and $v(t)$ of system (3.6) with $\bar{v}_0 = \varphi$ and $v_0 = \psi$, respectively, satisfy $\bar{v}_i(t) > v_i(t)$ for all $t > \check{\tau}$, $i = 1, 2$, and hence, $P(t)\varphi \gg P(t)\psi$ in $\Omega$ for all $t > \check{\tau} + \tilde{\tau}$, where $\check{\tau} = \min\{\bar{\tau}_L, \min_{t \in [0,\omega]}\{\tau_L(t) + \tau_A(h_L(t))\}\}$.*

*Proof.* Using a simple comparison argument on each interval $[n\check{\tau}, (n+1)\check{\tau}]$, $n \in \mathbb{N}$, we can show that $\bar{v}_i(t) \geq v_i(t)$ for all $t \geq 0$, $i = 1, 2$. Next we show that $P(t) : \Omega \to \Omega$ is eventually strongly monotone. Let $\varphi, \psi \in \Omega$ satisfy $\varphi > \psi$. Denote $\bar{v}(t) = v(t, \varphi) = (\overline{y}_1(t), \overline{y}_2(t))$ and $v(t) = v(t, \psi) = (y_1(t), y_2(t))$. Without loss of generality, we assume that $\varphi_2 > \psi_2$.

**Claim 1.** There exists $t_0 \in [0, \check{\tau}]$ such that $\overline{y}_1(t) > y_1(t)$ for all $t \geq t_0$.

We first prove that $\overline{y}_1(t_0) > y_1(t_0)$ for some $t_0 \in [0, \check{\tau}]$. Otherwise, we have $\overline{y}_1(t) = y_1(t)$, $\forall t \in [0, \check{\tau}]$, and hence $\frac{\mathrm{d}\overline{y}_1(t)}{\mathrm{d}t} = \frac{\mathrm{d}y_1(t)}{\mathrm{d}t}$ for all $t \in [0, \check{\tau}]$. Thus, for any $t \in [0, \check{\tau}]$, we have

$$\begin{aligned} & b_2(t)B(g_A(t), M^*(g_A(t)))[\overline{y}_1(g_A(t)) - y_1(g_A(t))] \\ & + b_3(t)\beta(h_L(t))\frac{M^*(h_L(t))}{N_B^*(h_L(t))}[\overline{y}_2(h_L(t)) - y_2(h_L(t))] = 0. \end{aligned} \tag{3.7}$$

Since for all $t \in [0, \check{\tau}]$, $-\tau_L(0) \leq h_L(t) \leq \check{\tau} - \tau_L(\check{\tau}) \leq 0$, $-\tau_L(0) - \tau_A(-\tau_L(0)) \leq g_A(t) \leq \check{\tau} - \tau_L(\check{\tau}) - \tau_A(\check{\tau} - \tau_L(\check{\tau})) \leq 0$, it follows that $\overline{y}_1(g_A(t)) = \varphi_1(g_A(t))$, $y_1(g_A(t)) = \psi_1(g_A(t))$, $\overline{y}_2(h_L(t)) = \varphi_2(h_L(t))$, $y_2(h_L(t)) = \psi_2(h_L(t))$. Since $\varphi_2 > \psi_2$, by (3.7), we have $\overline{y}_1(g_A(t)) = \varphi_1(g_A(t)) < y_1(g_A(t)) = \psi_1(g_A(t))$, which contradicts the fact that $\varphi > \psi$. Then there exists some $t_0 \in [0, \check{\tau}]$ such that $\overline{y}_1(t_0) > y_1(t_0)$.

Let $g_1(t, y) = b_2(t)B(g_A(t), M^*(g_A(t)))y_1(g_A(t)) + b_3(t)\beta(h_L(t))\frac{M^*(h_L(t))}{N_B^*(h_L(t))}y_2(h_L(t)) - d_M(t)y$. Since

$$\begin{aligned} \frac{\mathrm{d}\overline{y}_1(t)}{\mathrm{d}t} &= b_2(t)B(g_A(t), M^*(g_A(t)))\overline{y}_1(g_A(t)) + b_3(t)\beta(h_L(t))\frac{M^*(h_L(t))}{N_B^*(h_L(t))}\overline{y}_2(h_L(t)) \\ & \quad - d_M(t)\overline{y}_1(t) \\ &\geq b_2(t)B(g_A(t), M^*(g_A(t)))y_1(g_A(t)) + b_3(t)\beta(h_L(t))\frac{M^*(h_L(t))}{N_B^*(h_L(t))}y_2(h_L(t)) \\ & \quad - d_M(t)\overline{y}_1(t) = g_1(t, \overline{y}_1(t)), \end{aligned}$$

we have $\frac{\mathrm{d}\overline{y}_1(t)}{\mathrm{d}t} - g_1(t, \overline{y}_1(t)) \geq 0 = \frac{\mathrm{d}y_1(t)}{\mathrm{d}t} - g_1(t, y_1(t)), \forall t \geq t_0$. Since $\overline{y}_1(t_0) > y_1(t_0)$, it follows from Theorem 1.3.1 that $\overline{y}_1(t) > y_1(t)$ for all $t \geq t_0$.

**Claim 2.** $\overline{y}_2(t) > y_2(t)$ for all $t > t_0$.

Let $g_2(t, y) = c\beta(t)y_1(t) - (d_B(t) + \mu_B(t) + \gamma(t))y$. Then for all $t \geq t_0$, we have

$$\begin{aligned} \frac{\mathrm{d}\overline{y}_2(t)}{\mathrm{d}t} &= c\beta(t)\overline{y}_1(t) - (d_B(t) + \mu_B(t) + \gamma(t))\overline{y}_2(t) \\ &> c\beta(t)y_1(t) - (d_B(t) + \mu_B(t) + \gamma(t))\overline{y}_2(t) = g_2(t, \overline{y}_2(t)), \end{aligned}$$

we have $\frac{\mathrm{d}\overline{y}_2(t)}{\mathrm{d}t} - g_2(t, \overline{y}_2(t)) > 0 = \frac{\mathrm{d}y_2(t)}{\mathrm{d}t} - g_2(t, y_2(t))$, $\forall t \geq t_0$. Since $\overline{y}_2(t_0) \geq y_2(t_0)$, it follows from Theorem 1.3.1 that $\overline{y}_2(t) > y_2(t)$ for all $t > t_0$.

In view of the above two claims, we obtain $(\overline{y}_1(t), \overline{y}_2(t)) \gg (y_1(t), y_2(t)), \forall t > t_0$. Since $t_0 \in [0, \check{\tau}]$, it follows that $(\overline{y}_{1t}, \overline{y}_{2t}) \gg (y_{1t}, y_{2t})$, $\forall t > \check{\tau} + \tilde{\tau}$, that is, $v_t(\varphi) \gg v_t(\psi)$ for all $t > \check{\tau} + \tilde{\tau}$. This shows $P(t) : \Omega \to \Omega$ is strongly monotone for any $t > \check{\tau} + \tilde{\tau}$. $\square$

By [50, Theorem 3.6.1], it follows that for each $t \geq \hat{\tau}_2$, the linear operator $\hat{P}(t)$ is compact on $C([-\hat{\tau}_2, 0], \mathbb{R}^2)$, and hence, $P(t)$ is also compact on $\Omega$ for any $t \geq \hat{\tau}_2$. Then $P(t)$ is compact and strongly monotone on $\Omega$ for $t > \hat{\tau}_3 = \max\{\check{\tau} + \tilde{\tau}, \hat{\tau}_2\}$. Choose an integer $n_0 > 0$ such that $n_0\omega > \hat{\tau}_3$. Since $P^{n_0} = P(n_0\omega)$, [74, Lemma 3.1] implies that $r(P)$ is a simple eigenvalue of $P$ having a strongly positive eigenvector. By [135, Lemma 1], we have the following observation.

**Lemma 3.3.4.** *Let* $\mu = \frac{\ln r(P)}{\omega}$. *Then there is a positive* $\omega$*-periodic function* $v^*(t)$ *such that* $u^*(t) = e^{\mu t} v^*(t)$ *is a positive solution of linear system (3.6).*

By arguments similar to those in [82, Lemma 3.8], we have $r(\hat{P}) = r(P)$. It then follows from Lemma 3.3.1 that $R_0 - 1$ has the same sign as $r(P) - 1$.

Next we show that the disease is uniformly persistent in the case where $R_0 > 1$. Let

$$X := C([-\hat{\tau}, 0], \mathbb{R}_+) \times C([-\hat{\tau}_0, 0], \mathbb{R}^2_+) \times C([-\hat{\tau}_L, 0], \mathbb{R}^3_+),$$

$$\begin{aligned} X_\delta := \Big\{ &\varphi \in X : \textstyle\sum_{i=4}^{6} \varphi_i(s) \geq \delta, \forall s \in [-\hat{\tau}_L, 0], \\ &\varphi_2(0) = \textstyle\int_{h_L(0)}^{0} e^{-\int_\xi^0 d_M(r)dr} \big[\frac{b\beta(\xi)\varphi_1(\xi)\varphi_5(\xi)}{\sum_{i=4}^{6}\varphi_i(\xi)} + (1 - \tau_A'(\xi)) \\ &\times B(\xi - \tau_A(\xi), \textstyle\sum_{i=1}^{3} \varphi_i(\xi - \tau_A(\xi))) q\varphi_3(\xi - \tau_A(\xi)) e^{-\int_{M_A(\xi)}^{\xi} d_A(r)dr}\big] d\xi \Big\}. \end{aligned}$$

**Theorem 3.3.1.** *Let (C1) and (C2) hold. If* $R_0 > 1$, *then there exists a positive constant* $\eta$ *such that for any initial value* $\phi \in X_\delta$ *with* $\phi_3(0) > 0$ *and* $\phi_5(0) > 0$, *the solution* $(M_s(t, \phi), M_L(t, \phi), M_i(t, \phi), B_s(t, \phi), B_i(t, \phi), B_r(t, \phi))$ *of system (3.2) satisfies* $\liminf_{t\to\infty}(M_i(t, \phi), B_i(t, \phi)) \geq (\eta, \eta)$.

*Proof.* Let

$$X_0 := \{\phi = (\phi_1, \phi_2, \phi_3, \phi_4, \phi_5, \phi_6) \in X_\delta : \phi_3(0) > 0 \text{ and } \phi_5(0) > 0\},$$

$$\partial X_0 := X_\delta \setminus X_0 = \{\phi \in X_\delta : \phi_3(0) = 0 \text{ or } \phi_5(0) = 0\}.$$

Let $Q(t) : X_\delta \to X_\delta$ be the solution maps of system (3.2), that is, $Q(t)\phi = u_t(\phi)$, $t \geq 0$, where $u(t, \phi)$ is the unique solution of system (3.2) with $u_0 = \phi \in X_\delta$. Then $Q := Q(\omega)$ is the Poincaré map associated with system (3.2). From the third and fifth equations of system (3.2), it is easy to see that $Q(t)X_0 \subseteq X_0$ for all $t \geq 0$. Lemma 3.2.1 implies that the discrete-time dynamical system $\{Q^n : X_\delta \to X_\delta\}_{n\geq 0}$ is point dissipative. By [50, Theorem 3.6.1], for each $t \geq \hat{\tau}$, $Q(t)$ is compact, and hence, $Q^n$

is compact for sufficient large $n$. It follows from Theorem 1.1.3 that $Q : X_\delta \to X_\delta$ admits a global attractor. Now we prove that $Q$ is uniformly persistent with respect to $(X_0, \partial X_0)$.

Let $M_1 = (M_0^*, 0, 0, N_{B0}^*, 0, 0)$, $M_2 = (0, 0, 0, N_{B0}^*, 0, 0)$, where $M_0^*(\theta) = M^*(\theta)$ for $\theta \in [-\hat{\tau}, 0]$ and $N_{B0}^*(\theta) = N_B^*(\theta)$ for $\theta \in [-\hat{\tau}_L, 0]$. Since $\lim_{\phi\to M_1} \|Q(t)\phi - Q(t)M_1\| = 0$ uniformly for $t \in [0, \omega]$, for any given $\varepsilon > 0$, there exists an $\eta_1 > 0$ such that for any $\phi \in X_0$ with $\|\phi - M_1\| < \eta_1$, we have $\|Q(t)\phi - Q(t)M_1\| < \varepsilon$ for all $t \in [0, \omega]$.
**Claim 1.** $\limsup_{n\to\infty} \|Q(n\omega)\phi - M_1\| \geq \eta_1$ for all $\phi \in X_0$.

Suppose not, then $\limsup_{n\to\infty} \|Q(n\omega)\psi - M_1\| < \eta_1$ for some $\psi \in X_0$. Then there exists an integer $N_1 \geq 1$ such that $\|Q(n\omega)\psi - M_1\| < \eta_1$ for all $n \geq N_1$. For any $t \geq N_1\omega$, we have $t = n\omega + t_1$ with $n \geq N_1$, $t_1 \in [0, \omega]$, and $\|Q(t)\psi - Q(t)M_1\| = \|Q(t_1)Q(n\omega)\psi - Q(t_1)Q(n\omega)M_1\| = \|Q(t_1)Q(n\omega)\psi - Q(t_1)M_1\| < \varepsilon$. Therefore, $M^*(t)-\varepsilon < M_s(t) < M^*(t)+\varepsilon$, $0 \leq M_L(t) < \varepsilon$, $0 < M_i(t) < \varepsilon$, $N_B^*(t)-\varepsilon < B_s(t) < N_B^*(t) + \varepsilon$, $0 < B_i(t) < \varepsilon$, $0 \leq B_r(t) < \varepsilon$ for all $t \geq N_1\omega$. Let $P_\varepsilon(t)$ be the solution maps of the following perturbed linear system on $\Omega$:

$$\begin{aligned}
\tfrac{\mathrm{d}M_i(t)}{\mathrm{d}t} &= b_2(t)B(g_A(t), M^*(g_A(t)) + 3\varepsilon)M_i(g_A(t)) \\
&\quad + b_3(t)\beta(h_L(t))\tfrac{M^*(h_L(t))-\varepsilon}{N_B^*(h_L(t))+3\varepsilon}B_i(h_L(t)) - d_M(t)M_i(t), \qquad (3.8)\\
\tfrac{\mathrm{d}B_i(t)}{\mathrm{d}t} &= c\beta(t)M_i(t) - (d_B(t) + \mu_B(t) + \gamma(t))B_i(t).
\end{aligned}$$

and $P_\varepsilon := P_\varepsilon(\omega)$. Since $R_0 > 1$, $\lim_{\varepsilon\to 0^+} r(P_\varepsilon) = r(P) > 1$. Fix a sufficiently small $\varepsilon > 0$ such that $r(P_\varepsilon) > 1$, $M^*(h_L(t)) - \varepsilon > 0$, $N_B^*(t) - \varepsilon > 0$ for all $t \geq 0$. It is easy to verify that $P_\varepsilon(t)$ is also compact and strongly monotone on $\Omega$ for $t > \hat{\tau}_3$. By Lemma 3.3.4, there is a positive $\omega$-periodic function $v_\varepsilon^*(t) = (v_1(t), v_2(t))$ such that $w_\varepsilon^*(t) = e^{\lambda t}v_\varepsilon^*(t)$ is a positive solution of system (3.8), where $\lambda = \frac{\ln r(P_\varepsilon)}{\omega} > 0$. Then $\lim_{t\to\infty} w_\varepsilon^*(t) = \infty$. For all $t \geq N_1\omega + \hat{\tau}_2$, by system (3.2), we have

$$\begin{aligned}
\tfrac{\mathrm{d}M_i(t)}{\mathrm{d}t} &\geq b_2(t)B(g_A(t), M^*(g_A(t)) + 3\varepsilon)M_i(g_A(t)) \\
&\quad + b_3(t)\beta(h_L(t))\tfrac{M^*(h_L(t))-\varepsilon}{N_B^*(h_L(t))+3\varepsilon}B_i(h_L(t)) - d_M(t)M_i(t), \\
\tfrac{\mathrm{d}B_i(t)}{\mathrm{d}t} &\geq c\beta(t)M_i(t) - (d_B(t) + \mu_B(t) + \gamma(t))B_i(t).
\end{aligned}$$

Since $\psi \in X_0$, $M_i(t, \psi) > 0$ and $B_i(t, \psi) > 0$ for all $t \geq 0$, and hence, we can choose a sufficiently small $k > 0$ such that $(M_i(t, \psi), B_i(t, \psi)) \geq kw_\varepsilon^*(t)$, $\forall t \in [N_1\omega + \hat{\tau}_2, N_1\omega + 2\hat{\tau}_2]$. By Theorem 1.3.2, it follows that

$$(M_i(t, \psi), B_i(t, \psi)) \geq kw_\epsilon^*(t), \forall t \geq N_1\omega + 2\hat{\tau}_2.$$

Thus, we have $M_i(t,\psi) \to \infty$, $B_i(t,\psi) \to \infty$ as $t \to \infty$, a contradiction.

Since $\lim_{\phi \to M_2} \|Q(t)\phi - Q(t)M_2\| = 0$ uniformly for $t \in [0,\omega]$, for any given $\eta_0 > 0$, there exists an $\eta_2 > 0$ such that

$$\|Q(t)\phi - Q(t)M_2\| < \eta_0, \forall t \in [0,\omega], \|\phi - M_2\| < \eta_2.$$

**Claim 2.** $\limsup_{n\to\infty} \|Q(n\omega)\phi - M_2\| \geq \eta_2$ for all $\phi \in X_0$.

Assume, by contradiction, that $\limsup_{n\to\infty} \|Q(n\omega)\psi - M_2\| < \eta_2$ for some $\psi \in X_0$. Then there exists an integer $N_2 \geq 1$ such that $\|Q(n\omega)\psi - M_2\| < \eta_2$ for all $n \geq N_2$. For any $t \geq N_2\omega$, we have $t = n\omega + t_2$ with $n \geq N_2$, $t_2 \in [0,\omega]$, and $\|Q(t)\psi - Q(t)M_2\| = \|Q(t_2)Q(n\omega)\psi - Q(t_2)M_2\| < \eta_0$. Hence, $M_s(t) < \eta_0$, $M_L(t) < \eta_0$, $M_i(t) < \eta_0$, and $M(t) < 3\eta_0$ for all $t \geq N_2\omega$. Since $M(0) = \psi_1(0) + \psi_2(0) + \psi_3(0) > 0$, we have $\lim_{t\to\infty}(M(t) - M^*(t)) = 0$, a contradiction.

Define

$$M_\partial := \{\phi \in \partial X_0 : Q^n(\phi) \in \partial X_0, \forall n \geq 0\}.$$

Next we prove that

$$M_\partial = \{\phi \in \partial X_0 : \phi_3(0) = 0, \phi_5(0) = 0\}.$$

Indeed, it suffices to show that for any $\phi \in M_\partial$, $M_i(t,\phi) = 0$ and $B_i(t,\phi) = 0$ for all $t \geq 0$. Suppose not, then there exists some $t_0 \geq 0$ such that $M_i(t_0,\phi) > 0$ or $B_i(t_0,\phi) > 0$. We are left to consider two possibilities. In the case where $M_i(t_0,\phi) > 0$ and $B_i(t_0,\phi) > 0$, we have $M_i(t,\phi) > 0$ and $B_i(t,\phi) > 0$ for all $t \geqslant t_0$, which contradicts $\phi \in M_\partial$. In the case where $M_i(t_0,\phi) > 0$ and $B_i(t_0,\phi) = 0$, or $B_i(t_0,\phi) > 0$ and $M_i(t_0,\phi) = 0$, without loss of generality, we assume that $M_i(t_0,\phi) > 0$ and $B_i(t_0,\phi) = 0$. It follows from the third equation of system (3.2) that $\frac{\mathrm{d}M_i(t)}{\mathrm{d}t} \geq -d_M(t)M_i(t)$, and hence, $M_i(t,\phi) \geq M_i(t_0,\phi)e^{-\int_{t_0}^t d_M(r)dr} > 0$ for $t \geq t_0$. It is easy to see that $B_s(t) > 0$ for any $t \geq 0$. Thus, by the fifth equation of system (3.2), we get $B_i(t,\phi) = \int_{t_0}^t \frac{c\beta(r)M_i(r,\phi)B_s(r,\phi)}{B_s(r,\phi)+B_i(r,\phi)+B_r(r,\phi)} e^{\int_t^r (d_B(\xi)+\mu_B(\xi)+\gamma(\xi))d\xi} dr > 0$ for $t > t_0$. Then $M_i(t,\phi) > 0$ and $B_i(t,\phi) > 0$ for $t > t_0$. So we have some $k_1 > 0$ with $k_1\omega > t_0$ such that $Q^{k_1}(\phi) \notin \partial X_0$, a contradiction to the assumption $\phi \in M_\partial$. If $\phi \in M_\partial$, then $M_i(t,\phi) = 0$ and $B_i(t,\phi) = 0$, $\forall t \geq 0$. By the theory of internally chain transitive sets (see, e.g., Theorems 1.1.1 and 1.1.2 ), we see that $Q^n(\phi) \to M_1$ as $n \to \infty$, or $Q^n(\phi) \to M_2$ as $n \to \infty$. Thus, $\bigcup_{\phi \in M_\partial} \omega(\phi) = \{M_1, M_2\}$ and no subset of $\{M_1, M_2\}$ forms a cycle for $Q$ in $\partial X_0$.

By Claims 1 and 2 above, we see that $M_1$ and $M_2$ are isolated invariant sets for $Q$ in $X_\delta$, and $W^s(M_j)\bigcap X_0 = \emptyset$, $j = 1, 2$, where $W^s(M_j)$ is the stable set of $M_j$ for $Q$. By the acyclicity theory on uniform persistence for maps (see Theorem 1.2.1 ), it follows that $Q : X_\delta \to X_\delta$ is uniformly persistent with respect to $(X_0, \partial X_0)$ in the sense that there exists $\tilde{\eta} > 0$ such that

$$\liminf_{n\to\infty} d(Q^n(\phi), \partial X_0) \geq \tilde{\eta},\ \forall \phi \in X_0.$$

It remains to prove the practical uniform persistence. By Theorem 1.2.3, we know that $Q : X_0 \to X_0$ admits a global attractor $A_0$. For any $\phi \in A_0$, we have $\phi_i(0) > 0$ for all $i = 3, 5$. Let $B_0 := \bigcup_{t\in[0,\omega]} Q(t)A_0$. Then $\phi_3(0) > 0$ and $\phi_5(0) > 0$ for all $\phi \in B_0$. Moreover, $B_0 \subseteq X_0$ and $\lim_{t\to\infty} d(Q(t)\phi, B_0) = 0$ for all $\phi \in X_0$. Define a continuous function $p : X_\delta \to \mathbb{R}_+$ by

$$p(\phi) = \min\{\phi_3(0), \phi_5(0)\}, \forall \phi \in X_\delta.$$

Clearly, $p(\phi) > 0$ for all $\phi \in B_0$. Since $B_0$ is a compact subset of $X_0$, we have $\inf_{\phi\in B_0} p(\phi) = \min_{\phi\in B_0} p(\phi) > 0$. By the attractiveness of $B_0$, it then follows that there exists an $\eta > 0$ such that

$$\liminf_{t\to\infty} \min(M_i(t, \phi), B_i(t, \phi)) = \liminf_{t\to\infty} p(Q(t)\phi) \geq \eta,\ \forall \phi \in X_0.$$

This completes the proof. $\square$

For any given $K > 0$, denote

$$\begin{aligned}\mathcal{X}_K := \Big\{&\phi \in C([-\hat{\tau}, 0], [0, K]) \times C([-\hat{\tau}_0, 0], [0, K]^2) \times C([-\hat{\tau}_L, 0], [0, K]^3) :\\ &\textstyle\sum_{i=4}^6 \varphi_i(s) \geq \delta, \forall s \in [-\hat{\tau}_L, 0], \varphi_2(0) = \int_{h_L(0)}^0 e^{-\int_\xi^0 d_M(r)dr} [\frac{b\beta(\xi)\varphi_1(\xi)\varphi_5(\xi)}{\sum_{i=4}^6 \varphi_i(\xi)}\\ &+(1 - \tau_A'(\xi))B(\xi - \tau_A(\xi), \textstyle\sum_{i=1}^3 \varphi_i(\xi - \tau_A(\xi)))q\varphi_3(\xi - \tau_A(\xi))\\ &\times e^{-\int_{M_A(\xi)}^\xi d_A(r)dr}]d\xi\Big\}.\end{aligned}$$

Then we have the following result.

**Theorem 3.3.2.** *Let (C1) and (C2) hold. If* $R_0 < 1$, *then for every* $K > \max\{\frac{\widehat{B}_1}{\bar{d}_M}, \frac{\widehat{\Lambda}}{\bar{d}_B}\}$, *there exists a* $\zeta = \zeta(K) > 0$ *such that for any* $\phi \in \mathcal{X}_K \setminus (\{(0, 0, 0)\} \times C([-\hat{\tau}_L, 0], [0, K]^3))$ *with* $(\phi_3(\theta), \phi_5(\theta)) \in [0, \zeta]^2$ *for all* $\theta \in [-\hat{\tau}, 0]$, *the solution* $u(t, \phi)$ *of system (3.2) with* $u_0 = \phi$ *satisfies* $\lim_{t\to\infty} \|u(t, \phi) - (M^*(t), 0, 0, B_s^*(t), 0, 0)\| = 0$.

*Proof.* By Lemma 3.2.1 and its proof, we see that $\mathcal{X}_K$ is positively invariant for the periodic solution semiflow of system (3.2). We then have $u(t,\phi) \in [0,K]^6$, $\forall t \geq 0$, $\phi \in \mathcal{X}_K$.

Let $\widetilde{P}_\epsilon(t)$ be the solution maps of the following perturbed linear periodic system on $\Omega$:

$$\begin{aligned}
\frac{\mathrm{d}\widetilde{M}_i(t)}{\mathrm{d}t} &= b_2(t)B(g_A(t), M^*(g_A(t))-\epsilon)\widetilde{M}_i(g_A(t)) + b_3(t)\beta(h_L(t))\tfrac{M^*(h_L(t))+\epsilon}{N_B^*(h_L(t))-\epsilon}\widetilde{B}_i(h_L(t)) \\
&\quad -d_M(t)\widetilde{M}_i(t), \\
\frac{\mathrm{d}\widetilde{B}_i(t)}{\mathrm{d}t} &= c\beta(t)\widetilde{M}_i(t) - (d_B(t)+\mu_B(t)+\gamma(t))\widetilde{B}_i(t),
\end{aligned} \tag{3.9}$$

and $\widetilde{P}_\epsilon := \widetilde{P}_\epsilon(\omega)$. Since $R_0 < 1$, $\lim_{\epsilon \to 0^+} r(\widetilde{P}_\epsilon) = r(P) < 1$. Thus we can choose sufficiently small $\epsilon > 0$ such that $r(\widetilde{P}_\epsilon) < 1$. It follows from Lemma 3.3.4 that there is a positive $\omega$-periodic function $\widetilde{v}_\epsilon^*(t) = (\widetilde{v}_{\epsilon 1}^*(t), \widetilde{v}_{\epsilon 2}^*(t))$ such that $\widetilde{w}_\epsilon^*(t) = (\widetilde{w}_{\epsilon 1}^*(t), \widetilde{w}_{\epsilon 2}^*(t)) = e^{\mu_\epsilon t}\widetilde{v}_\epsilon^*(t)$ is a positive solution of system (3.9), where $\mu_\epsilon = \frac{\ln r(\widetilde{P}_\epsilon)}{\omega} < 0$.

Consider another auxiliary system:

$$\begin{aligned}
\frac{\mathrm{d}W_1(t)}{\mathrm{d}t} &= b_1(t)B(t-\tau_A(t), W_1(t-\tau_A(t)))W_1(t-\tau_A(t)) - d_M(t)W_1(t), \\
\frac{\mathrm{d}W_2(t)}{\mathrm{d}t} &= \Lambda(t) - d_B(t)W_2(t) - \mu_B(t)\xi_1.
\end{aligned}$$

We can choose small $\xi_1 > 0$ and large $T_1 = T_1(K) > \hat{\tau}_2$ such that for any solution $(W_1(t), W_2(t)) \in [0,K]^2$, we have

$$M^*(t) - \epsilon < W_1(t) < M^*(t) + \epsilon \text{ and } W_2(t) > N_B^*(t) - \epsilon, \forall t \geq T_1 - \hat{\tau}_2.$$

Then for all $t \geq T_1$, $M_i(t)$ and $B_i(t)$ satisfy

$$\begin{aligned}
\frac{\mathrm{d}M_i(t)}{\mathrm{d}t} &\leq b_2(t)B(g_A(t), M^*(g_A(t))-\epsilon)M_i(g_A(t)) + b_3(t)\beta(h_L(t))\tfrac{M^*(h_L(t))+\epsilon}{N_B^*(h_L(t))-\epsilon}B_i(h_L(t)) \\
&\quad -d_M(t)M_i(t), \\
\frac{\mathrm{d}B_i(t)}{\mathrm{d}t} &\leq c\beta(t)M_i(t) - (d_B(t)+\mu_B(t)+\gamma(t))B_i(t).
\end{aligned}$$

Choose $\xi_2 > 0$ such that $\xi_2\widetilde{v}_{\epsilon j}^*(t) < \xi_1$ for all $t \geq 0$, $j \in \{1,2\}$. Note that $(\widetilde{M}_i(t), \widetilde{B}_i(t)) = \xi_2\widetilde{w}_\epsilon^*(t)$ is also a solution of system (3.9). For a given solution $u(t,\phi)$ of system (3.2) with $u_0 = \phi$, if we denote $\bar{u}(t,\phi) = (\bar{u}_1(t,\phi), \bar{u}_2(t,\phi)) = (u_3(t,\phi), u_5(t,\phi))$, then there exists a $\zeta = \zeta(K) > 0$ such that

$$\bar{u}_j(t,\phi) < \xi_2\widetilde{w}_{\epsilon j}^*(t) \leq \xi_2\widetilde{v}_{\epsilon j}^*(t) < \xi_1, j \in \{1,2\}, t \in [0,T_1], \tag{3.10}$$

provided that $\phi_3(\theta) < \zeta, \phi_5(\theta) < \zeta$, $\forall \theta \in [-\hat{\tau}, 0]$. We further claim that

$$\bar{u}(t, \phi) \leq \xi_2 e^{\mu_\epsilon t} \widetilde{v}_\epsilon^*(t), \forall t \geq 0. \tag{3.11}$$

Suppose not, it follows from the comparison principle and (3.10) that there exists $j \in \{1, 2\}$ and $T_2 = T_2(\phi) > T_1$ such that

$$\begin{aligned} &\bar{u}(t, \phi) \leq \xi_2 e^{\mu_\epsilon t} \widetilde{v}_\epsilon^*(t), 0 \leq t \leq T_2, \\ &\bar{u}_j(T_2, \phi) = \xi_2 e^{\mu_\epsilon T_2} \widetilde{v}_{\epsilon j}^*(T_2), \\ &\bar{u}_j(t, \phi) > \xi_2 e^{\mu_\epsilon t} \widetilde{v}_{\epsilon j}^*(t), 0 < t - T_2 \ll 1. \end{aligned} \tag{3.12}$$

Since $(M_i(T_2, \phi), B_i(T_2, \phi)) \leq \xi_2 e^{\mu_\epsilon T_2} \widetilde{v}_\epsilon^*(T_2)$, again by the comparison principle, it follows that $(M_i(t, \phi), B_i(t, \phi)) \leq \xi_2 e^{\mu_\epsilon t} \widetilde{v}_\epsilon^*(t), 0 < t - T_2 \ll 1$, which is a contradiction. This proves the claim. Then $M_i(t, \phi) \to 0$, $B_i(t, \phi) \to 0$ as $t \to \infty$. By the theory of chain transitive sets (see, e.g., Theorem 1.1.1 and [83]), we further obtain that $\lim_{t\to\infty} M_L(t) = 0$, $\lim_{t\to\infty}(M_s(t) - M^*(t)) = 0$, $\lim_{t\to\infty}(B_s(t) - N_B^*(t)) = 0$, $\lim_{t\to\infty} B_r(t) = 0$, that is, $\lim_{t\to\infty} \|u(t, \phi) - (M^*(t), 0, 0, N_B^*(t), 0, 0)\| = 0$. □

It seems difficult to prove the global attractivity of the disease-free periodic solution in the case where $R_0 < 1$. However, we can do it under the additional condition that the disease-induced death rate of birds is zero.

**Theorem 3.3.3.** *Let (C1) and (C2) hold. If* $R_0 < 1$ *and* $\mu_B(t) \equiv 0$, *then the disease-free periodic solution* $(M^*(t), 0, 0, N_B^*(t), 0, 0)$ *is globally attractive for system (3.2) in* $X_\delta \setminus (\{(0, 0, 0)\} \times C([-\hat{\tau}_L, 0], \mathbb{R}_+^3))$.

*Proof.* Consider the following system with parameter $\epsilon > 0$:

$$\begin{aligned} \frac{\mathrm{d}M_i(t)}{\mathrm{d}t} &= b_2(t) B(g_A(t), M^*(g_A(t)) - \epsilon) M_i(g_A(t)) + b_3(t) \beta(h_L(t)) \tfrac{M^*(h_L(t)) + \epsilon}{N_B^*(h_L(t)) - \epsilon} B_i(h_L(t)) \\ &\quad - d_M(t) M_i(t), \\ \frac{\mathrm{d}B_i(t)}{\mathrm{d}t} &= c\beta(t) M_i(t) - (d_B(t) + \gamma(t)) B_i(t). \end{aligned} \tag{3.13}$$

Let $P_\epsilon(t)$ be the solution maps of the perturbed linear periodic system (3.13) on $\Omega$, and $P_\epsilon := P_\epsilon(\omega)$. Since $R_0 < 1$, $\lim_{\epsilon\to 0^+} r(P_\epsilon) = r(P) < 1$. Thus, we can fix a sufficiently small constant $\epsilon > 0$ such that $r(P_\epsilon) < 1$. According to Lemma 3.3.4, there is a positive $\omega$-periodic function $v_\epsilon^*(t) = (v_{\epsilon 1}^*(t), v_{\epsilon 2}^*(t))$ such that $u_\epsilon^*(t) = e^{\frac{\ln r(P_\epsilon)}{\omega} t} v_\epsilon^*(t)$

is a positive solution of system (3.13). Since $r(P_\epsilon) < 1$, $\lim_{t\to\infty} u_\epsilon^*(t) = 0$. The total number of vectors, $M(t)$, satisfies system (3.5), and hence, $M_s(t) \leq M(t)$ and $\lim_{t\to\infty}(M(t) - M^*(t)) = 0$. The total number of hosts, $N_B(t)$, satisfies $\frac{\mathrm{d}N_B(t)}{\mathrm{d}t} = \Lambda(t) - d_B(t)N_B(t)$, which has a globally attractive $\omega$-periodic solution $N_B^*(t)$, that is, $\lim_{t\to\infty}(N_B(t) - N_B^*(t)) = 0$. Then there exists a sufficiently large integer $n_1 > 0$ such that $n_1\omega > \hat{\tau}_2$ and $0 \leq M_s(t) \leq M(t) < M^*(t) + \epsilon$, $M(t) > M^*(t) - \epsilon > 0$, $N_B(t) > N_B^*(t) - \epsilon > 0$ for all $t \geq n_1\omega - \hat{\tau}_2$. We then have

$$\begin{aligned}\frac{\mathrm{d}M_i(t)}{\mathrm{d}t} &\leq b_2(t)B(g_A(t), M^*(g_A(t)) - \epsilon)M_i(g_A(t)) + b_3(t)\beta(h_L(t))\frac{M^*(h_L(t))+\epsilon}{N_B^*(h_L(t))-\epsilon}B_i(h_L(t))\\ &\quad -d_M(t)M_i(t),\\ \frac{\mathrm{d}B_i(t)}{\mathrm{d}t} &\leq c\beta(t)M_i(t) - (d_B(t) + \gamma(t))B_i(t),\end{aligned} \tag{3.14}$$

for all $t \geq n_1\omega$.

Let $\Theta > 0$ be large enough such that $(M_i(t), B_i(t)) \leq \Theta u_\epsilon^*(t)$ for $t \in [n_1\omega, n_1\omega + \hat{\tau}_2]$. Then Theorem 1.3.2 implies that $(M_i(t), B_i(t)) \leq \Theta u_\epsilon^*(t)$ for $t \geq n_1\omega + \hat{\tau}_2$. Hence, $M_i(t) \to 0$, $B_i(t) \to 0$ as $t \to \infty$. By using the chain transitive sets arguments (see, e.g., Theorem 1.1.1 and [83]), we have $M_L(t) \to 0$, $B_r(t) \to 0$, $M_s(t) - M^*(t) \to 0$, $B_s(t) - N_B^*(t) \to 0$ as $t \to \infty$. Thus, $(M^*(t), 0, 0, N_B^*(t), 0, 0)$ is globally attractive in $X_\delta \setminus (\{(0,0,0)\} \times C([-\hat{\tau}_L, 0], \mathbb{R}_+^3))$. □

## 3.4 Global attractivity in the case of constant coefficients

In this section, we study the global attractivity for the model system in the case where all coefficients are constants and the disease-induced death rate of birds $\mu_B$ is zero.

In this case, system (3.2) reduces to the following autonomous one:

$$\begin{aligned}
\frac{\mathrm{d}M_s(t)}{\mathrm{d}t} &= r_m e^{-\alpha M(t-\tau_A)}(M_s(t-\tau_A)+M_L(t-\tau_A)+(1-q)M_i(t-\tau_A))e^{-d_A\tau_A}\\
&\quad -d_M M_s(t)-\frac{b\beta M_s(t)B_i(t)}{N_B(t)},\\
\frac{\mathrm{d}M_L(t)}{\mathrm{d}t} &= r_m e^{-\alpha M(t-\tau_A)}qM_i(t-\tau_A)e^{-d_A\tau_A}-d_M M_L(t)+\frac{b\beta M_s(t)B_i(t)}{N_B(t)}-H(t),\\
\frac{\mathrm{d}M_i(t)}{\mathrm{d}t} &= H(t)-d_M M_i(t),\\
\frac{\mathrm{d}B_s(t)}{\mathrm{d}t} &= \Lambda-\frac{c\beta M_i(t)B_s(t)}{N_B(t)}-d_B B_s(t),\\
\frac{\mathrm{d}B_i(t)}{\mathrm{d}t} &= \frac{c\beta M_i(t)B_s(t)}{N_B(t)}-(d_B+\gamma)B_i(t),\\
\frac{\mathrm{d}B_r(t)}{\mathrm{d}t} &= \gamma B_i(t)-d_B B_r(t),
\end{aligned} \tag{3.15}$$

where

$$H(t)=\left[r_m e^{-\alpha M(t-\tau_L-\tau_A)}qM_i(t-\tau_A-\tau_L)e^{-d_A\tau_A}+\frac{b\beta M_s(t-\tau_L)B_i(t-\tau_L)}{N_B(t-\tau_L)}\right]e^{-d_M\tau_L}.$$

There are two disease-free equilibria, $E_0=(0,0,0,N_B^*,0,0)$ and $E_1=(M^*,0,0,N_B^*,0,0)$, where $M^*=\frac{1}{\alpha}\ln(\frac{r_m}{d_M e^{d_A\tau_A}})$ and $N_B^*=\frac{\Lambda}{d_B}$. In order to avoid the extinction of the mosquito population, we assume that

(H1) $d_M < r_m e^{-d_A\tau_A} < ed_M$.

It follows from Theorem A.4 that the scalar delay equation

$$\frac{\mathrm{d}M(t)}{\mathrm{d}t}=r_m e^{-\alpha M(t-\tau_A)}M(t-\tau_A)e^{-d_A\tau_A}-d_M M(t)$$

admits a globally attractive positive steady state $M^*$ in $C([-\tau_A,0],\mathbb{R}_+)\backslash\{0\}$ under the assumption (H1).

In the case of constant coefficients, let

$$F_1=\begin{bmatrix} r_m q e^{-d_A\tau_A}e^{-d_M\tau_L}e^{-\alpha M^*} & 0\\ 0 & 0\end{bmatrix},\quad F_2=\begin{bmatrix} 0 & \frac{b\beta M^* e^{-d_M\tau_L}}{N_B^*}\\ 0 & 0\end{bmatrix},\quad F_3=\begin{bmatrix} 0 & 0\\ c\beta & 0\end{bmatrix}.$$

It then follows that $F(\phi)=F_1\phi(-\tau_A-\tau_L)+F_2\phi(-\tau_L)+F_3\phi(0)$, and

$$V=\begin{bmatrix} d_M & 0\\ 0 & d_B+\gamma\end{bmatrix}.$$

According to [150, Corollary 2.1], $R_0=r(\hat{F}V^{-1})$, where $\hat{F}=F_1+F_2+F_3$. Since

$$\hat{F}V^{-1}=\begin{bmatrix} \frac{r_m q e^{-d_A\tau_A}e^{-d_M\tau_L}e^{-\alpha M^*}}{d_M} & \frac{b\beta M^* e^{-d_M\tau_L}}{N_B^*(d_B+\gamma)}\\ \frac{c\beta}{d_M} & 0\end{bmatrix},$$

we have

$$R_0 = \frac{1}{2}(C_1 + \sqrt{C_1^2 + 4C_0}),$$

where $C_0 = \frac{b\beta M^* e^{-d_M\tau_L} c\beta}{N_B^*(d_B+\gamma)d_M}$ and $C_1 = \frac{r_m q e^{-d_A\tau_A} e^{-d_M\tau_L} e^{-\alpha M^*}}{d_M}$. Define

$$\tilde{R}_0 = \frac{M^* b\beta e^{-d_M\tau_L} c\beta + d_M q e^{-d_M\tau_L} N_B^*(d_B+\gamma)}{d_M N_B^*(d_B+\gamma)}.$$

We can prove that $R_0 - 1$ has the same sign as $\tilde{R}_0 - 1$. When $R_0 > 1$, system (3.15) has a unique positive equilibrium $E^* = (M_s^*, M_L^*, M_i^*, B_s^*, B_i^*, B_r^*)$, where
$M_s^* = \frac{d_M(1-qe^{-d_M\tau_L})N_B^*(c\beta M_i^*+\Lambda)(d_B+\gamma)}{b\beta^2 c\Lambda e^{-d_M\tau_L}}$, $M_L^* = \frac{(1-e^{-d_M\tau_L})(d_M q M_i^* N_B^* + b\beta M_s^* B_i^*)}{N_B^* d_M}$,
$M_i^* = \frac{d_M N_B^* \Lambda (d_B+\gamma)(\tilde{R}_0-1)}{bc\beta^2\Lambda + (1-qe^{-d_M\tau_L})d_M N_B^* c\beta(d_B+\gamma)}$, $B_s^* = \frac{\Lambda N_B^*}{c\beta M_i^*+\Lambda}$, $B_i^* = \frac{c\beta M_i^*\Lambda}{(c\beta M_i^*+\Lambda)(d_B+\gamma)}$, $B_r^* = \frac{\gamma B_i^*}{d_B}$.

Define

$$Y_\delta := \Big\{\phi \in C([-\tau_A-\tau_L, 0], \mathbb{R}_+^6) : \Sigma_{i=4}^6 \phi_i(s) \geq \delta, \forall s \in [-\tau_A-\tau_L, 0], \varphi_2(0) = \int_{-\tau_L}^0 e^{d_M\xi}[\frac{b\beta\varphi_1(\xi)\varphi_5(\xi)}{\sum_{i=4}^6 \varphi_i(\xi)} + e^{-d_A\tau_A} B(\xi-\tau_A, \sum_{i=1}^3 \varphi_i(\xi-\tau_A))q\varphi_3(\xi-\tau_A)]d\xi\Big\}.$$

Then we have the following results on the global dynamics of system (3.15).

**Theorem 3.4.1.** *Let (H1) hold. If $R_0 < 1$, then the disease-free equilibrium $E_1$ is globally attractive for system (3.15) in $Y_\delta \setminus (\{(0,0,0)\} \times C([-\tau_A-\tau_L, 0], \mathbb{R}_+^3))$.*

*Proof.* The total vector and host populations satisfy the following system:

$$\begin{aligned} \tfrac{\mathrm{d}M(t)}{\mathrm{d}t} &= r_m e^{-\alpha M(t-\tau_A)} M(t-\tau_A) e^{-d_A\tau_A} - d_M M(t), \\ \tfrac{\mathrm{d}N_B(t)}{\mathrm{d}t} &= \Lambda - d_B N_B(t). \end{aligned} \tag{3.16}$$

Since (H1) holds, $(M^*, N_B^*)$ is globally attractive for system (3.16) in $(C([-\tau_A, 0], \mathbb{R}_+) \setminus \{0\}) \times \mathbb{R}_+$. Then for any $\epsilon > 0$, there exists $T_0 = T_0(\epsilon) > 0$ such that

$$M^* - \epsilon \leq M(t) \leq M^* + \epsilon, N_B^* - \epsilon \leq N_B(t) \leq N_B^* + \epsilon, \forall t \geq T_0.$$

Thus, for any $t \geq T_0 + \tau_A + \tau_L$,

$$\begin{aligned} \frac{\mathrm{d}M_i(t)}{\mathrm{d}t} \leq& [r_m e^{-\alpha(M^*-\epsilon)} q M_i(t-\tau_A-\tau_L) e^{-d_A\tau_A} + \frac{b\beta(M^*+\epsilon)B_i(t-\tau_L)}{N_B^*-\epsilon}]e^{-d_M\tau_L} \\ & - d_M M_i(t), \\ \frac{\mathrm{d}B_i(t)}{\mathrm{d}t} \leq& c\beta M_i(t) - (d_B+\gamma)B_i(t). \end{aligned}$$

In the case where $R_0 < 1$, by choosing sufficiently small $\epsilon > 0$ and using the comparison arguments similar to those in Theorem 3.3.3, we then obtain $\lim_{t\to\infty}(M_i(t), B_i(t)) = (0, 0)$. By the theory of asymptotically autonomous semiflows [123], it follows that $\lim_{t\to\infty}(M_s(t), M_L(t), M_i(t), B_s(t), B_i(t), B_r(t)) = (M^*, 0, 0, N_B^*, 0, 0)$. □

To obtain the global attractivity of the positive equilibrium, we need the following additional assumption:

(H2) $b\beta d_B > d_M(1 - qe^{-d_M\tau_L})(d_B + \gamma)$.

**Theorem 3.4.2.** *Let (H1) and (H2) hold. If $R_0 > 1$, then system (3.15) admits a unique positive equilibrium $u^* = E^*$ such that for any $\phi \in Y_\delta$ with $\phi_3(0) > 0$ and $\phi_5(0) > 0$, $\lim_{t\to\infty} u(t, \phi) = E^*$.*

*Proof.* Since (H1) holds, $(M^*, N_B^*)$ is globally attractive for system (3.16) in $(C([-\tau_A, 0], \mathbb{R}_+) \setminus \{0\}) \times \mathbb{R}_+$. Then we have the following limiting system:

$$\begin{aligned}
\tfrac{\mathrm{d}M_s(t)}{\mathrm{d}t} &= A - r_m e^{-\alpha M^*} qM_i(t-\tau_A)e^{-d_A\tau_A} - d_M M_s(t) - b\beta' M_s(t)B_i(t),\\
\tfrac{\mathrm{d}M_L(t)}{\mathrm{d}t} &= r_m e^{-\alpha M^*} qM_i(t-\tau_A)e^{-d_A\tau_A} - d_M M_L(t) + b\beta' M_s(t)B_i(t)\\
&\quad -[r_m e^{-\alpha M^*} qM_i(t-\tau_A-\tau_L)e^{-d_A\tau_A} + b\beta' M_s(t-\tau_L)B_i(t-\tau_L)]e^{-d_M\tau_L},\\
\tfrac{\mathrm{d}M_i(t)}{\mathrm{d}t} &= r_m e^{-\alpha M^*} qM_i(t-\tau_A-\tau_L)e^{-d_A\tau_A}e^{-d_M\tau_L} + b\beta' M_s(t-\tau_L)B_i(t-\tau_L)e^{-d_M\tau_L}\\
&\quad -d_M M_i(t),\\
\tfrac{\mathrm{d}B_s(t)}{\mathrm{d}t} &= \Lambda - c\beta' M_i(t)B_s(t) - d_B B_s(t),\\
\tfrac{\mathrm{d}B_i(t)}{\mathrm{d}t} &= c\beta' M_i(t)B_s(t) - (d_B+\gamma)B_i(t),\\
\tfrac{\mathrm{d}B_r(t)}{\mathrm{d}t} &= \gamma B_i(t) - d_B B_r(t),
\end{aligned} \tag{3.17}$$

where $A = d_M M^*$ and $\beta' = \frac{\beta}{N_B^*}$. Since the second and sixth equations are decoupled from others in system (3.17), we obtain the following system:

$$\begin{aligned}
\tfrac{\mathrm{d}M_s(t)}{\mathrm{d}t} &= A - r_m e^{-\alpha M^*} qM_i(t-\tau_A)e^{-d_A\tau_A} - d_M M_s(t) - b\beta' M_s(t)B_i(t),\\
\tfrac{\mathrm{d}M_i(t)}{\mathrm{d}t} &= r_m e^{-\alpha M^*} qM_i(t-\tau_A-\tau_L)e^{-d_A\tau_A}e^{-d_M\tau_L} + b\beta' M_s(t-\tau_L)B_i(t-\tau_L)e^{-d_M\tau_L}\\
&\quad -d_M M_i(t),\\
\tfrac{\mathrm{d}B_s(t)}{\mathrm{d}t} &= \Lambda - c\beta' M_i(t)B_s(t) - d_B B_s(t),\\
\tfrac{\mathrm{d}B_i(t)}{\mathrm{d}t} &= c\beta' M_i(t)B_s(t) - (d_B+\gamma)B_i(t).
\end{aligned} \tag{3.18}$$

Let $g(t) = M_s(t) + e^{d_M\tau_L}M_i(t+\tau_L)$. Then

$$\frac{\mathrm{d}g(t)}{\mathrm{d}t} = \frac{\mathrm{d}M_s(t)}{\mathrm{d}t} + e^{d_M\tau_L}\frac{dM_i(t+\tau_L)}{dt} = A - d_M g(t).$$

It is easy to see that $M^* = A/d_M$ is globally attractive for the above nonhomogeneous equation. For system (3.18), we consider the following limiting system:

$$\begin{aligned}\frac{\mathrm{d}\bar{M}_i(t)}{\mathrm{d}t} &= r_m e^{-\alpha M^*} q\bar{M}_i(t-\tau_A-\tau_L)e^{-d_A\tau_A}e^{-d_M\tau_L} - d_M\bar{M}_i(t)\\ &\quad + b\beta'(M^* - e^{d_M\tau_L}\bar{M}_i(t))\bar{B}_i(t-\tau_L)e^{-d_M\tau_L},\\ \frac{\mathrm{d}\bar{B}_s(t)}{\mathrm{d}t} &= \Lambda - c\beta'\bar{M}_i(t)\bar{B}_s(t) - d_B\bar{B}_s(t),\\ \frac{\mathrm{d}\bar{B}_i(t)}{\mathrm{d}t} &= c\beta'\bar{M}_i(t)\bar{B}_s(t) - (d_B+\gamma)\bar{B}_i(t).\end{aligned} \tag{3.19}$$

From the discussion in Lemma 3.2.1, it is easy to verify that the set

$$D := C([-\tau_A-\tau_L, 0], [0, M^*e^{-d_M\tau_L}] \times \mathbb{R}^2_+)$$

is positively invariant for system (3.19).

By arguments similar to those in Theorem 3.3.1, we can show that system (3.19) is uniformly persistent in the sense that there exists an $\eta_1 > 0$ such that for any initial value $\psi = (\psi_1, \psi_2, \psi_3) \in D$ with $\psi_1(0) > 0$, $\psi_3(0) > 0$, the solution $(\bar{M}_i(t,\psi), \bar{B}_s(t,\psi), \bar{B}_i(t,\psi))$ of system (3.19) satisfies

$$\liminf_{t\to\infty}(\bar{M}_i(t,\psi), \bar{B}_i(t,\psi)) \geq (\eta_1, \eta_1).$$

Next we use the method of fluctuations (see, e.g., [147]) to prove the global attractivity of the positive equilibrium for system (3.19). Given $\psi \in D$ with $\psi_1(0) > 0$, $\psi_3(0) > 0$, let $(\bar{M}_i(t), \bar{B}_s(t), \bar{B}_i(t)) = (\bar{M}_i(t,\psi), \bar{B}_s(t,\psi), \bar{B}_i(t,\psi))$. Define

$$\bar{M}_i^\infty = \limsup_{t\to\infty}\bar{M}_i(t), \bar{M}_{i\infty} = \liminf_{t\to\infty}\bar{M}_i(t), \bar{B}_s^\infty = \limsup_{t\to\infty}\bar{B}_s(t), \bar{B}_{s\infty} = \liminf_{t\to\infty}\bar{B}_s(t),$$

$$\bar{B}_i^\infty = \limsup_{t\to\infty}\bar{B}_i(t), \bar{B}_{i\infty} = \liminf_{t\to\infty}\bar{B}_i(t).$$

Clearly, $\bar{M}_i^\infty \geq \bar{M}_{i\infty} \geq \eta_1 > 0, \bar{B}_i^\infty \geq \bar{B}_{i\infty} \geq \eta_1 > 0, \bar{B}_s^\infty \geq \bar{B}_{s\infty} > 0$. Then there exist sequences $t_n^j \to \infty$ and $s_n^j \to \infty$, $j = 1, 2, 3$, such that

$$\lim_{n\to\infty}\bar{M}_i(t_n^1) = \bar{M}_i^\infty, \bar{M}_i'(t_n^1) = 0, \lim_{n\to\infty}\bar{M}_i(s_n^1) = \bar{M}_{i\infty}, \bar{M}_i'(s_n^1) = 0, \forall n \geq 1;$$

$$\lim_{n\to\infty}\bar{B}_s(t_n^2) = \bar{B}_s^\infty, \bar{B}_s'(t_n^2) = 0, \lim_{n\to\infty}\bar{B}_s(s_n^2) = \bar{B}_{s\infty}, \bar{B}_s'(s_n^2) = 0, \forall n \geq 1;$$

$$\lim_{n\to\infty}\bar{B}_i(t_n^3) = \bar{B}_i^\infty, \bar{B}_i'(t_n^3) = 0, \lim_{n\to\infty}\bar{B}_i(s_n^3) = \bar{B}_{i\infty}, \bar{B}_i'(s_n^3) = 0, \forall n \geq 1.$$

By the first equation of system (3.19), we have

$$\bar{B}_i^\infty b\beta'(M^* - e^{d_M\tau_L}\bar{M}_i^\infty)e^{-d_M\tau_L} + r_m e^{-\alpha M^*} q\bar{M}_i^\infty e^{-d_A\tau_A}e^{-d_M\tau_L} - d_M\bar{M}_i^\infty \geq 0$$

$$\geq \bar{B}_{i\infty} b\beta'(M^* - e^{d_M\tau_L}\bar{M}_i^{\infty})e^{-d_M\tau_L} + r_m e^{-\alpha M^*} q\bar{M}_i^{\infty} e^{-d_A\tau_A} e^{-d_M\tau_L} - d_M\bar{M}_i^{\infty},$$

$$\begin{aligned}&\bar{B}_i^{\infty} b\beta'(M^* - e^{d_M\tau_L}\bar{M}_{i\infty})e^{-d_M\tau_L} + r_m e^{-\alpha M^*} q\bar{M}_{i\infty} e^{-d_A\tau_A} e^{-d_M\tau_L} - d_M\bar{M}_{i\infty} \geq 0\\ &\geq \bar{B}_{i\infty} b\beta'(M^* - e^{d_M\tau_L}\bar{M}_{i\infty})e^{-d_M\tau_L} + r_m e^{-\alpha M^*} q\bar{M}_{i\infty} e^{-d_A\tau_A} e^{-d_M\tau_L} - d_M\bar{M}_{i\infty},\end{aligned}$$

and hence,

$$\bar{B}_i^{\infty} \geq \frac{d_M\bar{M}_i^{\infty}(1 - qe^{-d_M\tau_L})}{b\beta'(M^* - e^{d_M\tau_L}\bar{M}_i^{\infty})e^{-d_M\tau_L}} \geq \frac{d_M\bar{M}_{i\infty}(1 - qe^{-d_M\tau_L})}{b\beta'(M^* - e^{d_M\tau_L}\bar{M}_{i\infty})e^{-d_M\tau_L}} \geq \bar{B}_{i\infty}. \tag{3.20}$$

Similarly, by the second and third equations of system (3.19), we have

$$\frac{\Lambda}{d_B + c\beta'\bar{M}_{i\infty}} \geq \bar{B}_s^{\infty} \geq \bar{B}_{s\infty} \geq \frac{\Lambda}{d_B + c\beta'\bar{M}_i^{\infty}}, \tag{3.21}$$

$$\frac{c\beta'\bar{M}_i^{\infty}\bar{B}_s^{\infty}}{d_B + \gamma} \geq \bar{B}_i^{\infty} \geq \bar{B}_{i\infty} \geq \frac{c\beta'\bar{M}_{i\infty}\bar{B}_{s\infty}}{d_B + \gamma}. \tag{3.22}$$

Thus, combining (3.21) and (3.22) together, we obtain

$$\frac{\Lambda}{d_B + c\beta'\bar{M}_{i\infty}}\frac{c\beta'\bar{M}_i^{\infty}}{d_B + \gamma} \geq \bar{B}_i^{\infty} \geq \bar{B}_{i\infty} \geq \frac{\Lambda}{d_B + c\beta'\bar{M}_i^{\infty}}\frac{c\beta'\bar{M}_{i\infty}}{d_B + \gamma}. \tag{3.23}$$

By (3.20) and (3.23), it follows that

$$\begin{aligned}\frac{\Lambda}{d_B + c\beta'\bar{M}_{i\infty}}\frac{c\beta'\bar{M}_i^{\infty}}{d_B + \gamma} &\geq \frac{d_M\bar{M}_i^{\infty}(1 - qe^{-d_M\tau_L})}{b\beta'(M^* - e^{d_M\tau_L}\bar{M}_i^{\infty})e^{-d_M\tau_L}},\\ \frac{\Lambda}{d_B + c\beta'\bar{M}_i^{\infty}}\frac{c\beta'\bar{M}_{i\infty}}{d_B + \gamma} &\leq \frac{d_M\bar{M}_{i\infty}(1 - qe^{-d_M\tau_L})}{b\beta'(M^* - e^{d_M\tau_L}\bar{M}_{i\infty})e^{-d_M\tau_L}}.\end{aligned}$$

Therefore, $(\Lambda b\beta' - d_M(1 - qe^{-d_M\tau_L})(d_B + \gamma))\bar{M}_i^{\infty} \leq (\Lambda b\beta' - d_M(1 - qe^{-d_M\tau_L})(d_B + \gamma))\bar{M}_{i\infty}$. Since (H2) holds, we have $\bar{M}_i^{\infty} = \bar{M}_{i\infty}$. By (3.21) and (3.22), we get $\bar{B}_s^{\infty} = \bar{B}_{s\infty}$ and $\bar{B}_i^{\infty} = \bar{B}_{i\infty}$. Then $\lim_{t\to\infty}(\bar{M}_i(t), \bar{B}_s(t), \bar{B}_i(t)) = (M_i^*, B_s^*, B_i^*) := E_2$ for any $\psi \in D$ with $\psi_1(0) > 0$ and $\psi_3(0) > 0$. Thus, we have $W^S(E_2) = D \setminus \{(0, N_B^*, 0)\}$, where $W^S(E_2)$ is the stable set of $E_2$ for the solution semiflow of system (3.19).

For any given $\varphi \in E := C([-\tau_A - \tau_L, 0], \mathbb{R}_+^4)$, let $v(t, \varphi) = (v_1(t), v_2(t), v_3(t), v_4(t))$ be the unique solution of system (3.18) with $v_0 = \varphi$ for all $t \geq 0$. Then $(v_2(t), v_3(t), v_4(t))$ satisfies the following nonautonomous system:

$$\begin{aligned}\tfrac{\mathrm{d}M_i(t)}{\mathrm{d}t} &= r_m e^{-\alpha M^*} qM_i(t - \tau_A - \tau_L)e^{-d_A\tau_A}e^{-d_M\tau_L} - d_M M_i(t)\\ &\quad + b\beta'(g(t - \tau_L) - e^{d_M\tau_L}M_i(t))B_i(t - \tau_L)e^{-d_M\tau_L},\\ \tfrac{\mathrm{d}B_s(t)}{\mathrm{d}t} &= \Lambda - c\beta' M_i(t)B_s(t) - d_B B_s(t),\\ \tfrac{\mathrm{d}B_i(t)}{\mathrm{d}t} &= c\beta' M_i(t)B_s(t) - (d_B + \gamma)B_i(t).\end{aligned}$$

Now we define

$$\begin{aligned}\tilde{\omega} =& \{(\phi_2, \phi_3, \phi_4) \in C([-\tau_A - \tau_L, 0], \mathbb{R}^3_+) : \\ & \lim_{n\to\infty} (v_2(t_n + \cdot), v_3(t_n + \cdot), v_4(t_n + \cdot)) = (\phi_2, \phi_3, \phi_4) \text{ for some } t_n \to \infty\}.\end{aligned}$$

In view of Lemma 3.2.1 and its proof, it is easy to see that $\tilde{\omega}$ is a nonempty and compact subset of $C([-\tau_A - \tau_L, 0], \mathbb{R}^3_+)$. Since $\lim_{t\to\infty} g(t) = M^*$ and $0 \le v_2(t) \le g(t - \tau_L)e^{-d_M \tau_L}$ for all $t \ge 0$, we have $\tilde{\omega} \subseteq D$. By the continuous-time version of Lemma 1.1.3 (see also [92, Theorem 1.8 (d)]), it then follows that $\tilde{\omega}$ is an internally chain transitive set for the solution semiflow of system (3.19) on $D$. We further have the following observation.

**Claim.** $\lim_{t\to\infty} v(t, \varphi) \neq (M^*, 0, N_B^*, 0)$ for any $\varphi \in E$ with $\varphi_2(0) > 0$ and $\varphi_4(0) > 0$.

Suppose, by contradiction, that $\lim_{t\to\infty} v(t, \psi) = (M^*, 0, N_B^*, 0)$ for some $\psi \in E$ with $\psi_2(0) > 0$ and $\psi_4(0) > 0$. Thus, for any $\sigma > 0$, there exists $T_1 = T_1(\sigma) > 0$ such that $|M_s(t) - M^*| < \sigma$ and $|B_s(t) - N_B^*| < \sigma$ for all $t \ge T_1$. Consider the following perturbed linear system with parameter $\sigma > 0$:

$$\begin{aligned}\tfrac{\mathrm{d}M_i(t)}{\mathrm{d}t} &= r_m e^{-\alpha M^*} q M_i(t - \tau_A - \tau_L) e^{-d_A \tau_A} e^{-d_M \tau_L} + b\beta'(M^* - \sigma) B_i(t - \tau_L) e^{-d_M \tau_L} \\ &\quad - d_M M_i(t), \\ \tfrac{\mathrm{d}B_i(t)}{\mathrm{d}t} &= c\beta' M_i(t)(N_B^* - \sigma) - (d_B + \gamma) B_i(t).\end{aligned} \tag{3.24}$$

Let

$$\hat{F}_\sigma := \begin{bmatrix} r_m q e^{-d_A \tau_A} e^{-d_M \tau_L} e^{-\alpha M^*} & b\beta'(M^* - \sigma) e^{-d_M \tau_L} \\ c\beta'(N_B^* - \sigma) & 0 \end{bmatrix}.$$

Then we have $\lim_{\sigma\to 0^+} r(\hat{F}_\sigma V^{-1}) = r(\hat{F} V^{-1}) = R_0 > 1$. Fix a sufficiently small $\sigma > 0$ such that $r(\hat{F}_\sigma V^{-1}) > 1$. By arguments similar to those in Theorem 3.3.1, it follows that there is a positive vector $v_\sigma^*$ such that $w_\sigma^*(t) = e^{\ln r(\hat{F}_\sigma V^{-1}) t} v_\sigma^*$ is a positive solution of system (3.24). Then $\lim_{t\to\infty} w_\sigma^*(t) = \infty$. For all $t \ge T_1 + \tau_L$, we see from system (3.18) that

$$\begin{aligned}\tfrac{\mathrm{d}M_i(t)}{\mathrm{d}t} &\ge r_m e^{-\alpha M^*} q M_i(t - \tau_A - \tau_L) e^{-d_A \tau_A} e^{-d_M \tau_L} + b\beta'(M^* - \sigma) B_i(t - \tau_L) e^{-d_M \tau_L} \\ &\quad - d_M M_i(t), \\ \tfrac{\mathrm{d}B_i(t)}{\mathrm{d}t} &\ge c\beta' M_i(t)(N_B^* - \sigma) - (d_B + \gamma) B_i(t).\end{aligned}$$

Since $\psi_2(0) > 0$ and $\psi_4(0) > 0$, $M_i(t, \psi) > 0$ and $B_i(t, \psi) > 0$. By the comparison principle, it then easily follows that $\lim_{t\to\infty}(M_i(t, \psi), B_i(t, \psi)) = (\infty, \infty)$, which is a contradiction.

The above claim implies that for any given $\varphi \in E$ with $\varphi_2(0) > 0$ and $\varphi_4(0) > 0$, we have $\tilde{\omega} \neq \{(0, N_B^*, 0)\}$, and hence, $\tilde{\omega} \cap W^S(E_2) \neq \varnothing$. By Theorem 1.1.1 and [151, Remark 1.3.2], it follows that $\tilde{\omega} = E_2$, and hence, $\lim_{t\to\infty}(v_2(t), v_3(t), v_4(t)) = (M_i^*, B_s^*, B_i^*)$. Thus, we have $\lim_{t\to\infty} v_1(t) = \lim_{t\to\infty}(g(t) - e^{d_M \tau_L} M_i(t+\tau_L)) = M^* - e^{d_M \tau_L} M_i^* = M_s^*$. Consequently, the solution of system (3.18) satisfies $\lim_{t\to\infty} v(t, \varphi) = (M_s^*, M_i^*, B_s^*, B_i^*)$. By the theory of asymptotically periodic semiflows [151, Section 3.2] and the theory of chain transitive sets (see, e.g., Lemma 1.1.3, Theorems 1.1.1 and 1.2.1), we can further lift the global attractivity for system (3.18) to system (3.15). It follows that $\lim_{t\to\infty} u(t, \phi) = E^*$ for any $\phi \in Y_\delta$ with $\phi_3(0) > 0$ and $\phi_5(0) > 0$. □

## 3.5 A case study

In this section, we study the WNV transmission case in Orange County, California, United States. Since its arrival in California in 2003, WNV is now the most prevalent mosquito-borne disease in the United States. In the following, we take January of 2003 as the start time of all simulations. Let the period $\omega = 12$ months.

### 3.5.1 Parameter estimation

We first obtain and estimate the values for constant parameters in system (3.2) that do not heavily depend on temperature. They are listed in Table 3.2. According to [22], the recruitment rate of birds which can be infected by WNV in California is estimated to be $31.5253 \times 10^5$ birds $\times$ year$^{-1}$. The areas of California is 423970 km$^2$, yielding that the recruitment rate of birds is 7.4 birds $\times$ year$^{-1}$ per square kilometer. The areas of Orange County is 2455 km$^2$, then the recruitment rate of birds in Orange County is about 18000/12 birds $\times$ Month$^{-1}$.

Next, we use the monthly mean temperature for Orange County (see https://en.climate-data.org/north-america/united-states-of-america/california/orange-1441/), as shown in Table 3.3, to evaluate the periodic parameters in system (3.2).

*Estimation of* $r_m(t)$. It follows from [17] that the temperature-dependent per capita mosquito egg production rate per month can be expressed as

$$r_m(T) = \frac{1}{1432.5 \times T^{-2.12}} \times 30.4,$$

Table 3.2: Values (ranges) for constant parameters in system (3.2)

| Parameter | Value (range) | Resource |
|---|---|---|
| $\alpha$ | 0.00001 | estimated |
| $q$ | 0.007 | [32, 42] |
| $b$ | $0.24(0.02 \sim 0.24)$ | [111, 126, 127, 139] |
| $c$ | $1(0.80 \sim 1.00)$ | [111, 126, 127, 139] |
| $\Lambda$ | $18000/12$ birds $\times$ Month$^{-1}$ | see text |
| $d_B$ | $1/(8 \times 12)$ Month$^{-1}$ | [22, 70] |
| $\mu_B$ | $0.0014(0 \sim 0.5) \times 30.4$ Month$^{-1}$ | [67, 93] |
| $\gamma$ | $0.102(0 \sim 0.2) \times 30.4$ Month$^{-1}$ | [67] |

Table 3.3: Monthly mean tempreature for Orange County (in °C)

| Month | January | February | March | April | May | June |
|---|---|---|---|---|---|---|
| Temperature | 13.2 | 14.1 | 14.4 | 15.9 | 17.8 | 19.9 |
| Month | July | August | September | October | November | December |
| Temperature | 22.4 | 23 | 22.1 | 19.5 | 15.9 | 13.2 |

where T is the temperature in °C. Therefore, the per capita mosquito egg production rate $r_m(t)$ in Orange County can be approximated by:

$$\begin{aligned} r_m(t) =& (0.3202 - 0.1706\cos(\pi t/6) - 0.06493\sin(\pi t/6) + 0.01141\cos(2\pi t/6) \\ &+ 0.04363\sin(2\pi t/6) + 0.003083\cos(3\pi t/6) + 0.002633\sin(3\pi t/6) \\ &+ 0.004725\cos(4\pi t/6) + 0.004604\sin(4\pi t/6) - 0.00394\cos(5\pi t/6) \\ &+ 0.001008\sin(5\pi t/6) + 0.0009417\cos(6\pi t/6)) \times 30.4 \text{ Month}^{-1}. \end{aligned}$$

*Estimation of $\beta(t)$ and $\tau_A(t)$.* According to [70, 109], the temperature-dependent gonotrophic period (the duration period between blood meals) is the reciprocal of the biting rate, and the per capita biting rate of mosquitoes per month is given by

$$\beta(T) = \frac{0.344}{1 + 1.231e^{-0.184(T-20)}} \times 30.4.$$

Then the per capita biting rate of mosquitoes $\beta(t)$ in Orange County can be fitted by:

$$\begin{aligned} \beta(t) =& (0.1227 - 0.06352\cos(\pi t/6) - 0.02399\sin(\pi t/6) + 0.003592\cos(2\pi t/6) \\ &+ 0.01537\sin(2\pi t/6) + 0.00145\cos(3\pi t/6) + 0.001967\sin(3\pi t/6) \\ &+ 0.001942\cos(4\pi t/6) + 0.001342\sin(4\pi t/6) - 0.001482\cos(5\pi t/6) \end{aligned}$$

$$+ 0.0003116 \sin(5\pi t/6) + 0.0002583 \cos(6\pi t/6)) \times 30.4 \text{ Month}^{-1}.$$

By [51], the gonotrophic period is the ovarian maturation rate plus two days for oviposition and locating a blood meal host. Thus, we assume that the duration of immature stage of mosquitoes is the gonotrophic period minus two days, that is, $\tau_A(t) = 1/\beta(t) - 2/30.4$ Month.

*Estimation of $d_A(t)$ and $d_M(t)$.* The per capita mortality rate for immature mosquitoes $d_A(t)$ and for adult mosquitoes $d_M(t)$ per month can be evaluated as the following functions of temperature [70, 109], respectively,

$$d_A(T) = (0.0025T^2 - 0.094T + 1.0257) \times 30.4, \quad d_M(T) = d_A(T)/10.$$

Thus, the per capita mortality rate for immature mosquitoes $d_A(t)$ and for adult mosquitoes $d_M(t)$ in Orange County are given by:

$$\begin{aligned} d_A(t) =& (0.1765 + 0.02346 \cos(\pi t/6) - 0.001669 \sin(\pi t/6) + 0.02157 \cos(2\pi t/6) \\ &+ 0.0101 \sin(2\pi t/6) + 0.00105 \cos(3\pi t/6) - 0.01402 \sin(3\pi t/6) \\ &- 0.00115 \cos(4\pi t/6) - 0.004936 \sin(4\pi t/6) - 0.00151 \cos(5\pi t/6) \\ &- 0.002448 \sin(5\pi t/6) + 0.0005833 \cos(6\pi t/6)) \times 30.4 \text{ Month}^{-1}, \\ d_M(t) =& \frac{d_A(t)}{10} \text{ Month}^{-1}. \end{aligned}$$

*Estimation of $\tau_L(t)$.* By [29], the temperature-dependent EIP is estimated as

$$\tau_L(T) = \frac{10.45 - 0.21T}{(-0.27 + 0.03T) \times 30.4}.$$

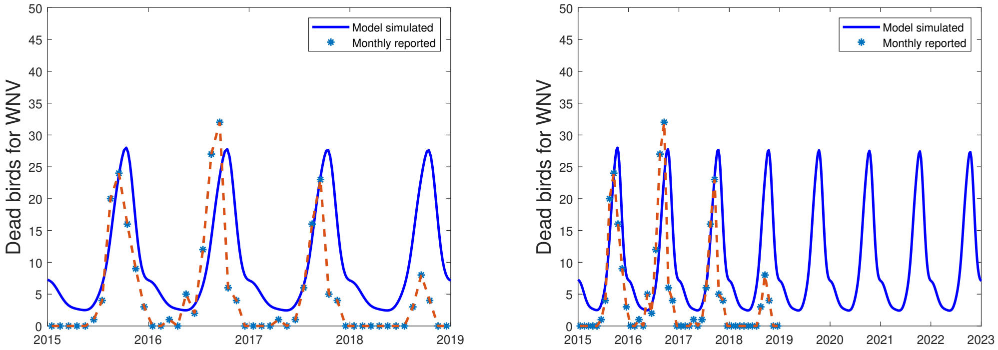
Then the periodic EIP in Orange County can be approximated by:

$$\begin{aligned} \tau_L(t) =& (32.72 + 22.27 \cos(\pi t/6) + 5.041 \sin(\pi t/6) + 5.288 \cos(2\pi t/6) \\ &- 2.445 \sin(2\pi t/6) + 1.109 \cos(3\pi t/6) - 3.395 \sin(3\pi t/6) - 0.2771 \cos(4\pi t/6) \\ &- 2.689 \sin(4\pi t/6) - 0.05495 \cos(5\pi t/6) - 1.347 \sin(5\pi t/6) \\ &- 0.1119 \cos(6\pi t/6) + 0.4898 \sin(6\pi t/6))/30.4 \text{ Month}. \end{aligned}$$

### 3.5.2 Model validation

From the California West Nile Virus Website (see http://www.westnile.ca.gov/), we can obtain the monthly reported numbers of dead birds testing positive for WNV in

Orange County from January 2015 to December 2018. We use the obtained parameter values above. From Figure 3.2, the monthly reported numbers of WNV-positive dead birds (stars in the dotted red curve) show an obvious seasonal fluctuation, with the seasonality peak in the summer, which is consistent with the seasonal variation of temperature in Orange County. The initial functions are chosen as the constant functions $M_s(\theta) = 43000$ for all $\theta \in [-\hat{\tau}, 0]$, $M_L(\theta) = 100$ and $M_i(\theta) = 100$ for all $\theta \in [-\hat{\tau}_0, 0]$, $B_s(\theta) = 18000$, $B_i(\theta) = 2$ and $B_r(\theta) = 10$ for all $\theta \in [-\hat{\tau}_L, 0]$. The reported data and the simulation result based on our model in Orange County are shown in Figure 3.2(a) and match well. Figure 3.2(b) gives the trends of the number of dead birds for WNV in the future severals years if no further effective control measure is taken in Orange County. In the year 2018, some personal protection measures may be introduced, and we choose the biting rate as $(1 - C)\beta(t)$, where $C = 0.21$ is the control effort. Then the simulation result until the year 2022 is shown in Figure 3.3, which has a less number of dead birds than that in Figure 3.2(b).



(a) (b)

Figure 3.2: Time series of monthly reported and model simulated dead birds cases. (a) From January 2015 to December 2018. (b) From January 2015 to December 2022.

### 3.5.3 Long-term behavior

Using Lemma 1.4.2, we compute the basic reproduction $R_0$ numerically under the same set of parameter values as Figure 3.2. We obtain $R_0 = 1.3672 > 1$ in Figure 3.2. In this case, the disease will persist and shows periodic fluctuation eventually (see Figure 3.4). By some WNV control measures to prevent bites, if we can decrease the biting rate to $0.6\beta(t)$, then $R_0 = 0.8217 < 1$. In this case, the long-term behaviors of the infectious mosquitoes and birds are shown in Figure 3.5, which implies that the disease will die out eventually. These simulations are consistent with our theoretical results.

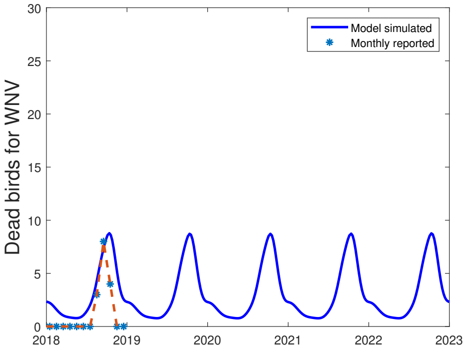
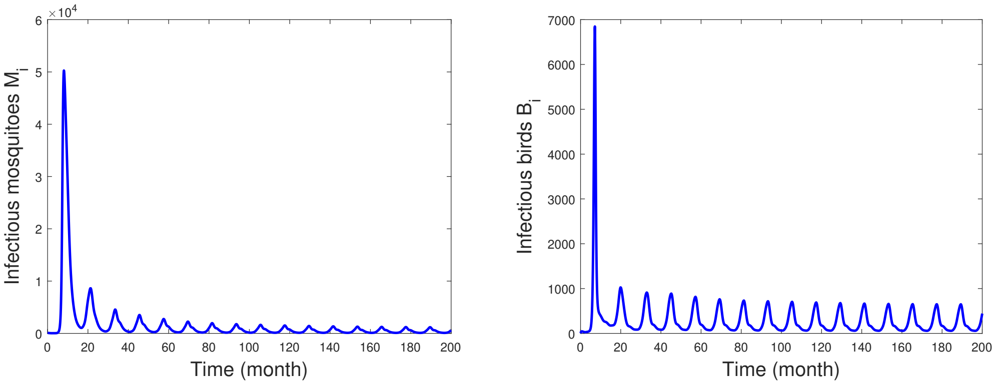


Figure 3.3: The monthly reported and model simulated dead birds cases from January 2018 to December 2022 when $\beta(t)$ is replaced by $0.79\beta(t)$.

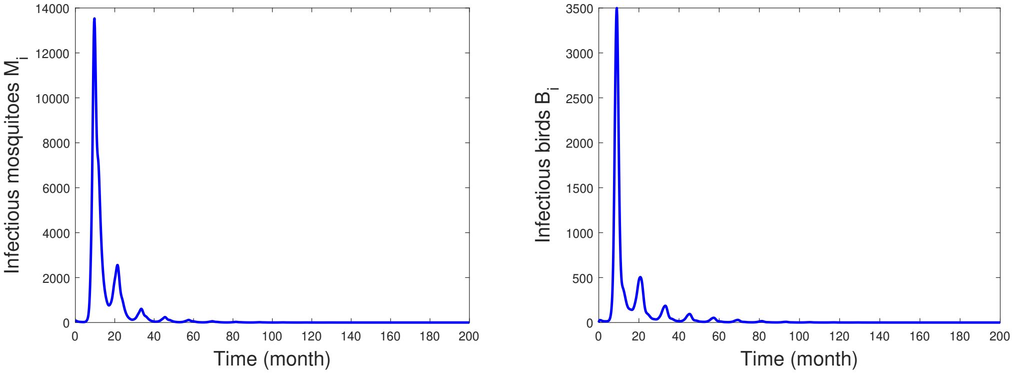


(a) (b)

Figure 3.4: Long-term behaviors of the infectious compartments in system (3.2) when $R_0 = 1.3672 > 1$.

### 3.5.4 Sensitivity analysis of $R_0$

In order to reduce the WNV mortality and morbidity in birds, it is important to explore the influence of different factors for WNV transmission. Then we explore the



(a) (b)

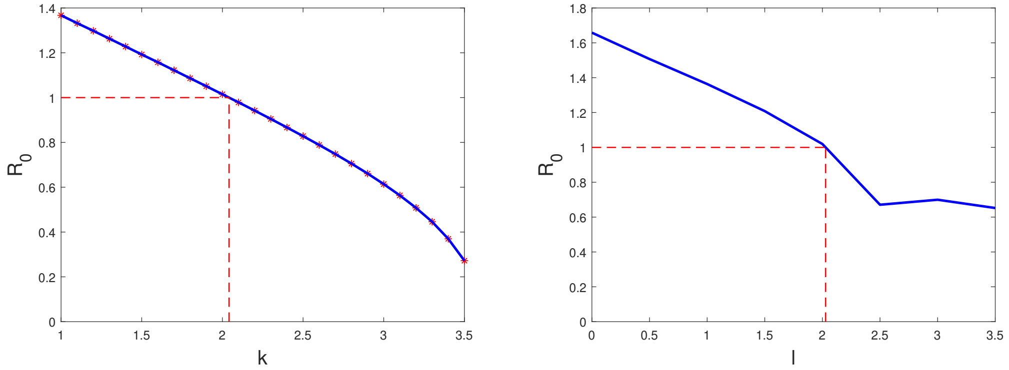
Figure 3.5: Long-term behaviors of the infectious compartments in system (3.2) when $R_0 = 0.8217 < 1$.

relationship between some parameters and $R_0$, and the possible measures to control WNV transmission.

We first discuss the effect of temperature-dependent maturation time and EIP on $R_0$. By replacing $\tau_A(t)$ and $\tau_L(t)$ with $k\tau_A(t)$ and $l\tau_L(t)$, $k \in [1, 3.5]$, $l \in [0, 3.5]$, respectively, and keeping the other parameter values the same as those in Figure 3.2, we observe that $R_0$ is a decreasing function of $k$ (see Figure 3.6(a)). Figure 3.6(b) shows that $R_0$ declines sharply when $l \in [2, 2.5]$ and reaches the relative minimum at $l = 2.5$, which implies that it is the “sweet spot”. Hence, we may try the prolong the maturation time and EIP to control WNV by using some drugs for mosquitoes. In the immature stage before mosquitoes reach adulthood, we may use larvicides in breeds areas which will kill the immature mosquitoes and reduce the mosquitoes population.

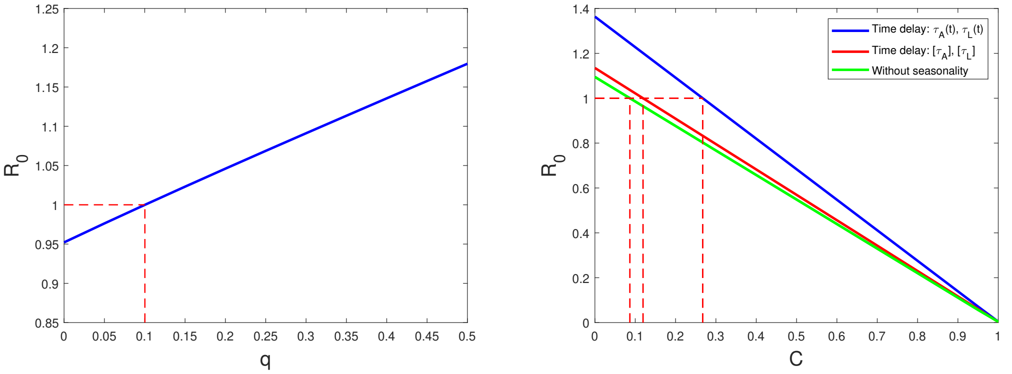
Secondly, we simulate the effect of the vertical transmission $q$ on $R_0$. Under other parameter values the same as those in Figure 3.5, we observe that there is a relative small change in $R_0$ as $q$ increases (see Figure 3.7(a)). A large enough vertical transmission rate in mosquitoes can make $R_0 > 1$, that is, the increase of vertical transmission could cause an endemic state of WNV. This is probably because the vertical transmission provides a survival mechanism for the virus during adverse conditions.

Thirdly, the biting rate plays a very important role in the spread of WNV. To simulate the effect of preventing bites, we replace $\beta(t)$ with $(1 - C)\beta(t)$ and other parameters values the same as those in Figure 3.2. The blue curve in Figure 3.7(b) shows that $R_0$ is a decreasing function of $C$. In order to eradicate disease, we should keep $C > 0.2673$ such that $R_0 < 1$.



(a) (b)

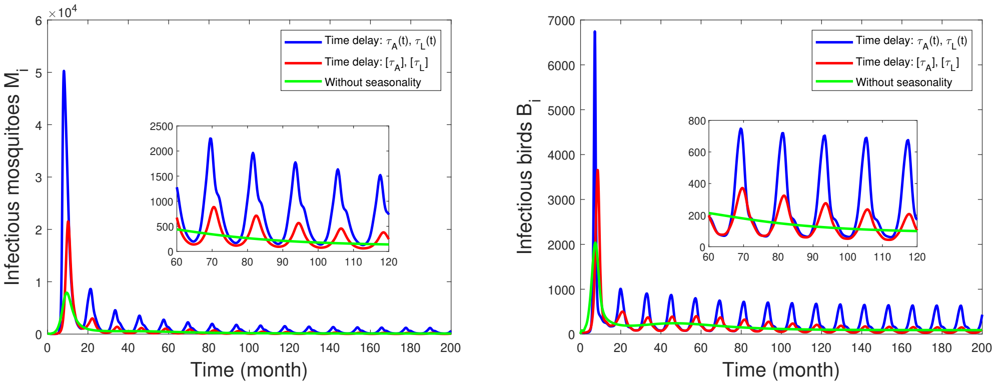
Figure 3.6: $R_0$ vs $k$ and $l$. (a) Relationship between $R_0$ and $k$. (b) Relationship between $R_0$ and $l$.



(a) (b)

Figure 3.7: $R_0$ vs $q$ and $C$. (a) Relationship between $R_0$ and $q$. (b) Relationship between $R_0$ and $C$.

Finally, we explore the influence of the seasonality and the periodic time delays on $R_0$. Define the time-averaged time delay as $[\tau] := \frac{1}{\omega}\int_0^{\omega} \tau(t)dt$. Figure 3.7(b) compares the effect of the periodic time delays, constant time delays, and without seasonality on $R_0$ keeping other parameters the same as those in Figure 3.2. We observe that the use of constant time delays, without seasonality parameters may underestimate the value of $R_0$. This implies that we need to take much more effort to control the spread of WNV. Figure 3.8 compares the long-term behaviors of mosquitoes and birds under three scenarios: periodic time delays, constant time delays, and without seasonality,



(a) (b)

Figure 3.8: Comparison of the long-term behaviors of the infectious compartments in system (3.2) with periodic time delay, time-averaged time delay, and without seasonality.

which implies that the amplitude of the periodic fluctuation of infectious mosquitoes and birds are greater than that in the case of constant time delays and parameters.

## 3.6 Discussion

In this chapter, we formulated and analyzed a WNV transmission model between mosquitoes and birds that includes the seasonal effects, the vertical transmission of virus in mosquitoes, the temperature-dependent maturation time, and the temperature-dependent EIP for mosquitoes. By the theory developed in [75, 150], we derived and numerically computed the basic reproduction ratio $R_0$. Since the maturation time and EIP are periodic, we need to define a suitable phase space on which the linearized system for infectious compartments generates an eventually strongly monotone periodic semiflow. By the persistence theory for periodic semiflows, we showed that $R_0$ is the threshold parameter for the extinction and persistence of the disease. More precisely, if $R_0 > 1$, then the disease will persist; if $R_0 < 1$, then the disease will be cleared provided that there is only a small invasion in infectious mosquitoes and birds. We further established the global attractivity of the disease-free periodic solution in the case where $R_0 < 1$ and the disease-induced death rate is zero. When all coefficients are constants and the disease-induced death rate of birds is zero, our model reduces to an autonomous system. For such a model, we obtained an explicit expression of $R_0$ and a threshold result on the global attractivity in terms of $R_0$.

By the perturbation method, we may prove the global attractivity of the disease-free periodic solution when the disease-induced death rate is sufficiently small. However, it remains an unsolved mathematical problem to prove it for the case of a general disease-induced death rate.

We have estimated all constant and periodic parameters from some published data and studied WNV transmission in Orange County, California, United States. The risk of the disease is measured by $R_0$. The simulated results based on our model exhibit the seasonal fluctuation and match with the reported data well. In the year 2018, since $R_0 = 1.0812 > 1$, the disease will persist if the control effort keeps $C = 21\%$. However, the number of dead birds has decreased significantly. If the control effort keeps $C = 26.73\%$ by reducing mosquitoes bites, then the disease will eventually be controlled and eliminated. This means that people need to make greater efforts and take more effective measures.

Our numerical simulations in Figures 3.6(a), 3.6(b), 3.7(a) indicate that an increase of the maturation time and the EIP, a decrease of the vertical transmission rate and the biting rate in mosquitoes could reduce the value of $R_0$. Control strategies focus mainly on the eradication of mosquitoes because birds' behavior is hard to control artificially. Therefore, we may try to prolong the maturation time, EIP, and reduce the vertical transmission rate by developing new drugs for mosquitoes. Moreover, in order to keep birds from mosquito bites, we may try to reduce the mosquito population. For such a purpose, we may reduce mosquito breeding sites by eliminating culverts, roadside ditches and standing water, or kill mosquito larvae by larvacides, or kill adult mosquitoes by fogging and spraying adulticides [97]. In addition, our simulated result shows that the risk of the disease will be underestimated if we only consider the constant parameters or time-averaged time delays. Thus, the model incorporating the seasonality and temperature-dependent time delays are more realistic for the control of WNV transmission.

## Appendix. A periodic delay differential equation

In this Appendix, we consider a scalar differential equation with periodic delay:

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = a(t)e^{-\alpha(t)u(t-\tau_A(t))}u(t-\tau_A(t)) - d(t)u(t), \tag{3.25}$$

where all coefficients are positive $\omega$-periodic functions. Let $Z := C([-\hat{\tau}_A, 0], \mathbb{R})$, $Z^+ := C([-\hat{\tau}_A, 0], \mathbb{R}_+)$. For any $\varphi \in Z^+$, define

$$\tilde{f}(t, \varphi) = a(t)e^{-\alpha(t)\varphi(-\tau_A(t))}\varphi(-\tau_A(t)) - d(t)\varphi(0).$$

It is easy to see that for any $\varphi \in Z^+$ with $\varphi(0) = 0$, we have $\tilde{f}(t, \varphi) \geq 0$. It then follows from [116, Theorem 5.2.1] that for any $\varphi \in Z^+$, system (3.25) has a unique nonnegative solution $w(t, \varphi)$ on its maximal interval $[0, \sigma_\varphi)$ of existence with $w_0 = \varphi$. Since

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} \leq \frac{a(t)}{\alpha(t)}e^{-1} - d(t)u(t),$$

system (3.25) is dominated by the following cooperative system:

$$\frac{\mathrm{d}\bar{u}(t)}{\mathrm{d}t} = \frac{a(t)}{\alpha(t)}e^{-1} - d(t)\bar{u}(t). \tag{3.26}$$

Clearly, system (3.26) has a globally attractive positive $\omega$-periodic solution $\bar{u}^*(t)$, that is, $\lim_{t\to\infty}(\bar{u}(t) - \bar{u}^*(t)) = 0$. Thus, solutions of system (3.26) are bounded and ultimately bounded. By the comparison principle, solutions of system (3.25) exist globally on $[0, \infty)$ and are ultimately bounded.

Let $P_1(t)$ be the solution maps of system (3.25), that is, $P_1(t)\psi = w_t(\psi)$, $\forall t \geq 0$, where $w(t, \psi)$ is the unique solution of system (3.25) satisfying $w_0 = \psi \in Z^+$. Then $P_1 := P_1(\omega)$ is the Poincaré map associated with system (3.25) on $Z^+$. Thus, $\{P_1^n\}_{n=0}^\infty$ is point dissipative on $Z^+$. Let $\rho(DP_1(0))$ be the spectral radius of the Frechét derivative of $P_1$ at zero. Note that the linearized system (3.25) at zero is

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = a(t)u(t - \tau_A(t)) - d(t)u(t). \tag{3.27}$$

Let $\tilde{P}$ be the Poincaré map associated with system (3.27) on $Z$. By the continuity and differentiability of solutions with respect to initial values, it follows that $P_1$ is differentiable at zero and $DP_1(0) = \tilde{P}$. Define

$$\mathcal{Z} := C([-\tau_A(0), 0], \mathbb{R}),\ \mathcal{Z}^+ := C([-\tau_A(0), 0], \mathbb{R}_+).$$

By the method of steps (see, e.g., [72, 82]), we have the following result.

**Lemma A.1.** *For any $\varphi \in \mathcal{Z}^+$, system (3.25) has a unique nonnegative solution $w(t, \varphi)$ with $w_0 = \varphi$ for all $t \geq 0$.*

For any given $t \geq 0$, let $S_1(t)$ be the solution map of system (3.25) on $\mathcal{Z}^+$. Let $\tilde{S}(t)$ be the solution maps of linear system (3.27) on $\mathcal{Z}$. Then $\tilde{S} := \tilde{S}(\omega)$ is the Poincaré map associated with linear system (3.27) and $DS_1(0) = \tilde{S}$. It is easy to see that $r(\tilde{P}) = r(\tilde{S})$ (see, e.g., [82]). Further, we have the following observations.

**Remark A.2.** *By the uniqueness of solutions, it follows that for any* $\psi \in Z^+$ *and* $\phi \in \mathcal{Z}^+$ *with* $\psi(\theta) = \phi(\theta)$ *for all* $\theta \in [-\tau_A(0), 0]$*, we have* $w(t,\psi) = \nu(t,\phi)$ *for all* $t \geq 0$*, where* $w(t,\psi)$ *and* $\nu(t,\phi)$ *are solutions of system (3.25) satisfying* $w_0 = \psi$ *and* $\nu_0 = \phi$*, respectively.*

**Lemma A.3.** $S_1(t)$ *is an* $\omega$*-periodic semiflow on* $\mathcal{Z}^+$ *in the sense that (i)* $S_1(0) = I$*; (ii)* $S_1(t+\omega) = S_1(t) \circ S_1(\omega)$ *for all* $t \geq 0$*; and (iii)* $S_1(t)\psi$ *is continuous in* $(t,\psi) \in [0,\infty) \times \mathcal{Z}^+$.

To obtain the global dynamics of system (3.25), we need the following assumptions:

(A1) $r(\tilde{P}) > 1$, where $r(\tilde{P})$ is the spectral radius of $\tilde{P}$.

(A2) $\bar{u}^*(t - \tau_A(t)) < \frac{1}{\alpha(t)}$ for all $t \in [0,\omega]$.

**Theorem A.4.** *Let (A1) and (A2) hold. Then system (3.25) admits a unique positive* $\omega$*-periodic solution* $u^*(t)$ *which is globally attractive in* $\mathcal{Z}^+ \setminus \{0\}$*.*

*Proof.* Define $W := [0, \bar{u}_0^*]_{\mathcal{Z}}$, where $\bar{u}_0^* \in \mathcal{Z}$, and $\bar{u}_0^*(\theta) = \bar{u}^*(\theta)$ for all $\theta \in [-\tau_A(0), 0]$. For any $\psi \in \mathcal{Z}^+$, we have $0 \leq u(t,\psi) \leq \bar{u}(t,\psi)$, $\forall t \geq 0$. Then $0 \leq u_t(\psi) \leq \bar{u}_t(\psi)$, $\forall t \geq 0$. Letting $t = n\omega$, we have

$$0 \leq u_{n\omega}(\psi) \leq \bar{u}_{n\omega}(\psi), \forall n \geq 0,$$

that is,

$$0 \leq S_1^n(\psi) \leq \bar{S}_1^n(\psi), \forall n \geq 0, \tag{3.28}$$

where $\bar{S}_1$ is the Poincaré map associated with linear system (3.26) on $\mathcal{Z}^+$.

Since $\lim_{t\to\infty}(\bar{u}(t) - \bar{u}^*(t)) = 0$, $\lim_{t\to\infty} \|\bar{u}_t(\psi) - \bar{u}_t^*\| = 0$. Letting $t = n\omega$, we have $\bar{u}_{n\omega}^* = \bar{u}_0^*$, and hence,

$$\lim_{n\to\infty} \|\bar{u}_{n\omega}(\psi) - \bar{u}_{n\omega}^*\| = \lim_{n\to\infty} \|\bar{S}_1^n(\psi) - \bar{u}_0^*\| = 0.$$

Combining with (3.28), it follows that the omega limit set $\omega(\psi)$ of $\psi$ for $S_1$ satisfies $\omega(\psi) \subseteq W$ for all $\psi \in \mathcal{Z}^+$.

Let $\tilde{S}_\epsilon(t)$ be the solution maps of the following perturbed linear periodic system on $\mathcal{Z}$:

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = a(t)(1-\epsilon)u(t-\tau_A(t)) - d(t)u(t), \tag{3.29}$$

and $\tilde{S}_\epsilon := \tilde{S}_\epsilon(\omega)$. Since $\lim_{\epsilon\to 0^+} r(\tilde{S}_\epsilon) = r(\tilde{S}) > 1$, we can fix a sufficiently small number $\epsilon_0 > 0$ such that $r(\tilde{S}_{\epsilon_0}) > 1$. It follows from [50, Theorem 3.6.1] and Remark A.2 that the linear operator $\tilde{S}_{\epsilon_0}(t)$ is compact on $\mathcal{Z}$ for all $t > \hat{\tau}_A$. By the same arguments as in [72, Lemma 6], it follows that $\tilde{S}_{\epsilon_0}(t)$ is also strongly monotone on $\mathcal{Z}$ for each $t \geq 2\hat{\tau}_A$. Choose an integer $n_0 > 0$ such that $n_0\omega \geq 2\hat{\tau}_A$. Since $\tilde{S}_{\epsilon_0}^{n_0} = \tilde{S}_{\epsilon_0}(n_0\omega)$, [74, Lemma 3.1] implies that $r(\tilde{S}_{\epsilon_0})$ is a simple eigenvalue of $\tilde{S}_{\epsilon_0}$ having a strongly positive eigenvector. By [135, Lemma 1], there is a positive $\omega$-periodic function $v^*(t)$ such that $w^*_{\epsilon_0}(t) = e^{\frac{\ln r(\tilde{S}_{\epsilon_0})}{\omega}t}v^*(t)$ is a positive solution of system (3.29).

For the above fixed $\epsilon_0 > 0$, there exists a sufficiently small positive number $\delta_0 = \delta_0(\epsilon_0) < \epsilon_0$ such that $e^{-\alpha(t)x} \geq 1-\epsilon_0, \forall t \geq 0, 0 \leq x \leq \delta_0$. Since $\lim_{\phi\to 0} S_{1t}(\phi) = 0$ uniformly for $t \in [0,\omega]$, there exists $\delta_1 > 0$ such that $\|S_{1t}(\phi)\| \leq \delta_0, \forall t \in [0,\omega], \|\phi\| \leq \delta_1$. We further have the following observation.

**Claim 1.** $\limsup_{n\to\infty} \|S_1^n(\psi)\| \geq \delta_1$ for all $\psi \in \mathcal{Z}^+ \setminus \{0\}$.

Suppose, by contradiction, that $\limsup_{n\to\infty} \|S_1^n(\phi)\| < \delta_1$ for some $\phi \in \mathcal{Z}^+ \setminus \{0\}$. Then there exists an integer $N_0 \geq 1$ such that $\|S_1^n(\phi)\| < \delta_1$ for all $n \geq N_0$. For any $t \geq N_0\omega$, we have $t = n\omega + t'$ with $n \geq N_0$, $t' \in [0,\omega]$, and $\|S_{1t}(\phi)\| = \|S_1(t')S_1(n\omega)\phi\| \leq \delta_0$. Then for all $t \geq N_0\omega + \hat{\tau}_A$, we have $\|u(t-\tau_A(t),\phi)\| \leq \delta_0$. Then

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} \geq a(t)(1-\epsilon_0)u(t-\tau_A(t)) - d(t)u(t),$$

for all $t \geq N_0\omega + \hat{\tau}_A$. Since $\phi \in \mathcal{Z}^+ \setminus \{0\}$, there exists $t_0 \in [0, \tau_A(0)]$ such that $u(t_0,\phi) > 0$. It then follows that $u(t,\phi) > 0$ for all $t \geq t_0$, and hence, $u(t,\phi) > 0$ for all $t \geq \tau_A(0)$. We can choose a sufficiently small number $k > 0$ such that $u(t,\phi) \geq kw^*_{\epsilon_0}(t)$, $\forall t \in [N_0\omega + \hat{\tau}_A, N_0\omega + 2\hat{\tau}_A]$. By Theorem 1.3.2, we have $u(t,\phi) \geq kw^*_{\epsilon_0}(t)$, $\forall t \geq N_0\omega + 2\hat{\tau}_A$. Thus, $\lim_{t\to 0} u(t,\phi) = \infty$, which is a contradiction.

For any $\phi \in W$, we have $\phi \leq \bar{u}^*_0$. Since system (3.25) is dominated by system (3.26), it follows that

$$u(t,\phi) \leq \bar{u}^*(t), \forall t \geq 0, \phi \in W.$$

For any given $\varphi, \psi \in W$ with $\varphi \geq \psi$, let $v(t,\varphi)$ and $v(t,\psi)$ be the unique solutions of system (3.25) with $v_0 = \varphi$ and $v_0 = \psi$, respectively. Define $B(t,x) := a(t)e^{-\alpha(t)x}x$.

In view of (A2), we see that for any $\phi \in W$,

$$\begin{aligned}\frac{\partial B}{\partial x}(t, u(t-\tau_A(t), \phi)) =&a(t)e^{-\alpha(t)u(t-\tau_A(t),\phi)}[1-\alpha(t)u(t-\tau_A(t),\phi)]\\ \geq&a(t)e^{-\alpha(t)u(t-\tau_A(t),\phi)}[1-\alpha(t)\bar{u}^*(t-\tau_A(t))] > 0.\end{aligned}$$

By arguments similar to those in [72], it is easy to show that we have $S_1(t): W \to W$ is monotone, that is, $v(t,\varphi) \geq v(t,\psi)$ for all $t \geq 0$. Next we prove that $S_1(t): W \to W$ is eventually strongly monotone. Let $\varphi, \psi \in W$ satisfy $\varphi > \psi$. Define $\bar{v}(t) = v(t,\varphi)$ and $v(t) = v(t,\psi)$. By the same arguments as in [72, Lemma 6], we have the following observation.

**Claim 2.** There exists $t_0 \in [0, \hat{\tau}_A]$ such that $\bar{v}(t) > v(t)$ for all $t \geq t_0$.

Letting $g(t,y) = B(t, v(t-\tau_A(t))) - d(t)y$. Since $\frac{\partial B}{\partial x}(t, u(t-\tau_A(t),\phi)) > 0$, we then have

$$\begin{aligned}\frac{\mathrm{d}\bar{v}(t)}{\mathrm{d}t} =&B(t, \bar{v}(t-\tau_A(t))) - d(t)\bar{v}(t)\\ >&B(t, v(t-\tau_A(t))) - d(t)\bar{v}(t) = g(t, \bar{v}(t)), \forall t > t_0 + \hat{\tau}_A,\end{aligned}$$

and hence,

$$\frac{\mathrm{d}\bar{v}(t)}{\mathrm{d}t} - g(t, \bar{v}(t)) > 0 = \frac{\mathrm{d}v(t)}{\mathrm{d}t} - g(t, v(t)), \forall t > t_0 + \hat{\tau}_A.$$

Since $\bar{v}(t_0 + \hat{\tau}_A) > v(t_0 + \hat{\tau}_A)$, it follows from Theorem 1.3.1 that $\bar{v}(t) > v(t)$ for all $t > t_0 + \hat{\tau}_A$. Since $t_0 \in [0, \hat{\tau}_A]$, it follows that $S_1^n(t): W \to W$ is strongly monotone for any $n\omega > 3\hat{\tau}_A$.

For any given $\phi \gg 0$ in $W$ and $\lambda \in (0,1)$, let $z(t,\phi)$ and $z(t,\lambda\phi)$ be the solutions of system (3.25) satisfying $z_0 = \phi$ and $z_0 = \lambda\phi$, respectively. Denote $w(t) = \lambda z(t,\phi)$ and $v(t) = z(t,\lambda\phi)$. By the method of steps, $w(t) > 0$ and $v(t) > 0$ for all $t \geq 0$. For all $\theta \in [-\tau_A(0), 0]$, we have $w(\theta) = \lambda\phi(\theta) = v(\theta)$. For any $t \in [0, \bar{\tau}_A]$, we have $-\tau_A(0) = 0 - \tau_A(0) \leq t - \tau_A(t) \leq \bar{\tau}_A - \tau_A(\bar{\tau}_A) \leq \bar{\tau}_A - \bar{\tau}_A = 0$, and hence, $w(t-\tau_A(t)) = \lambda\phi(t-\tau_A(t)) = v(t-\tau_A(t))$. Thus,

$$\begin{aligned}\frac{\mathrm{d}w(t)}{\mathrm{d}t}\,|_{t=0} &= a(0)e^{-\alpha(0)z(-\tau_A(0))}w(-\tau_A(0)) - d(0)w(0)\\ &< a(0)e^{-\alpha(0)w(-\tau_A(0))}w(-\tau_A(0)) - d(0)w(0)\\ &= a(0)e^{-\alpha(0)v(-\tau_A(0))}v(-\tau_A(0)) - d(0)v(0)\\ &= \frac{\mathrm{d}v(t)}{\mathrm{d}t}\,|_{t=0}\,.\end{aligned}$$

Since $w(0) = v(0) > 0$, there must be an $\xi \in (0, \bar{\tau}_A)$ such that $0 < w(t) < v(t)$ holds for all $t \in (0, \xi)$. We further claim that $w(t) < v(t)$ for all $0 < t \leq \bar{\tau}_A$. Assume not, then there exists $\bar{t} \in (0, \bar{\tau}_A]$ such that $w(t) < v(t)$ for all $t \in (0, \bar{t})$ and $w(\bar{t}) = v(\bar{t})$, which implies that $\frac{\mathrm{d}w(t)}{\mathrm{d}t} \mid_{t=\bar{t}} \geq \frac{\mathrm{d}v(t)}{\mathrm{d}t} \mid_{t=\bar{t}}$. However, we have

$$\begin{aligned}
\frac{\mathrm{d}w(t)}{\mathrm{d}t} \mid_{t=\bar{t}} &= a(\bar{t}) e^{-\alpha(\bar{t}) z(\bar{t} - \tau_A(\bar{t}))} w(\bar{t} - \tau_A(\bar{t})) - d(\bar{t}) w(\bar{t}) \\
&< a(\bar{t}) e^{-\alpha(\bar{t}) w(\bar{t} - \tau_A(\bar{t}))} w(\bar{t} - \tau_A(\bar{t})) - d(\bar{t}) w(\bar{t}) \\
&= a(\bar{t}) e^{-\alpha(\bar{t}) v(\bar{t} - \tau_A(\bar{t}))} v(\bar{t} - \tau_A(\bar{t})) - d(\bar{t}) v(\bar{t}) \\
&= \frac{\mathrm{d}v(t)}{\mathrm{d}t} \mid_{t=\bar{t}},
\end{aligned}$$

which is a contradiction. This shows that $w(t) < v(t)$ for all $0 < t \leq \bar{\tau}_A$. By the similar arguments for any interval $(n\bar{\tau}_A, (n+1)\bar{\tau}_A]$, $n = 1, 2, 3, \cdots$, we can get $w(t) < v(t)$ for all $t > 0$, that is, $u_t(\lambda\phi) \gg \lambda u_t(\phi)$ for all $t > \tau_A(0)$.

Now we fix an integer $n_0$ such that $n_0\omega > 3\hat{\tau}_A$. It then follows that $S_1^{n_0}$ is a strongly monotone and strictly subhomogeneous map on $W$. Note that $DS_1^{n_0}(0) = DS_1(n_0\omega)(0) = \tilde{S}(n_0\omega) = (\tilde{S}(\omega))^{n_0} = \tilde{S}^{n_0}$ and $r(\tilde{S}^{n_0}) = (r(\tilde{S}))^{n_0}$. Since (A1) holds, it follows from Theorem 1.3.6 that there exists a unique positive $n_0\omega$-periodic solution $\bar{w}(t) = u^*(t)$ which is globally attractive for system (3.25) in $W \setminus \{0\}$.

Next we show that $\bar{w}(t)$ is also an $\omega$-periodic solution of system (3.25). Let $\bar{w}(t) = w(t, \psi^*)$. By the properties of periodic semiflows, we have $S_1^{n_0}(S_1(\psi^*)) = S_1(S_1^{n_0}(\psi^*)) = S_1(\psi^*)$, which implies that $S_1(\psi^*)$ is also a positive fixed point of $S_1^{n_0}$. By the uniqueness of the positive fixed point of $S_1^{n_0}$, it follows that $S_1(\psi^*) = \psi^*$. Then $\bar{w}(t) = M^*(t)$ is an $\omega$-periodic solution of system (3.25).

For any $\psi \in \mathcal{Z}^+$, it follows from Lemma 1.1.2 that $\omega(\psi)$ is an internally chain transitive set for $S_1 : \mathcal{Z}^+ \to \mathcal{Z}^+$. Since $\omega(\psi) \subseteq W$, by Theorem 1.1.2, either $\omega(\psi) = 0$ or $\omega(\psi) = \psi^*$ for all $\psi \in \mathcal{Z}^+$. Claim 1 implies that $\omega(\psi) \neq 0$ for all $\psi \in \mathcal{Z}^+ \setminus \{0\}$. Thus, $\omega(\psi) = \psi^*$ for all $\psi \in \mathcal{Z}^+ \setminus \{0\}$. Therefore, system (3.25) admits a unique positive $\omega$-periodic solution $w(t, \psi^*) = u^*(t)$ which is globally attractive in $\mathcal{Z}^+ \setminus \{0\}$. $\square$

# Chapter 4

# A periodic Bluetongue model with a temperature-dependent incubation period

## 4.1 Introduction

Bluetongue virus (BTV) is the cause of bluetongue, an economically important, reemerging vector-borne disease of ruminants transmitted to and from the affected hosts by the biting female midges of the *Culicoides* genus [21, 89] and it is not transmitted by direct contact between animals in the absence of midges. BTV is known to have infected several ruminants, and cattle and sheep are identified as primary reservoirs in several endemic areas worldwide [101]. The World Organization for Animal Health (OIE) lists bluetongue as a notifiable disease.

Spreull [118] first reported the comprehensive clinical profile of the disease in 1905. Since its arrival in Europe in 1998, there has been a dramatic northward extension of the virus in Europe. In August 2006, the first outbreaks of bluetongue were reported in northern Europe in Belgium, France, Germany, and The Netherlands [49]. More recently, following initial elimination, BTV reemerged in France in 2015. There are many different serotypes of BTV (currently up to 27) [113]. Once infected, animals have high fever, swelling of the face and tongue, and cyanosis of the tongue.

Since 2008, numerous mathematical models for the time evolution of bluetongue disease have been developed (see, e.g., [21,49,89,122]). Gourley, Thieme, and van den Driessche [45] studied an autonomous system with a distributed delay and obtained necessary and sufficient conditions for local stability of the disease-free equilibrium and for disease uniform weak persistence in midges. Gourley, Röst, and Thieme [99] further improved the results in [45] and proved uniform persistence of the disease. Later, since the outbreaks in Europe were seasonal due to the seasonal activity of midges as their life cycle is temperature dependent [21,101,137], O'Farrell and Gourley [99] proposed a periodic system with constant delays but only obtained the linear stablility of the disease-free periodic solutions. However, few theoretical results are related to the global dynamics, including the extinction, persistence, and the global stability of the model system in terms of the basic reproduction ratio.

The life cycle of the *Culicoides* vector includes egg, larva, pupa, and adult. The first three stages are known as immature stages and the last one is called the mature stage. In general, adult *Culicoides* are short-lived and have an average life expectancy of approximately 20 days, but may survive up to 90 days [90]. For BTV transmission to occur, a midge must take a blood meal from an infected host and must ingest sufficient BTV. In the process, there is an incubation period for the midge to develop the disease and become infectious. More precisely, the time required for the entry of virus into the midgut of the midge, dissemination through the haemocoel, and subsequent infection of the salivary glands is termed the extrinsic incubation period (EIP) of BTV. Many population models with temperature-dependent delays have been developed (see, e.g., [12,72,82,100,136]). Indeed, the EIP of BTV is highly sensitive to temperature [90,101], varying from 26 days at 15°C to 4 days at 30°C [138]. Therefore, we should incorporate the temperature-dependent EIP into the mathematical model in a more realistic way.

In this chapter, we present a model to describe the dynamics of bluetongue transmission, which takes into account the seasonal effects, midges with a temperature-dependent EIP as vectors, and cattle and sheep as hosts, and then give a complete mathematical analysis. To our knowledge, this is the first research to incorporate the temperature-dependent delay in the complex periodic system (two hosts, one vector, and one infectious disease agent), which needs to define a new phase space. In addition, bluetongue affects the life cycles of two host species very differently, which gives rise to new challenges, because cattle may even play the role of a reservoir based on which bluetongue can eradicate the sheep without dying out itself.

The rest of the chapter is organized as follows. In Section 4.2, we present the model and study its well-posedness. In Section 4.3, we derive the basic disease reproduction ratio $R_0$ and the basic disease reproduction ratio in the absence of sheep $\widetilde{R}_0$, and prove the threshold dynamics in terms of these two reproduction ratios. Uniform disease persistence occurs in two different scenarios which are distinguished by $\widetilde{R}_0$ and need different mathematical treatment. In Section 4.4, we give a case study for bluetongue disease transmission in France. A brief discussion completes the chapter.

## 4.2 The model

The purpose of this section is to formulate a mathematical model of bluetongue transmission, and discuss its well-posedness.

### 4.2.1 Model formulation

We refer the readers to [45, 72, 99, 136] for the detailed explanation of the model and the derivation of the model system. Let $S_c(t)$ and $I_c(t)$ be the numbers of susceptible and infectious cattle at time $t$, respectively. Assume that the total number of cattle, $N_c(t) = S_c(t) + I_c(t)$, is described by

$$\frac{\mathrm{d}N_c(t)}{\mathrm{d}t} = b_c(t, N_c) - \mu_c(t)N_c,\ t > 0,$$

where $\mu_c(t)$ is the per capita natural death rate of cattle; $b_c(t, N_c)$ is the birth rate of cattle and is a nonnegative function. Since bluetongue generally does not cause death in cattle, we assume that the total number of cattle stabilizes at a positive periodic function $N_c^*(t)$, that is, $N_c(t) = N_c^*(t)$, $\forall t \geq 0$. Let $S_s(t)$, $I_s(t)$, $S_m(t)$, and $I_m(t)$ be the numbers of susceptible sheep, infectious sheep, susceptible, and infectious adult female midges at time $t$, respectively. We incorporate seasonal factors into the model by assuming all parameters are periodic functions. Let $\mu_l(t)$ be the per capita mortality rate for immature midges at time $t$, and $\tau_l$ be the maturation period. Then $b_m(t-\tau_l, S_m(t-\tau_l))e^{-\int_{t-\tau_l}^{t}\mu_l(s)ds}$ is the maturation rate at time $t$, which is produced by the mature midges at time $t-\tau_l$, and $e^{-\int_{t-\tau_l}^{t}\mu_l(s)ds}$ is the probability of egg-to-adult survival for midges. Here, $b_m(t, S_m)$ is the birth rate function of midges at time $t$, that is, the egg laying rate, assuming that only susceptible midges reproduce and compete for reproductive resources. The transmission coefficient $\beta_{mj}(t)$ ($\beta_{jm}(t)$) is a product of the per capita biting rate $a(t)$ of midges on hosts (i.e., the number of bites per midge per unit time at time $t$) and the transmission probability $\bar{\beta}_{mj}$ ($\bar{\beta}_{jm}$) from infectious vectors to susceptible hosts (from infectious hosts to susceptible vectors) per bite, where $j = c, s$, respectively. Since the temperature $T$ can be assumed to vary as a function of time $t$, we let $\tau_m(t)$ be the length of the EIP. Let $E_m(t)$ be the number of the exposed midges at time $t$ who are infected but not infectious yet. Let $\mu_{em}(t)$ be the per capita mortality rate of exposed adult female midges at time $t$, then the probability that a midge survives the EIP at time $t$ is $e^{-\int_{t-\tau_m(t)}^{t} \mu_{em}(\eta)d\eta}$. Let $\gamma(t)$ be the per capita recovery rate of infectious sheep and $b_s(t, S_s)$ be the birth rate function of sheep. Other assumptions are similar to those in [45, 99], including that sheep can recover from the disease, while midges and cattle do not (although cattle cannot show clinical symptoms, they are the main amplifying hosts and tend to be long term virus reservoirs [54]); only susceptible sheep produce offspring (since BTV tends to cause abortion and congenital anomalies in sheep); only adult female midges can contract the virus (since adult males and midges at immature stages do not take blood); there is no biting bias for midges. Therefore, we can obtain the following system with the temperature-dependent incubation period:

$$
\begin{aligned}
\frac{\mathrm{d}I_c(t)}{\mathrm{d}t} &= \frac{\beta_{mc}(t)(N_c^*(t)-I_c(t))I_m(t)}{I_s(t)+S_s(t)+N_c^*(t)} - \mu_c(t)I_c(t),\\
\frac{\mathrm{d}S_s(t)}{\mathrm{d}t} &= b_s(t, S_s(t)) - \frac{\beta_{ms}(t)S_s(t)I_m(t)}{I_s(t)+S_s(t)+N_c^*(t)} + \gamma(t)I_s(t) - \mu_s(t)S_s(t),\\
\frac{\mathrm{d}I_s(t)}{\mathrm{d}t} &= \frac{\beta_{ms}(t)S_s(t)I_m(t)}{I_s(t)+S_s(t)+N_c^*(t)} - \gamma(t)I_s(t) - \mu_{is}(t)I_s(t),\\
\frac{\mathrm{d}S_m(t)}{\mathrm{d}t} &= b_m(t-\tau_l, S_m(t-\tau_l))e^{-\int_{t-\tau_l}^{t}\mu_l(s)ds} - \frac{\beta_{cm}(t)I_c(t)+\beta_{sm}(t)I_s(t)}{I_s(t)+S_s(t)+N_c^*(t)}S_m(t)\\
&\quad -\mu_m(t)S_m(t),\\
\frac{\mathrm{d}E_m(t)}{\mathrm{d}t} &= \frac{\beta_{cm}(t)I_c(t)+\beta_{sm}(t)I_s(t)}{I_s(t)+S_s(t)+N_c^*(t)}S_m(t) - S_m(t-\tau_m(t))e^{-\int_{t-\tau_m(t)}^{t}\mu_{em}(\eta)d\eta}\\
&\quad \times(1-\tau_m'(t))\frac{\beta_{cm}(t-\tau_m(t))I_c(t-\tau_m(t))+\beta_{sm}(t-\tau_m(t))I_s(t-\tau_m(t))}{I_s(t-\tau_m(t))+S_s(t-\tau_m(t))+N_c^*(t-\tau_m(t))} - \mu_{em}(t)E_m(t),\\
\frac{\mathrm{d}I_m(t)}{\mathrm{d}t} &= (1-\tau_m'(t))\frac{\beta_{cm}(t-\tau_m(t))I_c(t-\tau_m(t))+\beta_{sm}(t-\tau_m(t))I_s(t-\tau_m(t))}{I_s(t-\tau_m(t))+S_s(t-\tau_m(t))+N_c^*(t-\tau_m(t))}\\
&\quad \times S_m(t-\tau_m(t))e^{-\int_{t-\tau_m(t)}^{t}\mu_{em}(\eta)d\eta} - \mu_{im}(t)I_m(t),
\end{aligned}
\tag{4.1}
$$

with $\mu_{em}(t) \geq \mu_m(t)$, $\mu_{ij}(t) = \mu_j(t) + \delta_j(t)$, where $\mu_{ij}(t)$ is the per capita death rate of infectious compartments (i.e., natural death rate $\mu_j(t)$ and disease-induced death rate $\delta_j(t)$) for $j = s, m$. We assume that all parameters are continuous and $\omega$-periodic functions in $t$ for some $\omega > 0$. And we assume that the temperature $T(t)$ is $\omega$-periodic, then $\tau_m(T(t)) = \tau_m(t)$ is $\omega$-periodic and is continuously differentiable in $[0, \infty)$. Thus, system (4.1) is an $\omega$-periodic functional differential system. Here note that the term

$1-\tau_m'(t)$ is involved the development rate from the $E_m$ state to the $I_m$ state, and $1-\tau_m'(t)>0$ [72,136]. In view of biological meaning, we should impose the following compatibility condition:

$$E_m(0)=\int_{-\tau_m(0)}^{0}\frac{\beta_{cm}(\eta)I_c(\eta)+\beta_{sm}(\eta)I_s(\eta)}{I_s(\eta)+S_s(\eta)+N_c^*(\eta)}S_m(\eta)e^{-\int_\eta^0\mu_{em}(s)ds}d\eta. \tag{4.2}$$

By the uniqueness of solutions, and systems (4.1) and (4.2), we have

$$E_m(t)=\int_{t-\tau_m(t)}^{t}\frac{\beta_{cm}(\eta)I_c(\eta)+\beta_{sm}(\eta)I_s(\eta)}{I_s(\eta)+S_s(\eta)+N_c^*(\eta)}S_m(\eta)e^{-\int_\eta^t\mu_{em}(s)ds}d\eta. \tag{4.3}$$

In the biological literature, there are three types of time periodic birth rate functions (see [25,84]): (C1) $b(t,x)=l(t)e^{-m(t)x}x$ with $l(t)>0$, $m(t)>0$; (C2) $b(t,x)=\frac{p(t)x}{q(t)+x^n}$ with $p(t)>0$, $q(t)>0$, $n>0$; (C3) $b(t,x)=A(t)+C(t)x$ with $A(t)>0$, $C(t)\geq 0$. To study the dynamics of system (4.1), we make the following assumptions:

(A1) $\beta_{mc}(t)$, $\beta_{ms}(t)$, $\beta_{cm}(t)$, $\beta_{sm}(t)$, $\mu_c(t)$, $\mu_s(t)$, $\mu_{is}(t)$, $\mu_m(t)$, $\mu_{em}(t)$, $\mu_{im}(t)$, and $\gamma(t)$ are all nonnegative and continuous functions with $\int_0^\omega\gamma(t)dt>0$, $\int_0^\omega\mu_a(t)dt>0$, $a=\{c,s,is,m,em,im\}$.

(A2) $b_s(\cdot,\cdot)\in C^1(\mathbb{R}\times\mathbb{R}_+,\mathbb{R}_+)$ is $\omega$-periodic in $t$ and has the following properties:

(i) $b_s(t,0)=0$ for all $t\in\mathbb{R}$; $\sup_{x\geq 0,t\in[0,\omega]}b_s(t,x)=\hat{b}_s<\infty$;

(ii) for each $t\geq 0$, $b_s(t,\cdot)$ is strictly subhomogeneous on $\mathbb{R}_+$ in the sense that $b_s(t,\alpha x)>\alpha b_s(t,x)$, $\forall x>0$, $\alpha\in(0,1)$.

(A3) $b_m(\cdot,\cdot)\in C^1(\mathbb{R}\times\mathbb{R}_+,\mathbb{R}_+)$ is $\omega$-periodic in $t$ and has the following properties:

(i) $b_m(t,0)=0$, $\frac{\partial b_m}{\partial x}>0$ for all $t\in\mathbb{R}$; $\sup_{x\geq 0,t\in[0,\omega]}b_m(t,x)=\hat{b}_m<\infty$;

(ii) for each $t\geq 0$, $b_m(t,\cdot)$ is strictly subhomogeneous on $\mathbb{R}_+$;

(iii) there exists a positive number $h_0$ such that $b_m(t-\tau_l,L)e^{-\int_{t-\tau_l}^t\mu_l(s)ds}-\mu_m(t)L\leq 0$ for all $L\geq h_0$.

Clearly, the birth rate functions in (C1), (C2) and (C3) are strictly subhomogeneous in $x\in\mathbb{R}_+$. Let

$$c(t):=e^{-\int_{t-\tau_l}^t\mu_l(s)ds}. \tag{4.4}$$

Since the fifth equation of system (4.1) is decoupled from the other equations, it suffices to study the decoupled system:

$$\begin{array}{l}
\frac{\mathrm{d}I_c(t)}{\mathrm{d}t} = \frac{\beta_{mc}(t)(N_c^*(t)-I_c(t))I_m(t)}{I_s(t)+S_s(t)+N_c^*(t)} - \mu_c(t)I_c(t), \\
\frac{\mathrm{d}S_s(t)}{\mathrm{d}t} = b_s(t, S_s(t)) - \frac{\beta_{ms}(t)S_s(t)I_m(t)}{I_s(t)+S_s(t)+N_c^*(t)} + \gamma(t)I_s(t) - \mu_s(t)S_s(t), \\
\frac{\mathrm{d}I_s(t)}{\mathrm{d}t} = \frac{\beta_{ms}(t)S_s(t)I_m(t)}{I_s(t)+S_s(t)+N_c^*(t)} - \gamma(t)I_s(t) - \mu_{is}(t)I_s(t), \\
\frac{\mathrm{d}S_m(t)}{\mathrm{d}t} = b_m(t-\tau_l, S_m(t-\tau_l))c(t) - \frac{\beta_{cm}(t)I_c(t)+\beta_{sm}(t)I_s(t)}{I_s(t)+S_s(t)+N_c^*(t)}S_m(t) - \mu_m(t)S_m(t), \\
\frac{\mathrm{d}I_m(t)}{\mathrm{d}t} = (1-\tau_m'(t))\frac{\beta_{cm}(t-\tau_m(t))I_c(t-\tau_m(t))+\beta_{sm}(t-\tau_m(t))I_s(t-\tau_m(t))}{I_s(t-\tau_m(t))+S_s(t-\tau_m(t))+N_c^*(t-\tau_m(t))} \\
\qquad\qquad \times S_m(t-\tau_m(t))e^{-\int_{t-\tau_m(t)}^{t}\mu_{em}(\eta)d\eta} - \mu_{im}(t)I_m(t).
\end{array} \tag{4.5}$$

## 4.2.2 The well-posedness

Let $\hat{\tau} = \max\{\tau_l, \max_{t\in[0,\omega]}\{\tau_m(t)\}\}$, $C := C([-\hat{\tau}, 0], \mathbb{R}^5)$, and $C^+ := C([-\hat{\tau}, 0], \mathbb{R}^5_+)$. Then $(C, C^+)$ is an ordered Banach space equipped with the maximum norm and the positive cone $C^+$. For any given continuous function $u : [-\hat{\tau}, \sigma) \longrightarrow \mathbb{R}^5$ with $\sigma > 0$, we define $u_t \in C$ by $u_t(\theta) = u(t+\theta)$, $\forall\theta \in [-\hat{\tau}, 0]$, for any $t \in [0, \sigma)$.

In view of the $E_m$ equation, we choose the initial data in the following set:

$$\begin{aligned}
D := \Bigg\{ & \psi \in C([-\hat{\tau}, 0], \mathbb{R}^6_+) : \\
& \psi_5(0) = \int_{-\tau_m(0)}^{0} \frac{\beta_{cm}(\eta)\psi_1(\eta)+\beta_{sm}(\eta)\psi_3(\eta)}{\psi_2(\eta)+\psi_3(\eta)+N_c^*(\eta)}\psi_4(\eta)e^{-\int_\eta^0 \mu_{em}(s)ds}d\eta \Bigg\}.
\end{aligned}$$

We first verify the global existence, nonnegativity and boundedness of solutions of system (4.5).

**Lemma 4.2.1.** *For any $\phi \in C^+$, system (4.5) has a unique nonnegative solution $u(t, \phi)$ with $u_0 = \phi$ for all $t \in [0, \infty)$, and all solutions are ultimately bounded.*

*Proof.* For any $\phi = (\phi_1, \phi_2, \phi_3, \phi_4, \phi_5) \in C^+$, we define

$$f(t, \phi) = \begin{pmatrix}
\frac{\beta_{mc}(t)(N_c^*(t)-\phi_1(0))\phi_5(0)}{\phi_2(0)+\phi_3(0)+N_c^*(t)} - \mu_c(t)\phi_1(0) \\
b_s(t, \phi_2(0)) - \frac{\beta_{ms}(t)\phi_2(0)\phi_5(0)}{\phi_2(0)+\phi_3(0)+N_c^*(t)} + \gamma(t)\phi_3(0) - \mu_s(t)\phi_2(0) \\
\frac{\beta_{ms}(t)\phi_2(0)\phi_5(0)}{\phi_2(0)+\phi_3(0)+N_c^*(t)} - \gamma(t)\phi_3(0) - \mu_{is}(t)\phi_3(0) \\
b_m(t-\tau_l, \phi_4(-\tau_l))c(t) - \frac{\beta_{cm}(t)\phi_1(0)+\beta_{sm}(t)\phi_3(0)}{\phi_2(0)+\phi_3(0)+N_c^*(t)}\phi_4(0) - \mu_m(t)\phi_4(0) \\
(1-\tau_m'(t))\frac{\beta_{cm}(t-\tau_m(t))\phi_1(-\tau_m(t))+\beta_{sm}(t-\tau_m(t))\phi_3(-\tau_m(t))}{\phi_2(-\tau_m(t))+\phi_3(-\tau_m(t))+N_c^*(t-\tau_m(t))} \\
\quad \times\phi_4(-\tau_m(t))e^{-\int_{t-\tau_m(t)}^{t}\mu_{em}(\eta)d\eta} - \mu_{im}(t)\phi_5(0)
\end{pmatrix}.$$

Note that $f(t,\phi)$ is continuous in $(t,\phi) \in \mathbb{R}_+ \times C^+$ and that $f(t,\phi)$ is Lipschitz in $\phi$ on each compact subset of $C^+$. By [50, Theorems 2.2.1 and 2.2.3] and [116, Theorem 5.2.1], it then follows that system (4.5) has a unique nonnegative solution $u(t,\phi)$ on its maximal interval $[0,\sigma_\phi)$ of existence with $u_0 = \phi$.

For any $\psi \in D$, let $v(t,\psi) = (I_c(t), S_s(t), I_s(t), S_m(t), E_m(t), I_m(t))$ be the unique solution of system (4.1) satisfying $v_0 = \psi$. In view of system (4.3), it follows that $v(t,\psi)$ are nonnegative on $[0,\sigma_\phi)$.

Since $\frac{\mathrm{d}I_c(t)}{\mathrm{d}t} \leq \beta_{mc}(t)I_m(t) - \mu_c(t)I_c(t)$, it follows that $I_c(t)$ is bounded whenever $I_m(t)$ is bounded on $[0,\sigma_\phi)$. For the total sheep population $N_s(t) = S_s(t) + I_s(t)$, we have

$$\begin{aligned}\frac{\mathrm{d}N_s(t)}{\mathrm{d}t} =& b_s(t,S_s(t)) - \mu_s(t)S_s(t) - \mu_{is}(t)I_s(t)\\ \leq& b_s(t,S_s(t)) - \mu_s(t)N_s(t) \leq \hat{b}_s - \bar{\mu}_s N_s(t),\end{aligned}$$

for all $t \in [0,\sigma_\phi)$, where $\bar{\mu}_s = \min_{t\in[0,\omega]} \mu_s(t)$. For the total midge population $N_m(t) = S_m(t) + E_m(t) + I_m(t)$, we have

$$\begin{aligned}\frac{\mathrm{d}N_m(t)}{\mathrm{d}t} =& b_m(t-\tau_l, S_m(t-\tau_l))c(t) - \mu_m(t)S_m(t) - \mu_{im}(t)I_m(t) - \mu_{em}(t)E_m(t)\\ \leq& b_m(t-\tau_l, S_m(t-\tau_l))c(t) - \mu_m(t)N_m(t) \leq M_m c(t) - \bar{\mu}_m N_m(t),\end{aligned}$$

for all $t \in [0,\sigma_\phi)$, where $\bar{\mu}_m = \min_{t\in[0,\omega]} \mu_m(t)$ and $M_m = \max\{\hat{b}_m, \sup_{\theta\in[-\tau_l,0]} N_m(\theta)\}$. Thus, the comparison argument implies that solutions of system (4.1) with initial data in $D$, and hence system (4.5) in $C^+$, exist globally on $[0,\infty)$ and also are ultimately bounded. □

## 4.3 Threshold dynamics

In this section, we first introduce the basic reproduction ratios and then study the global dynamics of system (4.5). Let $\hat{\tau}_m = \max_{t\in[0,\omega]} \tau_m(t)$ and $\bar{\tau}_m = \min_{t\in[0,\omega]} \tau_m(t)$. For each $t \geq 0$, we define

$$X(t) := [0, N_{ct}^*]_{C([-\hat{\tau}_m,0],\mathbb{R})} \times C([-\hat{\tau}_m,0],\mathbb{R}_+^2) \times C([-\hat{\tau},0],\mathbb{R}_+) \times \mathbb{R}_+,$$

where $[0,N_{ct}^*]_{C([-\hat{\tau}_m,0],\mathbb{R})} = \{\phi \in C([-\hat{\tau}_m,0],\mathbb{R}) : 0 \leq \phi \leq N_{ct}^*\}$ and $N_{ct}^*(\theta) = N_c^*(t+\theta)$, $-\hat{\tau}_m \leq \theta \leq 0$.

**Lemma 4.3.1.** *For any $\phi \in X(0)$, system (4.5) has a unique nonnegative solution $u(t,\phi)$ with $u_0 = \phi$ for all $t \in [0,\infty)$, and all solutions $u_t(\phi) = (u_{1t}(\phi), u_{2t}(\phi), u_{3t}(\phi), u_{4t}(\phi), u_5(t,\phi)) \in X(t)$ are ultimately bounded.*

*Proof.* Note that $f(t,\phi)$ is continuous in $(t,\phi) \in \mathbb{R}_+ \times X(0)$ and $f(t,\phi)$ is Lipschitz in $\phi$ on each compact subset of $X(0)$. By [50, Theorems 2.2.1 and 2.2.3] and [116, Theorem 5.2.1], it then follows that system (4.5) has a unique solution $u(t,\phi)$ on its maximal interval $[0,\sigma_\phi)$ of existence satisfying $u_t(\phi) \in C([-\hat{\tau}_m,0],\mathbb{R}^3_+) \times C([-\hat{\tau},0],\mathbb{R}_+) \times \mathbb{R}_+$ with $u_0 = \phi$.

It remains to prove that $u_1(t) \le N^*_c(t)$ for all $t \in [0,\sigma_\phi)$. Suppose this does not hold. Then there exists $t_0 \in [0,\sigma_\phi)$ and $\epsilon_0 > 0$ such that $u_1(t_0) = N^*_c(t_0)$ and $u_1(t) > N^*_c(t)$, $\forall t \in (t_0, t_0+\epsilon_0)$. Since

$$\frac{\mathrm{d}u_1(t_0)}{\mathrm{d}t} = -\mu_c(t_0)u_1(t_0) = -\mu_c(t_0)N^*_c(t_0) \le \frac{\mathrm{d}N^*_c(t_0)}{\mathrm{d}t},$$

there exists $\epsilon_1 \in (0,\epsilon_0)$ such that $u_1(t) \le N^*_c(t)$ for all $t \in (t_0, t_0+\epsilon_1)$, which is a contradiction. This proves that $u_t(\phi) \in X(t)$ for all $t \in [0,\sigma_\phi)$.

From the proof of Lemma 4.2.1, the solution of system (4.5) is bounded on $[0,\sigma_\phi)$, and hence, [50, Theorem 2.3.1] implies that $\sigma_\phi = \infty$. Thus, solutions of system (4.5) with initial data in $X(0)$ exist globally on $[0,\infty)$ and are ultimately bounded. □

### 4.3.1 The basic reproduction ratios

To find the disease-free state, letting $I_c = I_s = I_m = 0$, we then get

$$\frac{\mathrm{d}S_s(t)}{\mathrm{d}t} = b_s(t, S_s(t)) - \mu_s(t)S_s(t), \tag{4.6}$$

$$\frac{\mathrm{d}S_m(t)}{\mathrm{d}t} = b_m(t-\tau_l, S_m(t-\tau_l))c(t) - \mu_m(t)S_m(t). \tag{4.7}$$

We now introduce the basic reproduction radios $R^s_0$ for sheep and $R^m_0$ for midges. Linearizing system (4.6) at 0, we obtain the following system:

$$\frac{\mathrm{d}S_s(t)}{\mathrm{d}t} = \frac{\partial b_s(t,0)}{\partial S_s}S_s(t) - \mu_s(t)S_s(t).$$

From Lemma 1.4.1, we have $R^s_0 = \frac{\int_0^\omega \frac{\partial b_s(t,0)}{\partial S_s}dt}{\int_0^\omega \mu_s(t)dt}$. As a straightforward consequence of [151, Theorem 3.1.2], we have the following result.

**Lemma 4.3.2.** *Let (A1) and (A2) hold. The following statements are valid:*

*(i) If $R_0^s \leq 1$, then $0$ is a globally asymptotically stable periodic solution of system (4.6) in $\mathbb{R}_+$.*

*(ii) If $R_0^s > 1$, then system (4.6) has a unique positive $\omega$-periodic solution $S_s^*(t)$, which is globally asymptotically stable in $\mathbb{R}_+ \setminus \{0\}$.*

Similarly, linearizing system (4.7) at 0, we then obtain the following system:

$$\frac{\mathrm{d}S_m(t)}{\mathrm{d}t} = \frac{\partial b_m(t-\tau_l,0)}{\partial S_m} S_m(t-\tau_l)c(t) - \mu_m(t)S_m(t). \tag{4.8}$$

Let $\bar{C}_\omega$ be the ordered Banach space of all $\omega$-periodic functions from $\mathbb{R}$ to $\mathbb{R}$, which is equipped with the maximum norm and the positive cone $\bar{C}_\omega^+ = \{v \in \bar{C}_\omega : v(t) \geq 0, \forall t \in \mathbb{R}\}$. Let $\bar{F}(t)\phi = \frac{\partial b_m(t-\tau_l,0)}{\partial S_m}\phi(-\tau_l)c(t)$ and $\bar{V}(t) = \mu_m(t)$. According to [150], the next generation operator $\mathcal{L}_m : \bar{C}_\omega \to \bar{C}_\omega$ is given by

$$[\mathcal{L}_m v](t) = \int_0^\infty e^{-\int_{t-s}^t \mu_m(r)dr} \bar{F}(t-s)v(t-s+\cdot)ds, \forall t \in \mathbb{R}, v \in \bar{C}_\omega,$$

and hence, $R_0^m = r(\mathcal{L}_m)$, the spectral radius of $\mathcal{L}_m$. Let $P_m$ be the Poincaré map associated with system (4.8) on $C([-\tau_l, 0], \mathbb{R})$ and $r(P_m)$ be the spectral radius of $P_m$. By Theorem 1.4.1, $R_0^m - 1$ has the same sign as $r(P_m) - 1$. Then the following result is a straightforward consequence of [145, Theorem 2.1].

**Lemma 4.3.3.** *Let (A1) and (A3) hold. The following statements are valid:*

*(i) If $R_0^m \leq 1$, then $0$ is a globally asymptotically stable periodic solution of system (4.7) in $C([-\tau_l, 0], \mathbb{R}_+)$.*

*(ii) If $R_0^m > 1$, then system (4.7) has a unique positive $\omega$-periodic solution $S_m^*(t)$, which is globally asymptotically stable for any $\phi \in C([-\tau_l, 0], \mathbb{R}_+) \setminus \{0\}$.*

It then follows that there are four disease-free periodic solutions, $(0,0,0,0,0)$, $(0, S_s^*(t), 0,0,0)$, $(0,0,0,S_m^*(t),0)$, and $(0,S_s^*(t),0,S_m^*(t),0)$, where $S_s^*(t)$ and $S_m^*(t)$ are the positive $\omega$-periodic solutions of systems (4.6) and (4.7), respectively. Linearizing system (4.5) at the disease-free periodic solution $(0,S_s^*(t),0,S_m^*(t),0)$, we obtain the following periodic linear system for the infective variables $I_c$, $I_s$, and $I_m$:

$$\begin{array}{l}
\frac{\mathrm{d}I_c(t)}{\mathrm{d}t} = \frac{\beta_{mc}(t)N_c^*(t)I_m(t)}{S_s^*(t)+N_c^*(t)} - \mu_c(t)I_c(t), \\
\frac{\mathrm{d}I_s(t)}{\mathrm{d}t} = \frac{\beta_{ms}(t)S_s^*(t)I_m(t)}{S_s^*(t)+N_c^*(t)} - \gamma(t)I_s(t) - \mu_{is}(t)I_s(t), \\
\frac{\mathrm{d}I_m(t)}{\mathrm{d}t} = (1-\tau_m'(t))\frac{\beta_{cm}(t-\tau_m(t))I_c(t-\tau_m(t))+\beta_{sm}(t-\tau_m(t))I_s(t-\tau_m(t))}{S_s^*(t-\tau_m(t))+N_c^*(t-\tau_m(t))}S_m^*(t-\tau_m(t))d(t) \\
\qquad -\mu_{im}(t)I_m(t),
\end{array} \tag{4.9}$$

where $d(t) = e^{-\int_{t-\tau_m(t)}^{t}\mu_{em}(\eta)d\eta}$.

Let $E := C([-\hat{\tau}_m, 0], \mathbb{R}^3)$ and $E^+ := C([-\hat{\tau}_m, 0], \mathbb{R}^3_+)$. Then $(E, E^+)$ is an ordered Banach space equipped with the maximum norm and the positive cone $E^+$. For any given continuous function $v : [-\hat{\tau}_m, \sigma) \to \mathbb{R}^3$ with $\sigma > 0$, we define $v_t \in E$ by $v_t(\theta) = v(t+\theta)$, $\forall\theta \in [-\hat{\tau}_m, 0]$, for any $t \in [0, \sigma)$. Let $F : \mathbb{R} \to \mathcal{L}(E, \mathbb{R}^3)$ be a map and $V(t)$ be a continuous $3 \times 3$ matrix function on $\mathbb{R}$ defined as follows:

$$F(t)\phi = \begin{bmatrix} \frac{\beta_{mc}(t)N_c^*(t)\phi_3(0)}{S_s^*(t)+N_c^*(t)} \\ \frac{\beta_{ms}(t)S_s^*(t)\phi_3(0)}{S_s^*(t)+N_c^*(t)} \\ (1-\tau_m'(t))\frac{\beta_{cm}(t-\tau_m(t))\phi_1(-\tau_m(t))+\beta_{sm}(t-\tau_m(t))\phi_2(-\tau_m(t))}{S_s^*(t-\tau_m(t))+N_c^*(t-\tau_m(t))}S_m^*(t-\tau_m(t))d(t) \end{bmatrix},$$

$$V(t) = \begin{bmatrix} \mu_c(t) & 0 & 0 \\ 0 & \gamma(t)+\mu_{is}(t) & 0 \\ 0 & 0 & \mu_{im}(t) \end{bmatrix}.$$

Then the linear system (4.9) can be written as

$$\frac{dv(t)}{dt} = F(t)v_t - V(t)v(t).$$

Let $\Phi(t,s)$, $t \geq s$, be the evolution matrix associated with the following system:

$$\frac{dv(t)}{dt} = -V(t)v(t),$$

that is, $\Phi(t,s)$ satisfies

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

We then have

$$\Phi(t,s) = \begin{bmatrix} e^{-\int_s^t \mu_c(r)dr} & 0 & 0 \\ 0 & e^{-\int_s^t \gamma(r)+\mu_{is}(r)dr} & 0 \\ 0 & 0 & e^{-\int_s^t \mu_{im}(r)dr} \end{bmatrix}.$$

Let $C_\omega$ be the ordered Banach space of all continuous and $\omega$-periodic functions from $\mathbb{R}$ to $\mathbb{R}^3$, equipped with the maximum norm and the positive cone $C_\omega^+ = \{v \in C_\omega : v(t) \geq 0, \forall t \in \mathbb{R}\}$.

Suppose that $v \in C_\omega$ is the initial distribution of infectious cattle, sheep, and midges. Then for any given $s \geq 0$, $F(t-s)v_{t-s}$ is the distribution of newly infectious cattle, sheep and midges, at time $t-s$, which is produced by the infectious cattle, sheep and midges who were introduced over the time interval $[t-s-\hat{\tau}_m, t-s]$. Then $\Phi(t,t-s)F(t-s)v_{t-s}$ is the distribution of those infected cattle, sheep, and midges who were newly infected at time $t-s$ and remain in the infectious 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 new infections at time $t$ produced by all those infectious cattle, sheep, and midges introduced at all previous time to $t$.

We define the next generation operator $\mathcal{L} : C_\omega \longrightarrow C_\omega$ by

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

Following [150], we define the basic disease reproduction ratio for the whole system $R_0 = r(\mathcal{L})$, the spectral radius of $\mathcal{L}$. For any given $t \geq 0$, let $\hat{P}(t)$ be the solution map of system (4.9) on $E$ given by $\hat{P}(t)\psi = u_t(\psi)$, where $u(t,\psi)$ is the unique solution of system (4.9) with $u_0 = \psi \in E$. Then $\hat{P} := \hat{P}(\omega)$ is the Poincaré map associated with linear system (4.9). Let $r(\hat{P})$ be the spectral radius of $\hat{P}$. In view of Theorem 1.4.1, we have the following result.

**Lemma 4.3.4.** *$R_0 - 1$ has the same sign as $r(\hat{P}) - 1$.*

Let $P_\lambda$ be the Poincaré map on $E$ of the following linear periodic system with parameter $\lambda \in (0,\infty)$:

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = \frac{1}{\lambda}F(t)u_t - V(t)u(t), \quad t \geq 0.$$

The following observation comes from Theorem 1.4.3.

**Lemma 4.3.5.** *If $R_0 > 0$, then $\lambda = R_0$ is the unique solution of $r(P_\lambda) = 1$.*

To study the global dynamics of system (4.5), the key idea is to show that system (4.9) generates an eventually strongly monotone periodic semiflow on the following phase space:

$$\mathcal{W} := C([-\tau_m(0), 0], \mathbb{R}^2) \times \mathbb{R}.$$

Let $\tau = \max\{\tau_l, \tau_m(0)\}$ and, for each $t \geq 0$, define

$$\mathcal{X}(t) := [0, N^*_{ct}]_{C([-\tau_m(0),0],\mathbb{R})} \times C([-\tau_m(0), 0], \mathbb{R}^2_+) \times C([-\tau, 0], \mathbb{R}_+) \times \mathbb{R}_+.$$

Then we have the following result.

**Lemma 4.3.6.** *For any $\phi \in \mathcal{X}(0)$, system (4.5) has a unique nonnegative solution $v(t, \phi)$ with $v_0 = \phi$ and all solutions $v_t(\phi) = (v_{1t}(\phi), v_{2t}(\phi), v_{3t}(\phi), v_{4t}(\phi), v_5(t, \phi)) \in \mathcal{X}(t)$ for all $t \in [0, \infty)$.*

*Proof.* For any $t \in [0, \bar{\tau}_m]$, since $t - \tau_m(t)$ is strictly increasing in $t$, we have

$$-\tau \leq -\tau_m(0) = 0 - \tau_m(0) \leq t - \tau_m(t) \leq \bar{\tau}_m - \tau_m(\bar{\tau}_m) \leq \bar{\tau}_m - \bar{\tau}_m = 0,$$

and hence,

$$I_c(t - \tau_m(t)) = \phi_1(t - \tau_m(t)), S_s(t - \tau_m(t)) = \phi_2(t - \tau_m(t)),$$
$$I_s(t - \tau_m(t)) = \phi_3(t - \tau_m(t)), S_m(t - \tau_m(t)) = \phi_4(t - \tau_m(t)).$$

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

$$\begin{aligned}
\tfrac{\mathrm{d}I_c(t)}{\mathrm{d}t} &= \tfrac{\beta_{mc}(t)(N^*_c(t) - I_c(t))I_m(t)}{I_s(t) + S_s(t) + N^*_c(t)} - \mu_c(t)I_c(t),\\
\tfrac{\mathrm{d}S_s(t)}{\mathrm{d}t} &= b_s(t, S_s(t)) - \tfrac{\beta_{ms}(t)S_s(t)I_m(t)}{I_s(t) + S_s(t) + N^*_c(t)} + \gamma(t)I_s(t) - \mu_s(t)S_s(t),\\
\tfrac{\mathrm{d}I_s(t)}{\mathrm{d}t} &= \tfrac{\beta_{ms}(t)S_s(t)I_m(t)}{I_s(t) + S_s(t) + N^*_c(t)} - \gamma(t)I_s(t) - \mu_{is}(t)I_s(t),\\
\tfrac{\mathrm{d}S_m(t)}{\mathrm{d}t} &= b_m(t - \tau_l, \phi_4(t - \tau_l))c(t) - \tfrac{\beta_{cm}(t)I_c(t) + \beta_{sm}(t)I_s(t)}{I_s(t) + S_s(t) + N^*_c(t)} S_m(t) - \mu_m(t)S_m(t),\\
\tfrac{\mathrm{d}I_m(t)}{\mathrm{d}t} &= (1 - \tau'_m(t)) \tfrac{\beta_{cm}(t - \tau_m(t))\phi_1(t - \tau_m(t)) + \beta_{sm}(t - \tau_m(t))\phi_3(t - \tau_m(t))}{\phi_1(t - \tau_m(t)) + \phi_2(t - \tau_m(t)) + N^*_c(t - \tau_m(t))} \phi_4(t - \tau_m(t))d(t)\\
&\quad - \mu_{im}(t)I_m(t).
\end{aligned}$$

Given $\phi \in \mathcal{X}(0)$, the solution $(I_c(t), S_s(t), I_s(t), S_m(t), I_m(t))$ of the above system exists for all $t \in [0, \bar{\tau}_m]$. In other words, we have obtained the values of $\psi_1(\theta) := I_c(\theta)$, $\psi_2(\theta) := S_s(\theta)$, $\psi_3(\theta) := I_s(\theta)$ for all $\theta \in [-\tau_m(0), \bar{\tau}_m]$, $\psi_4(\theta) := S_m(\theta)$ for all $\theta \in [-\tau, \bar{\tau}_m]$ and $\psi_5(\theta) := I_m(\theta)$ for all $\theta \in [0, \bar{\tau}_m]$. By the proof of Lemma 4.3.1, $v_1(t, \phi) \leq N^*_c(t)$ for all $t \in [0, \bar{\tau}_m]$.

Repeating this procedure for $t \in [\bar{\tau}_m, 2\bar{\tau}_m]$, $[2\bar{\tau}_m, 3\bar{\tau}_m]$,$\cdots$, it then follows that for any $\phi \in \mathcal{X}(0)$, the solution $v(t, \phi)$ with $v_0 = \phi$ exists uniquely, and $v_t(\phi) \in \mathcal{X}(t)$ for all $t \geq 0$. ☐

**Remark 4.3.1.** *By the uniqueness of solutions in Lemmas 4.3.1 and 4.3.6, it follows that for any* $\psi \in X(0)$ *and* $\phi \in \mathcal{X}(0)$ *with* $\psi_1(\theta) = \phi_1(\theta)$, $\psi_2(\theta) = \phi_2(\theta)$, $\psi_3(\theta) = \phi_3(\theta)$ *for all* $\theta \in [-\tau_m(0), 0]$, $\psi_4(\theta) = \phi_4(\theta)$ *for all* $\theta \in [-\tau, 0]$, *and* $\psi_5 = \phi_5$, *we have* $w(t, \psi) = \nu(t, \phi)$ *for all* $t \geq 0$, *where* $w(t, \psi)$ *and* $\nu(t, \phi)$ *are solutions of system (4.5) satisfying* $w_0 = \psi$ *and* $\nu_0 = \phi$, *respectively.*

For any given $t \geq 0$, let $P(t)$ be the solution map of linear system (4.9) on $\mathcal{W}$. Then $P := P(\omega)$ is the Poincaré map associated with linear system (4.9). Let $r(P)$ be the spectral radius of $P$. The following lemma shows that the periodic semiflow $P(t)$ is eventually strongly monotone.

**Lemma 4.3.7.** *For any* $\varphi$ *and* $\psi$ *in* $\mathcal{W}$ *with* $\varphi > \psi$ *(that is,* $\varphi \geq \psi$, *but* $\varphi \neq \psi$*), the solutions* $\bar{v}(t)$ *and* $v(t)$ *of system (4.9) with* $\bar{v}_0 = \varphi$ *and* $v_0 = \psi$, *respectively, satisfy* $\bar{v}_i(t) > v_i(t)$, $i = 1, 2, 3$, *for all* $t > 2\hat{\tau}_m$, *and hence,* $P(t)\varphi \gg P(t)\psi$ *in* $\mathcal{W}$ *for all* $t > 3\hat{\tau}_m$.

*Proof.* By the proof of Lemma 4.3.6, it is easy to see that $P(t) : \mathcal{W} \to \mathcal{W}$ is monotone for each $t \geq 0$. Next we prove that the solution map $P(t)$ is eventually strongly monotone. Let $\varphi > \psi$ and denote $\bar{v}(t) = v(t, \varphi) = (\bar{y}_1(t), \bar{y}_2(t), \bar{y}_3(t))$, $v(t) = v(t, \psi) = (y_1(t), y_2(t), y_3(t))$. We assume that $\varphi_1 > \psi_1$. For the case where $\varphi_2 > \psi_2$ or $\varphi_3 > \psi_3$, we can do a similar analysis.

**Claim 1.** There exists $t_0 \in [0, \bar{\tau}_m]$ such that $\bar{y}_2(t) > y_2(t)$ for all $t \geq t_0$.

We first prove that $\bar{y}_2(t_0) > y_2(t_0)$ for some $t_0 \in [0, \bar{\tau}_m]$. Otherwise, we have $\bar{y}_2(t) = y_2(t)$ for all $t \in [0, \bar{\tau}_m]$, and hence, $\frac{\mathrm{d}\bar{y}_2(t)}{\mathrm{d}t} = \frac{\mathrm{d}y_2(t)}{\mathrm{d}t}$ for all $t \in [0, \bar{\tau}_m]$. Thus, we have

$$\frac{\beta_{ms}(t)S_s^*(t)}{S_s^*(t) + N_c^*(t)}[\bar{y}_3(t) - y_3(t)] = 0, \forall t \in [0, \bar{\tau}_m].$$

It follows that $\bar{y}_3(t) = y_3(t)$ for all $t \in [0, \bar{\tau}_m]$. Thus, $\frac{\mathrm{d}\bar{y}_3(t)}{\mathrm{d}t} = \frac{\mathrm{d}y_3(t)}{\mathrm{d}t}$ for all $t \in [0, \hat{\tau}_m]$. Then for any $t \in [0, \bar{\tau}_m]$, we have

$$\begin{aligned}(1 - \tau_m'(t))\frac{S_m^*(t - \tau_m(t))d(t)}{S_s^*(t - \tau_m(t)) + N_c^*(t - \tau_m(t))}&[\beta_{cm}(t - \tau_m(t))(\bar{y}_1(t - \tau_m(t)) \\ - y_1(t - \tau_m(t))) + \beta_{sm}(t - \tau_m(t))&(\bar{y}_2(t - \tau_m(t)) - y_2(t - \tau_m(t)))] = 0.\end{aligned}$$

Since $-\tau_m(0) = 0 - \tau_m(0) \leq t - \tau_m(t) \leq \bar{\tau}_m - \tau_m(\bar{\tau}_m) \leq 0, \forall t \in [0, \bar{\tau}_m]$, we have $\bar{y}_1(t - \tau_m(t)) = \varphi_1(t - \tau_m(t))$, $y_1(t - \tau_m(t)) = \psi_1(t - \tau_m(t))$, $\bar{y}_2(t - \tau_m(t)) = \varphi_2(t - \tau_m(t))$,

$y_2(t-\tau_m(t)) = \psi_2(t-\tau_m(t))$. Since $\varphi_1 > \psi_1$, we have $\varphi_2(t-\tau_m(t)) < \psi_2(t-\tau_m(t))$, which contradicts the fact that $\varphi > \psi$.

Let

$$g_1(t,y) := \frac{\beta_{ms}(t)S_s^*(t)}{S_s^*(t)+N_c^*(t)}y_3(t) - (\gamma(t)+\mu_{is}(t))y.$$

Since

$$\begin{aligned}\frac{\mathrm{d}\bar{y}_2(t)}{\mathrm{d}t} =& \frac{\beta_{ms}(t)S_s^*(t)}{S_s^*(t)+N_c^*(t)}\bar{y}_3(t) - (\gamma(t)+\mu_{is}(t))\bar{y}_2(t)\\ \geq& \frac{\beta_{ms}(t)S_s^*(t)}{S_s^*(t)+N_c^*(t)}y_3(t) - (\gamma(t)+\mu_{is}(t))\bar{y}_2(t)\\ =& g_1(t,\bar{y}_2(t)),\end{aligned}$$

we have

$$\frac{\mathrm{d}\bar{y}_2(t)}{\mathrm{d}t} - g_1(t,\bar{y}_2(t)) \geq 0 = \frac{\mathrm{d}y_2(t)}{\mathrm{d}t} - g_1(t,y_2(t)), \forall t \geq t_0.$$

Since $\bar{y}_2(t_0) > y_2(t_0)$, the comparison theorem for ordinary differential equations in Theorem 1.3.1 implies that $\bar{y}_2(t) > y_2(t)$ for all $t \geq t_0$.

**Claim 2.** $\bar{y}_3(t) > y_3(t)$ for all $t > t_0 + \hat{\tau}_m$.

Let

$$\begin{aligned}g_2(t,y) :=& (1-\tau_m'(t))\frac{\beta_{cm}(t-\tau_m(t))S_m^*(t-\tau_m(t))}{S_s^*(t-\tau_m(t))+N_c^*(t-\tau_m(t))}d(t)y_1(t-\tau_m(t))\\ &+ (1-\tau_m'(t))\frac{\beta_{sm}(t-\tau_m(t))S_m^*(t-\tau_m(t))}{S_s^*(t-\tau_m(t))+N_c^*(t-\tau_m(t))}d(t)y_2(t-\tau_m(t)) - \mu_{im}(t)y.\end{aligned}$$

It then follows that $\frac{\mathrm{d}\bar{y}_3(t)}{\mathrm{d}t} > g_2(t,\bar{y}_3(t)), \forall t \geq t_0 + \hat{\tau}_m$, and hence,

$$\frac{\mathrm{d}\bar{y}_3(t)}{\mathrm{d}t} - g_2(t,\bar{y}_3(t)) > 0 = \frac{\mathrm{d}y_3(t)}{\mathrm{d}t} - g_2(t,y_3(t)), \forall t \geq t_0 + \hat{\tau}_m.$$

Since $\bar{y}_3(t_0+\hat{\tau}_m) \geq y_3(t_0+\hat{\tau}_m)$, it follows from Theorem 1.3.1 that $\bar{y}_3(t) > y_3(t)$ for all $t > t_0 + \hat{\tau}_m$.

**Claim 3.** $\bar{y}_1(t) > y_1(t)$ for all $t > t_0 + \hat{\tau}_m$.

Let

$$g_3(t,y) := \frac{\beta_{mc}(t)N_c^*(t)}{S_s^*(t)+N_c^*(t)}y_3(t) - \mu_c(t)y.$$

Then we have $\frac{\mathrm{d}\bar{y}_1(t)}{\mathrm{d}t} > g_3(t,\bar{y}_1(t)), \forall t > t_0 + \hat{\tau}_m$, and hence,

$$\frac{\mathrm{d}\bar{y}_1(t)}{\mathrm{d}t} - g_3(t,\bar{y}_1(t)) > 0 = \frac{\mathrm{d}y_1(t)}{\mathrm{d}t} - g_3(t,y_1(t)), \forall t > t_0 + \hat{\tau}_m.$$

Since $\bar{y}_1(t_0+\hat{\tau}_m) \geq y_1(t_0+\hat{\tau}_m)$, it follows from Theorem 1.3.1 that $\bar{y}_1(t) > y_1(t)$ for all $t > t_0+\hat{\tau}_m$. In view of the above three claims, we obtain $(\bar{y}_1(t), \bar{y}_2(t), \bar{y}_3(t)) \gg (y_1(t), y_2(t), y_3(t)), \forall t > t_0+\hat{\tau}_m$. Since $t_0 \in [0, \hat{\tau}_m]$, it follows that $(\bar{y}_{1t}, \bar{y}_{2t}, \bar{y}_3(t)) \gg (y_{1t}, y_{2t}, y_3(t)), \forall t > 2\hat{\tau}_m + \tau_m(0)$, that is, $\bar{v}_t(\varphi) \gg v_t(\psi)$ for all $t > 2\hat{\tau}_m + \tau_m(0)$. This shows that the solution map $P(t)$ is strongly monotone for any $t > 3\hat{\tau}_m$. □

By [50, Theorem 3.6.1] and Remark 4.3.1, it follows that for each $t \geq \hat{\tau}_m$, the linear operator $P(t)$ is compact on $\mathcal{W}$. Then $P(t)$ is compact and strongly monotone on $\mathcal{W}$ for $t > 3\hat{\tau}_m$. Choose an integer $n_0 > 0$ such that $n_0\omega > 3\hat{\tau}_m$. Since $P^{n_0} = P(n_0\omega)$, [74, Lemma 3.1] implies that $r(P)$ is a simple eigenvalue of $P$ having a strongly positive eigenvector. By [135, Lemma 1], we have the following observation.

**Lemma 4.3.8.** *Let* $\mu = \frac{\ln r(P)}{\omega}$. *Then there is a positive* $\omega$*-periodic function* $v^*(t)$ *such that* $u^*(t) = e^{\mu t}v^*(t)$ *is a positive solution of linear system (4.9).*

By arguments similar to those in [82, Lemma 3.8], we have $r(P) = r(\hat{P})$. As a consequence of Lemma 4.3.4, we see that $R_0 - 1$ has the same sign as $r(P) - 1$.

### 4.3.2 Uniform persistence of midges

In order to obtain the uniform persistence of the bluetongue disease, we need to establish the uniform persistence of susceptible midges.

For each $t \geq 0$, we define

$$Y(t) := \{\phi \in X(t) : \phi_4(0) > 0\}, \quad \mathcal{Y}(t) := \{\phi \in \mathcal{X}(t) : \phi_4(0) > 0\}.$$

Let $Q(t) : \mathcal{X}(0) \to \mathcal{X}(t)$ be the solution maps of system (4.5). Then $Q := Q(\omega)$ is the Poincaré map associated with system (4.5). By arguments similar to those in [82, Lemma 3.5], we have the following result.

**Lemma 4.3.9.** $Q(t) : \mathcal{X}(0) \to \mathcal{X}(t)$, $\forall t \geq 0$, *is an* $\omega$*-periodic semiflow in the sense that (i)* $Q(0) = I$; *(ii)* $Q(t+\omega) = Q(t) \circ Q(\omega)$ *for all* $t \geq 0$; *and (iii)* $Q(t)\phi$ *is continuous in* $(t, \phi) \in [0, \infty) \times \mathcal{X}(0)$.

From the fourth equation of system (4.5), it is easy to see that $Q(t)\mathcal{Y}(0) \subseteq \mathcal{Y}(t)$ for all $t \geq 0$. By Lemma 4.3.1 and Remark 4.3.1, the discrete-time system $\{Q^n :$

$\mathcal{X}(0) \to \mathcal{X}(0)\}_{n\geq 0}$ is point dissipative. By [50, Theorem 3.6.1] and Remark 4.3.1, for each $t \geq \hat{\tau}$, $Q(t)$ is compact, and hence $Q^n := Q(n\omega)$ is compact for sufficiently large $n$. It then follows from Theorem 1.1.3 that $Q : \mathcal{X}(0) \to \mathcal{X}(0)$ admits a strong global attractor. By the proof of [72, Lemma 8], we have the following observation.

**Lemma 4.3.10.** *Assume that $f(t)$ is a nonnegative, continuous and $\omega$-periodic function on $\mathbb{R}_+$ with $\int_0^\omega f(t)dt > 0$, and $g(t)$ is a continuous and bounded function on $\mathbb{R}_+$. Then any solution $u(t)$ of the linear nonhomogeneous equation*

$$u'(t) = -f(t)u(t) + g(t), \ t \geq 0,$$

*satisfies* $\limsup_{t\to\infty} |u(t)| \leq \frac{K}{M} \limsup_{t\to\infty} |g(t)|$, *where $M = \frac{1}{\omega}\int_0^\omega f(t)dt$ and $K = e^{M\omega}$.*

**Theorem 4.3.1.** *Let (A1)-(A3) hold. If $R_0^m > 1$, then there exists some $\zeta_1 > 0$ such that any solution of system (4.5) with $\phi \in \mathcal{Y}(0)$ satisfies* $\liminf_{t\to\infty} S_m(t,\phi) \geq \zeta_1$.

*Proof.* We first prove the uniform weak persistence for susceptible midges. By Lemmas 4.3.1 and 4.3.10, there exists $M > 0$ such that

$$\limsup_{t\to\infty} |I_m(t)| \leq M \limsup_{t\to\infty} |S_m(t)|, \limsup_{t\to\infty} |I_c(t)| \leq M \limsup_{t\to\infty} |S_m(t)|,$$
$$\limsup_{t\to\infty} |I_s(t)| \leq M \limsup_{t\to\infty} |S_m(t)|.$$

Let $P_m^\epsilon(t)$ be the solution maps of the following perturbed linear periodic system on $C([-\tau_l, 0], \mathbb{R})$:

$$\frac{\mathrm{d}S_m(t)}{\mathrm{d}t} = (b_m'(t-\tau_l, 0) - \epsilon)c(t)S_m(t-\tau_l) - \mu_m(t)S_m(t) - \frac{(\beta_{cm}(t) + \beta_{sm}(t))M\epsilon}{N_c^*(t)}S_m(t),$$

and $P_m^\epsilon := P_m^\epsilon(\omega)$, where $b_m'$ denotes the derivative with respect to the second variable. Since $R_0^m > 1$, $\lim_{\epsilon\to 0} r(P_m^\epsilon) = r(P_m) > 1$. We can fix a sufficiently small $\epsilon > 0$ such that $r(P_m^\epsilon) > 1$. It is easy to verify that $P_m^\epsilon(t)$ is also compact and strongly monotone on $C([-\tau_l, 0], \mathbb{R})$ for each $t \geq 2\tau_l$. Choose an integer $N_0 > 0$ such that $N_0\omega \geq 2\tau_l$. Since $P_m^{\epsilon(N_0\omega)} = P_m^\epsilon(N_0\omega)$, [74, Lemma 3.1] implies that $r(P_m^\epsilon)$ is a simple eigenvalue of $P_m^\epsilon$ having a strongly positive eigenvector. Let $\mu_\epsilon = \frac{\ln r(P_m^\epsilon)}{\omega}$. By [135, Lemma 1 ], it then follows that there is a positive $\omega$-periodic function $v_\epsilon^*(t)$ such that $u_\epsilon^*(t) = e^{\mu_\epsilon t}v_\epsilon^*(t)$ is a positive solution of the above linear system. Clearly, $\lim_{t\to\infty} u_\epsilon^*(t) = \infty$. For the above fixed $\epsilon > 0$, there exists $\zeta = \zeta(\epsilon) < \epsilon$ such that

$b_m(t-\tau_l, x) \geq (b_m'(t-\tau_l, 0)-\epsilon)x, \forall x \in [0,\zeta], \forall t \geq \tau_l$. Since $\lim_{\phi\to 0} S_{mt}(\phi) = 0$ uniformly for $t \in [0,\omega]$, there exists $\zeta_0 > 0$ such that

$$|S_{mt}(\phi)| \leq \zeta, \forall t \in [0,\omega], \|\phi\| \leq \zeta_0.$$

**Claim.** $\limsup_{n\to\infty} S_m(n\omega)(\phi) \geq \zeta_0$ for all $\phi \in \mathcal{Y}(0)$.

Suppose, by contradiction, that $\limsup_{n\to\infty} S_m(n\omega)(\psi) < \zeta_0$ for some $\psi \in \mathcal{Y}(0)$. Then there exists an integer $N_0 \geq 1$ such that $S_m(n\omega)(\psi) < \zeta_0$ for all $n \geq N_0$. For any $t \geq N_0\omega$, we have $t = n\omega + t'$ with $n \geq N_0$, $t' \in [0,\omega]$, and $|S_{mt}(\psi)| = |S_m(t')S_m(n\omega)(\psi)| \leq \zeta$. Then for all $t \geq N_0\omega$, we have $0 \leq S_m(t,\psi) \leq \zeta < \epsilon$. Then there exists an integer $N_1 > N_0$ such that $0 \leq I_c(t) \leq M\epsilon$, $0 \leq I_s(t) \leq M\epsilon$, $\forall t \geq N_1\omega$. Therefore, for any $t \geq N_1\omega + \tau_l$,

$$\frac{\mathrm{d}S_m(t)}{\mathrm{d}t} \geq (b_m'(t-\tau_l,0)-\epsilon)S_m(t-\tau_l)c(t) - \mu_m(t)S_m(t) - \frac{(\beta_{cm}(t)+\beta_{sm}(t))M\epsilon}{N_c^*(t)}S_m(t).$$

Since $\psi \in \mathcal{Y}(0)$, $S_m(t,\psi) > 0$ for all $t \geq 0$, and hence, there exists a sufficiently small $l > 0$ such that $S_m(t,\psi) \geq lu_\epsilon^*(t), \forall t \in [N_1\omega+\tau_l, N_1\omega+2\tau_l]$. By Theorem 1.3.2, we have $S_m(t,\psi) \geq lu_\epsilon^*(t)$, $\forall t \geq N_1\omega + 2\tau_l$. Since $\mu_\epsilon > 0$, we have $\lim_{t\to\infty} S_m(t,\psi) = \infty$, which is a contradiction.

By Theorem 1.2.2, it follows that $Q : \mathcal{X}(0) \to \mathcal{X}(0)$ is uniformly persistent with respect to $\mathcal{Y}(0)$ in the sense that there exists $\zeta_1 > 0$ such that

$$\liminf_{n\to\infty} S_m(n\omega)(\phi) \geq \zeta_1, \forall \phi \in \mathcal{Y}(0).$$

Furthermore, Theorem 1.2.3 implies that $Q : \mathcal{Y}(0) \to \mathcal{Y}(0)$ has a global attractor $A_0$. For any $\phi \in A_0$, we have $\phi_4(0) > 0$. Let $B_0 := \cup_{t\in[0,\omega]} Q(t)A_0$. Then $\phi_4(0) > 0$ for all $\phi \in B_0$. It is easy to see that $\lim_{t\to\infty} d(Q(t)\phi, B_0) = 0$ for all $\phi \in \mathcal{Y}(0)$. Let $X_+ := C([-\hat{\tau}_m, 0], \mathbb{R}_+^3) \times C([-\hat{\tau}, 0], \mathbb{R}_+) \times \mathbb{R}_+$ and define a continuous function $p : X_+ \to \mathbb{R}_+$ by $p(\phi) = \phi_4(0), \forall \phi \in X_+$. Clearly, $p(\phi) > 0$ for all $\phi \in B_0$. Since $B_0$ is a compact subset of $X_+$, we have $\inf_{\phi\in B_0} p(\phi) = \min_{\phi\in B_0} p(\phi) > 0$. By the attractiveness of $B_0$, it then follows that there exists $\zeta_1 > 0$ such that

$$\liminf_{t\to\infty} S_m(t,\phi) = \liminf_{t\to\infty} p(Q(t)\phi) \geq \zeta_1, \forall \phi \in \mathcal{Y}(0).$$

This completes the proof. $\square$

### 4.3.3 Uniform persistence of bluetongue without sheep

In this subsection, we consider the situation where there are no sheep, that is, $S_s = 0$, $I_s = 0$. Then the subsystem without sheep is given by

$$\begin{aligned}
\tfrac{\mathrm{d}I_c(t)}{\mathrm{d}t} &= \tfrac{\beta_{mc}(t)(N_c^*(t)-I_c(t))I_m(t)}{N_c^*(t)} - \mu_c(t)I_c(t),\\
\tfrac{\mathrm{d}S_m(t)}{\mathrm{d}t} &= b_m(t-\tau_l, S_m(t-\tau_l))c(t) - \tfrac{\beta_{cm}(t)I_c(t)}{N_c^*(t)}S_m(t) - \mu_m(t)S_m(t),\\
\tfrac{\mathrm{d}I_m(t)}{\mathrm{d}t} &= (1-\tau_m'(t))\tfrac{\beta_{cm}(t-\tau_m(t))I_c(t-\tau_m(t))}{N_c^*(t-\tau_m(t))}S_m(t-\tau_m(t))d(t) - \mu_{im}(t)I_m(t).
\end{aligned} \tag{4.10}$$

In the following, we investigate the dynamics of system (4.10). For each $t \geq 0$, let

$$\widetilde{X}(t) := [0, N_{ct}^*]_{C([-\hat{\tau}_m,0],\mathbb{R})} \times C([-\hat{\tau},0],\mathbb{R}_+) \times \mathbb{R}_+,$$

$$\widetilde{Y}(t) := \{\phi \in \widetilde{X}(t) : \phi_2(0) > 0\}.$$

By arguments similar to those in Lemma 4.3.1, we have the following result.

**Lemma 4.3.11.** *For any $\phi \in \widetilde{X}(0)$, system (4.10) has a unique nonnegative solution $v(t,\phi)$ with $v_0 = \phi$ for all $t \in [0,\infty)$, and all solutions $v_t(\phi) = (v_{1t}(\phi), v_{2t}(\phi), v_3(t,\phi))$ $\in \widetilde{X}(t)$ are ultimately bounded.*

There are two disease-free periodic solutions, $(0,0,0)$ and $(0, S_m^*(t), 0)$, where $S_m^*(t)$ is globally attractive for system (4.7) in $C([-\tau_l,0],\mathbb{R}_+)\backslash\{0\}$ under assumptions (A1) and (A3). Linearizing system (4.10) at the disease-free solution $(0, S_m^*(t), 0)$, we obtain the following periodic linear system for the infective variables $I_c$ and $I_m$:

$$\begin{aligned}
\tfrac{\mathrm{d}I_c(t)}{\mathrm{d}t} &= \beta_{mc}(t)I_m(t) - \mu_c(t)I_c(t),\\
\tfrac{\mathrm{d}I_m(t)}{\mathrm{d}t} &= (1-\tau_m'(t))\tfrac{\beta_{cm}(t-\tau_m(t))I_c(t-\tau_m(t))}{N_c^*(t-\tau_m(t))}S_m^*(t-\tau_m(t))d(t) - \mu_{im}(t)I_m(t).
\end{aligned} \tag{4.11}$$

Set $\widetilde{E} := C([-\hat{\tau}_m,0],\mathbb{R}^2)$ and $\widetilde{E}^+ := C([-\hat{\tau}_m,0],\mathbb{R}^2_+)$. Let $\widetilde{C}_\omega$ be the ordered Banach space of all $\omega$-periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$, which is equipped with the maximum norm and the positive core $\widetilde{C}_\omega^+ = \{v \in \widetilde{C}_\omega : v(t) \geq 0, \forall t \in \mathbb{R}\}$. Let $\widetilde{F} : \mathbb{R} \to \mathcal{L}(E,\mathbb{R}^2)$ be a map and $\widetilde{V}(t)$ be a continuous $2\times 2$ matrix function on $\mathbb{R}$ defined as follows:

$$\widetilde{F}(t)\phi = \begin{bmatrix} \beta_{mc}(t)\phi_2(0) \\ (1-\tau_m'(t))\frac{\beta_{cm}(t-\tau_m(t))S_m^*(t-\tau_m(t))\phi_1(-\tau_m(t))}{N_c^*(t-\tau_m(t))}d(t) \end{bmatrix},$$

$$\widetilde{V}(t) = \begin{bmatrix} \mu_c(t) & 0 \\ 0 & \mu_{im}(t) \end{bmatrix}.$$

Let $\Phi(t,s)$, $t \geq s$, be the evolution matrix associated with the following system:

$$\frac{\mathrm{d}v(t)}{\mathrm{d}t} = -\widetilde{V}(t)v(t).$$

Then the next generation operator $\widetilde{\mathcal{L}} : \widetilde{C}_\omega \to \widetilde{C}_\omega$ is given by

$$[\widetilde{\mathcal{L}}v](t) = \int_0^\infty \Phi(t, t-s)\widetilde{F}(t-s)v(t-s+\cdot)ds, \forall t \in \mathbb{R}, v \in \bar{C}_\omega.$$

Following [150], the basic disease reproduction ratio in the absence of sheep is defined as $\widetilde{R}_0 = r(\widetilde{\mathcal{L}})$, the spectral radius of $\widetilde{\mathcal{L}}$. For any given $t \geq 0$, let $\widehat{S}(t)$ be the solution map of system (4.11) on $\widetilde{E}$. Then $\hat{S} := \hat{S}(\omega)$ is the Poincaré map associated with linear system (4.11) and $r(\hat{S})$ is the spectral radius of $\hat{S}$. In view of Theorem 1.4.1, we have the following result.

**Lemma 4.3.12.** *$\widetilde{R}_0 - 1$ has the same sign as $r(\hat{S}) - 1$.*

For each $t \geq 0$, we define

$$\widetilde{\mathcal{X}}(t) := [0, N^*_{ct}]_{C([-\tau_m(0),0],\mathbb{R})} \times C([-\tau, 0], \mathbb{R}_+) \times \mathbb{R}_+,$$

$$\widetilde{\mathcal{Y}}(t) := \{\phi \in \widetilde{\mathcal{X}}(t) : \phi_2(0) > 0\}, \quad \widetilde{\mathcal{W}} := C([-\tau_m(0), 0], \mathbb{R}) \times \mathbb{R}.$$

As argued in the proof of Lemma 4.3.6 and Remark 4.3.1, we have the following results.

**Lemma 4.3.13.** *For any $\phi \in \widetilde{\mathcal{X}}(0)$, system (4.10) has a unique nonnegative solution $v(t, \varphi)$ with $v_0 = \varphi$ and all solutions $v_t(\phi) = (v_{1t}(\phi), v_{2t}(\phi), v_3(t, \phi)) \in \widetilde{\mathcal{X}}(t)$ for all $t \in [0, \infty)$.*

**Remark 4.3.2.** *For any $\psi \in \widetilde{X}(0)$ and $\phi \in \widetilde{\mathcal{X}}(0)$ with $\psi_1(\theta) = \phi_1(\theta)$ for all $\theta \in [-\tau_m(0), 0]$, $\psi_2(\theta) = \phi_2(\theta)$ for all $\theta \in [-\tau, 0]$, and $\psi_3 = \phi_3$, we have $w(t, \psi) = \nu(t, \phi)$ for all $t \geq 0$, where $w(t, \psi)$ and $\nu(t, \phi)$ are solutions of system (4.10) satisfying $w_0 = \psi$ and $\nu_0 = \phi$, respectively.*

For any given $t \geq 0$, let $S(t)$ be the solution map of system (4.11) on $\widetilde{\mathcal{W}}$. Then $S := S(\omega)$ is the Poincaré map associated with linear system (4.11). Let $r(S)$ be the spectral radius of $S$. As argued for $P(t)$, we can prove $S(t)$ is strongly monotone for $t > 2\hat{\tau}_m$.

By [50, Theorem 3.6.1] and Remark 4.3.2, it follows that for each $t \geq \hat{\tau}_m$, the linear operator $S(t)$ is compact on $\widetilde{\mathcal{W}}$. Then $S(t)$ is compact and strongly monotone on $\widetilde{\mathcal{W}}$ for $t > 2\hat{\tau}_m$. Choose an integer $n_0 > 0$ such that $n_0\omega > 2\hat{\tau}_m$. Since $S^{n_0} = S(n_0\omega)$, [74, Lemma 3.1] implies that $r(S)$ is a simple eigenvalue of $S$ having a strongly positive eigenvector. By [135, Lemma 1 ], we have the following observation.

**Lemma 4.3.14.** *Let* $\mu = \frac{\ln r(S)}{\omega}$. *Then there is a positive* $\omega$*-periodic function* $v^*(t)$ *such that* $u^*(t) = e^{\mu t}v^*(t)$ *is a positive solution of system (4.11).*

By arguments similar to those in [82, Lemma 3.8], we have $r(S) = r(\hat{S})$. As a consequence of Lemma 4.3.12, we see that $\widetilde{R}_0 - 1$ has the same sign as $r(S) - 1$. By arguments similar to those in Theorem 4.3.1, we have the following result.

**Theorem 4.3.2.** *Let (A1) and (A3) hold. If* $R_0^m > 1$*, then there exists some* $\tilde{\zeta} > 0$ *such that any solution of system (4.10) with* $\phi \in \widetilde{\mathcal{Y}}(0)$ *satisfies* $\liminf_{t\to\infty} S_m(t,\phi) \geq \tilde{\zeta}$.

Let $\widetilde{Q}(t) : \widetilde{\mathcal{X}}(0) \to \widetilde{\mathcal{X}}(t)$ be the solution maps of system (4.10). Then $\widetilde{Q} := \widetilde{Q}(\omega)$ is the Poincaré map associated with system (4.10) on $\widetilde{\mathcal{X}}(0)$ and $\widetilde{Q}^n = \widetilde{Q}(n\omega)$, $\forall n \geq 0$. Then $\{\widetilde{Q}^n : \widetilde{\mathcal{X}}(0) \to \widetilde{\mathcal{X}}(0)\}_{n\geq 0}$ defines a discrete-time dynamical system. By Lemma 4.3.11 and Remark 4.3.2, the discrete-time system $\{\widetilde{Q}^n\}$ is point-dissipative. By [50, Theorem 3.6.1] and Remark 4.3.2, for each $t \geq \hat{\tau}$, $\widetilde{Q}(t)$ is compact, and hence $\widetilde{Q}^n$ is compact for all sufficiently large $n$. It then follows from Theorem 1.1.3 that $\widetilde{Q} : \widetilde{\mathcal{X}}(0) \to \widetilde{\mathcal{X}}(0)$ admits a strong global attractor. For each $t \geq 0$, we define

$$\widetilde{\mathcal{Y}}_0(t) := \{\phi = (\phi_1, \phi_2, \phi_3) \in \widetilde{\mathcal{Y}}(t) : \phi_1(0) > 0 \text{ and } \phi_3(0) > 0\},$$

$$\partial\widetilde{\mathcal{Y}}_0(t) := \widetilde{\mathcal{Y}}(t) \setminus \widetilde{\mathcal{Y}}_0(t) = \{\phi \in \widetilde{\mathcal{Y}}(t) : \phi_1(0) = 0 \text{ or } \phi_3(0) = 0\}.$$

**Theorem 4.3.3.** *Let (A1) and (A3) hold. Then the following statements are valid:*

*(i) If* $R_0^m \leq 1$*, then* $(0,0,0)$ *is globally attractive for system (4.10) in* $\widetilde{\mathcal{X}}(0)$.

*(ii) If* $\widetilde{R}_0 < 1$ *and* $R_0^m > 1$*, then the disease-free periodic solution* $(0, S_m^*(t), 0)$ *is globally attractive for system (4.10) in* $\widetilde{\mathcal{X}}(0) \setminus \{(0,0,0)\}$.

*(iii) If* $\widetilde{R}_0 > 1$ *and* $R_0^m > 1$*, then there exists some* $\widetilde{\eta} > 0$ *such that any solution* $v(t,\phi) = (I_c(t), S_m(t), I_m(t))$ *of system (4.10) with* $\phi \in \widetilde{\mathcal{Y}}_0(0)$ *satisfies* $\liminf_{t\to\infty}(I_c(t), I_m(t)) \geq (\widetilde{\eta}, \widetilde{\eta})$.

*Proof.* In the case where $R_0^m \leq 1$, we first prove $\lim_{t\to\infty} S_m(t) = 0$ by a simple comparison argument, and then obtain the global attractivity of $(0,0,0)$ by the theory of chain transitive sets.

In the case where $\widetilde{R}_0 < 1$, we have $r(S) < 1$. Consider the following system with parameter $\delta > 0$:

$$\begin{aligned} &\tfrac{\mathrm{d}I_c(t)}{\mathrm{d}t} = \beta_{mc}(t)I_m(t) - \mu_c(t)I_c(t), \\ &\tfrac{\mathrm{d}I_m(t)}{\mathrm{d}t} = (1-\tau'_m(t))\tfrac{\beta_{cm}(t-\tau_m(t))I_c(t-\tau_m(t))}{N_c^*(t-\tau_m(t))}(S_m^*(t-\tau_m(t))+\delta)d(t) - \mu_{im}(t)I_m(t). \end{aligned} \tag{4.12}$$

Let $S_\delta : \widetilde{\mathcal{W}} \to \widetilde{\mathcal{W}}$ be the Poincaré map of system (4.12) and $r(S_\delta)$ be the spectral radius of $S_\delta$. Since $\lim_{\delta\to 0} r(S_\delta) = r(S) < 1$, we can fix a sufficiently small number $\delta > 0$ such that $r(S_\delta) < 1$. It is easy to see that $S_\delta(t)$ is also compact and strongly positive for $t > 2\hat{\tau}_m$. By Lemma 4.3.14, there is a positive $\omega$-periodic function $v_\delta^*(t)$ such that $u_\delta^*(t) = e^{\mu_\delta t} v_\delta^*(t)$ is a positive solution of system (4.12), where $\mu_\delta = \frac{\ln r(S_\delta)}{\omega}$. Clearly, $\lim_{t\to\infty} u_\delta^*(t) = 0$.

By the global attractivity of $S_m^*(t)$ for system (4.7) when $R_0^m > 1$, and the comparison principle, there exists a sufficiently large integer $\widetilde{N}_1 > 0$ such that $\widetilde{N}_1\omega \geq \hat{\tau}_m$ and $S_m(t) \leq S_m^*(t) + \delta$, $\forall t \geq \widetilde{N}_1\omega - \hat{\tau}_m$. Then we have

$$\begin{aligned} &\tfrac{\mathrm{d}I_c(t)}{\mathrm{d}t} \leq \beta_{mc}(t)I_m(t) - \mu_c(t)I_c(t), \\ &\tfrac{\mathrm{d}I_m(t)}{\mathrm{d}t} \leq (1-\tau'_m(t))\tfrac{\beta_{cm}(t-\tau_m(t))I_c(t-\tau_m(t))}{N_c^*(t-\tau_m(t))}(S_m^*(t-\tau_m(t))+\delta)d(t) - \mu_{im}(t)I_m(t), \end{aligned}$$

for all $t \geq \widetilde{N}_1\omega$. For any given $\phi \in \widetilde{\mathcal{X}}(0)$, there exists a sufficiently large $\widetilde{k} > 0$ such that $(I_c(t,\phi), I_m(t,\phi)) \leq \widetilde{k}u_\delta^*(t), \forall t \in [\widetilde{N}_1\omega, \widetilde{N}_1\omega + \hat{\tau}_m]$. It then follows from Theorem 1.3.2 that $(I_c(t,\phi), I_m(t,\phi)) \leq \widetilde{k}u_\delta^*(t), \forall t \geq \widetilde{N}_1\omega + \hat{\tau}_m$. Then $\lim_{t\to\infty} I_c(t,\phi) = \lim_{t\to\infty} I_m(t,\phi) = 0$. By using the theory of internally chain transitive sets (see, e.g., [136, 151]), we can prove statement (ii).

In the case where $\widetilde{R}_0 > 1$, we have $r(\widetilde{P}) > 1$. From the first and third equations of system (4.10), it is easy to see that $\widetilde{Q}(t)\widetilde{\mathcal{Y}}_0(0) \subseteq \widetilde{\mathcal{Y}}_0(t)$ for all $t \geq 0$. Since susceptible midges persist uniformly, it follows from Theorem 1.2.3 that $\widetilde{Q} : \widetilde{\mathcal{Y}}(0) \to \widetilde{\mathcal{Y}}(0)$ has a global attractor. Now we prove that $\widetilde{Q} : \widetilde{\mathcal{Y}}(0) \to \widetilde{\mathcal{Y}}(0)$ is uniformly persistent with respect to $(\widetilde{\mathcal{Y}}_0(0), \partial\widetilde{\mathcal{Y}}_0(0))$.

Let $r_{\eta_0}$ be the spectral radius of the Poincaré map associated with the following system:

$$\begin{aligned}\frac{\mathrm{d}I_c(t)}{\mathrm{d}t} &= \frac{\beta_{mc}(t)(N_c^*(t)-\eta_0)I_m(t)}{N_c^*(t)} - \mu_c(t)I_c(t),\\ \frac{\mathrm{d}I_m(t)}{\mathrm{d}t} &= \frac{\beta_{cm}(t-\tau_m(t))I_c(t-\tau_m(t))}{N_c^*(t-\tau_m(t))}(S_m^*(t-\tau_m(t))-\eta_0)d(t) - \mu_{im}(t)I_m(t).\end{aligned} \tag{4.13}$$

Then $\lim_{\eta_0\to 0} r_{\eta_0} = r(\widetilde{P}) > 1$. Fix a sufficiently small $\eta_0 > 0$ such that $r_{\eta_0} > 1$. By Lemma 4.3.14, system (4.13) has a positive $\omega$-periodic function $v_{\eta_0}^*(t)$ such that $w_{\eta_0}^*(t) = e^{\mu_{\eta_0} t}v_{\eta_0}^*(t)$ is a positive solution of system (4.13), where $\mu_{\eta_0} = \frac{\ln r_{\eta_0}}{\omega}$. Clearly, $\lim_{t\to\infty} w_{\eta_0}^*(t) = \infty$.

Let $\widetilde{M} = (0, S_{m0}^*, 0)$, where $S_{m0}^*(\theta) = S_m^*(\theta)$ for all $\theta \in [-\tau, 0]$. Since $\lim_{\phi\to\widetilde{M}} \|\widetilde{Q}(t)\phi - \widetilde{Q}(t)\widetilde{M}\|=0$ uniformly for $t \in [0,\omega]$, there exists $\eta_1 = \eta_1(\eta_0) > 0$ such that for any $\phi \in \widetilde{\mathcal{Y}}_0(0)$ with $\|\phi - \widetilde{M}\| < \eta_1$, we have $\|\widetilde{Q}(t)\phi - \widetilde{Q}(t)\widetilde{M}\| < \eta_0$ for all $t \in [0,\omega]$. We further have the following claim.

**Claim.** $\limsup_{n\to\infty} \|\widetilde{Q}^n(\phi) - \widetilde{M}\| \geq \eta_1$ for all $\phi \in \widetilde{\mathcal{Y}}_0(0)$.

Suppose, by contradiction, that $\limsup_{n\to\infty} \|\widetilde{Q}^n(\psi) - \widetilde{M}\| < \eta_1$ for some $\psi \in \widetilde{\mathcal{Y}}_0(0)$. Then there exists an integer $\widetilde{N} \geq 1$ such that $\|\widetilde{Q}^n(\psi) - \widetilde{M}\| < \eta_1$ for all $n \geq \widetilde{N}$. For any $t \geq \widetilde{N}\omega$, we have $t = n\omega + t'$ with $n \geq \widetilde{N}$ and $t' \in [0,\omega]$, and hence, $\|\widetilde{Q}(t)\psi - \widetilde{Q}(t)\widetilde{M}\| = \|\widetilde{Q}(t')(\widetilde{Q}^n(\psi)) - \widetilde{Q}(t')\widetilde{M}\| < \eta_0, \forall t \geq \widetilde{N}\omega$. It follows that $0 < I_c(t) < \eta_0$ and $S_m(t) > S_m^*(t) - \eta_0$ for all $t \geq \widetilde{N}\omega$. For all $t \geq \widetilde{N}\omega + \hat{\tau}_m$, we have

$$\begin{aligned}\frac{\mathrm{d}I_c(t)}{\mathrm{d}t} &\geq \frac{\beta_{mc}(t)(N_c^*(t)-\eta_0)I_m(t)}{N_c^*(t)} - \mu_c(t)I_c(t),\\ \frac{\mathrm{d}I_m(t)}{\mathrm{d}t} &\geq (1-\tau_m'(t))\frac{\beta_{cm}(t-\tau_m(t))I_c(t-\tau_m(t))}{N_c^*(t-\tau_m(t))}(S_m^*(t-\tau_m(t))-\eta_0)d(t) - \mu_{im}(t)I_m(t).\end{aligned}$$

Since $\psi \in \widetilde{\mathcal{Y}}_0(0)$, $I_c(t,\psi) > 0$ and $I_m(t,\psi) > 0$ for all $t \geq 0$, and hence, we can choose a sufficiently small $k > 0$ such that $(I_c(t,\psi), I_m(t,\psi)) \geq kw_{\eta_0}^*(t), \forall t \in [\widetilde{N}\omega + \hat{\tau}_m, \widetilde{N}\omega + 2\hat{\tau}_m]$. By Theorem 1.3.2, it follows that $(I_c(t,\psi), I_m(t,\psi)) \geq kw_{\eta_0}^*(t), \forall t \geq \widetilde{N}\omega + 2\hat{\tau}_m$. Hence, $\lim_{t\to\infty} I_c(t,\psi) = \lim_{t\to\infty} I_m(t,\psi) = \infty$, which contradicts the boundedness of solutions of system (4.10).

The above claim implies that $\widetilde{M}$ is an isolated invariant set for $\widetilde{Q}$ in $\widetilde{\mathcal{Y}}(0)$ and $W^S(\widetilde{M}) \bigcap \widetilde{\mathcal{Y}}_0(0) = \emptyset$, where $W^S(\widetilde{M})$ is the stable set of $\widetilde{M}$ for $\widetilde{Q}$. Define

$$\widetilde{M}_\partial = \{\phi \in \partial\widetilde{\mathcal{Y}}_0(0) : \widetilde{Q}^n(\phi) \in \partial\widetilde{\mathcal{Y}}_0(0), \forall n \geq 0\}.$$

For any given $\psi \in \widetilde{M}_\partial$, $\widetilde{Q}^n(\psi) \in \partial\widetilde{\mathcal{Y}}_0(0)$, $\forall n \geq 0$. Thus, for each $n \in \mathbb{N}$, either $I_c(n\omega,\psi) \equiv 0$ or $I_m(n\omega,\psi) \equiv 0$. From the first and third equations of system (4.10), it follows that for each $t \geq 0$, $I_c(t,\psi) \equiv 0$ or $I_m(t,\psi) \equiv 0$. If $I_m(t,\psi) \equiv 0$ for all

$\forall t \geq 0$, then the $I_c$ equation of system (4.10) satisfies $\frac{\mathrm{d}I_c(t,\psi)}{\mathrm{d}t} \leq -\bar{\mu}_c I_c(t,\psi)$, where $\bar{\mu}_c = \min_{t\in[0,\omega]} \mu_c(t)$. By the comparison principle, we have $\lim_{t\to\infty} I_c(t,\psi) = 0$. Thus by the theory of internally chain transitive sets [151], $\lim_{t\to\infty}(S_m(t) - S_m^*(t)) = 0$ when $R_0^m > 1$. In this case, $\widetilde{Q}^n(\psi) \to \widetilde{M}$ as $n \to \infty$. If $I_m(t,\psi) \not\equiv 0$ for all $\forall t \geq 0$, there exists $t_0 \geq 0$ such that $I_m(t_0,\psi) > 0$. By the third equation of system (4.10), $I_m(t,\psi) > 0$ for all $t \geq t_0$. Thus, we have $I_c(t,\psi) \equiv 0$, $\forall t \geq t_0$. From the third equation of system (4.10), we see that $\lim_{t\to\infty} I_m(t,\psi) = 0$. Then the $S_m$ equation of system (4.10) is asymptotic to the periodic system (4.7). By the theory of internally chain transitive sets [151], we can prove that $\lim_{t\to\infty}(S_m(t)-S_m^*(t)) = 0$ when $R_0^m > 1$. In this case, $\widetilde{Q}^n(\psi) \to \widetilde{M}$ as $n \to \infty$. Thus, $\bigcup_{\phi\in\widetilde{M}_\partial} \omega(\phi) = \widetilde{M}$ and $\widetilde{M}$ cannot form a cycle for $\widetilde{Q}$ in $\partial\widetilde{\mathcal{Y}}_0(0)$. By the acyclicity theorem on uniform persistence for maps (see Theorem 1.2.1), it follows that $\widetilde{Q} : \widetilde{\mathcal{Y}}(0) \to \widetilde{\mathcal{Y}}(0)$ is uniformly persistent with respect to $(\widetilde{\mathcal{Y}}_0(0), \partial\widetilde{\mathcal{Y}}_0(0))$.

By taking $p(\phi) = \min\{\phi_1(0), \phi_3(0)\}$ and using an argument similar to that for Theorem 4.3.1, we can show that there exists $\tilde{\eta} > 0$ such that

$$\liminf_{t\to\infty} \min(I_c(t,\phi), I_m(t,\phi)) = \liminf_{t\to\infty} p(\widetilde{Q}(t)\phi) \geq \tilde{\eta}, \forall \phi \in \widetilde{\mathcal{Y}}_0(0).$$

This completes the proof. □

### 4.3.4 Uniform persistence of bluetongue

**Theorem 4.3.4.** *Let (A1)-(A3) hold. If* $R_0 > 1$, $\widetilde{R}_0 > 1$, *and* $R_0^m > 1$, *then there exists some* $\eta > 0$ *such that any solution* $u(t,\varphi) = (I_c(t), S_s(t), I_s(t), S_m(t), I_m(t))$ *of system (4.5) with* $\varphi \in \mathcal{Y}(0)$, $\varphi_5 > 0$ *satisfies* $\liminf_{t\to\infty} I_m(t) \geq \eta$. *Moreover, for some* $\bar{\eta} > 0$, $\liminf_{t\to\infty} I_c(t) \geq \bar{\eta}$; *the disease persists proportionally in the sheep in the sense that, for some* $\hat{\eta} > 0$,

$$\liminf_{t\to\infty} \frac{I_s(t)}{S_s(t) + I_s(t)} \geq \hat{\eta}.$$

*Proof.* For each $t \geq 0$, define

$$\mathcal{Y}_0(t) := \{\varphi \in \mathcal{Y}(t) : \varphi_5 > 0\} \quad \text{and} \quad \partial\mathcal{Y}_0(t) := \mathcal{Y}(t) \setminus \mathcal{Y}_0(t) = \{\varphi \in \mathcal{Y}(t) : \varphi_5 = 0\}.$$

From the fifth equation of system (4.5), it is easy to see that $Q(t)\mathcal{Y}_0(0) \subseteq \mathcal{Y}_0(t)$ for all $t \geq 0$. Since susceptible midges persist uniformly, it then follows from Theorem 1.2.3

that $Q : \mathcal{Y}(0) \to \mathcal{Y}(0)$ admits a global attractor. Now we prove that $Q : \mathcal{Y}(0) \to \mathcal{Y}(0)$ is uniformly persistent with respect to $(\mathcal{Y}_0(0), \partial\mathcal{Y}_0(0))$.

Let $M_1 = (0, 0, 0, S^*_{m0}, 0)$ and $M_2 = (0, S^*_{s0}, 0, S^*_{m0}, 0)$, where $S^*_{s0}(\theta) = S^*_s(\theta)$ for all $\theta \in [-\tau_m(0), 0]$, $S^*_{m0}(\theta) = S^*_m(\theta)$ for all $\theta \in [-\tau, 0]$. By Theorem 4.3.3 and arguments similar to those for the claim in its proof, we have the following observations.

**Claim 1.** There exists $\delta_1 > 0$, $\limsup_{n\to\infty} \|Q^n(\varphi) - M_1\| \geq \delta_1$ for all $\varphi \in \mathcal{Y}_0(0)$.

**Claim 2.** There exists $\gamma_1 > 0$, $\limsup_{n\to\infty} \|Q^n(\varphi) - M_2\| \geq \gamma_1$ for all $\varphi \in \mathcal{Y}_0(0)$.

Define

$$M_\partial = \{\varphi \in \partial\mathcal{Y}_0(0) : Q^n(\varphi) \in \partial\mathcal{Y}_0(0), \forall n \geq 0\}.$$

For any given $\psi \in M_\partial$, $Q^n(\psi) \in \partial\mathcal{Y}_0(0)$, $\forall n \geq 0$. Thus, for each $n \in \mathbb{N}$, $I_m(n\omega, \psi) \equiv 0$. From the $I_m$ equation of system (4.5), it follows that for each $t \geq 0$, $I_m(t, \psi) \equiv 0$. From the $I_c$ equation of system (4.5) and the comparison principle, we have that $\lim_{t\to\infty} I_c(t, \psi) = 0$. Similarly, from the $I_s$ equation of system (4.5), we see that $\lim_{t\to\infty} I_s(t, \psi) = 0$. Thus, $S_s(t, \psi)$ and $S_m(t, \psi)$ in system (4.5) are asymptotic to the periodic systems (4.6) and (4.7), respectively. Thus by the theory of internally chain transitive sets [151], $\lim_{t\to\infty}(S_m(t) - S^*_m(t)) = 0$ when $R^m_0 > 1$. If $R^s_0 \leq 1$, then $\lim_{t\to\infty} S_s(t) = 0$. In this case, $Q^n(\psi) \to M_1$ as $n \to \infty$. If $R^s_0 > 1$, then $\lim_{t\to\infty}(S_s(t) - S^*_s(t)) = 0$. In this case, $Q^n(\psi) \to M_2$ as $n \to \infty$. Thus, $\bigcup_{\varphi\in M_\partial} \omega(\varphi) = \{M_1, M_2\}$ and no subset of $\{M_1, M_2\}$ forms a cycle for $Q$ in $\partial\mathcal{Y}_0(0)$.

With the above two claims, we see that $M_1$ and $M_2$ are isolated invariant sets for $Q$ in $\mathcal{Y}(0)$, and $W^S(M_i) \cap \mathcal{Y}_0(0) = \emptyset$, $i = 1, 2$, where $W^S(M_i)$ is the stable of $M_i$ for $Q$. By the acyclicity theorem on uniform persistence for maps (see Theorem 1.2.1), it follows that $Q : \mathcal{Y}(0) \to \mathcal{Y}(0)$ is uniformly persistent with respect to $(\mathcal{Y}_0(0), \partial\mathcal{Y}_0(0))$. By taking $p(\varphi) = \varphi_5$, and using an argument similar to that for Theorem 4.3.1, there exists $\eta > 0$ such that

$$\liminf_{t\to\infty} I_m(t, \varphi) = \liminf_{t\to\infty} p(Q(t)\varphi) \geq \eta, \forall \varphi \in \mathcal{Y}_0(0).$$

To show the uniform persistence in cattle, we consider the $I_c$ equation of system (4.5). From the nonnegativity and boundedness of solutions, there exist $\bar{N}_c > 0$, $\hat{N}_c > 0$, $\bar{N}_s \geq 0$, and $\hat{N}_s \geq 0$ such that $\inf_{t\geq 0} N^*_c(t) \geq \bar{N}_c$, $\sup_{t\geq 0} N^*_c(t) \leq \hat{N}_c$, $\inf_{t\geq 0} (I_s(t) + S_s(t)) \geq \bar{N}_s$, $\sup_{t\geq 0} (I_s(t) + S_s(t)) \leq \hat{N}_s$. Thus,

$$\liminf_{t\to\infty} I_c(t) \geq \frac{\bar{\beta}_{mc}\bar{N}_c\eta(\bar{N}_s + \bar{N}_c)}{(\hat{N}_s + \hat{N}_c)(\hat{\beta}_{mc}\eta + \hat{\mu}_c(\bar{N}_s + \bar{N}_c))} := \bar{\eta},$$

where $\bar{\beta}_{mc} = \min_{t\in[0,\omega]} \beta_{mc}(t)$, $\hat{\beta}_{mc} = \max_{t\in[0,\omega]} \beta_{mc}(t)$, $\hat{\mu}_c = \max_{t\in[0,\omega]} \mu_c(t)$.

To show proportional disease persistence in the sheep motivated by [99], we introduce the proportion of infectious sheep: $p_s(t) = \frac{I_s(t)}{N_s(t)}$. Letting $b(t) := \frac{\partial b_s(t,0)}{\partial S_s}$, we then have

$$\begin{aligned} \frac{\mathrm{d}p_s(t)}{\mathrm{d}t} &\geq \frac{\beta_{ms}(t)(1-p_s(t))I_m(t)}{N_s(t)+N_c^*(t)} - \gamma(t)p_s(t) - \delta_s(t)p_s(t)(1-p_s(t)) - b(t)p_s(t) \\ &\geq \frac{\bar{\beta}_{ms}\eta}{\hat{N}_s+\hat{N}_c} - \left(\frac{\hat{\beta}_{ms}\eta}{\bar{N}_s+\bar{N}_c} + \hat{\gamma} + \hat{\delta}_s + \hat{b}\right) p_s(t), \end{aligned}$$

where $\bar{\beta}_{ms} = \min_{t\in[0,\omega]} \beta_{ms}(t)$, $\hat{\beta}_{ms} = \max_{t\in[0,\omega]} \beta_{ms}(t)$, $\hat{\gamma} = \max_{t\in[0,\omega]} \gamma(t)$, $\hat{\delta}_s = \max_{t\in[0,\omega]} \delta_s(t)$, $\hat{b} = \max_{t\in[0,\omega]} b(t)$. Thus,

$$\liminf_{t\to\infty} p_s(t) \geq \frac{\bar{\beta}_{ms}\eta(\bar{N}_s+\bar{N}_c)}{(\hat{N}_s+\hat{N}_c)(\hat{\beta}_{ms}\eta + (\hat{\gamma}+\hat{\delta}_s+\hat{b})(\bar{N}_s+\bar{N}_c))} := \hat{\eta}.$$

This completes the proof. □

### 4.3.5 Uniform disease persistence if sheep persist

The proof of uniform disease persistence needs to combine with the uniform persistence for midges and sheep, which ensures the existence of a global attractor in a state space. We first prove the uniform persistence in sheep when bluetongue cannot persist without sheep. By the same arguments as in Theorem 4.3.1, we have the following result.

**Theorem 4.3.5.** *Let (A1)-(A3) hold. If* $R_0^s > 1 \geq \widetilde{R}_0$, *then there exists some* $\zeta_2 > 0$ *such that any solution* $u(t,\phi)$ *of system (4.5) with* $\phi \in \mathscr{X}(0)$, $\phi_2(0) > 0$ *satisfies* $\liminf_{t\to\infty} S_s(t) \geq \zeta_2$.

**Theorem 4.3.6.** *Let (A1)-(A3) hold. If* $R_0 > 1 \geq \widetilde{R}_0$, $R_0^s > 1$, $R_0^m > 1$, *then system (4.5) admits a positive* $\omega$*-periodic solution, and there exists some* $\mathring{\zeta} > 0$ *such that any solution* $u(t,\phi)$ *of system (4.5) with* $\phi \in \mathscr{X}(0)$, $\phi_2(0) > 0$, $\phi_4(0) > 0$, $\phi_5 > 0$ *satisfies* $\liminf_{t\to\infty} I_m(t) \geq \mathring{\zeta}$. *Moreover, for some* $\bar{\zeta} > 0$ *and* $\hat{\zeta} > 0$, $\liminf_{t\to\infty} I_c(t) \geq \bar{\zeta}$ *and* $\liminf_{t\to\infty} I_s(t) \geq \hat{\zeta}$.

*Proof.* For each $t \geq 0$, we define $\mathscr{Z}(t) := \{\phi \in \mathscr{X}(t) : \phi_2(0) > 0, \phi_4(0) > 0\}$ and

$$\mathscr{Z}_0(t) := \{\phi \in \mathscr{Z}(t) : \phi_5 > 0\}, \quad \partial\mathscr{Z}_0(t) := \mathscr{Z}(t) \setminus \mathscr{Z}_0(t) = \{\phi \in \mathscr{Z}(t) : \phi_5 = 0\}.$$

From the fifth equation of system (4.5), it is easy to see that $Q(t)\mathcal{Z}_0(0) \subseteq \mathcal{Z}_0(t)$ for all $t \geq 0$. By Theorems 4.3.1 and 4.3.5, susceptible midges and susceptible sheep are uniformly persistent, and hence, $Q : \mathcal{Z}(0) \to \mathcal{Z}(0)$ has a global attractor by Theorem 1.2.3. Now we prove that $Q : \mathcal{Z}(0) \to \mathcal{Z}(0)$ is uniformly persistent with respect to $(\mathcal{Z}_0(0), \partial\mathcal{Z}_0(0))$.

Let $M = (0, S_{s0}^*, 0, S_{m0}^*, 0)$. By arguments similar to those for the claim in the proof of Theorem 4.3.3, we have the following observation.
**Claim.** There exists $\sigma_1 > 0$, $\limsup_{n\to\infty} \|Q^n(\phi) - M\| \geq \sigma_1$ for all $\phi \in \mathcal{Z}_0(0)$.

This claim implies that $M$ is an isolated invariant set for $Q$ in $\mathcal{Z}(0)$, and $W^S(M) \cap \mathcal{Z}_0(0) = \emptyset$, where $W^S(M)$ is the stable of $M$ for $Q$. Define

$$M_\partial = \{\phi \in \partial\mathcal{Z}_0(0) : Q^n(\phi) \in \partial\mathcal{Z}_0(0), \forall n \geq 0\}.$$

For any given $\psi \in M_\partial$, $Q^n(\psi) \in \partial\mathcal{Z}_0(0)$, $\forall n \geq 0$. Thus, for each $n \in \mathbb{N}$, $I_m(n\omega, \psi) \equiv 0$. From the fifth equation of system (4.5), it follows that for each $t \geq 0$, $I_m(t, \psi) \equiv 0$. By the $I_c$ equation of system (4.5) and the comparison principle, we have that $\lim_{t\to\infty} I_c(t, \psi) = 0$. Similarly, from the $I_s$ equation of system (4.5), we see that $\lim_{t\to\infty} I_s(t, \psi) = 0$. Then $S_s(t, \psi)$ and $S_m(t, \psi)$ are asymptotic to the periodic systems (4.6) and (4.7), respectively. Thus, by the theory of internally chain transitive sets [151], $\lim_{t\to\infty}(S_m(t) - S_m^*(t)) = 0$ when $R_0^m > 1$, $\lim_{t\to\infty}(S_s(t) - S_s^*(t)) = 0$ when $R_0^s > 1$. In this case, $Q^n(\psi) \to M$ as $n \to \infty$. Thus, $\bigcup_{\phi\in M_\partial} \omega(\phi) = M$ and $M$ cannot form a cycle for $Q$ in $\partial\mathcal{Z}_0(0)$. By the acyclicity theorem on uniform persistence for maps (see Theorem 1.2.1), it follows that $Q : \mathcal{Z}(0) \to \mathcal{Z}(0)$ is uniformly persistent with respect to $(\mathcal{Z}_0(0), \partial\mathcal{Z}_0(0))$. By letting $p(\phi) = \phi_5$ and using an argument similar to that for Theorem 4.3.1, we have that there exists $\mathring{\zeta} > 0$ such that

$$\liminf_{t\to\infty} I_m(t, \phi) = \liminf_{t\to\infty} p(Q(t)\phi) \geq \mathring{\zeta}, \forall \phi \in \mathcal{Z}_0(0).$$

As argued in the proof of Theorem 4.3.4, we can prove the uniform persistence in cattle and sheep. Let $\hat{\mu}_{is} = \max_{t\in[0,\omega]} \mu_{is}(t)$. Then

$$\begin{aligned}
\liminf_{t\to\infty} I_c(t) \geq & \frac{\bar{\beta}_{mc}\bar{N}_c\mathring{\zeta}(\bar{N}_s + \bar{N}_c)}{(\hat{N}_s + \hat{N}_c)(\hat{\beta}_{mc}\mathring{\zeta} + \hat{\mu}_c(\bar{N}_s + \bar{N}_c))} := \bar{\zeta}, \\
\liminf_{t\to\infty} I_s(t) \geq & \frac{\bar{\beta}_{ms}\zeta_2\mathring{\zeta}}{(\hat{N}_s + \hat{N}_c)(\hat{\gamma} + \hat{\mu}_{is})} := \hat{\zeta}.
\end{aligned}$$

Next we prove the existence of a positive periodic steady state. Let $\hat{Q}(t) : X(0) \to X(t)$ be the solution maps of system (4.5). For each $t \geq 0$, let

$$Z(t) := \{\phi \in X(t) : \phi_2(0) > 0, \phi_4(0) > 0\}, \quad Z_0(t) := \{\phi \in Z(t) : \phi_5 > 0\},$$

and $\partial Z_0(t) := Z(t) \setminus Z_0(t) = \{\phi \in Z(t) : \phi_5 = 0\}$. By [151, Theorem 3.5.1], there exists an equivalent norm on $C([-\hat{\tau}, 0], \mathbb{R}^5)$ such that for each $t > 0$, the solution map $\hat{Q}(t) : X(0) \to X(t)$ is an $\alpha$-contraction. Since $\overline{Z(0)} \subseteq X(0)$ and $\overline{Z(t)} \subseteq X(t)$ ($\overline{Z(t)}$ is a closure of $Z(t)$), it follows that $\hat{Q}(t) : \overline{Z(0)} \to \overline{Z(t)}$ is also an $\alpha$-contraction. Since susceptible midges and susceptible sheep are uniformly persistent by Theorems 4.3.1 and 4.3.5, then $\hat{Q} : X(0) \to X(0)$ is uniformly persistent with respect to $(Z(0), \partial Z(0))$, where $\partial Z(0) := X(0) \setminus Z(0)$. By Theorem 1.2.3, $\hat{Q} : Z(0) \to Z(0)$ has a global attractor. Similarly, $\hat{Q} : Z_0(0) \to Z_0(0)$ has a global attractor $A$. According to the proof of Theorem 1.2.4, if $\hat{Q} : \overline{Z(0)} \to \overline{Z(0)}$ is an $\alpha$-condensing, Theorem 1.2.4 still holds. It then follows that $\hat{Q} : Z_0(0) \to Z_0(0)$ has a fixed point $\psi^* \in A$, and hence, $w(t, \psi^*) = (\bar{I}_c(t), \bar{S}_s(t), \bar{I}_s(t), \bar{S}_m(t), \bar{I}_m(t))$ is an $\omega$-periodic solution of system (4.5) with $\psi^* \in Z_0(0)$. By the uniqueness of solutions, $v(t, \phi^*) = (\bar{I}_c(t), \bar{S}_s(t), \bar{I}_s(t), \bar{S}_m(t), \bar{I}_m(t))$ is also an $\omega$-periodic solution of system (4.5) with $\phi^* \in \mathcal{Z}_0(0)$, where $\psi^* \in Z_0(0)$ and $\phi^* \in \mathcal{Z}_0(0)$ with $\psi_i(\theta) = \phi_i(\theta)$, $i = 1, 2, 3$, for all $\theta \in [-\tau_m(0), 0]$, $\psi_4(\theta) = \phi_4(\theta)$ for all $\theta \in [-\tau, 0]$, and $\psi_5 = \phi_5$. By the second and fourth equations of system (4.5), it is also strictly positive. □

With the integral form (4.3), we can easily obtain the uniform persistence for $E_m$ from Theorems 4.3.4 and 4.3.6. Further, we can also discuss the attractivity of four disease-free periodic solutions in the case where $R_0 < 1$. We omitted details here.

## 4.4 A case study

In this section, we study the bluetongue transmission case in France, which has reemerged in late 2015. In this study, we let the period $\omega = 12$ months. Since some parameters do not vary too much with temperature, we assume they are temperature independent (constant). According to OIE, France has a cattle population of 19353497, which can be chosen as a constant value of $N_c^*(t)$, and the total number of sheep is $N_s = 5921047$ in 2014. According to farm animal life expectancy (see http://www.four-paws.us/campaigns/farm-animals-/farm-animal-life-expectancy/), the natural life expectancies of cattle and sheep are both 20 years. Then we estimate the cattle and sheep natural death rate as $\mu_c = \mu_s = \frac{1}{20\times 12} = \frac{1}{240}$ Month$^{-1}$. The survival probability $c(t) = e^{-\int_{t-\tau_l}^{t} \mu_l(s)ds}$ is 0.57 (see [14]). By [108,135], we assume that the birth rate of sheep with density-dependence is given by $b_s(t, S_s) = b_s e^{-\frac{S_s}{K_s}} S_s$, where $b_s$ is the maximal birth rate of sheep and $K_s$ is the carrying capacity for sheep. We estimate $K_s = 2N_s$. We give the temperature-independent parameters, as shown in Table 4.1.

Table 4.1: Relevant variables and parameters values (ranges)

| Parameter | Value(range) | Reference |
|---|---|---|
| $N_c^*$ | 19353497 | see text |
| $\bar{\beta}_{mc}$ | $0.8 \sim 1.0$ | [11] |
| $\bar{\beta}_{ms}$ | $0.8 \sim 1.0$ | [11] |
| $\bar{\beta}_{cm}$ | $0.001 \sim 0.15$ | [19,41] |
| $\bar{\beta}_{sm}$ | $0.001 \sim 0.15$ | [19,41] |
| $\gamma$ | $1/16.4 \times 30.4$ Month$^{-1}$ | [43,130] |
| $\delta_s$ | $(0.001 \sim 0.01)\times 30.4$ Month$^{-1}$ | [35,112] |
| $\mu_c$ | $1/240$ Month$^{-1}$ | see text |
| $\mu_s$ | $1/240$ Month$^{-1}$ | see text |
| $\mu_{is}$ | $\mu_s + \delta_s$ | see text |
| $b_s$ | $6.94 \times 10^{-4} \times 30.4$ Month$^{-1}$ | [21] |
| $\tau_l$ | $0.5 \sim 0.7$ Month | [105] |
| $K_s$ | $2 \times 5921047$ | see text |

Next, we use the average monthly temperatures and the relationship between the biting rate, vector mortality rate, EIP, and temperature to estimate the temperature-dependent parameters. In this case study, the average monthly temperatures for France from 1991-2015 (obtained from the Climate Change Knowledge Portal website: http://sdwebx.worldbank.org/climateportal) is as shown in Table 4.2.

*Estimation of the biting rate.* It follows from [94] that the temperature-dependent midge biting rate is given by

$$a(T) = 0.000171 \times T \times (T - 3.6966) \times (41.8699 - T)^{1/2.7056} \times 30.4,$$

where $T$ is the temperature in °C. Then the temperature dependence of the duration of the midge gonotrophic cycle (i.e., the duration period for oviposition) can be expressed as the reciprocal of this rate, $1/a(T)$. The biting rate of midges in France can be fitted by

$$\begin{aligned} a(t) =& 30.4(0.07021 - 0.07731\cos(\pi t/6) - 0.01151\sin(\pi t/6) + 0.01452\cos(\pi t/3) \\ & + 0.00941\sin(\pi t/3) - 0.001083\cos(\pi t/2) - 0.001767\sin(\pi t/2) \\ & + 0.0006667\cos(2\pi t/3) - 0.0002021\sin(2\pi t/3) + 0.0008927\cos(5\pi t/6) \\ & - 0.001902\sin(5\pi t/6) + 8.34\times 10^{-6}\cos(\pi t))\ \text{Month}^{-1}. \end{aligned}$$

Therefore, $\beta_{mc}(t) = \bar{\beta}_{mc}a(t)$, $\beta_{ms}(t) = \bar{\beta}_{ms}a(t)$, $\beta_{cm}(t) = \bar{\beta}_{cm}a(t)$, $\beta_{sm}(t) = \bar{\beta}_{sm}a(t)$. According to [64], the per capita oviposition rate is derived by dividing the fecundity (number of eggs layed per oviposition) by the mean gonotrophic period and, further, dividing by two (since half of the eggs laid are destined to emerge as males and are not included in our adult population density measure which represents only females). The number of eggs layed per oviposition is about 25 to 150. We assume that density-dependence occurs, and it follows from [25, 84] that the birth rate of midges is given by $b_m(t, S_m) = \frac{p(t)S_m}{q(t)+S_m^r}$, where the maximum per capita birth rate of midges $p(t) = 150a(t)$, the maximum capacity related parameter $q(t) = 5$, and the dimensionless parameter $r = 0.196$.

Table 4.2: Monthly mean temperatures for France (in °C)

| Month | January | February | March | April | May | June |
|---|---|---|---|---|---|---|
| Temperature | 5.8 | 6.0 | 8.5 | 10.6 | 13.9 | 17.1 |
| Month | July | August | September | October | November | December |
| Temperature | 19.3 | 19.2 | 16.3 | 12.7 | 8.5 | 6.2 |

*Estimation of $\mu_m(t)$.* The temperature-dependent midge mortality rate can be approximated by [40]:

$$\mu_m(T) = 0.008941e^{0.1547\times T} \times 30.4,$$

where $T$ is the temperature in °C. We assume that the mortality rate of susceptible, exposed, and infectious midges are the same, that is, $\mu_m(t) = \mu_{em}(t) = \mu_{im}(t)$. Hence, the midge mortality rate in France can be fitted by

$$\mu_m(t) = 2.305 - 2.21\cos(\pi t/6) - 0.3654\sin(\pi t/6) + 0.6834\cos(\pi t/3)$$

$$+ 0.3605\sin(\pi t/3) - 0.1704\cos(\pi t/2) - 0.159\sin(\pi t/2) + 0.04236\cos(2\pi t/3)$$
$$+ 0.05758\sin(2\pi t/3) + 0.02236\cos(5\pi t/6) - 0.06244\sin(5\pi t/6)$$
$$- 0.006183\cos(\pi t) \text{ Month}^{-1}.$$

*Estimation of* $\tau_m(t)$. According to [94], the temperature-dependent EIP is reflected in the reciprocal of $\nu$ which is given by

$$\nu = \nu(T) = \begin{cases} 0 & T \le T_{\min}, \\ 0.0003 \times T \times (T - T_{\min}) \times 30.4 & T > T_{\min}, \end{cases}$$

where $T_{\min} = 10.4057$°C. Temperatures only in the summer months for France are above the baseline temperature for EIP of 10.4057 °C, see Figure 4.1. Low temperatures mean that the period of virus replication (the EIP) is longer than the life span of any midge and hence there is no incubation below $T_{min}$. In the case of favorable temperature, we take $\tau_m(T) = \frac{1}{\nu(T)}$, while in the case of unfavorable temperature, we assume that the EIP for the current month is longer than that for its last month by about one month. For simplicity, we choose the EIP to be 2.0413 Month for October, 2.9413 Month for November, 3.7413 Month for December, 3.2575 Month for April, 3.7413 Month for January, February and March, respectively. It then follows that the periodic time delay $\tau_m(t)$ in France can be approximated by

$$\begin{aligned} \tau_m(t) =& 2.404 + 1.639\cos(\pi t/6) + 0.505\sin(\pi t/6) - 0.2357\cos(\pi t/3) \\ & - 0.09017\sin(\pi t/3) - 0.03022\cos(\pi t/2) - 0.1513\sin(\pi t/2) \\ & + 0.01554\cos(2\pi t/3) + 0.001111\sin(2\pi t/3) - 0.05729\cos(5\pi t/6) \\ & - 0.04817\sin(5\pi t/6) + 0.006067\cos(\pi t) \text{ Month}. \end{aligned}$$

In the following, we will present some numerical analyses based on the above parameter values. Firstly, let us choose the following parameter values and the others stay the same as above: $\beta_{mc}(t) = 0.8a(t), \beta_{ms}(t) = 0.8a(t), \beta_{cm}(t) = 0.15a(t)$, $\beta_{sm}(t) = 0.15a(t), \delta_s(t) = 0.005 \times 30.4$, $\tau_l = 0.5$. Using Lemmas 4.3.5 and 1.4.2, we can numerically compute the basic reproduction ratios. We obtain $R_0^m = 14.9069 > 1$, $\widetilde{R}_0 = 15.0391 > 1$, and $R_0 = 7.5443 > 1$. Setting the initial function values as $I_c(\theta) = 41$, $S_s(\theta) = 2664471$, $I_s(\theta) = 0$ for all $\theta \in [-\hat{\tau}_m, 0]$, $S_m(\theta) = 41071134$ for all $\theta \in [-\hat{\tau}, 0]$, $I_m(0) = 6318636$; in this case, the long term behaviors of the $I_c$, $S_s$, $I_s$, and $I_m$ are shown in Figure 4.4, which is coincident with Theorem 4.3.4. It shows that bluetongue can persist and exhibit periodic fluctuations in cattle and midges even though it may eradicate the sheep. If we choose $\beta_{cm}(t) = 0.0005a(t)$, $\beta_{ms}(t) = 1.4a(t)$, and $\beta_{sm}(t) = a(t)$, then $R_0^s = 5.064 > 1$, $R_0^m = 14.9069 > 1$, $\widetilde{R}_0 = 0.8674 < 1$, and $R_0 = 1.1762 > 1$. In this case, a positive periodic solution is observed. The periodic fluctuations of the infectious compartments are shown in Figure 4.3, which is consistent with Theorem 4.3.6. This implies that bluetongue will persist and exhibit periodic fluctuation in cattle, sheep, and midges if no further control measure is taken in France. By taking some measures, if we can decrease the above contact rate $\beta_{cm}(t)$ and $\beta_{sm}(t)$ to $0.0005a(t)$ and $0.001a(t)$ and keep other parameters as in Figure 4.4, respectively, then $R_0 = 0.4366 < 1$. In this case, the infectious compartments all tend to zero, which implies that the disease will die out eventually (see Figure 4.4). We also observe that a large first epidemic peak occurs in cattle and sheep populations and subsequently continues to decline.

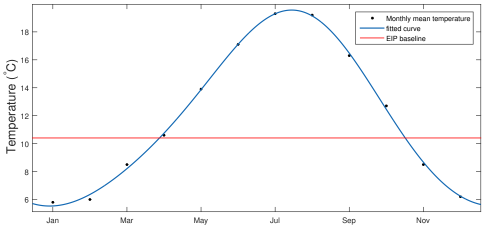
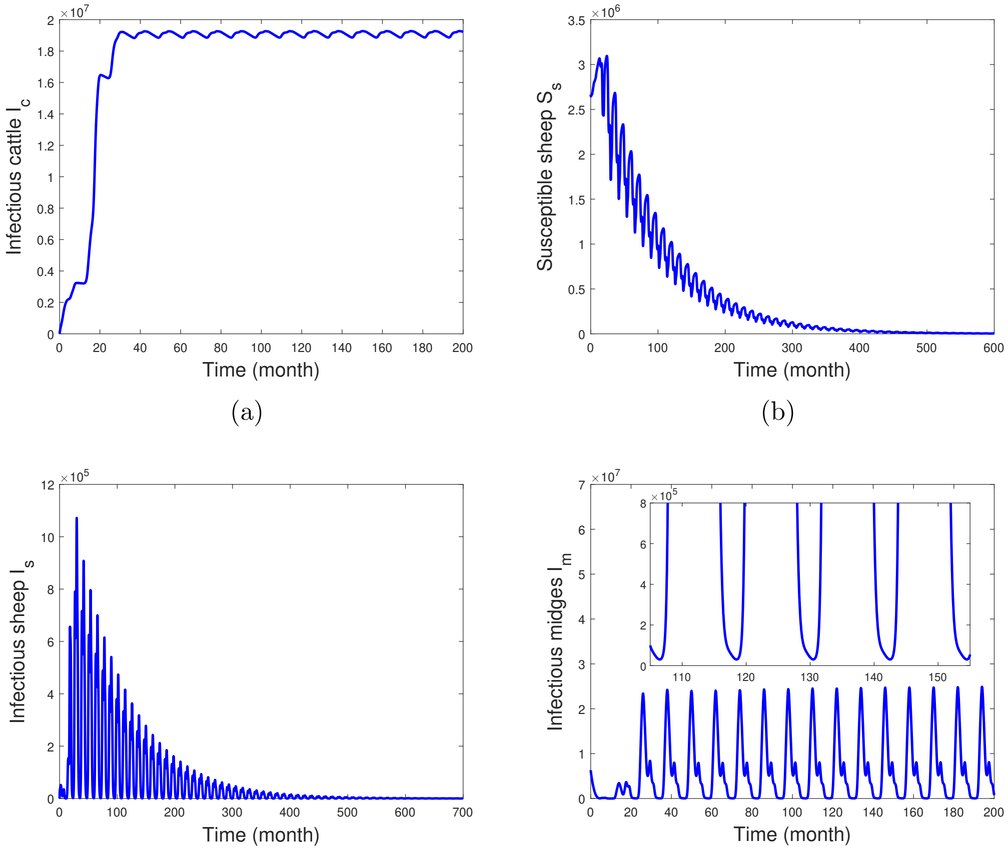


Figure 4.1: Fitted curve of the average monthly temperature in France and the baseline temperature at which extrinsic incubation is possible.

Second, it is important to know the influences of different factors on the disease transmission. It is well known that the disease transmission is directly related to $R_0$, then we will analyze the relationship between $R_0$ and some coefficients in our system.

*Increasing the mortality rate of adult midges.* To explore the effect of the mortality rate of adult midges, we replace $\mu_m(t)$ with $k\mu_m(t)$, $k \in [1, 2]$, in our model and the other parameter values are the same as those in Figure 4.4. Figure 4.5(a) shows that $R_0$ is an increasing function of $k$. Clearly, by taking some vectors control measures such as the using of insecticides, if we can keep $k > 1.7925$, then $R_0 < 1$, which implies that it is effective to control BTV spread, see Figure 4.5(a).

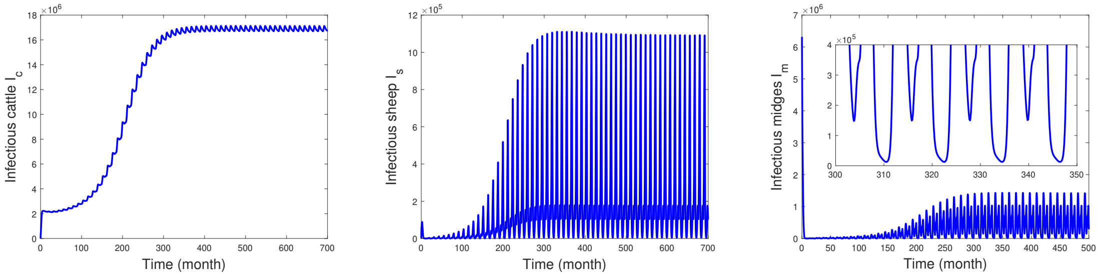
*Prolonging the duration of the EIP.* By multiplying $\tau_m(t)$ by $l$, $l \in [1, 5]$, we observe that $R_0$ and $\widetilde{R}_0$ are both decreasing functions of $l$ as shown in Figure 4.5(b). Hence, we can try to prolong the EIP duration to control BTV spread by developing some



(a) (b)

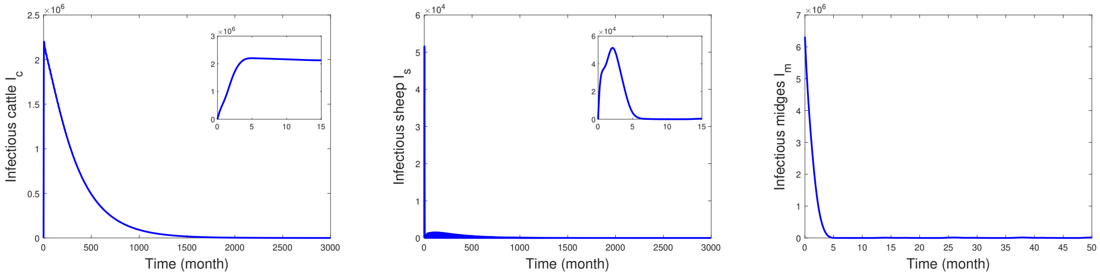
(c) (d)

Figure 4.2: Long-term behaviors of the infectious compartments and susceptible sheep when $\widetilde{R}_0 = 15.0391 > 1$ and $R_0 = 7.5443 > 1$.



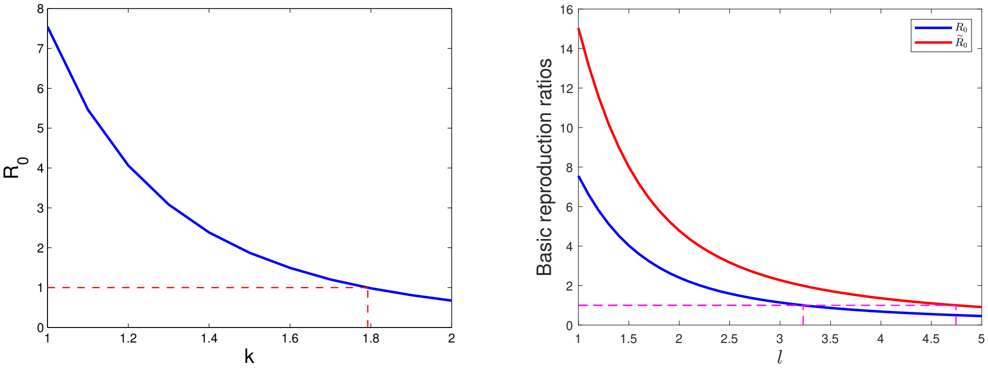
(a) (b) (c)

Figure 4.3: Long-term behaviors of the infectious compartments when $\widetilde{R}_0 = 0.8674 < 1$ and $R_0 = 1.1762 > 1$.

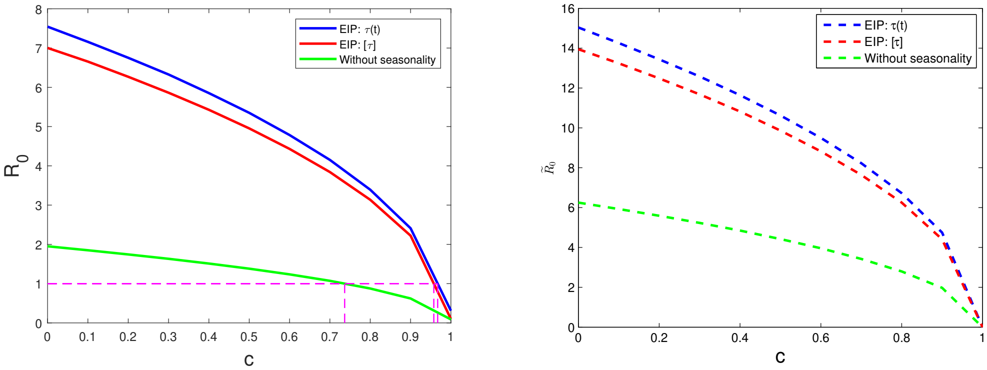


(a) (b) (c)

Figure 4.4: Long-term behaviors of the infectious compartments when $R_0 = 0.4366 < 1$.



(a) $R_0$ as a function of $k$. (b) $R_0$ and $\widetilde{R}_0$ as a function of $l$.



(c) $R_0$ as a function of $c$. (d) $\widetilde{R}_0$ as a function of $c$.

Figure 4.5: $R_0$ vs $k$, $l$, $c$, and the effect of EIP and seasonality.

drugs. From the expression of $\tau_m(T)$, we know that high temperatures can shorten the duration of the EIP, and hence, global warming may facilitate the spread of disease. Moreover, the blue curve always lies below the red one, which reveals that $R_0$ for two hosts tends to be lower than $\widetilde{R}_0$ for only cattle in these parameter values. This could be because sheep are assumed to be a poorer host compared with cattle in terms of the duration of infection.

*Prevention of host-vector contact.* Here we only consider the effect of $\beta_{mc}$ on $R_0$. Assuming that the control effort is $c$, $c \in [0, 1]$, we replace $\beta_{mc}$ with $(1 - c)\beta_{mc}$ in our model. The blue curve in Figure 4.5(c) shows that $R_0$ is a decreasing function of $c$ and we should keep $c > 0.9672$ to control BTV spread by isolation or vaccination effort.

Third, we explore the influence of the seasonality and the periodic EIP on $R_0$. Define the time-averaged EIP duration as $[\tau_m] := \frac{1}{\omega}\int_0^\omega \tau_m(t)dt$. It follows that $[\tau_m] =$ 2.404 Month. Figures 4.5(c) and 4.5(d) compare the effect of periodic $\tau_m(t)$, constant $[\tau_m]$, and without seasonality on $R_0$ and $\widetilde{R}_0$, respectively, keeping the other parameter values the same as those in Figure 4.4. They imply that the uses of the time-averaged EIP, parameters without seasonality may both underestimate $R_0$ and $\widetilde{R}_0$. If the contact rate from midges to cattle is less than $(1 - 0.7366)\beta_{mc}$ without seasonality, or $(1 - 0.9576)\beta_{mc}$ with constant $[\tau_m]$, or $(1 - 0.9672)\beta_{mc}$ with periodic $\tau_m(t)$, then $R_0 < 1$. This implies that the control efforts of 73.66%, 95.76% are not adequate to control the BTV spread. For example, if vaccination covering 96.72% of susceptible cattle and sheep would be needed, then the disease will be controlled.

## 4.5 Discussion

In this chapter, we developed and analyzed a bluetongue transmission model by incorporating the effect of seasonality and temperature-dependent EIP. By using the theory developed in [133,150], we can derive the basic sheep reproduction ratio $R_0^s$, the basic midge reproduction ratio $R_0^m$, the basic disease reproduction ratio in the absence of sheep $\widetilde{R}_0$, and the basic disease reproduction ratio for the whole system $R_0$, which serve as very important threshold parameters for the persistence and extinction of the disease (population). Following the theoretical approach in [82], we define a suitable phase space on which the linearized system of infectious compartments generates an eventually strongly monotone periodic semiflow. By using the theorem of uniform persistence for periodic semiflows and the theory of chain transitive sets, we have obtained a threshold dynamics of system in term of $R_0$ and $\widetilde{R}_0$ under some additional conditions. More precisely, if $R_0 > 1$ and $\widetilde{R}_0 > 1$, then bluetongue can persist even though it may eradicate the sheep; if $R_0 > 1 \geq \widetilde{R}_0$, then there is a positive periodic solution, that is, bluetongue coexists with cattle, sheep, and midges, and the sheep are not eradicated.

Numerically, we have estimated all constant and periodic parameters by using some published data and simulated the BTV transmission case in France. We have numerically calculated the basic reproduction ratios, and explored the relationship between $R_0$ and some parameters in our model. The numerical simulation results of the long term behaviors of the infectious compartments are consistent with the obtained analytic results. In addition, we have observed that these three temperature-dependent parameters, the mortality rate of midges, the duration of the EIP, and the host-vector contact, have a strong influence on $R_0$. This provides us three possible measures for controlling BTV spread. The results predict that increasing the mortality rate of midges, prolonging the duration of the EIP, and preventing host-vector contact are effective measures in controlling BTV spread. Therefore, the use of insecticides in the cattle and sheep premises and in the areas where these midges live, keeping cattle and sheep in stables as adult midges cannot enter buildings very easily, restriction to the movements of cattle and sheep from affected areas to noninfected regions where the midges are present, and the use of vaccines are all helpful to reduce the transmission of BTV. New control measures are urgently needed to completely eliminate BTV and prevent reemergence of disease. Moreover, we observe that the adoption of the time-averaged EIP and without seasonality parameters may both underestimate $R_0$. Therefore, in order to obtain more realistic and effective control measures, it is important for the time-dependent EIP to be incorporated into models.

# Chapter 5

# A nonlocal periodic reaction-diffusion model of Bluetongue disease

## 5.1 Introduction

Bluetongue is a noncontagious midge-borne infectious disease of ruminants caused by bluetongue virus (BTV) via vector-competent biting female midges in the *Culicoides*. Bluetongue outbreaks cause substantial economic losses for farmers due to the direct effects on livestocks, trade restrictions, and the cost of surveillance and control [59]. In recent decades, bluetongue is one of the most common diseases of livestocks. To date, 27 BTV-serotypes have been identified [13] whose geographic distribution differs by region. Since 1998 into Europe, BTV has caused a series of disease outbreaks across the whole of Europe. In late 2000, BTV-2 was recorded in French Corsica Island, and BTV-4 in 2003 and BTV-16 were detected in 2004. Since then, no other outbreaks have been reported in Corsica. Until 2013, BTV-1 has been introduced to Corsica from the island of Sardinia. In 2016, BTV-4 reemerged in Corsica and then has been introduced to the mainland France [110].

Quite a few mathematical models have been developed to describe the spread of BTV (see, e.g., [21, 44, 49, 73, 89, 99]). Cattle and sheep are susceptible to BTV infection [49]. Gourley, Röst, and Thieme [44] proposed an autonomous delay differential equation model that includes cattle and sheep as hosts, midges as vectors. Seasonal spread of bluetongue can be explained by seasonal activities of vectors since temperature influences the midge developmental rate and life history parameters [94]. Then bluetongue models with seasonality have been proposed in [49, 73, 99]. Gubbins et al. [49] presented an ordinary differential equation model with explicit temperature-dependent midge parameters and estimated the effect of each parameter on the basic reproduction ratio. The extrinsic incubation period (EIP) describes the interval between virus ingestion and the subsequent ability to transmit virus (development time of the virus in the vector). The EIP of BTV is strongly dependent on temperature, varying from 26 days at 15°C to 4 days at 30°C [49]. Higher temperature can reduce the duration of the EIP. Recently, Li and Zhao [73] introduced a periodic bluetongue model with temperature-dependent EIP and investigated the effect of temperature-dependent EIP on the basic reproduction ratio. The temperature-dependent EIP was also incorporated in other vector-borne diseases (see, e.g., [82, 142]).

Spatiotemporal heterogeneity has a strong impact on the BTV spread. Sumner et al. [120] found that about 90% of BTV transmission between farms is due to midge dispersal. The vector spread pathways are the long-distance passive movements by winds and the short-distance fights (about 100 metres per day) by active movements [103]. Midge in the absence of winds or other directional stimuli, its active movements perform randomly in all directions and regard as a local spread. Charron et al. [20] proposed a spatiotemporal spread of bluetongue model which neglects the host movements and wind-induced passive vector movements. These authors considered the impact of spatiotemporal heterogeneities in abundance and distribution of vectors and hosts on the occurrence and amplitude of epidemics, but they did not study the global dynamics on persistence and extinction of bluetongue in terms of the basic reproduction ratio.

In this chapter, we modify the bluetongue model in [20] by incorporating the temperature-dependent EIP of BTV, seasonality in vectors, and spatial heterogeneity in hosts and vectors. Note that the modelling process is nontrivial because the temperature-dependent EIP induces a new nonlocal term. Since livestock populations are managed by farmers, host movements are controlled, and hence, the spatial spread of BTV is due to only vector movements. This leads to the lack of compactness for solution maps of our model system since some equations have no diffusion terms. Thus, we need to prove the asymptotic compactness of solution maps to obtain the existence of the global attractor for the associated Poincaré map. Numerically, we estimate the relevant model parameters and study the impact of the seasonal and spatial heterogeneities in hosts and vectors on the spread of BTV.

The rest of the chapter is organized as follows. In Section 5.2, we present the model and study its well-posedness. In Section 5.3, we derive the basic reproduction ratio $R_0$. In Section 5.4, we establish the threshold dynamics in terms of $R_0$. In Section 5.5, in the case where all coefficients are constants, we obtain a sufficient condition for the global attractivity of the positive steady state for the autonomous system. In Section 5.6, a case study in French Corsica Island for BTV-4 transmission is presented. A brief discussion then concludes the chapter.

## 5.2 The model

Cattle are much more attractive to midges than sheep and they show longer duration of viraemia, and hence, cattle are a major reservoir of infection [15]. This may be the reason why some models only chose cattle as hosts [21, 89]. To develop our spatial model for the spread of bluetongue, we consider the dynamics of infection in hosts (cattle) and vectors (midges). We assume that all populations remain in a bounded spatial habitat $\Omega$ with smooth boundary $\partial\Omega$. Since we focus on a local to regional scale, the spatial spread of bluetongue is assumed to be only due to active movements. The cattle population is divided into susceptible ($S_h$), infectious ($I_h$) and recovered ($R_h$) classes. Let the density of total cattle population be $H_p(t, x) = S_h(t, x) + I_h(t, x) + R_h(t, x)$ at time $t$ and location $x$. Since cattle's movements are controlled by farmers, the diffusion coefficient of cattle is zero. According to [20], we assume that the per capita birth rate of cattle $b_h$ equals the per capita exit (mortality, selling, culling) rate $m_h$, and hence, $H_p(t, x)$ stablizes at a positive steady state $H_p^*(x)$.

Adult males and immature midges can not transmit and acquire the virus since they do not take blood meals, thereby only female adult midges are modelled. The vector population $V_p$ is divided into susceptible, exposed (i.e., infected but not infective), infectious midges, and their densities are denoted by $S_v$, $E_v$ and $I_v$, respectively, and hence, $V_p(t, x) = S_v(t, x) + E_v(t, x) + I_v(t, x)$, $\forall t \geq 0$, $x \in \Omega$.

For model parameters, since the impact of climate change on cattle is much less than that on midges activities, the parameters related to cattle are assumed be constants. Let $\alpha_1$ be the per capita recovery rate of cattle. The seasonal and spatial dependent parameters are as follows: the per capita biting rate $n(t,x)$ of midges is the average number of bites per midge per unit time at time $t$ and location $x$; $b_v(t,x)$ is the per capita birth rate of midges at time $t$ and location $x$; $m_v(t,x)$ is the per capita natural mortality rate of midges; and $k_v(t,x)$ is the per capita density-dependent mortality rate of midges at time $t$ and location $x$. Then $n(t,x)I_v/H_p^*(x)$ is the average number of infectious midge bites received by per cattle per unit time at time $t$ and location $x$. Thus, the force of infection for cattle and midges per unit time at time $t$ and location $x$ are given, respectively, by

$$c_{vh}n(t,x)\frac{I_v}{H_p^*(x)}S_h \text{ and } \; c_{hv}n(t,x)\frac{I_h}{H_p^*(x)}S_v,$$

where $c_{vh}$ and $c_{hv}$ represent the transmission probability of BTV per bite from infectious midges to susceptible cattle and from infectious cattle to susceptible midges, respectively. Similar to [20], we assume that the vector population has a logistic growth with $K = (b_v - m_v)/k_v$ being the carrying capacity of the environment dependent on the midge birth rate $b_v(t,x)$, mortality $m_v(t,x)$, and density-dependent mortality rate $k_v(t,x)$, at the disease-free state and with seasonality. In order to guarantee a positive growth rate of the midge population, we further assume that

(A1) $b_v(t,x) > m_v(t,x)$ on $\mathbb{R} \times \bar{\Omega}$.

Since the temperature $T$ is assumed to vary as a function of time $t$, we let $\tau(t)$ be the length of the temperature-dependent EIP. Further, we consider the midge active movements and assume that they perform an unbiased random walk and that the dispersion of midges is homogeneous in space described by $D > 0$. We do not consider immigration or emigration of individuals, that is, no population flux crosses the boundary $\partial\Omega$. Let $\Delta$ be the Laplacian operator, $\nu$ be the outward unit normal vector on $\partial\Omega$, and $M(t,x)$ be the density of newly occurred infectious midges per unit time at time $t$ and location $x$. By the same arguments as in [142], we can derive the expression of $M(t,x)$ as

$$M(t,x) = (1-\tau'(t)) \int_{\Omega} \Gamma(t, t-\tau(t), x, y) c_{hv} n(t-\tau(t), y) \frac{I_h(t-\tau(t), y)}{H_p^*(y)} S_v(t-\tau(t), y)dy,$$

where $\Gamma(t, t_0, x, y)$ with $t > t_0 \geq 0$ and $x, y \in \Omega$ is the Green function associated with $\frac{\partial u}{\partial t} = D\Delta u - m_v(t, \cdot)u$ subject to the Neumann boundary condition. Therefore, we have the following nonlocal reaction-diffusion system with the temperature-dependent EIP:

$$\begin{aligned}
&\frac{\partial S_h}{\partial t} = b_h H_p^*(x) - c_{vh} n(t,x) \frac{I_v}{H_p^*(x)} S_h - m_h S_h, \\
&\frac{\partial I_h}{\partial t} = c_{vh} n(t,x) \frac{I_v}{H_p^*(x)} S_h - (\alpha_1 + m_h) I_h, \\
&\frac{\partial R_h}{\partial t} = \alpha_1 I_h - m_h R_h, \\
&\frac{\partial S_v}{\partial t} = D\Delta S_v + b_v(t,x) V_p - c_{hv} n(t,x) \frac{I_h}{H_p^*(x)} S_v - m_v(t,x) S_v - k_v(t,x) V_p S_v, \\
&\frac{\partial E_v}{\partial t} = D\Delta E_v + c_{hv} n(t,x) \frac{I_h}{H_p^*(x)} S_v - m_v(t,x) E_v - k_v(t,x) V_p E_v - M(t,x), \\
&\frac{\partial I_v}{\partial t} = D\Delta I_v + M(t,x) - m_v(t,x) I_v - k_v(t,x) V_p I_v, \\
&\frac{\partial S_v}{\partial \nu} = \frac{\partial E_v}{\partial \nu} = \frac{\partial I_v}{\partial \nu} = 0, t > 0, x \in \partial\Omega.
\end{aligned} \tag{5.1}$$

Let $\rho(r)$ be the developmental proportion of bluetongue virus in midges at time $r$. When the accumulative proportion from $t - \tau(t)$ to $t$ reaches 1, the individual moves to the next stage (see, e.g., [82, 143]). It follows that

$$\int_{t-\tau(t)}^{t} \rho(r) dr = 1. \tag{5.2}$$

Differentiating both sides of (5.2) with respect to $t$, we then obtain $1 - \tau'(t) = \frac{\rho(t)}{\rho(t-\tau(t))} > 0$. Here we assume that $\tau(t)$ is $\omega$-periodic in $t$ and $\tau'(t)$ is Hölder continuous on $\mathbb{R}$. All constant parameters are positive, and functions $n(t,x)$, $b_v(t,x)$ and $k_v(t,x)$ are Hölder continuous and nonnegative nontrivial on $\mathbb{R} \times \bar{\Omega}$ and $\omega$-periodic in $t$. The function $m_v(t,x)$ is Hölder continuous and positive on $\mathbb{R} \times \bar{\Omega}$, and $\omega$-periodic in $t$.

Let $\mathbb{X} := C(\bar{\Omega}, \mathbb{R}^6)$ be the Banach space with the supremum norm $\|\cdot\|_{\mathbb{X}}$. Let $\hat{\tau} = \max_{t\in[0,\omega]} \tau(t)$. Define $X := C([-\hat{\tau}, 0], \mathbb{X})$ with the norm $\|\phi\| = \max_{\theta\in[-\hat{\tau},0]} \|\phi(\theta)\|_{\mathbb{X}}$, $\forall \phi \in X$. Define $\mathbb{X}^+ := C(\bar{\Omega}, \mathbb{R}^6_+)$ and $X^+ := C([-\hat{\tau}, 0], \mathbb{X}^+)$, then $(\mathbb{X}, \mathbb{X}^+)$ and $(X, X^+)$ are ordered spaces. As usual, we identity $\phi \in X$ defined by $\phi(\theta, x) = \phi(\theta)(x)$, $\forall \theta \in [-\hat{\tau}, 0]$, $\forall x \in \bar{\Omega}$. Given a function $z : [-\hat{\tau}, \sigma) \to \mathbb{X}$ for $\sigma > 0$, we define $z_t \in X$ by $z_t(\theta) = z(t + \theta)$, $\forall \theta \in [-\hat{\tau}, 0]$, for any $t \in [0, \sigma)$.

Let $\mathbb{Y} := C(\bar{\Omega}, \mathbb{R})$ and $\mathbb{Y}^+ := C(\bar{\Omega}, \mathbb{R}_+)$. Define the linear evolution operators $T_i(t,s)$, $i = 1, 2, 3$, on $\mathbb{Y}$ by $T_1(t,s)\phi_1 = e^{-m_h(t-s)}\phi_1$, $T_2(t,s)\phi_2 = e^{-(\alpha_1+m_h)(t-s)}\phi_2$ and $T_3(t,s) = T_1(t,s)$, $\forall t \geq s$, respectively. Let $T_4(t,s) : \mathbb{Y} \to \mathbb{Y}$ be the evolution operator associated with $\frac{\partial u}{\partial t} = D\Delta u - m_v(t,x)u := A_4(t)u$, $t \geq s$, $x \in \bar{\Omega}$, subject to the Neumann boundary condition. Since $m_v(t, \cdot)$ is $\omega$-periodic in $t$, [28, Lemma 6.1] implies that $T_4(t+\omega, s+\omega) = T_4(t,s)$ for $(t,s) \in \mathbb{R}^2$ with $t \geq s$. Moreover, for $(t,s) \in \mathbb{R}^2$ with $t > s$, $T_4(t,s)$ is compact and strongly positive (see, e.g., [52, Chaper II] and [141, Theorem 2.1.8]). Let $T(t,s) = \operatorname{diag}\{T_1(t,s), T_2(t,s), T_3(t,s), T_4(t,s), T_4(t,s), T_4(t,s)\} : \mathbb{X} \to \mathbb{X}$, and $\mathcal{A}(t) = \operatorname{diag}\{A_1, A_2, A_3, A_4(t),\ A_4(t), A_4(t)\}$, where $A_i$ $(i = 1,2,3)$ is defined by

$$D(A_i) = \{\varphi \in C^2(\bar{\Omega}) : \tfrac{\partial \varphi}{\partial \nu} = 0 \text{ on } \partial\Omega\},\ i = 1,2,3,$$

$$A_1\varphi = A_3\varphi = -m_h\varphi,\ \varphi \in D(A_1),$$

$$A_2\varphi = -(\alpha_1 + m_h)\varphi,\ \varphi \in D(A_2).$$

Define $F = (F_1, F_2, F_3, F_4, F_5, F_6) : [0, +\infty) \times X^+ \to \mathbb{X}$ by

$$\begin{aligned}
F_1(t,\phi) &= b_h H_p^*(\cdot) - \tfrac{c_{vh} n(t,\cdot)\phi_1(0,\cdot)\phi_6(0,\cdot)}{H_p^*(\cdot)},\\
F_2(t,\phi) &= \tfrac{c_{vh} n(t,\cdot)\phi_1(0,\cdot)\phi_6(0,\cdot)}{H_p^*(\cdot)},\\
F_3(t,\phi) &= \alpha_1 \phi_2(0,\cdot),\\
F_4(t,\phi) &= b_v(t,\cdot)(\phi_4(0,\cdot) + \phi_5(0,\cdot) + \phi_6(0,\cdot)) - \tfrac{c_{hv} n(t,\cdot)\phi_2(0,\cdot)\phi_4(0,\cdot)}{H_p^*(\cdot)}\\
&\quad -k_v(t,\cdot)(\phi_4(0,\cdot) + \phi_5(0,\cdot) + \phi_6(0,\cdot))\phi_4(0,\cdot),\\
F_5(t,\phi) &= \tfrac{c_{hv} n(t,\cdot)\phi_2(0,\cdot)\phi_4(0,\cdot)}{H_p^*(\cdot)} - k_v(t,\cdot)(\phi_4(0,\cdot) + \phi_5(0,\cdot) + \phi_6(0,\cdot))\phi_5(0,\cdot)\\
&\quad -(1 - \tau'(t)) \int_\Omega \Gamma(t, t-\tau(t), \cdot, y) c_{hv} n(t-\tau(t), y) \tfrac{\phi_2(-\tau(t),y)\phi_4(-\tau(t),y)}{H_p^*(y)} dy,\\
F_6(t,\phi) &= (1 - \tau'(t)) \int_\Omega \Gamma(t, t-\tau(t), \cdot, y) c_{hv} n(t-\tau(t), y) \tfrac{\phi_2(-\tau(t),y)\phi_4(-\tau(t),y)}{H_p^*(y)} dy\\
&\quad -k_v(t,\cdot)(\phi_4(0,\cdot) + \phi_5(0,\cdot) + \phi_6(0,\cdot))\phi_6(0,\cdot),
\end{aligned}$$

for all $t \geq 0$ and $\phi = (\phi_1, \phi_2, \phi_3, \phi_4, \phi_5, \phi_6) \in X^+$. Then system (5.1) can be written as

$$\begin{aligned}
&\tfrac{\mathrm{d}u}{\mathrm{d}t} = \mathcal{A}(t)u + F(t, u_t), t > 0,\\
&u_0 = \phi \in X^+.
\end{aligned} \tag{5.3}$$

From the expression of $F$, we see that $F$ is locally Lipschitz continuous. For any $(t,\phi) \in \mathbb{R}_+ \times X^+$, we have

$$\lim_{k \to 0^+} \frac{1}{k} \operatorname{dist}(\phi(0,\cdot) + kF(t,\phi), \mathbb{X}) = 0.$$

Obviously, $T(t,s) : \mathbb{X} \to \mathbb{X}$, $\forall t \geq s \geq 0$. By [87, Corollary 4] with $K = \mathbb{X}$ and $S(t,s) = T(t,s)$, it then follows that for any $\phi \in X^+$, system (5.1) has a unique noncontinuable mild solution $u(t,\cdot,\phi) = (S_h(t,\cdot), I_h(t,\cdot), R_h(t,\cdot),\ S_v(t,\cdot),\ E_v(t,\cdot), I_v(t,\cdot))$

with $u_0 = \phi$ on its maximal existence interval $t \in [0, t_\phi)$, where $t_\phi \leq +\infty$, and $u(t, \cdot, \phi) \in \mathbb{X}$, $\forall t \in [0, t_\phi)$. Moreover, the semigroup theory arguments in [87, Theorem 1] implies that $u(t, \cdot, \phi)$ is a classical solution of system (5.1) for $t > \hat{\tau}$.

Choose

$$K = \{\phi \in \mathbb{X} : \phi_i \geq 0, \forall i \neq 5,\ \phi_4 + \phi_5 + \phi_6 \geq 0\}.$$

For any given $(t, \phi) \in \mathbb{R}_+ \times C([-\hat{\tau}, 0], K)$, we have $\phi(0, \cdot) + kF(t, \phi) \in K$ for sufficiently small $k > 0$, and hence, $\lim_{k \to 0^+} \frac{1}{k} \text{dist}(\phi(0, \cdot) + kF(t, \phi), K) = 0$. Clearly, $T(t, s) : K \to K$, $\forall t \geq s \geq 0$. It follows from [87, Corollary 4] that for any $\phi \in C([-\hat{\tau}, 0], K)$, the solution $u(t, \cdot, \phi)$ with $u_0 = \phi$ satisfies $S_h(t, \cdot) \geq 0$, $I_h(t, \cdot) \geq 0$, $R_h(t, \cdot) \geq 0$, $S_v(t, \cdot) \geq 0$ and $I_v(t, \cdot) \geq 0$ for all $t \in [0, t_\phi)$. In view of the biological meaning of $\tau(t)$, we impose the following compatibility condition:

$$E_v(0, \cdot) = \int_{-\tau(0)}^{0} T_4(0, s) c_{hv} n(s, \cdot) \frac{I_h(s, \cdot)}{H_p^*(\cdot)} S_v(s, \cdot) ds. \tag{5.4}$$

Define

$$D := \left\{ \phi \in X^+ : \phi_5(0, \cdot) = \int_{-\tau(0)}^{0} T_4(0, s) c_{hv} n(s, \cdot) \frac{\phi_2(s, \cdot)\phi_4(s, \cdot)}{H_p^*(\cdot)} ds \right\}.$$

By the uniqueness of solutions of system (5.1) and the compatibility condition (5.4), it follows that

$$E_v(t, \cdot) = \int_{t-\tau(t)}^{t} T_4(t, s) c_{hv} n(s, \cdot) \frac{I_h(s, \cdot)}{H_p^*(\cdot)} S_v(s, \cdot) ds, \tag{5.5}$$

and hence, $E_v(t, \cdot) \geq 0$ for all $t \in [0, t_\phi)$. Therefore, for any $\phi \in D$, $u(t, \cdot, \phi)$ with $u_0 = \phi$ is nonnegative for all $t \in [0, t_\phi)$.

Note that the density of total vector population $V_p(t, x) = S_v(t, x) + E_v(t, x) + I_v(t, x)$ satisfies

$$\frac{\partial V_p}{\partial t} = D\Delta V_p + b_v(t, x)V_p - m_v(t, x)V_p - k_v(t, x)V_p^2,\ t > 0,\ x \in \Omega, \tag{5.6}$$

subject to the Neumann boundary condition. For system (5.6), we have

$$\frac{\partial V_p}{\partial t} \leq D\Delta V_p + \overline{b}_v V_p - \underline{m_v} V_p - \underline{k_v} V_p^2,$$

where $\overline{b}_v = \max_{t \in [0, \omega], x \in \bar{\Omega}} b_v(t, x)$, $\underline{k_v} = \min_{t \in [0, \omega], x \in \bar{\Omega}} k_v(t, x)$, $\underline{m_v} = \min_{t \in [0, \omega], x \in \bar{\Omega}} m_v(t, x)$. Then $S_v(t, \cdot)$, $E_v(t, \cdot)$, and $I_v(t, \cdot)$ are bounded on $t \in [0, t_\phi)$. From the first three equations of system (5.1), we see that the density of total cattle population satisfies

$$\frac{\partial H_p(t, x)}{\partial t} = b_h H_p^*(x) - m_h H_p(t, x), \tag{5.7}$$

and hence, $S_h(t,\cdot)$, $I_h(t,\cdot)$, and $R_h(t,\cdot)$ are bounded on $t \in [0, t_\phi)$, which implies $t_\phi = \infty$. Further, $\lim_{t\to\infty}(H_p(t,x) - H_p^*(x)) = 0$ uniformly for $x \in \bar{\Omega}$. It then follows from the comparison argument that solutions of system (5.1) with initial data in $D$, and hence in $X^+$, exist globally on $[0, +\infty)$ and are also ultimately bounded.

It is easy to see that there exists a positive vector $\zeta = (\zeta_1, \zeta_2) = (\frac{b_h \bar{H}_p}{m_h}, \frac{\bar{b}_v - \underline{m}_v}{\underline{k}_v})$ such that

$$b_h H_p^*(x) - m_h \zeta_1 \leq 0,\ b_v(t,x)\zeta_2 - (m_v(t,x) + k_v(t,x)\zeta_2)\zeta_2 \leq 0,$$

where $\bar{H}_p = \max_{x\in\bar{\Omega}} H_p^*(x)$. This implies that for any $m \geq 1$, $m\zeta$ is an upper solution of systems (5.6) and (5.7). This implies that solutions of system (5.6) are uniformly bounded. Thus, we have the following result.

**Lemma 5.2.1.** *Let (A1) hold. For any $\phi \in X^+$, system (5.1) has a unique nonnegative solution $u(t,\cdot,\phi)$ on $[0,+\infty)$ with $u_0 = \phi$, and solutions are ultimately bounded and uniformly bounded.*

## 5.3 The basic reproduction ratio

Now we define the basic reproduction ratio $R_0$ by using the theory developed in [75,150]. According to [52], let $\mu$ be the principal eigenvalue of the periodic parabolic problem

$$\begin{aligned} \tfrac{\partial V_p}{\partial t} &= D\Delta V_p - m_v(t,x)V_p + b_v(t,x)V_p + \mu V_p, \\ \tfrac{\partial V_p}{\partial \nu} &= 0, t > 0, x \in \partial\Omega. \end{aligned}$$

From [52, Section 17.2], we have $\mu < 0$ since $(A1)$ holds. Then by a standard convergence result on the periodic-parabolic logistic equations (see, e.g., [52, Theorem 28.1] and [151, Theorem 3.1.5]), it follows that system (5.6) admits a globally asymptotically stable positive $\omega$-periodic solution $V_p^*(t,\cdot)$ in $\mathbb{Y}^+ \setminus \{0\}$. Thus, system (5.1) has the following limiting system:

$$\begin{aligned}
&\tfrac{\partial S_h}{\partial t} = b_h H_p^*(x) - c_{vh} n(t,x) \tfrac{I_v}{H_p^*(x)} S_h - m_h S_h,\\
&\tfrac{\partial I_h}{\partial t} = c_{vh} n(t,x) \tfrac{I_v}{H_p^*(x)} S_h - (\alpha_1 + m_h) I_h,\\
&\tfrac{\partial R_h}{\partial t} = \alpha_1 I_h - m_h R_h,\\
&\tfrac{\partial S_v}{\partial t} = D\Delta S_v + b_v(t,x) V_p^*(t,x) - c_{hv} n(t,x) \tfrac{I_h}{H_p^*(x)} S_v - (m_v(t,x) + k_v(t,x) V_p^*(t,x)) S_v,\\
&\tfrac{\partial E_v}{\partial t} = D\Delta E_v + c_{hv} n(t,x) \tfrac{I_h}{H_p^*(x)} S_v - (m_v(t,x) + k_v(t,x) V_p^*(t,x)) E_v\\
&\qquad\qquad -(1-\tau'(t)) \textstyle\int_\Omega \Gamma(t, t-\tau(t), x, y) c_{hv} n(t-\tau(t), y) \tfrac{I_h(t-\tau(t),y)}{H_p^*(x)} S_v(t-\tau(t), y) dy,\\
&\tfrac{\partial I_v}{\partial t} = D\Delta I_v - (m_v(t,x) + k_v(t,x) V_p^*(t,x)) I_v\\
&\qquad\qquad +(1-\tau'(t)) \textstyle\int_\Omega \Gamma(t, t-\tau(t), x, y) c_{hv} n(t-\tau(t), y) \tfrac{I_h(t-\tau(t),y)}{H_p^*(y)} S_v(t-\tau(t), y) dy,\\
&\tfrac{\partial S_v}{\partial \nu} = \tfrac{\partial E_v}{\partial \nu} = \tfrac{\partial I_v}{\partial \nu} = 0, t > 0, x \in \partial\Omega.
\end{aligned}\tag{5.8}$$

Similarly, the fifth equation of system (5.8) can be rewritten as the integral form (5.5). Since the third and fifth equations are decoupled from others, we focus on the following system:

$$\begin{aligned}
&\tfrac{\partial S_h}{\partial t} = b_h H_p^*(x) - c_{vh} n(t,x) \tfrac{I_v}{H_p^*(x)} S_h - m_h S_h,\\
&\tfrac{\partial I_h}{\partial t} = c_{vh} n(t,x) \tfrac{I_v}{H_p^*(x)} S_h - (\alpha_1 + m_h) I_h,\\
&\tfrac{\partial S_v}{\partial t} = D\Delta S_v + b_v(t,x) V_p^*(t,x) - c_{hv} n(t,x) \tfrac{I_h}{H_p^*(x)} S_v - (m_v(t,x) + k_v(t,x) V_p^*(t,x)) S_v,\\
&\tfrac{\partial I_v}{\partial t} = D\Delta I_v - (m_v(t,x) + k_v(t,x) V_p^*(t,x)) I_v\\
&\qquad\qquad +(1-\tau'(t)) \textstyle\int_\Omega \Gamma(t, t-\tau(t), x, y) c_{hv} n(t-\tau(t), y) \tfrac{I_h(t-\tau(t),y)}{H_p^*(y)} S_v(t-\tau(t), y) dy,\\
&\tfrac{\partial S_v}{\partial \nu} = \tfrac{\partial I_v}{\partial \nu} = 0, t > 0, x \in \partial\Omega.
\end{aligned}\tag{5.9}$$

Define $\mathbb{Z} := C(\bar{\Omega}, \mathbb{R}^4)$, $Z := C([-\hat{\tau}, 0], \mathbb{Z})$, $\mathbb{Z}^+ := C(\bar{\Omega}, \mathbb{R}_+^4)$, and $Z^+ := C([-\hat{\tau}, 0], \mathbb{Z}^+)$. By arguments similar to those in the proof of Lemma 5.2.1, together with [87, Corollary 4, Theorem 1 and Remark 1.1] and the proof of [148, Lemma 2.1], we have the following result.

**Lemma 5.3.1.** *Let (A1) hold. For any $\phi \in Z^+$, system (5.9) has a unique nonnegative solution $w(t, \cdot, \phi)$ on $[0, +\infty)$ with $w_0 = \phi$, and solutions are ultimately bounded and uniformly bounded. Moreover, system (5.9) generates an $\omega$-periodic semiflow*

$Q(t) := w_t(\cdot) : Z^+ \to Z^+$.

Let $\mathbb{E} := C(\bar{\Omega}, \mathbb{R}^2)$, $\mathbb{E}^+ := C(\bar{\Omega}, \mathbb{R}^2_+)$ and $C_\omega(\mathbb{R}, \mathbb{E})$ be the Banach space consisting of all $\omega$-periodic and continuous functions from $\mathbb{R}$ to $\mathbb{E}$, where $\|\phi\|_{C_\omega(\mathbb{R},\mathbb{E})} := \max_{\theta\in[0,\omega]} \|\phi(\theta)\|_{\mathbb{E}}$ for any $\phi \in C_\omega(\mathbb{R}, \mathbb{E})$. Setting $I_h = I_v = 0$ in system (5.9), we obtain the equations for the density of susceptible populations:

$$\begin{aligned}\frac{\partial S_h}{\partial t} &= b_h H_p^*(x) - m_h S_h, \\ \frac{\partial S_v}{\partial t} &= D\Delta S_v + b_v(t,x)V_p^*(t,x) - (m_v(t,x) + k_v(t,x)V_p^*(t,x))S_v,\end{aligned} \tag{5.10}$$

where $S_v$ is subject to Neumann boundary condition. By [148, Lemma 2.1], it is easy to see that system (5.10) admits a globally attractive positive $\omega$-periodic solution $(H_p^*(\cdot), V_p^*(t,\cdot))$ in $\mathbb{E}^+$. Linearizing system (5.9) at disease-free periodic solution $(H_p^*, 0, V_p^*, 0)$, we then consider the following system of infectious compartments:

$$\begin{aligned}&\tfrac{\partial I_h}{\partial t} = c_{vh} n(t,x) I_v - (\alpha_1 + m_h) I_h, \\ &\tfrac{\partial I_v}{\partial t} = D\Delta I_v - (m_v(t,x) + k_v(t,x)V_p^*(t,x))I_v \\ &\qquad +(1-\tau'(t)) \int_\Omega \Gamma(t, t-\tau(t), x, y) c_{hv} n(t-\tau(t), y) \tfrac{I_h(t-\tau(t),y)}{H_p^*(y)} V_p^*(t-\tau(t), y) dy, \\ &\tfrac{\partial I_v}{\partial \nu} = 0, t > 0, x \in \partial\Omega.\end{aligned} \tag{5.11}$$

Let $E := C([-\hat{\tau}, 0], \mathbb{E})$ and $E^+ := C([-\hat{\tau}, 0], \mathbb{E}^+)$. We define the operator $F(t) : E \to \mathbb{E}$ by

$$F(t)\phi = (F_1(t)\phi_2, F_2(t)\phi_1), \forall \phi = (\phi_1, \phi_2) \in E, t \in \mathbb{R},$$

where $F_1(t)\phi_2 = c_{vh} n(t,\cdot)\phi_2(0,\cdot)$ and $F_2(t)\phi_1 = (1-\tau'(t)) \int_\Omega \Gamma(t, t-\tau(t), \cdot, y) c_{hv} n(t-\tau(t), y) \times \frac{\phi_1(-\tau(t),y)}{H_p^*(y)} V_p^*(t-\tau(t), y) dy$. Let

$$-V(t)v = \mathbf{D}\Delta v - W(t)v,$$

where $\mathbf{D} = \mathrm{diag}(0, \mathrm{D})$ and

$$-[W(t)](x) = \begin{pmatrix} -(\alpha_1 + m_h) & 0 \\ 0 & -(m_v(t,x) + k_v(t)V_p^*(t,x)) \end{pmatrix}, \forall x \in \bar{\Omega}.$$

Then system (5.11) can be written as

$$\frac{dv}{dt} = F(t)v_t - V(t)v, t \geq 0.$$

Suppose that $T_5(t,s)$, $t \geq s$, is the evolution operator on $\mathbb{Y}$ associated with

$$\frac{\partial u}{\partial t} = D\Delta u - (m_v(t,\cdot) + k_v(t,\cdot)V_p^*(t,\cdot))u, t > 0,$$

subject to the Neumann boundary condition. Let $\Phi(t,s) = \operatorname{diag}(T_2(t,s), T_5(t,s))$, $t \geq s$, be the evolution family on $\mathbb{E}$ associated with the following linear system:

$$\frac{\mathrm{d}v}{\mathrm{d}t} = -V(t)v.$$

Recall that the exponential growth bound of $\Phi(t,s)$ is defined as

$$\tilde{\omega}(\Phi) = \inf\{\bar{\omega} : \exists M_0 \geq 1 \text{ such that } \|\Phi(t+s,s)\| \leq M_0 e^{\bar{\omega}t},\ \forall s \in \mathbb{R},\ t \geq 0\}.$$

By [124, Proposition A.2], we have

$$\tilde{\omega}(\Phi) = \frac{\ln r(\Phi(\omega,0))}{\omega} = \frac{\ln r(\Phi(\omega+\zeta,\zeta))}{\omega}, \forall \zeta \in [0,\omega].$$

From Theorem 1.3.3 and [52, Lemma 14.2], we have

$$0 < r(\Phi(\omega,0)) = \max\{r(T_2(\omega,0)), r(T_5(\omega,0))\} < 1,$$

where $r(\Phi(\omega,0))$ is the spectral radius of $\Phi(\omega,0)$. It follows from [124, Proposition 5.6] that $\tilde{\omega}(\Phi) < 0$. Note that $\Phi(t,s)$ is a positive operator in the sense that $\Phi(t,s)\mathbb{E}^+ \subseteq \mathbb{E}^+$ for all $t \geq s$. Then [124, Theorem 3.12] implies that $-V(t)$ is resolvent positive. Therefore, $F(t)$ and $V(t)$ satisfy the following assumptions:

(H1) $F(t) : E^+ \to \mathbb{E}^+$ is positive.

(H2) $-V(t)$ is resolvent positive and $\tilde{\omega}(\Phi) < 0$.

Following [75,150], we introduce the basic reproduction ratio $R_0$ for system (5.9). Suppose that $v \in C_\omega(\mathbb{R},\mathbb{E})$ and $v(t)$ is the initial distribution of infectious cattle and midges at time $t \in \mathbb{R}$. Then for any given $s \geq 0$, $F(t-s)v_{t-s}$ is the density distribution of newly infectious cattle and midges at time $t-s$, which is produced by the infectious cattle and midges who were introduced over the time interval $[t-s-\hat{\tau}_m, t-s]$. Then $\Phi(t,t-s)F(t-s)v_{t-s}$ is the density distribution of those infected cattle and midges who were newly infected at time $t-s$ and remain in the infectious 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 density distribution of accumulative new infectious at time $t$ produced by all those infectious cattle and midges introduced at all previous time to $t$. In fact, for any given $s \geq 0$, $\Phi(t, t-s)v(t-s)$ is the density distribution of those infectious individuals who were introduced at time $t-s$ and remain in the infectious compartments at time $t$, and hence, $\int_0^{+\infty} \Phi(t, t-s)v(t-s)ds$ is the density distribution of accumulative infectious individuals who were introduced at all previous time to $t$ and remain in the infected compartments at time $t$. Then the density distribution of newly infectious cattle and midges at time $t$ is $F(t)\int_0^{+\infty} \Phi(t+\cdot, t-s+\cdot)v(t-s+\cdot)ds$.

Now we define two linear next generation operators on $C_\omega(\mathbb{R}, \mathbb{E})$ by

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

and

$$[\mathcal{L}v](t) := F(t)\int_0^{+\infty} \Phi(t+\cdot, t-s+\cdot)v(t-s+\cdot)ds, \ \forall t \in \mathbb{R}, \ v \in C_\omega(\mathbb{R}, \mathbb{E}).$$

Let $A$ and $B$ be two bounded linear operators on $C_\omega(\mathbb{R}, \mathbb{E})$ defined by

$$[Av](t) = \int_0^{+\infty} \Phi(t, t-s)v(t-s)ds, \ [Bv](t) = F(t)v_t, \ \forall t \in \mathbb{R}, \ v \in C_\omega(\mathbb{R}, \mathbb{E}).$$

Further,

$$Av = (A_1v_1, A_2v_2), \ Bv = (B_1v_2, B_2v_1), \ \forall v \in C_\omega(\mathbb{R}, \mathbb{E}),$$

where

$$[A_1v_1](t) = \int_0^{+\infty} T_2(t, t-s)v(t-s)ds, \ [A_2v_2](t) = \int_0^{+\infty} T_5(t, t-s)v(t-s)ds, \ \forall t \in \mathbb{R},$$

$$B_1v_2(t) = F_1(t)v_{2t}, B_2v_1(t) = F_2(t)v_{1t}, \forall t \in \mathbb{R}, \ \forall v_t = (v_{1t}, v_{2t}) \in E.$$

We then have $L = A \circ B$ and $\mathcal{L} = B \circ A$, and hence, $L$ and $\mathcal{L}$ have the same spectral radius. Motivated by [8, 124, 150], we define the basic reproduction ratio as $R_0 := r(L) = r(\mathcal{L})$, where $r(L)$ and $r(\mathcal{L})$ are the spectral radius of $L$ and $\mathcal{L}$, respectively.

For any given $t \geq 0$, let $\hat{P}(t)$ be the solution map of system (5.11) on $E$, that is, $\hat{P}(t)\phi = v_t(\phi)$, where $v_t(\phi)(\theta, x) = v(t+\theta, x, \phi) = (v_1(t+\theta, x, \phi), v_2(t+\theta, x, \phi))$, $\forall(\theta, x) \in [-\hat{\tau}, 0] \times \bar{\Omega}$, and $v(t, x, \phi)$ is the unique solution of system (5.11) with $v(\theta, x, \phi) = \phi(\theta, x)$, $\forall(\theta, x) \in [-\hat{\tau}, 0] \times \bar{\Omega}$. Then $\hat{P} := \hat{P}(\omega)$ is the Poincaré map associated with system (5.11). Let $r(\hat{P})$ be the spectral radius of $\hat{P}$.

In order to apply the generalized Krein-Rutman theorem (see, e.g., [98, 151]), the key idea is to prove that linear system (5.11) can generate an (eventually) strongly monotone periodic semiflow on a suitable phase space. Since the periodic semiflow $\hat{P}(t)$ is monotone but not strongly monotone on $E$, we define

$$\mathcal{E} := C([-\tau(0), 0], Y) \times Y \text{ and } \mathcal{E}^+ := C([-\tau(0), 0], Y^+) \times Y^+.$$

Then $(\mathcal{E}, \mathcal{E}^+)$ is an ordered Banach space. Given a function $w : [-\tau(0), +\infty) \times [0, +\infty) \to \mathbb{E}$, we define $w_t \in \mathcal{E}$ by $w_t(\theta) = (w_1(t+\theta), w_2(t))$, $\forall \theta \in [-\tau(0), 0]$, $\forall t \geq 0$.

**Lemma 5.3.2.** *Let (A1) hold. For any $\psi \in \mathcal{E}^+$, system (5.11) has a unique nonnegative solution $w(t, \cdot, \psi)$ on $[0, +\infty)$ with $w_0 = \psi$.*

*Proof.* Let $\bar{\tau} = \min_{t \in [0,\omega]} \tau(t)$. For any $t \in [0, \bar{\tau}]$, since $t - \tau(t)$ is strictly increasing in $t$, we have $-\tau(0) = 0 - \tau(0) \leq t - \tau(t) \leq \bar{\tau} - \tau(\bar{\tau}) \leq \bar{\tau} - \bar{\tau} = 0$, and hence, $I_h(t - \tau(t), \cdot) = \psi_1(t - \tau(t), \cdot)$. Thus,

$$\begin{aligned}
&\tfrac{\partial I_h}{\partial t} = c_{vh} n(t,x) I_v - (\alpha_1 + m_h) I_h,\\
&\tfrac{\partial I_v}{\partial t} = D\Delta I_v - (m_v(t,x) + k_v(t,x) V_p^*(t,x)) I_v\\
&\qquad\qquad + (1 - \tau'(t)) \textstyle\int_\Omega \Gamma(t, t-\tau(t), x, y) c_{hv} n(t - \tau(t), y) \tfrac{\psi_1(t-\tau(t),y)}{H_p^*(y)} V_p^*(t - \tau(t), y) dy,\\
&\tfrac{\partial I_v}{\partial \nu} = 0, x \in \partial\Omega.
\end{aligned}$$

Given $\psi \in \mathcal{E}^+$, the solution $(w_1(t, \cdot), w_2(t, \cdot))$ of the above linear system exists uniquely for $t \in [0, \bar{\tau}]$. This implies that $\Psi_1(\theta, \cdot) := w_1(\theta, \cdot)$, $\forall \theta \in [-\tau(0), \bar{\tau}]$ and $\Psi_2(\theta, \cdot) := w_2(\theta, \cdot)$, $\forall \theta \in [0, \bar{\tau}]$.

We can repeat this procedure to $[n\bar{\tau}, (n+1)\bar{\tau}]$ for all $n \in \mathbb{N}$ by the method of steps. Thus, for any $\psi \in \mathcal{E}^+$, the solution $w(t, \cdot, \psi)$ exists uniquely and is nonnegative for all $t \geq 0$. □

**Remark 5.3.1.** *By the uniqueness of solutions in Lemmas 5.3.1 and 5.3.2, it follows that for any $\varphi \in E^+$ and $\psi \in \mathcal{E}^+$ with $\varphi_1(\theta, \cdot) = \psi_1(\theta, \cdot)$, $\forall \theta \in [-\tau(0), 0]$, and $\varphi_2(0, \cdot) = \psi_2(\cdot)$, then $v(t, \cdot, \varphi) = w(t, \cdot, \psi)$, $t \geq 0$, where $v(t, \cdot, \varphi)$ and $w(t, \cdot, \psi)$ are solutions of system (5.11) satisfying $v_0 = \varphi$ and $w_0 = \psi$, respectively.*

For any given $t \geq 0$, let $P(t) : \mathcal{E} \to \mathcal{E}$ be the solution map of system (5.11) on $\mathcal{E}$, that is, $P(t)\phi = w_t(\phi)$, where $w_t(\phi)(\theta, x) = w(t+\theta, x, \phi) = (w_1(t+\theta, x, \phi), w_2(t, x, \phi))$,

$\forall(\theta, x) \in [-\tau(0), 0] \times \bar{\Omega}$, and $w(t, x, \phi)$ is the unique solution of system (5.11) with $w(\theta, x, \phi) = \phi(\theta, x)$, $\forall(\theta, x) \in [-\tau(0), 0] \times \bar{\Omega}$. Then $P := P(\omega)$ is the Poincaré map associated with system (5.11). Let $r(P)$ be the spectral radius of $P$. Now we show that the periodic semiflow $P(t)$ is eventually strongly monotone.

**Lemma 5.3.3.** *Let (A1) hold. For any $\varphi$ and $\psi$ in $\mathcal{E}$ with $\varphi > \psi$ (that is, $\varphi \geq \psi$, but $\varphi \not\equiv \psi$), the solutions $\bar{w}(t, \cdot, \varphi)$ and $w(t, \cdot, \psi)$ of system (5.11) with $\bar{w}_0 = \varphi$ and $w_0 = \psi$, respectively, satisfy $\bar{w}_i(t, \cdot, \varphi) > w_i(t, \cdot, \psi)$ for all $t > \hat{\tau}$, $i = 1, 2$, and hence, $P(t)\varphi \gg P(t)\psi$ in $\mathcal{E}$ for all $t > 2\hat{\tau}$.*

*Proof.* Using a simple comparison argument on each interval $[n\bar{\tau}, (n+1)\bar{\tau}]$, $n \in \mathbb{N}$, we can prove that $\bar{w}_i(t, \cdot, \varphi) \geq w_i(t, \cdot, \psi)$ for all $t \geq 0$, $i = 1, 2$.

Let $\varphi, \psi \in \mathcal{E}$ satisfy $\varphi > \psi$. Denote $\bar{w}(t, \cdot) = \bar{w}(t, \cdot, \varphi) = (\bar{w}_1(t, \cdot), \bar{w}_2(t, \cdot))$ and $w(t, \cdot) = w(t, \cdot, \psi) = (w_1(t, \cdot), w_2(t, \cdot))$. Without loss of generality, we assume that $\varphi_1 > \psi_1$.

**Claim 1.** There exists $t_0 \in [0, \hat{\tau}]$ such that $\bar{w}_2(t, \cdot) > w_2(t, \cdot)$ for all $t \geq t_0$.

We first prove that $\bar{w}_2(t_0, \cdot) > w_2(t_0, \cdot)$ for some $t_0 \in [0, \hat{\tau}]$. Otherwise, we have $\bar{w}_2(t, \cdot) = w_2(t, \cdot)$, $\forall t \in [0, \hat{\tau}]$, and hence $\frac{\partial \bar{w}_2}{\partial t} = \frac{\partial w_2}{\partial t}$ for all $t \in [0, \hat{\tau}]$. Thus, we have

$$(1 - \tau'(t)) \int_\Omega \Gamma(t, t - \tau(t), \cdot, y) c_{hv} n(t - \tau(t), y) \frac{V_p^*(t - \tau(t), y)}{H_p^*(y)} \times (\bar{w}_1(t - \tau(t), y) - w_1(t - \tau(t), y)) dy = 0,$$

for any $t \in [0, \hat{\tau}]$. It follows that $\bar{w}_1(t - \tau(t), \cdot) = w_1(t - \tau(t), \cdot)$ for all $t \in [0, \hat{\tau}]$. Since $-\tau(0) \leq t - \tau(t) \leq \hat{\tau} - \tau(\hat{\tau})$, $\forall t \in [0, \hat{\tau}]$, and $\hat{\tau} - \tau(\hat{\tau}) \geq 0$, we have $\varphi_1(\theta, \cdot) = \psi_1(\theta, \cdot)$ for all $\theta \in [-\tau(0), 0]$, which is a contradiction to the assumption $\varphi_1 > \psi_1$ in $\mathcal{E}$.

Let

$$g_1(t, x, \xi) := D\Delta\xi - (m_v(t, x) + k_v(t, x) V_p^*(t, x))\xi + (1 - \tau'(t)) \int_\Omega \Gamma(t, t - \tau(t), x, y) \times c_{hv} n(t - \tau(t), y) \frac{w_1(t - \tau(t), y)}{H_p^*(y)} V_p^*(t - \tau(t), y) dy, x \in \bar{\Omega}.$$

Since

$$\frac{\partial \bar{w}_2}{\partial t} = D\Delta\bar{w}_2 - (m_v(t, x) + k_v(t, x) V_p^*(t, x))\bar{w}_2 + (1 - \tau'(t)) \int_\Omega \Gamma(t, t - \tau(t), x, y) \times c_{hv} n(t - \tau(t), y) \frac{\bar{w}_1(t - \tau(t), y)}{H_p^*(y)} V_p^*(t - \tau(t), y) dy,$$

$$\geq D\Delta\bar{w}_2 - (m_v(t,x) + k_v(t,x)V_p^*(t,x))\bar{w}_2 + (1-\tau'(t))\int_\Omega \Gamma(t, t-\tau(t), x, y)$$
$$\times\, c_{hv} n(t-\tau(t), y)\frac{w_1(t-\tau(t), y)}{H_p^*(y)} V_p^*(t-\tau(t), y)dy = g_1(t, x, \bar{w}_2),$$

we have $\frac{\partial \bar{w}_2}{\partial t} - g_1(t,x,\bar{w}_2) \geq 0 = \frac{\partial w_2}{\partial t} - g_1(t,x,w_2)$, $\forall t \geq t_0$, $x \in \Omega$, with $\frac{\partial \bar{w}_2}{\partial \nu} = \frac{\partial w_2}{\partial \nu} = 0$, $x \in \partial\Omega$. Since $\bar{w}_2(t_0,\cdot) > w_2(t_0,\cdot)$, it follows that $\bar{w}_2(t,\cdot) > w_2(t,\cdot)$ for all $t \geq t_0$ due to the parabolic maximum principle.

**Claim 2.** $\bar{w}_1(t,\cdot) > w_1(t,\cdot)$ for all $t > t_0$.

Let $g_2(t,x,\xi) := c_{vh} n(t,x) w_2 - (\alpha_1 + m_h)\xi$, $\forall x \in \Omega$. Then for all $t \geq t_0$, we have

$$\begin{aligned}\frac{\partial \bar{w}_1}{\partial t} =& c_{vh} n(t,x)\bar{w}_2 - (\alpha_1 + m_h)\bar{w}_1\\ >& c_{vh} n(t,x) w_2 - (\alpha_1 + m_h)\bar{w}_1 = g_2(t,x,\bar{w}_1).\end{aligned}$$

Then $\frac{\partial \bar{w}_1}{\partial t} - g_2(t,x,\bar{w}_1) > 0 = \frac{\partial w_1}{\partial t} - g_2(t,x,w_1)$, $\forall t \geq t_0$, $x \in \Omega$, with $\frac{\partial \bar{w}_1}{\partial \nu} = \frac{\partial w_1}{\partial \nu} = 0$, $x \in \partial\Omega$. Since $\bar{w}_2(t_0,\cdot) > w_2(t_0,\cdot)$, it follows that $\bar{w}_1(t,\cdot) > w_1(t,\cdot)$ for all $t > t_0$ due to the parabolic maximum principle.

From the above two claims, we obtain that $\bar{w}_i(t,\cdot) > w_i(t,\cdot)$, $i = 1, 2$, $\forall t > t_0$. Since $t_0 \in [0, \hat{\tau}]$, we have $\bar{w}_i(t,\cdot) > w_i(t,\cdot)$, $i = 1, 2$, for all $t > \hat{\tau}$. This implies that $P(t) : \mathcal{E} \to \mathcal{E}$ is strongly monotone for all $t > 2\hat{\tau}$. □

Since the first equation of system (5.11) has no diffusion term, its solution map $\hat{P}(t)$ is not compact. But we are able to prove that for each $t > 0$, $\hat{P}(t)$ is $\alpha$-contraction on $E$, where $\alpha$ is the Kuratowski measure of noncompactness in the space $E$.

**Lemma 5.3.4.** *Let (A1) hold. If $r(\hat{P}) \geq 1$, then $r(\hat{P})$ is an eigenvalue of $\hat{P}$ with a strongly positive eigenvector on $E$. Moreover, $r(\hat{P}) = r(P)$.*

*Proof.* Let $v(t,x,\phi) = (v_1(t,x,\phi), v_2(t,x,\phi))$ be the solution of system (5.11) with $v(\theta,x,\phi) = \phi(\theta,x)$, $\forall(\theta,x) \in [-\hat{\tau}, 0] \times \bar{\Omega}$. We first prove that $r_e(\hat{P}) < 1$, where $r_e(\hat{P})$ is the essential spectral radius of $\hat{P}$.

Let $\Lambda(t)\phi = (T_2(t,0)\phi_1, T_5(t,0)\phi_2)$ is a linear semigroup on $\mathbb{E}$. Define

$$J(t,\phi) = (J_1(t,\phi), J_2(t,\phi)), \forall t > 0, \phi = (\phi_1, \phi_2) \in E,$$

where

$$J_1(t,\phi)(x) := c_{vh} n(t,x)\phi_2(0,x), \forall x \in \bar{\Omega},$$

$$\begin{aligned}J_2(t,\phi)(x) :=&(1-\tau'(t))\int_{\Omega}\Gamma(t,t-\tau(t),x,y)c_{hv}n(t-\tau(t),y)\frac{\phi_1(-\tau(t),y)}{H_p^*(y)}\\ &\times V_p^*(t-\tau(t),y)dy, \forall x\in\bar{\Omega}.\end{aligned}$$

By the constant variation formula, we have

$$v(t,x,\phi)=\Lambda(t)[\phi(0,\cdot)]+\int_0^t\Lambda(t-s)J(s,v_s(\phi))ds, \forall t>0.$$

Define a linear operator

$$(S_1(t)\phi)(\theta)=(T_2(t+\theta,0)\phi_1(0,\cdot),0), \forall\phi\in E, t+\theta>0, t\geq 0, \theta\in[-\hat{\tau},0],$$

and a nonlinear operator

$$(S_2(t)\phi)(\theta)=(\int_0^{t+\theta}T_2(t+\theta,s)J_1(s,v_s(\phi))ds, v_2(t+\theta,\cdot,\phi)),$$

$\forall\phi\in E, t+\theta>0, t\geq 0, \theta\in[-\hat{\tau},0]$. Then $\hat{P}(t)\phi=S_1(t)\phi+S_2(t)\phi$, $\phi\in E$, $t\geq 0$. It is easy to choose an integer $K>0$ such that $K\omega>\hat{\tau}$ and

$$\|T_2(K\omega+\theta,0)\|_{\mathbb{Y}}\leq\frac{1}{2}, \ \forall\theta\in[-\hat{\tau},0].$$

Since the boundedness of $\hat{P}(t)$ and the compactness of $T_5(t,s)$ for all $t>s$, by the same argument as in the proof of [75, Lemma 4.3], it then follows that for any bounded subset $B$ of $E$, $S_2(K\omega)B$ is precompact, and hence, $\alpha(S_2(K\omega)B)=0$. Note that there exists $C_0>0$ such that $\|\frac{d}{d\theta}T_2(K\omega+\theta,0)\|_{\mathbb{Y}}\leq C_0$, $\forall\theta\in[-\hat{\tau},0]$ due to $K\omega>\hat{\tau}$. According to [30, Section 7.4], we have

$$\alpha(S_1(K\omega)B)=\max_{\theta\in[-\hat{\tau},0]}\alpha((S_1(K\omega)B)(\theta))=\max_{\theta\in[-\hat{\tau},0]}\alpha(T_2(K\omega+\theta,0)[B(0)]),$$

where $(S_1(K\omega)B)(\theta):=\{(S_1(K\omega)\phi)(\theta):\phi\in B\}$ and $B(0):=\{\phi(0):\phi\in B\}$. It follows from the proof of [30, Section 7.4] that $\alpha(B(0))\leq\alpha(B)$. Thus, we have

$$\begin{aligned}\alpha(\hat{P}(K\omega)B)&\leq\alpha(S_1(K\omega)B))+\alpha(S_2(K\omega)B))=\alpha(S_1(K\omega)B))\\ &\leq\max_{\theta\in[-\hat{\tau},0]}\|T_2(K\omega+\theta,0)\|\alpha(B(0))\leq\frac{1}{2}\alpha(B).\end{aligned}$$

This implies that $r_e(\hat{P}(K\omega))\leq\frac{1}{2}$ due to [30, Theorem 9.9], and hence, $r_e(\hat{P}(\omega))\leq(\frac{1}{2})^{\frac{1}{K}}<1$. Thus, $r_e(\hat{P})<r(\hat{P})$.

By the weak version of the generalized Krein-Rutman theorem in Theorem 1.3.4 (see also [76]), $r(\hat{P})$ is an eigenvalue of $\hat{P}$ with a positive eigenfunction $\phi^* \in E$. Now we prove that $\phi^*$ is strongly positive on $E$. Let $\psi^* = (\psi_1^*, \psi_2^*) \in \mathcal{E}$ with $\psi_1^*(\theta, \cdot) = \phi_1^*(\theta, \cdot)$ for all $\theta \in [-\tau(0), 0]$ and $\psi_2^*(\cdot) = \phi_2^*(0, \cdot)$, and $\phi_1^*(\theta) = \psi_1^*(-\tau(0))$, $\forall \theta \in [-\hat{\tau}, -\tau(0)]$, $\phi_2^*(\theta) = \psi_2^*(0))$, $\forall \theta \in [-\hat{\tau}, 0]$. By Remark 5.3.1, $w(t, \cdot, \psi^*) = v(t, \cdot, \phi^*)$ for all $t \geq 0$, where $w(t, \cdot, \psi^*)$ and $v(t, \cdot, \phi^*)$ are solutions of system (5.11) satisfying $w(\theta, \cdot, \psi^*) = \psi^*(\theta, \cdot) \in \mathcal{E}^+$ and $v(\theta, \cdot, \phi^*) = \phi^*(\theta, \cdot) \in E^+$, respectively. From Lemma 5.3.3, we obtain that $w(t, \cdot, \psi^*)$ is strongly positive on $\mathcal{E}$ for any $t > 2\hat{\tau}$, and hence, $\psi^*$ is strongly positive on $\mathcal{E}$ due to [87, Theorem 3]. Since $w(t, \cdot, \psi^*) = v(t, \cdot, \phi^*)$ and the uniqueness of eigenfunctions, $\phi^*$ is also strongly positive on $E$.

Moreover, by arguments similar to those in [82, Lemma 3.8], we can obtain that $r(\hat{P}) = r(P)$. □

Let $\{U(t, s, \lambda) : t \geq s\}$ be the evolution family on $E$ of the following linear periodic system with parameter $\lambda \in [0, +\infty)$:

$$\frac{\mathrm{d}v(t)}{\mathrm{d}t} = \lambda F(t) v_t - V(t) v(t), t \geq 0. \tag{5.12}$$

In order to obtain the relationship between the sign of $R_0 - 1$ and $r(\hat{P}) - 1$, according to Theorem 1.4.2, we only need to verify the following assumptions:

(H3) The positive linear operator $L$ possesses the principal eigenvalue.

(H4) The positive linear operators $U(\omega, 0, \lambda)$ possesses the isolated principal eigenvalue with finite multiplicity for any $\lambda \in [0, +\infty)$ whenever $r(U(\omega, 0, \lambda)) \geq 1$.

(H5) Either the principal eigenvalue of $L$ is isolated, or there exists an integer $n_0 > 0$ such that $L^{n_0}$ is strongly positive.

**Lemma 5.3.5.** *$R_0 - 1$ has the same sign as $r(\hat{P}) - 1$.*

*Proof.* Our arguments are motivated by [75, Lemma 4.7]. We have known that (H1) and (H2) hold. Next we prove that (H3)-(H5) are valid.
**Claim 1.** $L^2$ is compact on $C_\omega(\mathbb{R}, \mathbb{E})$.

Clearly, $A_1$, $B_1$, $A_2$ and $B_2$ are bounded in $C_\omega(\mathbb{R}, \mathbb{E})$. By [116, Chapter 7], $A_2$ is compact on $C_\omega(\mathbb{R}, \mathbb{E})$. Since $A_1 B_1 A_2 B_2$ and $A_2 B_2 A_1 B_1$ are compact on $C_\omega(\mathbb{R}, \mathbb{Y})$, we

have $L^2$ is compact on $C_\omega(\mathbb{R},\mathbb{E})$ due to $L^2v = ABABv = (A_1B_1A_2B_2v_1, A_2B_2A_1B_1v_2)$.
**Claim 2.** $L$ admits the principal eigenvalue.

Obviously, $A_1$, $B_1$, $A_2$ and $B_2$ are strictly positive and map $\mathrm{Int}(Y^+)$ to $\mathrm{Int}(Y^+)$. Note that $T_5(t,s)$ is strongly positive on $\mathbb{Y}$ for any $t > s$. Then for any $v_2 \in C_\omega(\mathbb{R},\mathbb{Y}^+)\setminus\{0\}$, $\int_0^{+\infty} T_5(t,t-s)v_2(t-s)ds$, $t \in \mathbb{R}$ is strongly positive on $\mathbb{Y}$. That is, $A_2$ is strongly positive on $C_\omega(\mathbb{R},\mathbb{Y})$, and hence, $A_2B_2A_1B_1$ are strongly positive on $C_\omega(\mathbb{R},\mathbb{Y})$.

Now we prove that $r(L) > 0$. For a fixed $v_2 \in C_\omega(\mathbb{R},\mathbb{Y}^+) \setminus \{0\}$, there exists $r > 0$ such that $A_2B_2A_1B_1v_2 \geq rv_2$ in $\mathbb{Y}$. Then $L^2v \geq rv$, where $v = (0, v_2)$, and hence, $r(L^2) > 0$ due to the Gelfand's formula. It follows from the Krein-Rutman theorem (see, e.g., [30, Theorem 19.2]) that $L^2$ possesses the principal eigenvalue with an eigenfunction $\tilde{v} \in C_\omega(\mathbb{R},\mathbb{E}^+) \setminus \{0\}$. Since $r^2(L) = r(L^2)$ and $(r^2(L) - L^2)\tilde{v} = 0$, we have $(r(L) - L)\hat{v} = 0$, where $\hat{v} = (r(L) + L)\tilde{v} \in C_\omega(\mathbb{R},\mathbb{E}^+) \setminus \{0\}$. This implies that $L$ possesses the principal eigenvalue with positive eigenfunction in $C_\omega(\mathbb{R},\mathbb{E}^+)$. Therefore, (H3) and (H5) hold true.

It remains to prove (H4). Let $\hat{P}_\lambda := U(\omega, 0, \lambda)$ be the Poincaré map on $E$ associated with system (5.12). We repeat the arguments in Lemma 5.3.4 to obtain that $r(\hat{P}_\lambda)$ is the principal eigenvalue whenever $r(\hat{P}_\lambda) \geq 1$. Then (H4) holds. Thus, by Theorem 1.4.2, $R_0 - 1$ has the same sign as $r(\hat{P}) - 1$. □

By Lemma 5.3.1, we can define the solution maps $Q(t) : Z^+ \to Z^+$ associated with system (5.9) by $Q(t)\phi = u_t(\phi)$, where $u_t(\phi)(\theta,x) = u(t+\theta,x,\phi)$, $t \geq 0$, $(\theta,x) \in [-\hat{\tau},0]\times\bar{\Omega}$, and $u(t,x,\phi)$ is the unique solution of system (5.9) with $u(\theta,x) = \phi(\theta,x)$, $(\theta,x) \in [-\hat{\tau},0]\times\bar{\Omega}$. Then $Q := Q(\omega)$ is the Poincaré map associated with system (5.9). Since the first two equations in system (5.9) have no diffusion terms, its solution map $Q(t)$ is not compact. Due to the lack of compactness, we need to prove the following observation.

**Lemma 5.3.6.** *Let (A1) hold. Then $Q$ is $\alpha$-contracting in the sense that*

$$\lim_{n\to\infty} \alpha(Q^n(B)) = 0 \text{ for any bounded set } B \subseteq Z^+.$$

*Proof.* Let $B$ be a given bounded subset of $Z^+$. Motivated by [55, Lemma 4.1], we first show that $Q^n = Q(n\omega)$ is asymptotically compact on $B$ in the sense that for any sequences $\psi_k = (\psi_{k1}, \psi_{k2}, \psi_{k3}, \psi_{k4}) \in B$ and $n_k \to \infty$, there exist subsequences $k_j \to \infty$ and $\psi_{k_j} \in B$ such that $Q^{n_{k_j}}(\psi_{k_j})$ converges in $Z$ as $j \to \infty$. By Lemma 5.3.1, the solution $\{u(n_k\omega,\cdot,\psi_k)\}_{k\geq 1}$ is uniformly bounded on $\bar{\Omega}$ for all $k\geq 1$, and hence, there exists an $\eta>0$ such that

$$|S_h(t,x,\psi_k)|<\eta, |I_h(t,x,\psi_k)|<\eta,$$

$$|S_v(t,x,\psi_k)|<\eta, |I_v(t,x,\psi_k)|<\eta, \forall k\geq 1, t\geq 0, x\in\bar{\Omega}.$$

Since $n_k\omega>\hat{\tau}$ for all sufficiently large $k$, in view of the generalized Arzela-Ascoli theorem for space $Z^+=C([-\hat{\tau},0],\mathbb{Z}^+)$, it suffices to prove that (i) for each $\theta\in[-\hat{\tau},0]$, the set $\{Q^{n_k}(\psi_k)(\theta)\}_{k\geq 1}$ is precompact in $\mathbb{Z}^+$; (ii) the sequence $\{Q^{n_k}(\psi_k)\}_{k\geq 1}$ is equicontinuous in $\theta\in[-\hat{\tau},0]$.

Now we prove the statement (i). By the Arzela-Ascoli theorem, it suffices to prove for any given $\theta\in[-\hat{\tau},0]$, $\{Q^{n_k}(\psi_k)(\theta,x)\}_{k\geq 1}$ is equicontinuous in $x\in\bar{\Omega}$ for all $k\geq 1$. Note that $\{S_v(n_k\omega+\theta,x,\psi_k)\}_{k\geq 1}$ and $\{I_v(n_k\omega+\theta,x,\psi_k)\}_{k\geq 1}$ are equicontinuous in $x\in\bar{\Omega}$ for all $k\geq 1$, $\theta\in[-\hat{\tau},0]$. Then we first show that $\{S_h(n_k\omega+\theta,x,\psi_k)\}_{n\geq 1}$ is equicontinuous in $x\in\bar{\Omega}$ for all $k\geq 1$, $\theta\in[-\hat{\tau},0]$. Let

$$g_k(x,t):=b_hH_p^*(x)-c_{vh}n(t,x)\frac{I_v(t,x,\psi_k)}{H_p^*(x)}S_h(t,x,\psi_k),$$

and hence, for each $k\geq 1$, $g_k(x,t)$ is a continuous function on $\bar{\Omega}\times\mathbb{R}_+$. Let $v_k(t,x)=S_h(t,x,\psi_k)$, $t\geq 0$, $x\in\bar{\Omega}$. Define $\overline{v}_k(t,x):=v_k(t+n_k\omega,x)$, $\forall t\geq -n_k\omega$, $x\in\bar{\Omega}$. Clearly,

$$\begin{aligned}
&\frac{\partial}{\partial t}[(\overline{v}_k(t+\theta,x_1)-\overline{v}_k(t+\theta,x_2))^2]\\
=&2(\overline{v}_k(t+\theta,x_1)-\overline{v}_k(t+\theta,x_2))\frac{\partial}{\partial t}[\overline{v}_k(t+\theta,x_1)-\overline{v}_k(t+\theta,x_2)]\\
=&2(\overline{v}_k(t+\theta,x_1)-\overline{v}_k(t+\theta,x_2))[g_k(x_1,t+n_k\omega+\theta)-g_k(x_2,t+n_k\omega+\theta)\\
&-m_h(\overline{v}_k(t+\theta,x_1)-\overline{v}_k(t+\theta,x_2))]\\
\leq&4\eta|g_k(x_1,t+n_k\omega+\theta)-g_k(x_2,t+n_k\omega+\theta)|-2m_h[\overline{v}_k(t+\theta,x_1)-\overline{v}_k(t+\theta,x_2)]^2,
\end{aligned}$$

for all $t\geq -n_k\omega-\theta$, $\theta\in[-\hat{\tau},0]$, $x_1,x_2\in\bar{\Omega}$. Set $h_k(t,x,y):=|g_k(x,t+n_k\omega+\theta)-g_k(y,t+n_k\omega+\theta)|$. By the constant variation formula and the comparison argument, we obtain

$$\begin{aligned}
|\overline{v}_k(t+\theta,x_1)-\overline{v}_k(t+\theta,x_2)|^2\leq&e^{-2m_h(t-s)}|\overline{v}_k(s+\theta,x_1)-\overline{v}_k(s+\theta,x_2)|^2\\
&+4\eta\int_s^t e^{-2m_h(t-r)}h_k(r,x_1,x_2)dr, \qquad (5.13)
\end{aligned}$$

for all $t \geq s \geq -n_k\omega - \theta$. Letting $t = 0$ and $s = -n_k\omega - \theta$ in (5.13), we have

$$\begin{aligned}|\overline{v}_k(\theta, x_1) - \overline{v}_k(\theta, x_2)|^2 \leq & e^{-2m_h(n_k\omega+\theta)}|\overline{v}_k(-n_k\omega, x_1) - \overline{v}_k(-n_k\omega, x_2)|^2 \\ & + 4\eta \int_{-n_k\omega-\theta}^{0} e^{2m_h r} h_k(r, x_1, x_2) dr,\end{aligned}$$

and hence,

$$\begin{aligned}|S_h(n_k\omega + \theta, x_1, \psi_k) - S_h(n_k\omega + \theta, x_2, \psi_k)|^2 \leq & e^{-2m_h(n_k\omega+\theta)}|\psi_{k1}(0, x_1) - \psi_{k1}(0, x_2)|^2 \\ & + 4\eta \int_{-n_k\omega-\theta}^{0} e^{2m_h r} h_k(r, x_1, x_2) dr,\end{aligned} \tag{5.14}$$

for all $k \geq 1$, $x_1, x_2 \in \bar{\Omega}$. We further prove that for any $\epsilon > 0$, there exists $\delta > 0$ such that

$$|S_h(n_k\omega + \theta, x_1, \psi_k) - S_h(n_k\omega + \theta, x_2, \psi_k)| < \epsilon, \forall k \geq 1, \forall x_1, x_2 \in \bar{\Omega} \text{ with } |x_1 - x_2| < \delta.$$

Suppose, by contradiction, that there exist $\epsilon_0 > 0$, $k_j \to \infty$, $x_j, y_j \in \bar{\Omega}$ with $|x_j - y_j| < 1/j$ such that

$$|S_h(n_{k_j}\omega + \theta, x_j, \psi_{n_{k_j}}) - S_h(n_{k_j}\omega + \theta, y_j, \psi_{n_{k_j}})| \geq \epsilon_0, \forall j \geq 1.$$

It then follows from (5.14) that

$$\begin{aligned}\epsilon_0^2 &\leq \limsup_{j\to\infty} |S_h(n_{k_j}\omega + \theta, x_j, \psi_{n_{k_j}}) - S_h(n_{k_j}\omega + \theta, y_j, \psi_{n_{k_j}})|^2 \\ &\leq 4\eta \limsup_{j\to\infty} \int_{-n_{k_j}\omega-\theta}^{0} e^{2m_h r} h_{n_{k_j}}(r, x_j, y_j) dr.\end{aligned} \tag{5.15}$$

For each $r \leq 0$, we can choose an integer $k_0 > 0$ such that $\{I_v(r + n_k\omega + \theta, x, \psi_k)\}_{k\geq k_0}$ is equicontinuous in $x \in \bar{\Omega}$ for all $k \geq k_0$. It is easy to see that for each $k \geq 1$, $g_k(x, t)$ is uniformly continuous in $(x, t) \in \bar{\Omega} \times \mathbb{R}_+$. Since $\lim_{j\to\infty} |I_v(r + n_{k_j}\omega + \theta, x_j, \psi_{n_{k_j}}) - I_v(r + n_{k_j}\omega + \theta, y_j, \psi_{n_{k_j}})| = 0$, for any given $r \leq 0$, we have $\lim_{j\to\infty} h_{n_{k_j}}(r, x_j, y_j) = 0$. According to Fatou's lemma, (5.15) becomes

$$\epsilon_0^2 \leq 4\eta \int_{-\infty}^{0} e^{2m_h r} \limsup_{j\to\infty} h_{n_{k_j}}(r, x_j, y_j) dr = 0,$$

which is a contradiction. Similarly, we can verify that $\{I_h(n_k\omega + \theta, x, \psi_k)\}_{k\geq 1}$ is also equicontinuous in $x \in \bar{\Omega}$ for all $k \geq 1$. This shows that statement (i) holds true.

Next we prove statement (ii). Since $n_k \to \infty$, without loss of generality, we assume that $n_1\omega > \hat{\tau}$ and $n_k \geq n_1$, $\forall k \geq 1$. By the mean value theorem, we easily see that $S_h(n_k\omega + \theta, \cdot, \psi_k)$ and $I_h(n_k\omega + \theta, \cdot, \psi_k)$ are equicontinuous in $\theta \in [-\hat{\tau}, 0]$ on $C(\bar{\Omega}, \mathbb{R})$. Since $Q^{n_k}(\psi_k) = Q^{n_1}(Q^{n_k - n_1}(\psi_k)) = Q(n_1\omega)(Q^{n_k-n_1}(\psi_k))$, $\forall k \geq 1$, it follows that the sequence $\{(S_v)_{n_k\omega}(\psi_k), (I_v)_{n_k\omega}(\psi_k)\}_{k\geq 1}$ is precompact in $C([-\hat{\tau}, 0], C(\bar{\Omega}, \mathbb{R}^2))$ (see, e.g., the proof of [151, Theorem 3.5.1]). This implies that the sequence of functions $\{S_v(n_k\omega + \theta, \cdot, \psi_k), I_v(n_k\omega + \theta, \cdot, \psi_k)\}_{k\geq 1}$ is equicontinuous in $\theta \in [-\hat{\tau}, 0]$ on $C(\bar{\Omega}, \mathbb{R}^2)$. Consequently, the sequence $\{S_h(n_k\omega + \theta, \cdot, \psi_k), I_h(n_k\omega + \theta, \cdot, \psi_k), S_v(n_k\omega + \theta, \cdot, \psi_k), I_v(n_k\omega + \theta, \cdot, \psi_k)\}_{k\geq 1}$ is equicontinuous in $\theta \in [-\hat{\tau}, 0]$ on $C(\bar{\Omega}, \mathbb{R}^4)$. Thus, $Q^n$ is asymptotically compact on $B$.

Now we consider the omega limit set of $B$ for $Q$ on $Z^+$, defined by

$$\omega(B) = \{\psi \in Z^+ : \lim_{k\to\infty} Q^{n_k}(\psi_k) = \psi \text{ for some sequence } \psi_k \in B \text{ and } n_k \to \infty\}.$$

Since $Q^n$ is asymptotically compact on $B$, it follows that $\omega(B)$ is a nonempty, compact and invariant set for $Q$ in $Z^+$, and $\omega(B)$ attracts $B$ (see, e.g., the proof of [114, Lemma 23.1(2)]). By Lemma 1.1.1(b), we have

$$\alpha(Q^n(B)) \leq \alpha(\omega(B)) + \delta(Q^n(B), \omega(B)) = \delta(Q^n(B), \omega(B)) \to 0 \text{ as } n \to \infty,$$

where $\delta(B, A) = \sup_{x\in B} d(x, A) = \sup_{x\in B} \inf_{y\in A} d(x, y)$ for any subsets $A$, $B$ of Banach space. □

In view of Lemma 5.3.1, we see that $Q$ is point dissipative on $Z^+$, the positive orbits of bounded subsets for $Q$ are bounded, and $Q$ is $\alpha$-contracting on $Z^+$. It follows from Theorem 1.1.3 (ii) that $Q$ has a global attractor that attracts each bounded set in $Z^+$.

## 5.4 Global dynamics

Now we are ready to prove the main results of the global dynamics for system (5.9). Using the comparison principle and Lemma 5.3.1, we can obtain the following result.

**Lemma 5.4.1.** *Assume that (A1) holds. Let* $u(t, \cdot, \phi)$ *be the solution of system (5.9) with* $u_0 = \phi \in Z^+$. *If there exists some* $t_0 \geq 0$ *such that* $u_i(t_0, \cdot, \phi) \not\equiv 0$ *for some* $i \in \{2, 4\}$, *then* $u_i(t, x, \phi) > 0$ *for all* $t > t_0$, $x \in \bar{\Omega}$. *Moreover, for any* $\phi \in Z^+$, *we* *have* $u_i(t,x,\phi) > 0$*,* $i = 1,3$*,* $t > 0$*,* $x \in \bar{\Omega}$*, and* $\liminf_{t\to\infty} u_i(t,x,\phi) \geq \bar{\eta}$*,* $i = 1,3$*, uniformly for* $x \in \bar{\Omega}$*, where* $\bar{\eta}$ *is a* $\phi$*-independent positive constant.*

*Proof.* For any $\phi \in Z^+$, it is easy to see that $u_2(t,x,\phi)$ and $u_4(t,x,\phi)$ satisfy

$$\begin{aligned}
&\tfrac{\partial u_2}{\partial t} \geq -(\alpha_1 + m_h)u_2,\\
&\tfrac{\partial u_4}{\partial t} \geq D\Delta u_4 - (\overline{m}_v + \overline{k}_v\overline{V}_p^*)u_4,\\
&\tfrac{\partial u_4}{\partial \nu} = 0, t > 0, x \in \partial\Omega,
\end{aligned}$$

where

$$\overline{k}_v = \max_{t\in[0,\omega],x\in\bar{\Omega}} k_v(t,x), \overline{m}_v = \max_{t\in[0,\omega],x\in\bar{\Omega}} m_v(t,x), \text{ and } \overline{V}_p^* = \max_{t\in[0,\omega],x\in\bar{\Omega}} V_p^*(t,x).$$

If $u_i(t_0,\cdot,\phi) \not\equiv 0$ for some $t_0 \geq 0$, $i = 2,4$, then $u_i(t_0,\cdot,\phi) > 0$ for all $t > t_0$, $x \in \bar{\Omega}$ due to the comparison principle.

By Lemma 5.3.1, solutions of system (5.9) are uniformly bounded, and hence, there exists a constant $C > 0$ such that $u_2(t,x,\phi) < C$ and $u_4(t,x,\phi) < C$, $\forall t > 0$, $x \in \bar{\Omega}$. Let $v_1(t,x,\phi_1)$ be the solution of

$$\begin{aligned}
&\tfrac{\partial v_1}{\partial t} = b_h H_p^*(x) - (c_{vh} n(t,x)\tfrac{C}{H_p^*(x)} + m_h)v_1, t > 0, x \in \Omega,\\
&\tfrac{\partial v_1}{\partial \nu} = 0, t > 0, x \in \partial\Omega, \qquad (5.16)\\
&v_1(0,x) = \phi_1(0,x), x \in \Omega.
\end{aligned}$$

Then we have $u_1(t,x,\phi) \geq v_1(t,x,\phi_1) > 0$, $t > 0$, $x \in \bar{\Omega}$. Since system (5.16) admits a globally attractive positive periodic solution $v_1^*(t,x)$, we have

$$\liminf_{t\to\infty} u_1(t,x,\phi) \geq \bar{\eta}_1 := \min_{t\in[0,\omega],x\in\bar{\Omega}} v_1^*(t,x) > 0,$$

uniformly for $x \in \bar{\Omega}$. Similarly, we can obtain $\liminf_{t\to\infty} u_3(t,x,\phi) \geq \bar{\eta}_2 > 0$ uniformly for $x \in \bar{\Omega}$. Setting $\bar{\eta} := \min\{\bar{\eta}_1, \bar{\eta}_2\}$, this completes the proof. □

**Theorem 5.4.1.** *Let (A1) hold. The following statements are valid:*

*(i) If* $R_0 < 1$*, then the disease-free periodic solution* $(H_p^*(x), 0, V_p^*(t,x), 0)$ *is globally attractive for system (5.9) in* $Z^+$*.*

*(ii) If $R_0 > 1$, then there exists an $\hat{\eta} > 0$ such that for any $\phi \in Z^+$ with $\phi_2(0,\cdot) \not\equiv 0$ and $\phi_4(0,\cdot) \not\equiv 0$, we have*

$$\liminf_{t\to\infty} \min_{x\in\bar{\Omega}} (S_h(t,x,\phi), I_h(t,x,\phi), S_v(t,x,\phi), I_v(t,x,\phi)) \geq (\hat{\eta},\hat{\eta},\hat{\eta},\hat{\eta}).$$

*Proof.* (i) In the case where $R_0 < 1$, Lemmas 5.3.4 and 5.3.5 imply that $r(\hat{P}) < 1$. Consider the following system with parameter $\varepsilon > 0$:

$$\begin{aligned}
\tfrac{\partial I_h}{\partial t} &= c_{vh} n(t,x) \tfrac{H_p^*(x)+\varepsilon}{H_p^*(x)} I_v - (\alpha_1 + m_h) I_h,\\
\tfrac{\partial I_v}{\partial t} &= D\Delta I_v - (m_v(t,x) + k_v(t,x) V_p^*(t,x)) I_v + (1-\tau'(t)) \textstyle\int_\Omega \Gamma(t, t-\tau(t), x, y)\\
&\qquad \times c_{hv} n(t-\tau(t), y) \tfrac{I_h(t-\tau(t),y)}{H_p^*(x)} (V_p^*(t-\tau(t),y)+\varepsilon) dy,\\
\tfrac{\partial I_v}{\partial \nu} &= 0, t > 0, x \in \partial\Omega.
\end{aligned} \tag{5.17}$$

For any $\varphi \in E$, let $v^\varepsilon(t,s,\varphi)$ be the unique solution of system (5.17) with $v_s^\varepsilon(s,\varphi) = \varphi$, where $v_t^\varepsilon(s,\varphi)(\theta,x) = v^\varepsilon(t+\theta,s,x,\varphi)$, $\theta \in [-\hat{\tau},0]$. Let $V_\varepsilon(t,s)$, $t \geq s$, be the evolution operator of system (5.17) on $E$, and then $V_\varepsilon(t,s)\varphi = v_t^\varepsilon(s,\varphi)$. Since $\lim_{\varepsilon\to 0} r(V_\varepsilon(\omega,0)) = r(\hat{P}) < 1$, we can fix a sufficiently small number $\varepsilon > 0$ such that $r(V_\varepsilon(\omega,0)) < 1$. Hence, the exponential growth bound $\tilde{\omega}(V_\varepsilon) < 0$, then there exists $\gamma > 0$ such that $\tilde{\omega}(V_\varepsilon) + \gamma < 0$. By the definition of $\tilde{\omega}(V_\varepsilon)$, there exists $M_0 > 0$ such that

$$\|V_\varepsilon(t+s,s)\varphi\|_E \leq M_0 e^{(\tilde{\omega}(V_\varepsilon)+\gamma)t} \|\varphi\|_E, \forall t \geq 0, \forall s \in \mathbb{R}, \varphi \in E.$$

Then $\|V_\varepsilon(t+s,s)\varphi\|_E \to 0$ as $t \to \infty$, $\forall s \in \mathbb{R}$, and hence, $\|v^\varepsilon(t+s+\theta,s,x,\varphi)\| \to 0$ as $t \to \infty$, $\forall s \in \mathbb{R}$, $x \in \bar{\Omega}$, $\theta \in [-\hat{\tau},0]$.

By the global attractivity of $(H_p^*(\cdot), V_p^*(t,\cdot))$ for system (5.10) and the comparison principle, there exists a sufficiently large integer $N_0 > 0$ such that $N_0\omega > \hat{\tau}$ and $S_h^*(t,x) \leq H_p^*(x) + \varepsilon$ and $S_v^*(t,x) \leq V_p^*(t,x) + \varepsilon$, $\forall t \geq N_0\omega - \hat{\tau}$, $x \in \bar{\Omega}$. Clearly, the solution $(I_h(t,x,\phi), I_v(t,x,\phi))$ of system (5.9) satisfies

$$\begin{aligned}
\tfrac{\partial I_h}{\partial t} &\leq c_{vh} n(t,x) \tfrac{H_p^*(x)+\varepsilon}{H_p^*(x)} I_v - (\alpha_1 + m_h) I_h,\\
\tfrac{\partial I_v}{\partial t} &\leq D\Delta I_v - (m_v(t,x) + k_v(t,x) V_p^*(t,x)) I_v + (1-\tau'(t)) \textstyle\int_\Omega \Gamma(t, t-\tau(t), x, y)\\
&\qquad \times c_{hv} n(t-\tau(t), y) \tfrac{I_h(t-\tau(t),y)}{H_p^*(y)} (V_p^*(t-\tau(t),y)+\varepsilon) dy,\\
\tfrac{\partial I_v}{\partial \nu} &= 0, t > N_0\omega, x \in \partial\Omega.
\end{aligned}$$

For any given $\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in Z^+$, there exists $m_0 > 0$ such that

$$(I_h(t, x, \phi), I_v(t, x, \phi)) \le m_0 v^\varepsilon(t, N_0\omega, x, \varphi_0), \forall t \in [N_0\omega, N_0\omega + \hat{\tau}], x \in \bar{\Omega}, \varphi_0 = (\phi_2, \phi_4).$$

By the comparison principle, we have

$$(I_h(t, x, \phi), I_v(t, x, \phi)) \le m_0 v^\varepsilon(t, N_0\omega + \hat{\tau}, x, \varphi_0), \forall t \ge N_0\omega + \hat{\tau}, x \in \bar{\Omega}.$$

Then $\lim_{t\to\infty}(I_h(t, x, \phi), I_v(t, x, \phi)) = (0, 0)$ uniformly for $x \in \bar{\Omega}$, $\forall \phi \in Z^+$. Then the $S_h$, $S_v$ equations in system (5.9) are asymptotic to system (5.10). Now we use the theory of internally chain transitive sets (see, e.g., [151]) to prove that

$$\lim_{t\to\infty} \|(S_h(t, x, \phi), S_v(t, x, \phi)) - (H_p^*(x), V_p^*(t, x))\| = 0 \text{ uniformly for } x \in \bar{\Omega}.$$

For any $\varphi \in E^+$, let $\nu(t, x, \varphi(0, \cdot))$ be the solution of system (5.11) with $\nu(0, x) = \varphi(0, x)$. Define a solution semiflow of system (5.11) on $E^+$ by

$$\nu_t(\theta, x, \varphi) = \begin{cases} \nu(t + \theta, x, \varphi(0, x)), & \text{if } t + \theta > 0, t > 0, \theta \in [-\hat{\tau}, 0], \\ \varphi(t + \theta, x), & \text{if } t + \theta \le 0, t > 0, \theta \in [-\hat{\tau}, 0]. \end{cases}$$

Let $\bar{P}(\varphi) = \nu_\omega(\varphi)$. For convenience, we rewrite the solution map $Q(t)$ for system (5.9) as $\hat{Q}(t)$ in the following way:

$$\hat{Q}(t)\phi = (S_h(t + \theta, \cdot, \phi), S_v(t + \theta, \cdot, \phi), I_h(t + \theta, \cdot, \phi), I_v(t + \theta, \cdot, \phi)),$$

for any $\theta \in [-\hat{\tau}, 0]$, $t \ge 0$. Let $\mathcal{W} = \omega(\phi)$ be the omega limit set of $\phi \in Z^+$ for the Poincaré map $\hat{Q}$. Since $\lim_{t\to\infty}(I_h(t, x, \phi), I_v(t, x, \phi)) = (0, 0)$ uniformly for $x \in \bar{\Omega}$, there holds $\mathcal{W} = \bar{\omega} \times \{(\hat{0}, \hat{0})\}$, where $\hat{0}(\theta, \cdot) = 0$, $\forall \theta \in [-\hat{\tau}, 0]$. By the proof of Lemma 5.3.6, it follows that the discrete forward orbit $\gamma^+(\phi) = \{\hat{Q}^{n\omega}(\phi) : n \ge 0\}$ is asymptotically compact. Thus, its omega limit set $\omega(\phi)$ is nonempty, compact and invariant for $\hat{Q}$. It then follows from Lemma 1.1.2 that $\mathcal{W}$ is an internally chain transitive set for $\hat{Q}$, and hence, $\bar{\omega}$ is an internally chain transitive set for $\bar{P}$. Define $(H_p^*, V_{p0}^*) \in E^+$ by $V_{p0}^*(\theta, \cdot) = V_p^*(\theta, \cdot)$, $\theta \in [-\hat{\tau}, 0]$. Since $\bar{\omega} \ne \{(\hat{0}, \hat{0})\}$ due to Lemma 5.4.1, and $(H_p^*, V_{p0}^*)$ is globally attractive in $E^+$, we have $\bar{\omega} \bigcap W^S((H_p^*, V_{p0}^*)) \ne \emptyset$, where $W^S((H_p^*, V_{p0}^*))$ is the stable set of $(H_p^*, V_{p0}^*)$. By Theorem 1.1.2, we get $\bar{\omega} = \{(H_p^*, V_{p0}^*)\}$. Thus, $\mathcal{W} = \{(H_p^*, V_{p0}^*, \hat{0}, \hat{0})\}$, and we have

$$\lim_{t\to\infty} \|(S_h(t, \cdot, \phi), I_h(t, \cdot, \phi), S_v(t, \cdot, \phi), I_v(t, \cdot, \phi)) - (H_p^*(\cdot), 0, V_p^*(t, \cdot), 0)\| = 0.$$

(ii) In the case where $R_0 > 1$, we have $r(\hat{P}) > 1$, and hence, $\tilde{\omega}(\hat{P}) > 0$. Let

$$Z_0 := \{\psi = (\psi_1, \psi_2, \psi_3, \psi_4) \in Z^+ : \psi_2(0, \cdot) \not\equiv 0 \text{ and } \psi_4(0, \cdot) \not\equiv 0\},$$

and

$$\partial Z_0 := Z^+ \setminus Z_0 = \{\psi \in Z^+ : \psi_2(0, \cdot) \equiv 0 \text{ or } \psi_4(0, \cdot) \equiv 0\}.$$

For any $\psi \in Z_0$, it then follows from Lemma 5.4.1 that $I_h(t, x, \psi) > 0$ and $I_v(t, x, \psi) > 0$, $t \geq 0$, $x \in \bar{\Omega}$. This implies that $Q^n(Z_0) \subseteq Z_0$, $\forall n \in \mathbb{N}$. Now we prove that $Q$ is uniformly persistent with respect to $(Z_0, \partial Z_0)$.

Let $M = (H_p^*, 0, V_{p0}^*, 0)$, where $V_{p0}^*(\theta) = V_p^*(\theta)$ for $\theta \in [-\hat{\tau}, 0]$. Since $\lim_{\psi \to M} \|Q(t)\psi - Q(t)M\| = 0$ uniformly for $t \in [0, \omega]$, for any given $\delta > 0$, there exists a $\delta_0 > 0$ such that for any $\psi \in Z_0$ with $\|\psi - M\| < \delta_0$, we have $\|Q(t)\psi - Q(t)M\| < \delta$ for all $t \in [0, \omega]$.

**Claim 1.** $\limsup_{n\to\infty} \|Q(n\omega)\psi - M\| \geq \delta_0$ for all $\psi \in Z_0$.

Suppose, by contradiction, that there exists $\psi_0 \in Z_0$ such that $\limsup_{n\to\infty} \|Q(n\omega)\psi_0 - M\| < \delta_0$. Then there exists an integer $n_0 \geq 1$ such that $\|Q(n\omega)\psi_0 - M\| < \delta_0$ for all $n \geq n_0$. For any $t \geq n_0\omega$, we have $t = t' + n\omega$ with $n \geq n_0$, $t' \in [0, \omega)$, and

$$\|Q(t)\psi_0 - Q(t)M\| = \|Q(t')Q(n\omega)\psi_0 - Q(t')M\| < \delta.$$

Therefore, $S_h(t, x, \psi_0) > H_p^*(x) - \delta$ and $S_v(t, x, \psi_0) > V_p^*(t, x) - \delta$ for all $t \geq n_0\omega$ and $x \in \bar{\Omega}$. Let $\hat{P}_\delta : E \to E$ be the Poincaré map of the following perturbed linear system:

$$\begin{aligned}
&\tfrac{\partial I_h}{\partial t} = c_{vh} n(t,x) \tfrac{H_p^*(x)-\delta}{H_p^*(x)} I_v - (\alpha_1 + m_h) I_h, \\
&\tfrac{\partial I_v}{\partial t} = D\Delta I_v - (m_v(t,x) + k_v(t,x)V_p^*(t,x)) I_v + (1 - \tau'(t)) \\
&\qquad \times \int_\Omega \Gamma(t, t-\tau(t), x, y) c_{hv} n(t-\tau(t), y) \tfrac{I_h(t-\tau(t),y)}{H_p^*(y)} (V_p^*(t-\tau(t), y) - \delta) dy, \\
&\tfrac{\partial I_v}{\partial \nu} = 0, t > 0, x \in \partial\Omega.
\end{aligned} \tag{5.18}$$

Since $\lim_{\delta\to 0^+} r(\hat{P}_\delta) = r(\hat{P}) > 1$, we can fix a sufficiently small $\delta > 0$ such that

$$\delta < \min\{\min_{x\in\bar{\Omega}} H_p^*(x), \min_{t\in[0,\omega], x\in\bar{\Omega}} V_p^*(t,x)\} \text{ and } r(\hat{P}_\delta) > 1.$$

Thus, $I_h(t,x,\psi_0)$ and $I_v(t,x,\psi_0)$ in system (5.9) satisfy

$$\begin{aligned}
&\tfrac{\partial I_h}{\partial t} \geq c_{vh} n(t,x) \tfrac{H_p^*(x)-\delta}{H_p^*(x)} I_v - (\alpha_1 + m_h) I_h, \\
&\tfrac{\partial I_v}{\partial t} \geq D\Delta I_v - (m_v(t,x) + k_v(t,x) V_p^*(t,x)) I_v + (1-\tau'(t)) \\
&\qquad \times \textstyle\int_\Omega \Gamma(t, t-\tau(t), x, y) c_{hv} n(t-\tau(t), y) \tfrac{I_h(t-\tau(t),y)}{H_p^*(y)} (V_p^*(t-\tau(t), y) - \delta) dy, \\
&\tfrac{\partial I_v}{\partial \nu} = 0, \ t \geq n_0\omega + \hat{\tau}, \ x \in \partial\Omega.
\end{aligned} \tag{5.19}$$

By repeating the arguments in Lemma 5.3.4, we can obtain that $\hat{P}_\delta$ possesses the principal eigenvalue with strongly positive vector on $E$. Thus, by arguments similar to [9, Lemma 5], there exists a positive $\omega$-periodic function $v_\delta^*(t,x)$ such that $e^{\mu_\delta t} v_\delta^*(t,x)$ is a solution of system (5.19), where $\mu_\delta = \frac{\ln r(\hat{P}_\delta)}{\omega}$.

Since $\psi_0 \in Z_0$, $I_h(t,x,\psi_0) > 0$ and $I_v(t,x,\psi_0) > 0$ for all $t \geq 0$ and $x \in \bar{\Omega}$, and hence, there exists a $\kappa > 0$ such that

$$(I_h(t,x,\psi_0), I_v(t,x,\psi_0)) \geq \kappa e^{\mu_\delta t} v_\delta^*(t,x), \forall t \in [n_0\omega - \hat{\tau}, n_0\omega], x \in \bar{\Omega}.$$

By the comparison theorem, we have

$$(I_h(t,x,\psi_0), I_v(t,x,\psi_0)) \geq \kappa e^{\mu_\delta t} v_\delta^*(t,x), \forall t \geq n_0\omega, x \in \bar{\Omega}.$$

Since $\mu_\delta = \tilde{\omega}(\hat{P}) > 0$, it follows that $I_h(t,\cdot,\psi_0) \to \infty$ and $I_v(t,\cdot,\psi_0) \to \infty$ as $t \to \infty$, a contradiction.

This claim implies that $M$ is an isolated invariant set for $Q$ in $Z^+$, and $W^S(M) \bigcap Z_0 = \emptyset$, where $W^S(M)$ is the stable set of $M$ for $Q$. Let

$$M_\partial := \{\psi \in \partial Z_0 : Q^n(\psi) \in \partial Z_0, \forall n \in \mathbb{N}\},$$

and $\omega(\psi)$ be the omega limit set of the forward orbit $\gamma^+(\psi) = \{Q^n(\psi) : \forall n \in \mathbb{N}\}$. Further we claim $M$ cannot form a cycle for $Q$ in $\partial Z_0$.

**Claim 2.** The omega limit set $\omega(\psi) = M$ for any $\psi \in M_\partial$.

For any given $\psi \in M_\partial$, $Q^n(\psi) \in \partial Z_0$, $\forall n \in \mathbb{N}$, that is, for each $n \in \mathbb{N}$, either $I_h(n\omega,\cdot,\psi) \equiv 0$ or $I_v(n\omega,\cdot,\psi) \equiv 0$. It follows that for each $t \geq 0$, $I_h(t,\cdot,\psi) \equiv 0$ or $I_v(t,\cdot,\psi) \equiv 0$. Otherwise, it contradicts Lemma 5.4.1. If $I_v(t,\cdot,\psi) \equiv 0$ for all $t \geq 0$, then $\lim_{t\to\infty}(S_h(t,x,\psi) - H_p^*(x)) = 0$ uniformly for $x \in \bar{\Omega}$. Note that the $I_h$ equation in system (5.9) satisfies $\frac{\partial I_h}{\partial t} = -(\alpha_1 + m_h) I_h$. It follows from the comparison principle that $\lim_{t\to\infty} I_h(t,x,\psi) = 0$ uniformly for $x \in \bar{\Omega}$. Then the $S_v$ equation in system (5.9) is asymptotic to

$$\frac{\partial S_v}{\partial t} = D\Delta S_v + b_v(t,x)V_p^*(t,x) - (m_v(t,x) + k_v(t,x)V_p^*(t,x))S_v, \tag{5.20}$$

which admits a globally attractive positive $\omega$-periodic solution $V_p^*(t,\cdot)$ in $\mathbb{Y}^+$. By the theory of internally chain transitive sets as argued in (i), we have $\lim_{t\to\infty}(S_v(t,x,\psi) - V_p^*(t,x)) = 0$ uniformly for $x \in \bar{\Omega}$. If $I_v(t,\cdot,\psi) \not\equiv 0$ for some $t_0 \geq 0$, then $I_v(t,\cdot,\psi) > 0$, $\forall t \geq t_0$. Then $I_h(t,\cdot,\psi) \equiv 0$, $\forall t \geq t_0$, and hence, $\lim_{t\to\infty}(S_v(t,x,\psi) - V_p^*(t,x)) = 0$ uniformly for $x \in \bar{\Omega}$. From the $I_v$ equation in system (5.9), we have $\lim_{t\to\infty} I_v(t,x,\psi) = 0$ uniformly for $x \in \bar{\Omega}$ due to the comparison principle. Then the $S_h$ equation is asymptotic to $\frac{\partial S_h}{\partial t} = b_h H_p^*(x) - m_h S_h$. Similarly, we obtain $\lim_{t\to\infty}(S_h(t,x,\psi) - H_p^*(x)) = 0$ uniformly for $x \in \bar{\Omega}$. Therefore, $\omega(\psi) = M$ for any $\psi \in M_\partial$.

Since $Q$ admits a global attractor on $Z^+$, it then follows from the acyclicity theory on uniform persistence for maps (see., e.g., Theorem 1.2.1) that $Q : Z^+ \to Z^+$ is uniformly persistent with respect to $(Z_0, \partial Z_0)$ in the sense that there exists an $\tilde{\eta} > 0$ such that

$$\liminf_{n\to\infty} d(Q^n(\psi), \partial Z_0) \geq \tilde{\eta},\ \forall \psi \in Z_0.$$

By Theorem 1.2.3, we obtain that $Q : Z_0 \to Z_0$ admits a global attractor $A_0$. Since $A_0 = Q(\omega)A_0 = Q(A_0)$, we have $\psi_2(0,\cdot) > 0$ and $\psi_4(0,\cdot) > 0$ for all $\psi \in A_0$. Let $B_0 := \bigcup_{t\in[0,\omega]} Q(t)A_0$. Then $B_0 \subseteq Z_0$ and $\lim_{t\to\infty} d(Q(t)\psi, B_0) = 0$ for all $\psi \in Z_0$. Define a continuous function $p : Z^+ \to \mathbb{R}_+$ by

$$p(\psi) = \min\{\min_{x\in\bar{\Omega}} \psi_2(0,x), \min_{x\in\bar{\Omega}} \psi_4(0,x)\}, \forall \psi = (\psi_1,\psi_2,\psi_3,\psi_4) \in Z^+.$$

Clearly, $p(\psi) > 0$ for all $\psi \in B_0$. Since $B_0$ is a compact subset of $Z_0$, we have $\inf_{\psi\in B_0} p(\psi) = \min_{\psi\in B_0} p(\psi) > 0$. By the attractiveness of $B_0$, it follows that there exists an $\check{\eta} > 0$ such that

$$\liminf_{t\to\infty} \min(\min_{x\in\bar{\Omega}} I_h(t,x,\psi), \min_{x\in\bar{\Omega}} I_v(t,x,\psi)) \geq \check{\eta}, \forall \psi \in Z_0.$$

Moreover, by Lemma 5.4.1, there exists an $\hat{\eta} \in (0,\check{\eta})$ such that

$$\liminf_{t\to\infty} \min_{x\in\bar{\Omega}}(S_h(t,x,\psi), I_h(t,x,\psi), S_v(t,x,\psi), I_v(t,x,\psi)) \geq (\hat{\eta},\hat{\eta},\hat{\eta},\hat{\eta}), \forall \psi \in Z_0.$$

□

By the theory of asymptotically periodic semiflows [151, Section 3.2] and the theory of chain transitive sets (see, e.g., Lemma 1.1.3 and Theorems 1.1.1 and 1.2.1), we can lift the threshold type result for system (5.9) to system (5.1). Thus, we have the following result.

**Theorem 5.4.2.** *Let (A1) hold. The following statements are valid:*

*(i) If $R_0 < 1$, then the disease-free periodic solution $(H_p^*(x), 0, 0, V_p^*(t,x), 0, 0)$ is globally attractive for system (5.1) in $D \setminus (C([-\hat{\tau}, 0], C(\bar{\Omega}, \mathbb{R}_+^3)) \times \{(0,0,0)\})$.*

*(ii) If $R_0 > 1$, then there exists an $\mathring{\eta} > 0$ such that for any $\phi \in D$ with $\phi_2(0,\cdot) \not\equiv 0$ and $\phi_6(0,\cdot) \not\equiv 0$, we have*

$$\liminf_{t\to\infty} \min_{x\in\bar{\Omega}} (S_h(t,x,\phi), I_h(t,x,\phi), R_h(t,x,\phi), S_v(t,x,\phi), E_v(t,x,\phi), I_v(t,x,\phi)) \geq (\mathring{\eta}, \mathring{\eta}, \mathring{\eta}, \mathring{\eta}, \mathring{\eta}, \mathring{\eta}).$$

## 5.5 Global attractivity in the case of constant coefficients

In the case where all coefficients are positive constants and spatially homogeneous, system (5.1) reduces to the following autonomous reaction-diffusion system:

$$\begin{aligned}
&\tfrac{\partial S_h}{\partial t} = b_h H_p^* - c_{vh} n \tfrac{I_v}{H_p^*} S_h - m_h S_h,\\
&\tfrac{\partial I_h}{\partial t} = c_{vh} n \tfrac{I_v}{H_p^*} S_h - (\alpha_1 + m_h) I_h,\\
&\tfrac{\partial R_h}{\partial t} = \alpha_1 I_h - m_h R_h,\\
&\tfrac{\partial S_v}{\partial t} = D\Delta S_v + b_v V_p - c_{hv} n \tfrac{I_h}{H_p^*} S_v - m_v S_v - k_v V_p S_v,\\
&\tfrac{\partial E_v}{\partial t} = D\Delta E_v + c_{hv} n \tfrac{I_h}{H_p^*} S_v - m_v E_v - k_v V_p E_v\\
&\qquad\quad - e^{-m_v\tau} \int_\Omega \Gamma(D\tau, x, y) c_{hv} n \tfrac{I_h(t-\tau, y)}{H_p^*} S_v(t-\tau, y) dy,\\
&\tfrac{\partial I_v}{\partial t} = D\Delta I_v + e^{-m_v\tau} \int_\Omega \Gamma(D\tau, x, y) c_{hv} n \tfrac{I_h(t-\tau, y)}{H_p^*} S_v(t-\tau, y) dy - m_v I_v - k_v V_p I_v,\\
&\tfrac{\partial S_v}{\partial \nu} = \tfrac{\partial E_v}{\partial \nu} = \tfrac{\partial I_v}{\partial \nu} = 0, t > 0, x \in \partial\Omega.
\end{aligned} \tag{5.21}$$

where $\Gamma(t,x,y)$ is the Green function associated with $\frac{\partial u}{\partial t} = \Delta u$ subject to the Neumann boundary condition. It is easy to see that $\lim_{t\to\infty} \|V_p(t,x) - V_p^*\| = 0$ uniformly for $x \in \bar{\Omega}$, where $V_p^* = \frac{b_v - m_v}{k_v}$. In order to avoid the extinction of the vector population, we assume that the vector birth rate $b_v$ is large enough, relative to its natural death rate $m_v$, that is,

(A2) $b_v > m_v$,

which corresponds to assumption (A1) for periodic system (5.1). We then have the following limiting system:

$$\begin{aligned}
&\tfrac{\partial S_h}{\partial t} = b_h H_p^* - c_{vh} n \tfrac{I_v}{H_p^*} S_h - m_h S_h,\\
&\tfrac{\partial I_h}{\partial t} = c_{vh} n \tfrac{I_v}{H_p^*} S_h - (\alpha_1 + m_h) I_h,\\
&\tfrac{\partial R_h}{\partial t} = \alpha_1 I_h - m_h R_h,\\
&\tfrac{\partial S_v}{\partial t} = D\Delta S_v + b_v V_p^* - c_{hv} n \tfrac{I_h}{H_p^*} S_v - (m_v + k_v V_p^*) S_v,\\
&\tfrac{\partial E_v}{\partial t} = D\Delta E_v + c_{hv} n \tfrac{I_h}{H_p^*} S_v - (m_v + k_v V_p^*) E_v\\
&\qquad\quad - e^{-m_v\tau} \int_\Omega \Gamma(D\tau, x, y) c_{hv} n \tfrac{I_h(t-\tau,y)}{H_p^*} S_v(t-\tau, y)dy,\\
&\tfrac{\partial I_v}{\partial t} = D\Delta I_v + e^{-m_v\tau} \int_\Omega \Gamma(D\tau, x, y) c_{hv} n \tfrac{I_h(t-\tau,y)}{H_p^*} S_v(t-\tau, y)dy - (m_v + k_v V_p^*) I_v,\\
&\tfrac{\partial S_v}{\partial \nu} = \tfrac{\partial E_v}{\partial \nu} = \tfrac{\partial I_v}{\partial \nu} = 0, t > 0, x \in \partial\Omega.
\end{aligned} \tag{5.22}$$

Thus, we obtain the following decoupled limiting system:

$$\begin{aligned}
&\tfrac{\partial S_h}{\partial t} = b_h H_p^* - c_{vh} n \tfrac{I_v}{H_p^*} S_h - m_h S_h,\\
&\tfrac{\partial I_h}{\partial t} = c_{vh} n \tfrac{I_v}{H_p^*} S_h - (\alpha_1 + m_h) I_h,\\
&\tfrac{\partial S_v}{\partial t} = D\Delta S_v + b_v V_p^* - c_{hv} n \tfrac{I_h}{H_p^*} S_v - (m_v + k_v V_p^*) S_v,\\
&\tfrac{\partial I_v}{\partial t} = D\Delta I_v + e^{-m_v\tau} \int_\Omega \Gamma(D\tau, x, y) c_{hv} n \tfrac{I_h(t-\tau,y)}{H_p^*} S_v(t-\tau, y)dy - (m_v + k_v V_p^*) I_v,\\
&\tfrac{\partial S_v}{\partial \nu} = \tfrac{\partial I_v}{\partial \nu} = 0, t > 0, x \in \partial\Omega.
\end{aligned} \tag{5.23}$$

By the arguments in [134, Theorem 3.4] and [150, Corollary 2.1], the basic reproduction ratio $R_0$ is defined by the spectral radius of the following $2 \times 2$ matrix

$$M = \begin{pmatrix} 0 & \frac{c_{vh} n}{b_v} \\ \frac{e^{-m_v\tau} c_{hv} n V_p^*}{(\alpha_1 + m_h) H_p^*} & 0 \end{pmatrix},$$

and hence,

$$R_0 = \sqrt{\frac{c_{vh}c_{hv}n^2V_p^*e^{-m_v\tau}}{b_v(\alpha_1+m_h)H_p^*}}.$$

When $R_0 > 1$, system (5.23) has a unique positive equilibrium $u^* = (S_h^*, I_h^*, S_v^*, I_v^*)$ with

$$\begin{aligned} S_h^* =& \frac{b_hH_p^*}{c_{vh}n\frac{I_v^*}{H_p^*}+m_h}, I_h^* = \frac{c_{vh}nI_v^*S_h^*}{(\alpha_1+m_h)H_p^*}, \\ S_v^* =& V_p^* - I_v^*e^{m_v\tau}, I_v^* = \frac{b_hb_v(\alpha_1+m_h)H_p^*(R_0^2-1)}{b_v(\alpha_1+m_h)+c_{vh}c_{hv}n^2b_h}. \end{aligned}$$

Define $\mathbb{G} := C(\bar{\Omega}, \mathbb{R})$, $\mathbb{G}^+ := C(\bar{\Omega}, \mathbb{R}_+)$, and $G := \mathbb{G}^+ \times C([-\tau, 0], \mathbb{G}^+ \times \mathbb{G}^+) \times \mathbb{G}^+$.

**Theorem 5.5.1.** *Let (A2) hold. Let $u(t, x, \phi)$ be the solution of system (5.23) with $u_0 = \phi \in G$. The following statements are valid:*

*(i) If $R_0 < 1$, then the disease-free equilibrium $(H_p^*, 0, V_p^*, 0)$ is globally attractive for system (5.23) in $G$.*

*(ii) If $R_0 > 1$, then system (5.23) has a unique constant equilibrium $u^* = (S_h^*, I_h^*, S_v^*, I_v^*)$ such that for any $\phi \in G$ with $\phi_2(0, \cdot) \not\equiv 0$ and $\phi_4(\cdot) \not\equiv 0$, we have*

$$\lim_{t\to\infty} u(t, x, \phi) = u^* \textit{ uniformly for all } x \in \bar{\Omega}.$$

*Proof.* We return to system (5.22), and then find that

$$\begin{aligned} &\tfrac{\partial H_p}{\partial t} = b_hH_p^* - m_hH_p, \\ &\tfrac{\partial V_p}{\partial t} = D\Delta V_p + b_vV_p^* - (m_v + k_vV_p^*)V_p, \\ &\tfrac{\partial V_p}{\partial \nu} = 0, t > 0, x \in \partial\Omega. \end{aligned}$$

Therefore, the set

$$\begin{aligned} H :=& \{\phi \in G : \phi_1(0, x) \le H_p^*, \phi_2(\theta, x) \le H_p^*, \phi_3(\theta, x) \le V_p^*, \phi_4(0, x) \le V_p^*, \\ & \forall\theta \in [-\tau, 0], x \in \bar{\Omega}\}. \end{aligned}$$

is positive invariant for the solution map $Q(t)$ of system (5.23) and every forward orbit of system (5.23) from $G$ enters $H$ eventually. Thus, it suffices to study the dynamics of system (5.23) on $H$. In the case where $R_0 < 1$, statement (i) follows from Theorem 5.4.1 (i).

It remains to prove statement (ii). Since $R_0 > 1$, Theorem 5.4.1 (ii) implies that system (5.23) is uniformly persistent in the sense that there exists a $\xi > 0$ such that for any $\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in H$ with $\phi_2(0, \cdot) \not\equiv 0$ and $\phi_4(\cdot) \not\equiv 0$, the solution $u(t, x, \phi)$ satisfies

$$\liminf_{t\to\infty}(S_h(t,\cdot,\phi), I_h(t,\cdot,\phi), S_v(t,\cdot,\phi), I_v(t,\cdot,\phi)) \geq (\xi,\xi,\xi,\xi). \tag{5.24}$$

Let

$$H_0 := \{\phi \in H : \phi_i(0,x) > 0,\ \forall x \in \bar{\Omega},\ i = 1,2,3,4\}.$$

Set $f(u) = u-1-\ln u, u \in (0,\infty)$, with $f(u) \geq 0$ for all $u \in (0,\infty)$ and $\min_{0<u<\infty} f(u) = f(1) = 0$. Define a continuous functional $V : H_0 \to \mathbb{R}$:

$$V(\phi) = \int_\Omega [V_1(x,\phi) + V_2(x,\phi)]\, dx,$$

where

$$V_1(x,\phi) = \frac{H_p^*}{c_{vh} n I_v^*} f\Big(\frac{\phi_1(0,x)}{S_h^*}\Big) + \frac{I_h^* H_p^*}{c_{vh} n I_v^* S_h^*} f\Big(\frac{\phi_2(0,x)}{I_h^*}\Big),$$

and

$$\begin{aligned} V_2(x,\phi) =& \frac{H_p^*}{c_{hv} n I_h^*} f\Big(\frac{\phi_3(0,x)}{S_v^*}\Big) + \frac{H_p^* I_v^*}{e^{-m_v\tau} I_h^* S_v^* c_{hv} n} f\Big(\frac{\phi_4(0,x)}{I_v^*}\Big) \\ &+ \int_{-\tau}^0 \int_\Omega \Gamma(D(-s),x,y) f\Big(\frac{\phi_3(s,y)\phi_2(s,y)}{S_v^* I_h^*}\Big) dyds. \end{aligned}$$

In what follows, we fix $\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in H$ with $\phi_2(0,\cdot) \not\equiv 0$ and $\phi_4(\cdot) \not\equiv 0$. In view of (5.24), without loss of generality, we assume that $u_t(\phi) \in H_0$, $\forall t \geq 0$. Let $\omega(\phi)$ be the omega limit set of the orbit $\gamma^+(\phi)$ for the semiflow $Q(t)$. Clearly, $\omega(\phi) \subset H_0$. Now we calculate the time derivative of $V(u_t(\phi))$ along the solution of system (5.23). Note that

$$\begin{aligned} \frac{\partial V_1(x,u_t(\phi))}{\partial t} =& \frac{H_p^*}{c_{vh} n I_v^*}\Big(1 - \frac{S_h^*}{S_h(t,x)}\Big)\frac{1}{S_h^*}\frac{\partial S_h(t,x)}{\partial t} + \frac{I_h^* H_p^*}{c_{vh} n I_v^* S_h^*}\Big(1 - \frac{I_h^*}{I_h(t,x)}\Big)\frac{1}{I_h^*}\frac{\partial I_h(t,x)}{\partial t} \\ =& -\frac{H_p^* m_h (S_h(t,x) - S_h^*)^2}{c_{vh} n I_v^* S_h^* S_h(t,x)} + \frac{1}{I_v^* S_h^*}\Big(1 - \frac{S_h^*}{S_h(t,x)}\Big)(I_v^* S_h^* - I_v(t,x) S_h(t,x)) \\ &+ \frac{1}{I_v^* S_h^*}\Big(1 - \frac{I_h^*}{I_h(t,x)}\Big)\Big(I_v(t,x)S_h(t,x) - \frac{I_v^* S_h^*}{I_h^*} I_h(t,x)\Big) \\ =& -\frac{H_p^* m_h (S_h(t,x) - S_h^*)^2}{c_{vh} n I_v^* S_h^* S_h(t,x)} + 2 - \frac{S_h^*}{S_h(t,x)} + \frac{I_v(t,x)}{I_v^*} - \frac{I_h(t,x)}{I_h^*} \\ &- \frac{I_v(t,x) S_h(t,x) I_h^*}{I_v^* S_h^* I_h(t,x)}, \end{aligned}$$

and

$$
\begin{aligned}
\frac{\partial V_2(x,u_t(\phi))}{\partial t} =& \frac{H_p^*}{c_{hv}nI_h^*}(1-\frac{S_v^*}{S_v(t,x)})\frac{1}{S_v^*}\frac{\partial S_v(t,x)}{\partial t} + \frac{I_v^*H_p^*}{e^{-m_v\tau}c_{hv}nI_h^*S_v^*}(1-\frac{I_v^*}{I_v(t,x)})\frac{\partial I_v(t,x)}{\partial t} \\
& \times \frac{1}{I_v^*} + [f(\frac{S_v(t,x)I_h(t,x)}{S_v^*I_h^*}) - \int_\Omega \Gamma(D\tau,x,y)f(\frac{S_v(t-\tau,y)I_h(t-\tau,y)}{S_v^*I_h^*})dy] \\
=& -\frac{H_p^*(m_v+k_vV_p^*)(S_v(t,x)-S_v^*)^2}{c_{hv}nI_h^*S_v(t,x)S_v^*} + \frac{1}{I_h^*S_v^*}\Big(1-\frac{S_v^*}{S_v(t,x)}\Big)(I_h^*S_v^* \\
& - I_h(t,x)S_v(t,x)) + \frac{H_p^*}{c_{hv}nI_h^*}\Big(1-\frac{S_v^*}{S_v(t,x)}\Big)\frac{1}{S_v^*}D\Delta S_v + \frac{H_p^*}{e^{-m_v\tau}c_{hv}nI_h^*S_v^*}\Big(1 \\
& - \frac{I_v^*}{I_v(t,x)}\Big)D\Delta I_v + \Big(\int_\Omega \Gamma(D\tau,x,y)\frac{I_h(t-\tau,y)S_v(t-\tau,y)}{I_h^*S_v^*}dy \\
& - \frac{I_v(t,x)}{I_v^*}\Big)\Big(1-\frac{I_v^*}{I_v(t,x)}\Big) + \frac{S_v(t,x)I_h(t,x)}{S_v^*I_h^*} - \ln\frac{S_v(t,x)I_h(t,x)}{S_v^*I_h^*} \\
& - \int_\Omega \Gamma(D\tau,x,y)\Big(\frac{S_v(t-\tau,y)I_h(t-\tau,y)}{S_v^*I_h^*} - \ln\frac{S_v(t-\tau,y)I_h(t-\tau,y)}{S_v^*I_h^*}\Big)dy \\
=& -\frac{H_p^*(m_v+k_vV_p^*)(S_v(t,x)-S_v^*)^2}{c_{hv}nI_h^*S_v(t,x)S_v^*} + \frac{H_p^*}{c_{hv}nI_h^*S_v^*}\Big(1-\frac{S_v^*}{S_v(t,x)}\Big)D\Delta S_v \\
& + \frac{H_p^*}{e^{-m_v\tau}c_{hv}nI_h^*S_v^*}\Big(1-\frac{I_v^*}{I_v(t,x)}\Big)D\Delta I_v + 2 - \frac{S_v^*}{S_v(t,x)} + \frac{I_h(t,x)}{I_h^*} - \frac{I_v(t,x)}{I_v^*} \\
& - \ln\frac{S_v(t,x)I_h(t,x)}{S_v^*I_h^*} - \int_\Omega \Gamma(D\tau,x,y)\Big(\frac{S_v(t-\tau,y)I_h(t-\tau,y)I_v^*}{S_v^*I_h^*I_v(t,x)} \\
& - \ln\frac{S_v(t-\tau,y)I_h(t-\tau,y)}{S_v^*I_h^*}\Big)dy \\
=& -\frac{H_p^*(m_v+k_vV_p^*)(S_v(t,x)-S_v^*)^2}{c_{hv}nI_h^*S_v(t,x)S_v^*} + \frac{H_p^*}{c_{hv}nI_h^*S_v^*}\Big(1-\frac{S_v^*}{S_v(t,x)}\Big)D\Delta S_v \\
& + \frac{H_p^*}{e^{-m_v\tau}c_{hv}nI_h^*S_v^*}\Big(1-\frac{I_v^*}{I_v(t,x)}\Big)D\Delta I_v + 1 - \frac{S_v^*}{S_v(t,x)} + \ln\frac{S_v^*}{S_v(t,x)} \\
& + \frac{I_h(t,x)}{I_h^*} - \frac{I_v(t,x)}{I_v^*} - \ln\frac{I_v^*}{I_v(t,x)} - \ln\frac{I_h(t,x)}{I_h^*} - \int_\Omega \Gamma(D\tau,x,y) \\
& \times \Big(\frac{S_v(t-\tau,y)I_h(t-\tau,y)I_v^*}{S_v^*I_h^*I_v(t,x)} - \ln\frac{S_v(t-\tau,y)I_h(t-\tau,y)I_v^*}{S_v^*I_h^*I_v(t,x)} - 1\Big)dy \\
=& -\frac{H_p^*(m_v+k_vV_p^*)(S_v(t,x)-S_v^*)^2}{c_{hv}nI_h^*S_v(t,x)S_v^*} + \frac{H_p^*}{c_{hv}nI_h^*S_v^*}\Big(1-\frac{S_v^*}{S_v(t,x)}\Big)D\Delta S_v \\
& + \frac{H_p^*}{e^{-m_v\tau}c_{hv}nI_h^*S_v^*}\Big(1-\frac{I_v^*}{I_v(t,x)}\Big)D\Delta I_v - f\Big(\frac{S_v^*}{S_v(t,x)}\Big) + \frac{I_h(t,x)}{I_h^*} \\
& - \frac{I_v(t,x)}{I_v^*} - \ln\frac{I_v^*}{I_v(t,x)} - \ln\frac{I_h(t,x)}{I_h^*}
\end{aligned}
$$

$$-\int_\Omega \Gamma(D\tau,x,y) f\Big(\frac{S_v(t-\tau,y)I_h(t-\tau,y)I_v^*}{S_v^* I_h^* I_v(t,x)}\Big)dy.$$

Since $\ln v \leq \frac{v}{u} + \ln u - 1$, $\forall u, v > 0$, we have $2 - u - \frac{v}{u} + \ln v \leq 0$, and $2 - u - \frac{v}{u} + \ln v = 0$ if and only if $u = v = 1$. Recall that $\int_\Omega \Delta u dx = 0$ and $\int_\Omega \frac{\Delta u}{u} dx = \int_\Omega \frac{\|\nabla u\|^2}{u^2} dx$. It then follows that

$$\begin{aligned}
\frac{dV(u_t(\phi))}{dt} =& -\int_\Omega \frac{H_p^* m_h (S_h(t,x) - S_h^*)^2}{c_{vh} n I_v^* S_h^* S_h(t,x)} dx - \int_\Omega \frac{H_p^* (m_v + k_v V_p^*)(S_v(t,x) - S_v^*)^2}{c_{hv} n I_h^* S_v(t,x) S_v^*} dx \\
&+ \frac{H_p^* D}{c_{hv} n I_h^* S_v^*} \int_\Omega \Delta S_v dx - \frac{H_p^* D}{c_{hv} n I_h^*} \int_\Omega \frac{1}{S_v(t,x)} \Delta S_v dx \\
&+ \frac{H_p^* D e^{m_v \tau}}{c_{hv} n I_h^* S_v^*} \int_\Omega \Delta I_v dx - \frac{H_p^* D e^{m_v \tau} I_v^*}{c_{hv} n I_h^* S_v^*} \int_\Omega \frac{1}{I_v(t,x)} \Delta I_v dx \\
&- \int_\Omega \int_\Omega \Gamma(D\tau,x,y) f\Big(\frac{S_v(t-\tau,y)I_h(t-\tau,y)I_v^*}{S_v^* I_h^* I_v(t,x)}\Big) dy dx + \int_\Omega \Big(2 \\
&- \frac{S_h^*}{S_h(t,x)} - \frac{I_v(t,x) S_h(t,x) I_h^*}{I_v^* S_h^* I_h(t,x)} - \ln \frac{I_v^* I_h(t,x)}{I_v(t,x) I_h^*}\Big) dx - \int_\Omega f\Big(\frac{S_v^*}{S_v(t,x)}\Big) dx \\
=& -\int_\Omega \frac{H_p^* m_h (S_h(t,x) - S_h^*)^2}{c_{vh} n I_v^* S_h^* S_h(t,x)} dx - \int_\Omega \frac{H_p^* (m_v + k_v V_p^*)(S_v(t,x) - S_v^*)^2}{c_{hv} n I_h^* S_v(t,x) S_v^*} dx \\
&- \frac{H_p^* D}{c_{hv} n I_h^*} \int_\Omega \frac{\|\nabla S_v(t,x)\|^2}{S_v^2(t,x)} dx - \frac{H_p^* D e^{m_v \tau} I_v^*}{c_{hv} n I_h^* S_v^*} \int_\Omega \frac{\|\nabla I_v(t,x)\|^2}{I_v^2(t,x)} dx \\
&- \int_\Omega \int_\Omega \Gamma(D\tau,x,y) f\Big(\frac{S_v(t-\tau,y)I_h(t-\tau,y)I_v^*}{S_v^* I_h^* I_v(t,x)}\Big) dy dx + \int_\Omega \Big(2 \\
&- \frac{S_h^*}{S_h(t,x)} - \frac{I_v(t,x) S_h(t,x) I_h^*}{I_v^* S_h^* I_h(t,x)} - \ln \frac{I_v^* I_h(t,x)}{I_v(t,x) I_h^*}\Big) dx - \int_\Omega f\Big(\frac{S_v^*}{S_v(t,x)}\Big) dx \\
\leq& -\int_\Omega \frac{H_p^* m_h (S_h(t,x) - S_h^*)^2}{c_{vh} n I_v^* S_h^* S_h(t,x)} dx - \int_\Omega \frac{H_p^* (m_v + k_v V_p^*)(S_v(t,x) - S_v^*)^2}{c_{hv} n I_h^* S_v(t,x) S_v^*} dx \\
&- \int_\Omega \int_\Omega \Gamma(D\tau,x,y) f\Big(\frac{S_v(t-\tau,y)I_h(t-\tau,y)I_v^*}{S_v^* I_h^* I_v(t,x)}\Big) dy dx + \int_\Omega \Big(2 \\
&- \frac{S_h^*}{S_h(t,x)} - \frac{I_v(t,x) S_h(t,x) I_h^*}{I_v^* S_h^* I_h(t,x)} - \ln \frac{I_v^* I_h(t,x)}{I_v(t,x) I_h^*}\Big) dx - \int_\Omega f\Big(\frac{S_v^*}{S_v(t,x)}\Big) dx \\
:=& U_\phi(t).
\end{aligned}$$

Since $V(u_t(\phi))$ is nonincreasing and bounded below on $[0, \infty)$, it follows that there exists a real number $L \geq 0$ such that $\lim_{t\to\infty} V(u_t(\phi)) = L$. For any $\psi \in \omega(\phi)$, there exists a sequence $t_n \to \infty$ such that $\lim_{n\to\infty} u_{t_n}(\phi) = \psi$ in $H_0$. This implies that $V(\psi) = L$, $\forall \psi \in \omega(\phi)$. Since $u_t(\psi) \in \omega(\phi)$, we have $V(u_t(\psi)) = L$, $\forall t \geq 0$, and hence, $\frac{\mathrm{d}V(u_t(\psi))}{\mathrm{d}t} = 0$. Replacing $\phi$ in the above inequality with $\psi$, we obtain $0 = \frac{\mathrm{d}V(u_t(\psi))}{\mathrm{d}t} \leq U_\psi(t) \leq 0$. This gives rise to $U_\psi(t) = 0$, $\forall t \geq 0$. Combining with system (5.23), we have $u_t(\psi) = u^*$, $\forall t \geq \tau$. Since $\psi \in \omega(\phi)$ is arbitrary, there holds $u_t(\omega(\phi)) = u^*, \forall t \geq \tau$. It follows from the invariance of omega limit sets that $\omega(\phi) = u_\tau(\omega(\phi)) = u^*$, which implies that $\lim_{t\to\infty} u_t(\phi) = u^*$. □

It is easy to see that system (5.21) has a unique positive equilibrium $E^* = (S_h^*, I_h^*, R_h^*, S_v^*, E_v^*, I_v^*)$ if $R_0 > 1$, where $R_h^* = \frac{\alpha_1 I_h^*}{m_h}$ and $E_v^* = \frac{c_{hv} n I_h^* S_v^* (1-e^{-m_v\tau})}{m_v + k_v H_p^*}$. By the thoery of chain transitive sets, we can also lift the above threshold type result for system (5.23) to system (5.21) to obtain the following result.

**Theorem 5.5.2.** *Let (A2) hold. The following statements are valid:*

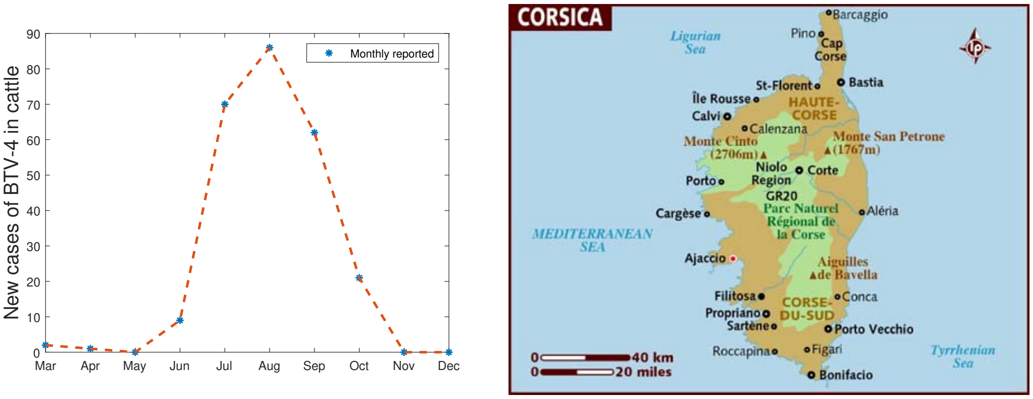
*(i) If $R_0 < 1$, then the disease-free steady state $(H_p^*, 0, 0, V_p^*, 0, 0)$ is globally attractive for system (5.21) in $D \setminus (C([-\tau, 0], C(\bar{\Omega}, \mathbb{R}_+^3)) \times \{(0,0,0)\})$.*

*(ii) If $R_0 > 1$, then there exists unique positive steady state $(S_h^*, I_h^*, R_h^*, S_v^*, E_v^*, I_v^*)$ such that for any $\phi \in D$ with $\phi_2(0,\cdot) \not\equiv 0$ and $\phi_6(0,\cdot) \not\equiv 0$, the solution $v(t,x,\phi)$ of system (5.21) with $v_0 = \phi$ satisfies $\lim_{t\to\infty} v(t,x,\phi) = (S_h^*, I_h^*, R_h^*, S_v^*, E_v^*, I_v^*)$ uniformly for all $x \in \bar{\Omega}$.*

## 5.6 A case study

In this section, we apply the model system (5.1) to study the bluetongue transmission in French Corsica Island with an area of 8,680 km$^2$, lying in the Mediterranean Sea, and the influence of some parameters on $R_0$. Since the end of October 2016, a sheep located in the south of Corsica island was found positive for BTV-4 [110]. And then the first cattle case of BTV-4 was reported in March 2017. In the following, we choose March to be the starting point. Set the period $\omega = 12$ months.

According to the Weekly Disease Information of OIE World Organisation for Animal Health, we count the monthly new case data for Corsica which is given from March 2017 through December 2017 (see, Figure 5.1(a)), with the higher number of cases during June-September. From the Map of Corsica (see, Figure 5.1(b)), the whole island is much longer in the North-South direction. For the sake of convenience, we assume that the spatial units are kilometers (km) and that the spatial domain $\Omega$ is one dimensional. Without loss of generality, we set $\Omega = (0, \pi)$. The Office of Agricultural and Rural Development of Corsica (see http://www.odarc.fr) estimated the total number of cattle herd is about 80,000 and about 2/3 of them on Haute-Corse. Balagne and the Corsican Center contain 40% of the total population of the region. Then to describe the spatial heterogeneity on domain $\Omega$, we assume that the geographical cattle density function is $H_p^*(x) = \frac{80{,}000}{8{,}680}(1.0 - 0.4\cos(0.4-2x)) = 9.2166(1.0-0.4\cos(0.4-2x))$. We set the location-dependent fertility rate of midges $b_v = 6.1 \times 30.4(1.0-0.3\cos(0.4-2x))$ $\text{Month}^{-1}$, where $6.1 \times 30.4$ $\text{Month}^{-1}$ is the parameter in homogeneous environment according to [20].



(a) (b)

Figure 5.1: (a) The monthly reported new cases for BTV-4 from March to December 2017. (b) The map of Corsica (Source: https://www.lonelyplanet.com/maps/europe/france/corsica/).

Table 5.1: Values (ranges) for constant parameters in system (5.1)

| Parameter | Value(range) | Reference |
|---|---|---|
| $b_h$ | $6.94 \times 10^{-4} \times 30.4$ $\text{Month}^{-1}$ | [20] |
| $m_h$ | $b_h$ | [20] |
| $\alpha_1$ | $1/60 \times 30.4$ $\text{Month}^{-1}$ | [20, 115] |
| $c_{vh}$ | $0.8 \sim 1.0$ | [11] |
| $c_{hv}$ | $0.001 \sim 0.15$ | [41] |
| $D$ | $1.25 \times 0.01 \times 30.4$ $\text{km}^2/\text{Month}$ | [20] |

The constant parameters are listed in Table 5.1 using some published data. For four of these model parameters, the biting rate, the mortality rate of midges, the EIP and the carrying capacity in vectors, they exhibit a strong temperature dependence. We apply the given expression of temperature-dependent and location-independent parameters in [73], including the biting rate $n$, the mortality rate of midges $m_v$ under

Table 5.2: Monthly mean temperatures for Corsica (in °C)

| Month | March | April | May | June | July | August |
|---|---|---|---|---|---|---|
| Temperature | 9 | 12 | 16 | 20 | 22 | 22 |
| Month | September | October | November | December | January | February |
| Temperature | 19 | 17 | 12 | 9 | 8 | 8 |

the temperature $T$ (in °C of month $t$), where

$$n(T) = 0.000171 \times T \times (T - 3.6966) \times (41.8699 - T)^{1/2.7056} \times 30.4,$$

$$m_v(T) = 0.008941 e^{0.1547 \times T} \times 30.4.$$

We use the mosquito temperature-dependent carrying capacity of the environment [51] to evaluate that of the midge, which is given by

$$K(T) = pop_{base} \times e^{0.05326 + \frac{3.11241}{1 + e^{\frac{14.56325 - T}{2.93955}}}},$$

where $pop_{base}$ is an arbitrary baseline that scaled annual fluctuations in abundance. Using the mean monthly temperature at Corsica in Table 5.2 (see https://www.holiday-weather.com /corsica/averages/), to evaluate the temperature-dependent coefficients, we obtain

$$\begin{aligned}
n(t) =& (0.1008 - 0.06914 \cos(\pi t/6) + 0.06848 \sin(\pi t/6) - 0.001483 \cos(2\pi t/6) \\
&- 0.01452 \sin(2\pi t/6) + 0.00095 \cos(3\pi t/6) - 0.004233 \sin(3\pi t/6) \\
&- 0.0028 \cos(4\pi t/6) + 0.002136 \sin(4\pi t/6) + 0.003986 \cos(5\pi t/6) \\
&- 0.0003662 \sin(5\pi t/6) - 0.002592 \cos(6\pi t/6)) \times 30.4 \text{ Month}^{-1}, \\
m_v(t) =& (0.1152 - 0.0819 \cos(\pi t/6) + 0.08259 \sin(\pi t/6) - 0.003242 \cos(2\pi t/6) \\
&- 0.03673 \sin(2\pi t/6) + 0.009317 \cos(3\pi t/6) + 0.00165 \sin(3\pi t/6) \\
&- 0.005608 \cos(4\pi t/6) + 0.002555 \sin(4\pi t/6) + 0.006086 \cos(5\pi t/6) \\
&- 0.0002893 \sin(5\pi t/6) - 0.003833 \cos(6\pi t/6)) \times 30.4 \text{ Month}^{-1}, \\
K(t) =& pop_{base} \times (7.875 - 6.516 \cos(\pi t/6) + 6.411 \sin(\pi t/6) - 0.1768 \cos(2\pi t/6) \\
&- 2.713 \sin(2\pi t/6) + 0.1474 \cos(3\pi t/6) - 0.5164 \sin(3\pi t/6) \\
&+ 0.176 \cos(4\pi t/6) + 0.2812 \sin(4\pi t/6) + 0.4105 \cos(5\pi t/6) \\
&+ 0.0474 \sin(5\pi t/6) - 0.3319 \cos(6\pi t/6) + 0.506 \sin(6\pi t/6)).
\end{aligned}$$

We use equation (5.2) to determine the EIP $\tau(t)$ at time $t$ and hence, we need to know the development rate of bluetongue virus (the virus replication rate) in midges $\rho(s)$ on the interval for $s \in [t-\tau(t), t]$. According to [94], the development rate is given by $0.0003 \times T(s) \times (T(s) - 10.4057) \times 30.4$, where 10.4057°C is the threshold temperature for virus replication. That is, the rate of virus replication below the threshold temperature would be almost zero. Here we assume that the virus development may not pause completely with the extreme weather while the development rate is very small below the threshold temperature, which is given by

$$\rho(T) = \begin{cases} 0.0003 \times T \times (T - 10.4057) \times 30.4, & T > 10.4057, \\ 0.0054 \times 30.4, & T \leq 10.4057. \end{cases}$$

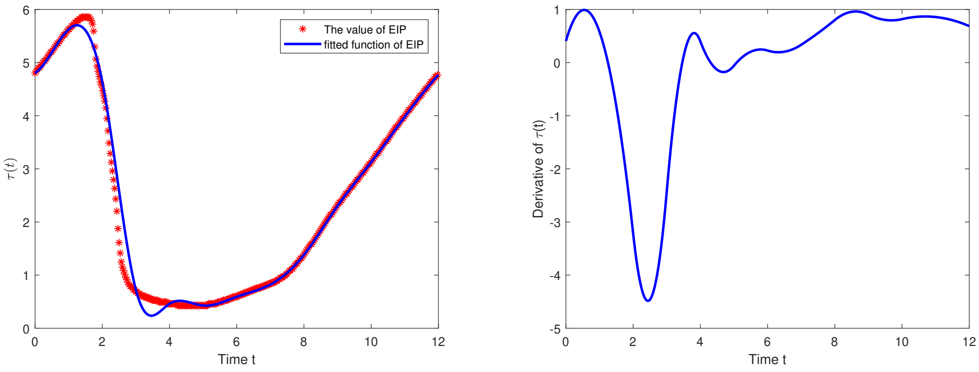
By discretizing the formula

$$\int_{t-\tau(t)}^{t} \rho(T(s))ds = 1,$$

we obtain the corresponding value of EIP for each day. Then the EIP $\tau(t)$ can be approximated by the following periodic function in $[0, 12]$ Month by using the cubic spline fitting, see Figure 5.2(a).

$$\tau(t) = \begin{cases} -0.6609t^3 + 1.078t^2 + 0.4053t + 4.8026, & 0 \leq t < 1, \\ -0.6609(t-1)^3 - 0.9046(t-1)^2 + 0.5786(t-1) + 5.6250, & 1 \leq t < 2, \\ 2.1859(t-2)^3 - 2.8872(t-2)^2 - 3.2132(t-2) + 4.6382, & 2 \leq t < 3, \\ -1.5037(t-3)^3 + 3.6704(t-3)^2 - 2.430(t-3) + 0.7237, & 3 \leq t < 4, \\ 0.4077(t-4)^3 - 0.8406(t-4)^2 + 0.400(t-4) + 0.4605, & 4 \leq t < 5, \\ -0.1602(t-5)^3 + 0.3827(t-5)^2 - 0.058(t-5) + 0.4276, & 5 \leq t < 6, \\ 0.1015(t-6)^3 - 0.098(t-6)^2 + 0.2267(t-6) + 0.5921, & 6 \leq t < 7, \\ 0.0175(t-7)^3 + 0.2065(t-7)^2 + 0.3353(t-7) + 0.8224, & 7 \leq t < 8, \\ -0.1386(t-8)^3 + 0.259(t-8)^2 + 0.8007(t-8) + 1.3816, & 8 \leq t < 9, \\ 0.0763(t-9)^3 - 0.1568(t-9)^2 + 0.9029(t-9) + 2.3026, & 9 \leq t < 10, \\ -0.035(t-10)^3 + 0.0721(t-10)^2 + 0.8182(t-10) + 3.125, & 10 \leq t < 11, \\ -0.035(t-11)^3 - 0.0329(t-11)^2 + 0.8574(t-11) + 3.9803, & 11 \leq t < 12. \end{cases}$$

Figure 5.2(b) numerically validates that $1 - \tau'(t) > 0$ holds. It can be also observed that the derivative of $\tau(t)$ is very close to 1 under a low temperature period, which implies low temperatures will slow the spread of the disease.



(a)

(b)

Figure 5.2: The time-dependent EIP $\tau(t)$ and its derivative.

Choose $c_{vh} = 0.8$, $c_{hv} = 0.0035$ and $pop_{base} = 10^7$. With this set of parameters, we numerically compute $R_0 = 3.6404 > 1$. Applying the difference method to the system with Neumann boundary condition, Figure 5.3 shows the evolution of each compartment in system (5.1), with the initial data

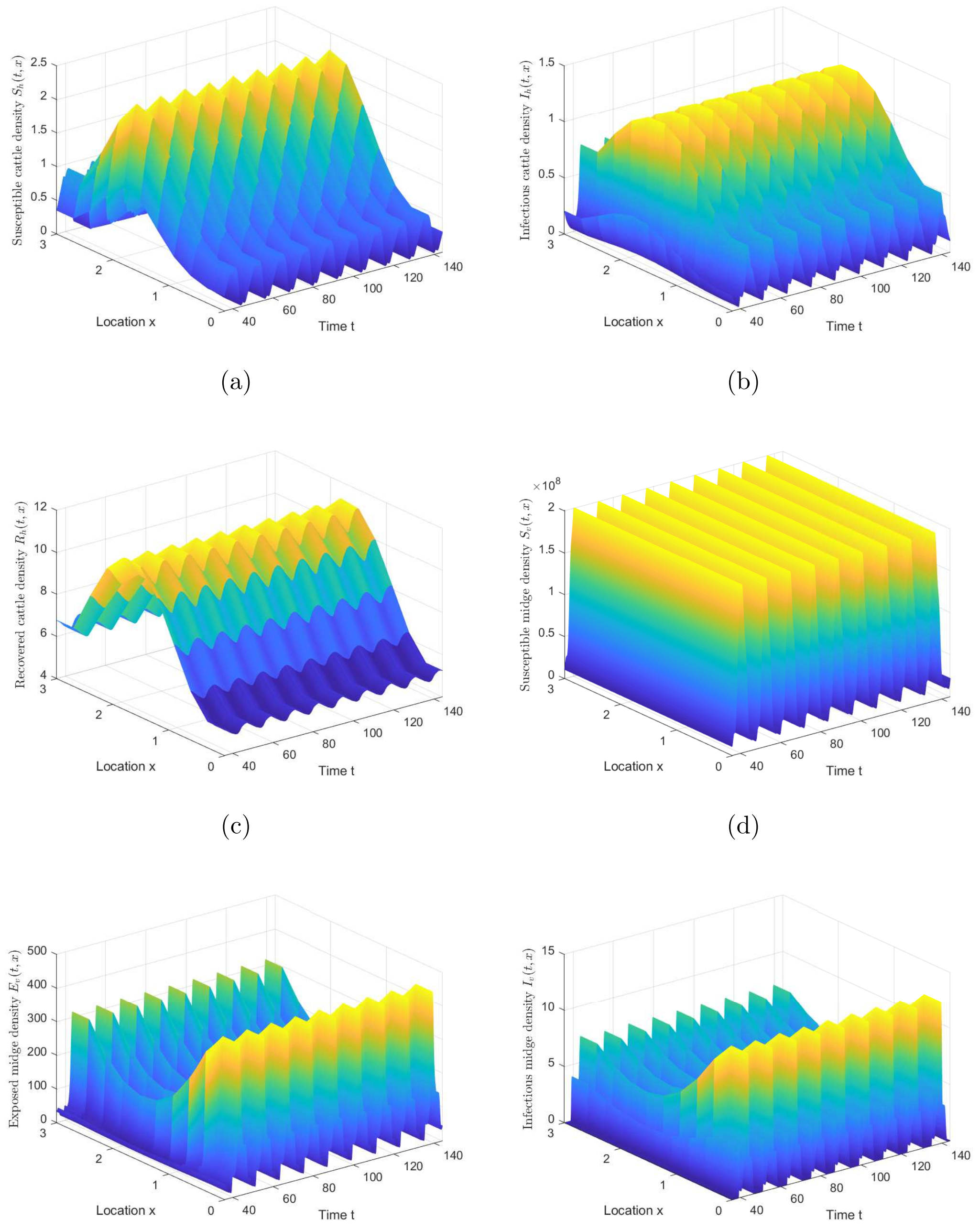
$$S_h(\theta, x) = 1 - 0.6\cos(0.4 - 2x), I_h(\theta, x) = 1 - 0.2\cos(0.4 - 2x),$$

$$R_h(\theta, x) = 7.2166 - 2.88664\cos(0.4 - 2x), S_v(\theta, x) = 10^8 - 200\cos(0.4 - 2x),$$

$$E_v(\theta, x) = 180 - 10\cos(0.4 - 2x), I_v(\theta, x) = 15 - 2\cos(0.4 - 2x),$$

$\theta \in [-\hat{\tau}, 0]$, $x \in [0, \pi]$, which implies that the disease is persistent in cattle and midges. If the biting rate reduces to $0.2n(t)$ by some preventive measures, e.g., keeping cattle in stables, we numerically calculate $R_0 = 0.7281 < 1$. In this case, Figure 5.4 shows that the infectious cattle and midges both approach zero eventually. These simulation results are consistent to Theorem 5.4.2. If $H_p(x) \equiv 9.2166$ and $b_v(x) \equiv 6.1 \times 30.4$, we obtain $R_0 = 2.9379$ and $R_0 = 0.5876$ in the above two cases, respectively. This implies that the spatial averaged system may be underestimate the disease risk.

Since $R_0$ provides a powerful tool to assess the level of disease risk, we investigate the influence of some model parameters on $R_0$. Firstly, the biting rate has often been regarded as a critical parameter for the transmission of vector-borne diseases. To study the effect of preventing bites, we replace $n(t)$ with $(1 - C)n(t)$ and other parameters are the same as those in Figure 5.3. Figure 5.5(a) shows that $R_0$ is a decreasing function of $C$ on $[0, 1)$. Thus in order to eliminate the disease, we should reduce the biting rate to $(1-72.53\%)n(t)$ such that $R_0 < 1$. Charron et al. [20] showed



(a)

(b)

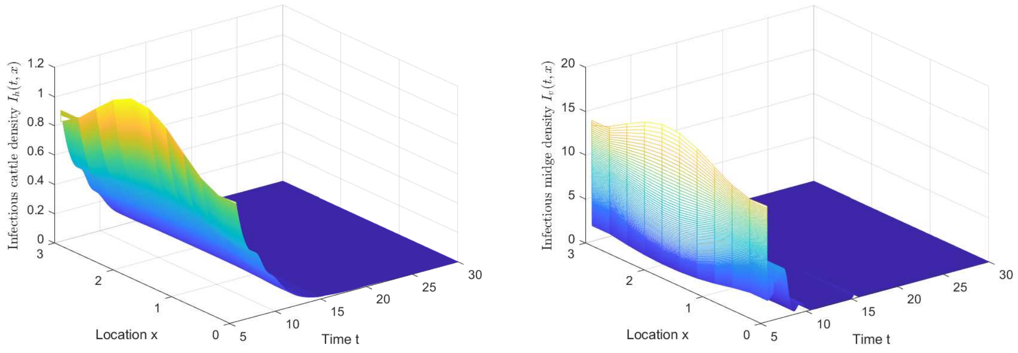
(c)

(d)

(e)

(f)

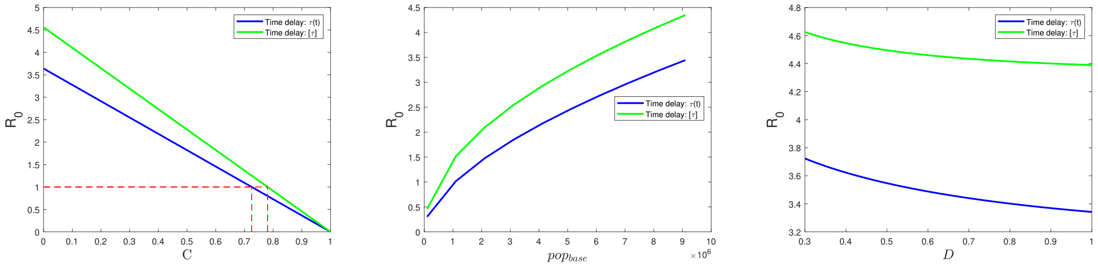
Figure 5.3: The evolution of $S_h$, $I_h$, $R_h$, $S_v$, $E_v$, and $I_v$ when $R_0 = 3.6404 > 1$.



(a) (b)

Figure 5.4: The evolution of the infectious cattle and midges when $R_0 = 0.7281 < 1$.

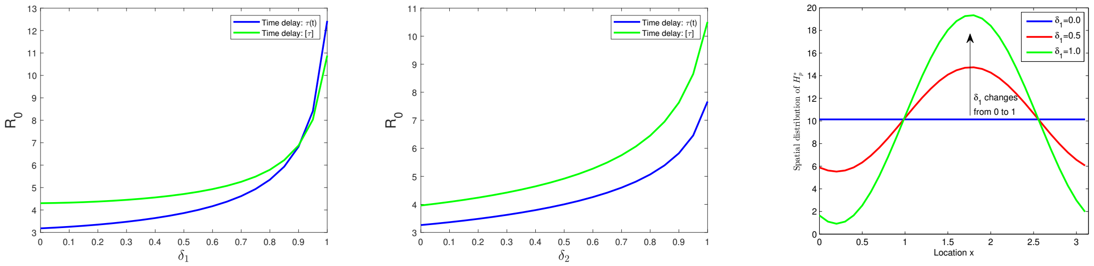
that a larger maximum of carrying capacity in vectors (i.e., maximum of $K(t)$) leads to a higher disease risk and an earlier peak. Here, we give the relationship between $R_0$ and $pop_{base}$. Figure 5.5(b) also shows that $R_0$ decreases as $pop_{base}$ increases, which highlights the importance of the carrying capacity in midges and its influence on the spread of disease. Then we might not want a place where the carrying capacity in vectors is large and we should reduce the areas suitable for midges living. In addition, Figure 5.5(c) shows that $R_0$ is a decreasing function of the diffusion coefficient $D$, which means that the random diffusion movement of midges has an impact on the control of disease, but there is only a relatively small change in $R_0$.



(a) (b) (c)

Figure 5.5: $R_0$ as funtions of $C$, $pop_{base}$ and $D$ with $\tau(t)$ and $[\tau]$.

Secondly, to study the spatial heterogeneity effect on $R_0$, we assume that the total cattle density is $H_p^*(x) = 9.2166(1.0 - \delta_1 \cos(0.4 - 2x))$ and that the fertility rate is $b_v = 6.1 \times 30.4(1.0 - \delta_2 \cos(0.4 - 2x))$ with $\delta_1, \delta_2 \in [0, 1)$. Note that if $\delta_1 = 0$, cattle is homogeneous distribution in Corsica. As $\delta_1$ increases from 0 to 1, more and more



(a) (b) (c)

Figure 5.6: $R_0$ as funtions of $\delta_1$, $\delta_2$ with $\tau(t)$ and $[\tau]$, and the distribution of $H_p^*$.

cattle keep in the north of Corsica (i.e., $x = \pi/2 + 0.4$) (see, Figure 5.6(c)), but the total cattle density on $\Omega$ is not changed (i.e., $\int_0^\pi H_p^*(x)dx = 9.2166\pi$). Figure 5.6(a) shows the relationship between $R_0$ and $\delta_1$. In particular, there is a very sharp increase after $\delta_1 = 0.8$. This figure implies that the spatial heterogeneity in cattle strongly influences the value of $R_0$. We also have a similar observation for spatial heterogeneity in midges. Comparing the range of $R_0$ as $\delta_i$ $(i = 1, 2)$ changing form 0 to 1 in these two figures, there is a difference between the impacts of cattle heterogeneity and midge heterogeneity on $R_0$ in this set of model parameters. Intensive farming promotes the spread of the virus.

Thirdly, we analyse the seasonality of vectors in the spread of disease. Here we focus on the impact of periodic EIP. Define the time-averaged EIP $[\tau]$ as $[\tau] := \frac{1}{\omega}\int_0^\omega \tau(t)dt$, which represents that the EIP is a constant and hence the development rate of bluetongue virus has a constant development rate for a whole year. The green curves in Figures 5.5(a), 5.5(b), and 5.5(c) 5.6(b) represent system (5.1) with a time-averaged EIP $[\tau] = 2.0202$ Month, which always lies above the blue one in each case. However, the blue curve crosses the green one when $\delta_1 = 0.906$ in Figure 5.6(a). These means that the use of time-averaged EIP can either overestimate or underestimate the value of $R_0$.

## 5.7 Discussion

In this chapter, we proposed a nonlocal reaction-diffusion model of BTV spread which accounts for the time-periodic EIP, the seasonality in vectors, the density-dependent mortality in vectors and the spatial heterogeneity in hosts and vectors. Since host movements are controlled, the spatial spread of the disease is caused only by vector movements, and hence, the solution maps of the model system are not compact since some equations have no diffusion terms. Applying the theory developed in [75] and [150], we derived the basic reproduction ratio $R_0$ for this model. Since the time delay is time-periodic, we constructed a new phase space, motivated by [82], and to prove that the linearized system for infectious compartments can generate an eventually strongly monotone periodic semiflow on it. We showed that $R_0$ serves as a threshold value for the extinction and persistence of the disease by the persistence theory for periodic semiflows. More precisely, if $R_0 < 1$, then the disease will be cleared; if $R_0 > 1$, then the disease will persist. On the other side, our numerical results suggest that there exists a positive periodic solution when $R_0 > 1$ (see, Figure 5.3), but we did not prove it by Theorem 1.2.4 because we only proved that the Poincaré map of system (5.9) is $\alpha$-contracting but not is $\alpha$-condensing. When $H_p^*(x)$ and $b_v(x)$ are spatial homogeneous, and all time-periodic coefficients are constants, we further obtained an explicit formulation of $R_0$ and the global attractivity of the positive steady state for system (5.21) in terms of $R_0$ by using the method of Lyapunov functionals.

From published works, we obtained some feasible coefficients and temperature-dependent model parameters to study the spread of BTV-4 in Corsica, France. Our numerical results showed that the biting rate strongly influences the value of $R_0$. If we can keep it less than $(1 - 72.53\%)n(t)$ through reducing the midges bites or vaccination, then the disease will be controlled. We also highlighted the importance of the environment carrying capacity in vectors and its influence on $R_0$. If a region possesses a larger environment carrying capacity in midges, then it might lead to a larger epidemic when BTV outbreaks. Moreover, we found that the disease risk will be highly underestimated if we ignore the spatial heterogeneity in hosts and vectors since $R_0$ is influenced by $\delta_i$ $(i = 1, 2)$. When $\delta_i$ becomes closer and closer to 1, $R_0$ will grow several folds. Then the very high-density livestock farming makes the spread of BTV easier. Lower livestock density might have restricted the spread of the disease. The active dispersal of vectors $(D)$ can also influence the disease risk and the high dispersion of midges may help to reduce the spread of infections but it is hard to control the midge mobility. In addition, the seasonality in vectors can not be ignored. In particular, the periodic EIP brings us some difficulties in mathematical analysis and numerical simulations. To distinguish between the time-averaged and periodic EIP, we give Figures 5.5 and 5.6 to illustrate it, which shows that there is a difference of the values of $R_0$ between the use of $\tau(t)$ and its average $[\tau]$. Thus, we should try to avoid using the time-averaged EIP since it may lead to a bad estimate of the basic reproduction ratio and cause an inaccurate prediction of disease transmission. Based on the above analyses, in order to control the transmission of the disease, we should clear the dirty water in bullpens, clear the weeds, and use the insecticides in cattle premises and in midges habitats, to avoid midge bites and minimise the breeding grounds of the midges. Culling the positive animals and reducing the cattle trade exchange from BTV restricted areas, and vaccination measures are believed to be effective methods.

# Chapter 6

# Summary and future works

In this chapter, we first briefly summarize the main results in this thesis, and then present some possible future works.

## 6.1 Research summary

In Chapters 2-4, we studied the global dynamics of some time-delayed infectious disease models with seasonality and time-dependent delays in a spatially homogeneous environment. In Chapter 5, we investigated the threshold dynamics for a nonlocal and time-delayed reaction-diffusion bluetongue model with temporal and spatial heterogeneities in terms of its basic reproduction ratio.

In Chapter 2, we considered a class of periodic SEIRS epidemic models with the general incidence rate and time-dependent delay. We first formulated the model and derived the basic reproduction ratio $R_0$ for this model system. By applying the comparison argument and the theorem of uniform persistence for periodic semiflows, we then established a threshold type result on its global dynamics in terms of $R_0$, that is, the disease-free periodic solution is globally attractive if $R_0 < 1$, while the system admits a positive periodic solution and the disease is uniformly persistent if $R_0 > 1$. Numerical simulations are also carried out to illustrate the analytic results. In addition, we find that the use of the temporal average of the periodic delay may underestimate or overestimate the real value of $R_0$.

In Chapter 3, we formulated and analyzed a West Nile virus transmission model between mosquitoes and birds, which includes seasonality, the vertical transmission of the virus, the temperature-dependent maturation delay, and the temperature-dependent extrinsic incubation period (EIP) for mosquitoes. We first introduced the basic reproduction ratio $R_0$ for this model system, and then showed that the disease is uniformly persistent if $R_0 > 1$. It was also shown that the disease-free periodic solution is attractive if $R_0 < 1$, provided that there is only a small invasion in infectious mosquitoes and birds. When $R_0 < 1$ and the disease-induced death rate of birds is zero, we could prove that the disease-free periodic solution is attractive. In the case where all coefficients are constants and the disease-induced death rate of birds is zero, we established a threshold result on the global attractivity in terms of $R_0$. Numerically, we carry out a case study for West Nile virus transmission in Orange County, California, USA. Our numerical simulations indicate that it is important for controlling West Nile virus spread to prolong the maturation time and EIP, reduce the vertical transmission rate by developing new drugs for mosquitoes, and keep birds from mosquito bites.

In Chapter 4, motivated by the autonomous time-delayed differential equation model in [44], we proposed a bluetongue model with seasonality and temperature-dependent incubation period. We introduced the basic disease reproduction ratio for the whole system $R_0$ and the basic disease reproduction ratio in the absence of sheep $\widetilde{R}_0$, and obtained $R_0$ and $\widetilde{R}_0$ serve as threshold parameters for the persistence and extinction of the disease. Bluetongue affects the life cycles of two host species very differently, which gives rise to new challenges. Then uniform disease persistence occurs in two different scenarios which are distinguished by $\widetilde{R}_0$. Meanwhile, since the disease can only persist if the vector is present, the state space for the semiflow must be restricted to states where the vector (in another case also the sheep) is present. In other words, the uniform persistence of midges and sheep first needs to be established, which ensures the existence of a global attractor for this restricted semiflow in a state space and then makes it possible to prove the uniform persistence of the disease. More precisely, bluetongue persists in cattle and midges but it may eradicate the sheep if $R_0 > 1$ and $\widetilde{R}_0 > 1$; the system admits a positive periodic solution, the disease is uniformly persistent in cattle, sheep, and midges, and bluetongue cannot eradicate the sheep if $R_0 > 1 \geq \widetilde{R}_0$. As an application, we study the bluetongue virus (BTV) transmission case in France. The simulation results predict that increasing the mortality rate of midges, prolonging the duration of the EIP, and preventing host-vector contact are effective measures in controlling BTV spread. We also find that if 96.72% vaccination coverage for cattle and sheep is provided, then the disease will be controlled.

In Chapter 5, we developed a nonlocal reaction-diffusion model of bluetongue disease with seasonality, spatial heterogeneous structure, and periodic EIP. Since livestock populations are managed by farmers, host movements are controlled, and hence, the spatial spread of BTV is due to only vector movements. This leads to the lack of compactness for solution maps of our model system since some equations have no diffusion terms. Thus, we proved the asymptotic compactness of solution maps to obtain the existence of the global attractor for the associated Poincaré map. Applying the theory developed in [75] and [150], we derived the basic reproduction ratio $R_0$ for this model system. By using the comparison argument, the theory of chain transitive, and the theorem of uniform persistence for periodic semiflows, we showed that the disease-free periodic solution is globally attractive if $R_0 < 1$, while the disease is uniformly persistent if $R_0 > 1$. Further, we obtained the global attractivity of the positive steady state in the case where all the coefficients are constants. Numerically, we gave a case study for the bluetongue transmission in Corsica Island, France, and investigated the impact of some model parameters on $R_0$. We found that the disease risk may be underestimated if the spatial heterogeneity is ignored.

## 6.2 Future works

Related to the projects in this thesis, there are some challenging issues for future investigation.

In Chapter 2, we proposed a class of SEIRS epidemic model with the general incidence rate $f(t, S(t), I(t))$. However, it is still a simple case of most general situations. A possible extension of our model is to consider the case where the incidence rate also depends on the total population size $N(t)$ (see, e.g., [88]). As such, the incidence function is of the form $f(t, S(t), I(t), N(t))$, which makes the mathematical analysis of the resulting model more challenging.

To incorporate more biological factors, a West Nile virus model, as shown in Chapter 3, should contain spatial diffusion of birds and mosquitoes, as well as latitudinal variation in host and vector population. In addition, the biting rates vary across stages of birds, for example, juvenile birds are bitten at a higher rate than adult birds [106]. Then to explore the effect of birds stage-structure (nestling, fledgling, and adult) exposure to mosquitoes is important. Thus, it should be more reasonable to consider a periodic WNV model with time-dependent delays accounting for bird stage-structure and stage-specific biting rates of mosquitoes on birds.

In Chapter 4, the temperature-dependent EIP in midges is incorporated into BTV transmission models. Indeed, the BTV transmission in cattle and sheep also undergoes the intrinsic incubation period, so after that amount of time the infected cattle and sheep become infectious and enter the $I_c$ and $I_s$ compartments, respectively. From Figures 4.2(d) and 4.3(c), we see that the number of infectious midges reaches an extremely low minimum, which may be zero in reality. This also suggests that we may take into account the case where the midge population is subject to an Allee effect, see [18] for a related study.

In Chapter 5, our model has shown that the landscape heterogeneity, seasonal pattern in abundance and activities of midge population, and the active dispersal of midges all impact on the BTV spatial-temporal transmission. It was noticed in [64] that the long distance, 100 km over water and lesser distances over land, is driven by wind. This might be the reason why BTV-4 has been introduced to Corsica from Italy, probably from Sardinia (12 km between the two islands); BTV-4 has been introduced to mainland France from Corsica or Italy [110]. Therefore, when the spatial scale is large enough, it would be interesting to incorporate host movements and the long-range directed movement of midge population due to the wind-induced passive movements into our model. And we leave the study of such a reaction-diffusion-advection compartmental system in distant sites for further investigation.

Throughout this thesis, we assume that $1 - \tau'(t)$ is positive which means that the infection transmission takes place all time during the year. However, the development rate of virus would cease at unfavorable environmental conditions such as harsh winters. From the expression of the development rate function in Chapters 4 and 5, we see that it is zero below some threshold temperature. In order to address this issue, we may approximate these coefficients by strictly positive functions and then study the limiting behaviors, or we may use the piecewise parameter functions to describe the infection progress and the evolution dynamics in each interval.

For almost all infectious diseases, vaccination is a pertinent strategy to control the spread of diseases even through it is hard to eradication of the disease. Estimation the critical vaccination coverage and vaccine efficacy is important. Thus, it is meaningful to introduce the vaccination strategy into the existing model systems and to study the best period of the year to implement a vaccination program. Moreover, it would be interesting to study spreading speeds and traveling waves for some spatial models of infectious diseases in unbounded domain.

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