

Global dynamics of a vector-borne disease model with infection ages and general incidence rates

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Abstract A vector-borne disease model with general incidence rates is proposed and investigated in this paper, where both vector and host are stratified by infection ages in the form of a hyperbolic system of partial differential equations coupled with ordinary differential equations. The existence, uniqueness, nonnegativeness, and boundedness of solution of the model are studied for biologically reasonable purpose. Furthermore, a global threshold dynamics of the system is established by constructing suitable Lyapunov functionals, which is determined by the basic reproduction number \mathcal{R}_0 : the infection-free equilibrium is globally asymptotically stable when $\mathcal{R}_0 > 1$.

Keywords Vector-borne disease model · Infection age · General incidence rate · Uniform persistence · Fluctuation lemma · Lyapunov functional

Mathematics Subject Classification 34D05 · 34D23 · 35E99 · 58J32

1 Introduction

The infectious disease transmission between hosts and vectors is one of the dominant themes in epidemic dynamics. Vector-borne infectious diseases are emerging or resurging as a result of changes in public health policy (Brand et al. 2016). Vector-borne diseases are transmitted by arthropod insects such as mosquitoes, ticks, flies, midges, and fleas. They account for

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about 17% of the estimated burden of all infectious diseases affecting humans, and they also exert pressure on food security through their impacts on animal health and plants (Caminade et al. 2016).

Among all the vector-borne diseases, mosquito-borne types such as malaria, dengue fever, and West Nile Virus are of recent particular interests due to their serious impact on the public health in the world. For example, dengue virus infection is the most commonest mosquito borne viral disease and is a major public health problem (globally). More than 2.5 billion people in over 112 countries of the world are at risk from dengue virus (Tahir 2017). One recent estimate indicates 390 million dengue infections per year (95% credible interval 284–528 million), of which 96 million (67–136 million) manifest clinically (with some severity of the disease) (Bhatt et al. 2013). West Nile virus was discovered in 1937 in the West Nile region of Uganda. Since its first incursion into North America in 1999 (Nash et al. 2001), numerous cases of WNV infection in humans have been recorded in the USA (see details in Bowman et al. 2005; Centers for Disease Control and Prevention 2002). As one of the most important parasitic diseases in the world, Malaria is endemic in over 100 countries and it leads to 214 million cases and 438,000 deaths in WHO (2016). Up to now, there is no effective and safe vaccine for malaria. It is well recognized that the successful control of vector-borne diseases depends on our understanding of its transmission dynamics of them (Hollingsworth et al. 2015).

Mathematical models have been widely used to provide an explicit framework for understanding dynamics of vector-borne diseases in the last 20 years (see, for instance, Altizer et al. 2006; Avila-Vales and Buonomo 2015; Bowman et al. 2005; Forouzannia and Gumel 2014; Hollingsworth et al. 2015; Mandal et al. 2011; McCallum et al. 2001; Ngwa and Shu 2000; Saul 1996). A fundamental issue of epidemic modeling is the incidence rate of disease transmission, which is defined as the number of infection per unit time at which susceptible individuals contract the infection (Avila-Vales and Buonomo 2015; Maidana and Yang 2008; McCallum et al. 2001), and it plays an important role in the study of mathematical epidemiology. Since host–vector models were first developed at the beginning of the 20th century, the 'mass action' (if the density of susceptible hosts is represented as *S*, and that of infected hosts as *I*, then the number of new infected hosts per unit area and per unit of time is βSI (Anderson and May 1978; Anderson and May 1978, where β is the transmission coefficient)) assumption has been commonly used. If susceptible and infected hosts were randomly mixed, this would lead to the following frequency-dependent (or density-independent) transmission $\frac{\beta SI}{N}$ (Antonovics et al. 1995; Begon et al. 1999), where *N* is total host density.

In many works, the infection rate is assumed to proportional to the size of the infectious compartment (Lutambi et al. 2013; Maidana and Yang 2008). However, Capasso et al. (1977, 1978) have considered the importance of introducing a nonlinear incidence rate. From then on, various forms of nonlinear incidence rates have been proposed (Feng et al. 2015; Georgescu and Hsieh 2006; Korobeinikov 2009, 2007; Novoseltsev et al. 2012; Park 2004; Roop-O et al. 2015; Vargas-De-León et al. 2014; Wang et al. 2017a). For example, an asymptotic relationship between the contact rate and host density is proposed, which includes $\beta S^p I^q$ ($0) (Hochberg 1991; Knell et al. 1996), <math>kS \ln(1 + \frac{\beta I}{k})$ (negative binomial. Here, small *k* corresponds to highly aggregated infection. As $k \to \infty$, the expression reduces to the mass action) (Barlow 2000; Briggs and Godfray 1995), $\frac{\beta SI}{1+aS+bI}$ (*a*, *b* > 0 are constants) (Diekmann and Kretzschmar 1991; McCallum et al. 2001). In general, Korobeinikov (2007, 2009) assumed the incidence rate to be a more general form $\varphi(S(t), I(t))$.

The Ross–Macdonald model on vector-borne diseases was described by ordinary differential equations (Macdonald 1952; Ross 1910, 1911). Macdonald (1952) established a threshold condition on the invasion and persistence of infection, which is determined by the basic reproduction number (defined as the average number of secondary cases produced by an index case during its infectious period). Most of the existing vector-borne disease models, especially those on malaria that investigate complications arising from host superinfection, immunity, and other factors, are based on this fundamental model (Dietz et al. 1974; Feng and Velasco-Hernández 1997; Hethcote 2000; Lashari and Zaman 2011; Qiu 2008; Ruan et al. 2008; Tumwiine et al. 2007; Vargas-De-León 2012). The obtained results greatly helped us to understand the underlying mechanisms on disease spread and to make appropriate control strategies.

Furthermore, infection age of a vector and/or host can affect the number of secondary infections resulting from introducing an infected individual (Hollingsworth et al. 2015; Rock et al. 2015), and hence infection-age structures of vector and host may change the transmission dynamics. As a matter of fact, malaria burden differs due to infection age and gender in humans. Therefore, infection age becomes an important inter-related factor for transmission of malaria in a population. Many epidemiological studies (Browne and Pilyugin 2013; Chen et al. 2016; Forouzannia and Gumel 2014; Iannelli 1995; Inaba and Sekine 2004; Kuniya 2014; Liu et al. 2006; Magal et al. 2010; Melnik and Korobeinikov 2013; Soufiane and Touaoula 2016) have focused on this important aspect by including age structure of the epidemic models and obtained results including threshold dynamics. Up to now, a general vector–host infection model with nonlinear incidence rate and infection-age-dependence in both vector and host is not common. As a result, it is necessary and meaningful for one to construct novel models with infection ages in both vector and host and consider their effects on the transmission dynamics.

Motivated by the above discussions, in this paper we will introduce infection ages into both host and vector in the vector–host models studied in Aron (1988), Bowman et al. (2005), Brand et al. (2016), Lashari and Zaman (2011), Kuniya (2014), McCallum et al. (2001), Melnik and Korobeinikov (2013), Qiu (2008), Ruan et al. (2008), and Tumwiine et al. (2007) and we assume that the forces of infection are generally nonlinear (we refer to Feng et al. 2015; Georgescu and Hsieh 2006; Korobeinikov 2009; Korobeinikov 2007; Novoseltsev et al. 2012; Park 2004; Vargas-De-León et al. 2014; Wang et al. 2017a for justifications). For the modeling methods on infection-age-dependent incidence rate of age-structured epidemic models, we refer to Chen et al. (2016), Wang et al. (2017a, b, c, d), Wang et al. (2015), and Yang et al. (2017). Our model will be described by a system of ordinary differential equations coupled with two partial differential equations, which is very challenging in analysis. The main purpose of this paper is to consider the transmission dynamics of vectors that infect hosts due to the infection-age-dependent incidence rate.

Many epidemic models including infection-age-dependent incidence rates have been studied (Chen et al. 2016; Kuniya and Oizumi 2015; Wang et al. 2017a, c, d, 2015; Yang et al. 2017). The results there implied that decreasing the initial transmission rate and drawing up efficient prevention ways played a very important role on controlling the spreading of diseases. In addition, humans can influence the outcome of a host-parasite interaction in multiple ways (for example, environmental degradation). But, the relationship of the conditions for extinction or uniform persistence of the vector–host model with general infection-age-dependent incidence rates still remains unclear. Analysis of such a model is not trivial. To the best of our knowledge, our work is likely the first study on the effects of both infection ages and general incidence rates on vector-borne disease models.

The rest of the paper is organized as follows. In the next section, we will formulate the vector-borne disease model with both infection ages and general incidence rates. We also present results on the existence, uniqueness, non-negativeness, and boundedness of solutions of the model system. In Sect. 3, we study the existence of equilibria and their local

stability. We establish the threshold dynamics (which is determined by the basic reproduction number) in Sect. 4. The global stability of the disease-free equilibrium is obtained by applying the fluctuation lemma while the global stability of the endemic equilibrium is obtained by constructing an appropriate Lyapunov functional. The paper ends with a brief conclusion.

2 Model formulation

Motivated by the vector-borne compartmental models in Aron (1988) and Lashari and Zaman (2011), we propose an age-structured vector-host model with permanent immunity for recovered hosts and general nonlinear incidences between vectors and hosts. The model is based on the following assumptions.

- (A₁) The host population size (N_h) is divided into three subclasses, the susceptible class S_h , the infected class I_h , and the recovered class R_h (to be permanently immune and hence there is no need to consider the evolution of R_h), while the vector population size (N_v) is divided into two subclasses, the susceptible class S_v and the infected class I_v . The infected vectors are assumed to never recover until their death and hence there is no recovered class for the vector population.
- (A₂) There is a constant recruitment rate, λ , for the susceptible host. The natural death rate of the host is μ_h . The susceptible hosts can be infected by infectious vectors with a general nonlinear incidence $\varphi(S_h(t), \int_0^\infty k(a)i_v(t, a)da)$. Here, $i_v(t, a)$ is the density of infected vectors of infection age *a* at time *t* and k(a) is the age-dependent biting rate of a susceptible host by an infected vector. Note that $I_v(t) = \int_0^\infty i_v(t, a)da$ is the total number of infected vectors at time *t*. We assume that the per capita recovery rate of the infected host at infection age *a* is $\gamma(a)$.
- (A₃) The vector population size N_v is assumed to be constant and hence the birth rate and the natural death rate are the same, denoted by μ_v . The susceptible vectors can be infected by biting an infected host and the transmission rate is taken as $\psi(S_v(t), \int_0^\infty \beta(a)i_h(t, a)da)$, another general incidence. Here, $i_h(t, a)$ is the density of the infected hosts of infection age *a* at time *t* and $\beta(a)$ is the age-dependent biting rate of an infected host by a susceptible vector. Notice that $I_h(t) = \int_0^\infty i_h(t, a)da$ is the total number of infected hosts at time *t*.

The above assumptions lead to the following vector-borne disease model:

$$\frac{\mathrm{d}S_{h}(t)}{\mathrm{d}t} = \lambda - \mu_{h}S_{h}(t) - \varphi\left(S_{h}(t), \int_{0}^{\infty}k(a)i_{v}(t, a)\mathrm{d}a\right),$$

$$\frac{\partial i_{h}(t,a)}{\partial t} + \frac{\partial i_{h}(t,a)}{\partial a} = -\delta(a)i_{h}(t, a),$$

$$i_{h}(t, 0) = \varphi(S_{h}(t), \int_{0}^{\infty}k(a)i_{v}(t, a)\mathrm{d}a),$$

$$\frac{\partial i_{v}(t,a)}{\partial t} + \frac{\partial i_{v}(t,a)}{\partial a} = -\mu_{v}i_{v}(t, a),$$

$$i_{v}(t, 0) = \psi(N_{v} - \int_{0}^{\infty}i_{v}(t, a)\mathrm{d}a, \int_{0}^{\infty}\beta(a)i_{h}(t, a)\mathrm{d}a),$$

$$S_{h}(0) = S_{h0} \in R_{+}, i_{h}(0, \cdot) = i_{h0} \in L^{1}_{+}(0, \infty), i_{v}(0, \cdot) = i_{v0} \in L^{1}_{+}(0, \infty),$$
(2.1)

where $\delta(a) = \mu_h + \gamma(a)$ and $R_+ = [0, \infty)$. For (2.1), there should be an inherent relationship between the initial values and the boundary values, that is, $i_h(0, 0) = i_{h0}(0)$ and $i_v(0, 0) = i_{v0}(0)$. Therefore, in the sequel, we always assume that

$$\varphi(S_{h0}, \int_0^\infty k(a)i_{v0}(a)\mathrm{d}a) = i_{h0}(0)$$

and

$$\psi(N_v - \int_0^\infty i_{v0}(a) \mathrm{d}a, \int_0^\infty \beta(a) i_{h0}(a) \mathrm{d}a) = i_{v0}(0).$$

To study the dynamics of (2.1), we make the following hypotheses.

(H₁) k and β are bounded and uniformly continuous functions from R_+ to R_+ .

(H₂) $\varphi(u, v)$ and $\psi(u, v)$ are differentiable such that $\varphi_1(u, v) > 0$ and $\psi_1(u, v) > 0$ for u > 0 and v > 0, and $\varphi_2(u, v) > 0$ and $\psi_2(u, v) > 0$ for u > 0 and $v \ge 0$. Moreover, $\varphi(u, 0) = \varphi(0, v) = \psi(u, 0) = \psi(0, v) = 0$ for all $u, v \in R_+$. Here, $\varphi_1(u, v)$ and $\varphi_2(u, v)$ represent the first-order partial derivatives of $\varphi(u, v)$ with respect to u and v, respectively; while $\psi_1(u, v)$ and $\psi_2(u, v)$ represent the first-order partial derivatives of $\psi(u, v)$ with respect to u and v, respectively.

(H₃) $\varphi_2(u, v)$ and $\psi_2(u, v)$ are continuous, respectively, at $(\frac{\lambda}{\mu_h}, 0)$ and $(N_v, 0)$. Furthermore, $\frac{\partial^2 \varphi(u, v)}{\partial v^2} \leq 0$ and $\frac{\partial^2 \varphi(u, v)}{\partial v^2} \leq 0$ for u > 0 and v > 0.

(H₄) $\varphi(u, v)$ and $\psi(u, v)$ are locally Lipschitz continuous on R^2_+ , namely for any C > 0, there exist $L_u(C) > 0$, $L_v(C) > 0$, $K_u(C) > 0$, and $K_v(C) > 0$ such that

$$\begin{aligned} |\varphi(u, v) - \varphi(\widetilde{u}, v)| &\leq L_u |u - \widetilde{u}|, \\ |\varphi(u, v) - \varphi(u, \widetilde{v})| &\leq L_v |v - \widetilde{v}|, \\ |\psi(u, v) - \psi(\widetilde{u}, v)| &\leq K_u |u - \widetilde{u}|, \\ |\psi(u, v) - \psi(u, \widetilde{v})| &\leq K_v |v - \widetilde{v}| \end{aligned}$$

for all $0 \le u, \widetilde{u}, v, \widetilde{v} \le C$.

It is obvious that $\varphi(u, v)$ and $\psi(u, v)$ are always positive for u > 0 and v > 0, $\varphi(u, \cdot)$ and $\psi(u, \cdot)$ are strictly increasing for u > 0, and $\varphi(\cdot, v)$ and $\psi(\cdot, v)$ are strictly increasing for v > 0 by hypotheses (H₂).

According to the methods of characteristic lines, the following two partial differential equations

$$\begin{cases} \frac{\partial i_h(t,a)}{\partial t} + \frac{\partial i_h(t,a)}{\partial a} = -\delta(a)i_h(t,a),\\ i_h(t,0) = \varphi(S_h(t), \int_0^\infty k(a)i_v(t,a)da),\\ i_h(0,0) = i_{h0}, \end{cases}$$

and

$$\begin{cases} \frac{\partial i_v(t,a)}{\partial t} + \frac{\partial i_v(t,a)}{\partial a} = -\mu_v i_v(t,a), \\ i_v(t,0) = \psi(N_v - \int_0^\infty i_v(t,a) \mathrm{d}a, \int_0^\infty \beta(a) i_h(t,a) \mathrm{d}a), \\ i_v(0,0) = i_{v0}, \end{cases}$$

can be solved, respectively, as:

$$i_{h}(t,a) = \begin{cases} \sigma(a)\varphi(S_{h}(t-a), \int_{0}^{\infty} k(a)i_{v}(t-a,a)da), \ 0 \le a < t, \\ \frac{\sigma(a)}{\sigma(a-t)}i_{h0}(a-t), & a \ge t > 0, \end{cases}$$

and

$$i_{v}(t,a) = \begin{cases} \pi(a)\psi(N_{v} - \int_{0}^{\infty} i_{v}(t-a,a)\mathrm{d}a, \int_{0}^{\infty} \beta(a)i_{h}(t-a,a)\mathrm{d}a), \ 0 \le a < t, \\ \frac{\pi(a)}{\pi(a-t)}i_{v0}(a-t), & a \ge t > 0, \end{cases}$$

where $\sigma(a) = \exp(-\int_0^a \delta(s) ds)$ and $\pi(a) = \exp(-\int_0^a \mu_v ds)$, which are, respectively, the survival probabilities of an infected host and an infected vector to age *a*. Then, (2.1) can be rewritten as the following equivalent integro-differential equation:

$$\begin{cases} \frac{dS_{h}(t)}{dt} = \lambda - \mu_{h}S_{h}(t) - \varphi(S_{h}(t), \int_{0}^{\infty} k(a)i_{v}(t, a)da), \\ i_{h}(t, a) = \sigma(a)\varphi(S_{h}(t - a), \int_{0}^{\infty} k(a)i_{v}(t - a, a)da)\mathbf{1}_{t>a} + \frac{\sigma(a)}{\sigma(a-t)}i_{h0}(a - t)\mathbf{1}_{a>t}, \\ i_{v}(t, a) = \pi(a)\psi(N_{v} - \int_{0}^{\infty} i_{v}(t - a, a)da, \int_{0}^{\infty} \beta(a)i_{h}(t - a, a)da)\mathbf{1}_{t>a} \\ + \frac{\pi(a)}{\pi(a-t)}i_{v0}(a - t)\mathbf{1}_{a>t}, \end{cases}$$
(2.2)

where

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

Let

$$X_{+} = R_{+} \times L^{1}_{+}(0, \infty) \times L^{1}_{+}(0, \infty),$$

which is a positive cone of the Banach space $X = R \times L^1(0, \infty) \times L^1(0, \infty)$ with the product norm $\|\cdot\|$. The following result on the existence and nonnegativeness of solutions to (2.2) and hence to (2.1) can be proved with a modification of the proofs of Theorem 2.1 and Lemma 2.2 in Browne and Pilyugin (2013). Therefore, we omit the proof here.

Theorem 2.1 Suppose (H₁), (H₂), and (H₄) hold. Then, for any initial value $x \in X_+$, system (2.1) has a unique solution on R_+ , which depends continuously on the initial value and time *t*. Moreover, $(S_h(t), i_h(t, \cdot), i_v(t, \cdot)) \in X_+$ for $t \in R_+$ and they are bounded.

In fact, let

$$G(t) = S_h(t) + \int_0^\infty i_h(t, a) \mathrm{d}a.$$

Then

$$\begin{aligned} \frac{dG(t)}{dt} \\ &= \lambda - \mu_h S_h(t) - \varphi(S_h(t), \int_0^\infty k(a)i_v(t, a)da) + \int_0^\infty \frac{\partial i_h(t, a)}{\partial t}da \\ &= \lambda - \mu_h S_h(t) - \varphi(S_h(t), \int_0^\infty k(a)i_v(t, a)da) - \int_0^\infty \left(\frac{\partial i_h(t, a)}{\partial a} + \delta(a)i_h(t, a)\right) da \\ &= \lambda - \mu_h S_h(t) - \varphi(S_h(t), \int_0^\infty k(a)i_v(t, a)da) + i_h(t, 0) - i_h(t, a)\Big|_{a=\infty} \\ &- \int_0^\infty \delta(a)i_h(t, a)da \\ &\leq \lambda - \mu_h S_h(t) - \mu_h \int_0^\infty i_h(t, a)da \\ &= \lambda - \mu_h(S_h(t) + \int_0^\infty i_h(t, a)da). \end{aligned}$$

It follows that

$$\limsup_{t\to\infty} G(t) \le \frac{\lambda}{\mu_h}.$$

Moreover,

$$\int_0^\infty i_v(t,a)\mathrm{d}a = N_v - S_v(t) \le N_v.$$

Then, one can easily see that Ω is a positively invariant and attracting subset for system (2.1), where

$$\Omega = \left\{ x = (x_1, \rho_1, \rho_2) \in X_+ \Big| x_1 + |\rho_1||_1 \le \frac{\lambda}{\mu_h}, \|\rho_2\|_1 \le N_v \right\}.$$

In the sequel, for the purpose of global dynamics of (2.1), we always assume that the initial values are in Ω . Moreover, L_u , L_v , K_u , and K_v are the constants in (H₄) corresponding to $C = \max \left\{ \frac{\lambda}{\mu_h}, \|\beta\|_{\infty} \frac{\lambda}{\mu_h}, \|k\|_{\infty} N_v \right\}.$

3 Equilibria and their local stability

Obviously, system (2.1) always has the disease-free equilibrium $E^0 = (S_h^0, i_h^0, i_v^0)$, where $S_h^0 = \frac{\lambda}{\mu_h}, i_h^0 = 0, i_v^0 = 0$. For convenience of notation, we introduce

$$\xi = \int_0^\infty k(a)\pi(a)da$$
 and $\eta = \int_0^\infty \beta(a)\sigma(a)da$

Define the basic reproduction number \mathcal{R}_0 by

$$\mathcal{R}_0 = \psi_2(N_v, 0)\varphi_2(S_h^0, 0)\xi\eta.$$
(3.1)

In fact, $\psi_2(N_v, 0)\eta$ is the number of infected vector produced by introducing an infected host in the system and $\varphi_2(S_h^0, 0)\xi$ is the number of infected host produced with one infected vector in the system. Therefore, \mathcal{R}_0 is the number of infected host when an infected host is introduced into the system, which agrees with the definition of the basic reproduction number.

Now, we study the existence of other equilibria. If $E^* = (S_h^*, i_h^*, i_v^*) \in \Omega$ is an equilibrium, then it must satisfy

$$\begin{cases} \lambda - \mu_h S_h^* - \varphi(S_h^*, \int_0^\infty k(a) i_v^*(a) da) = 0, \\ \frac{di_h^*(a)}{da} = -\delta(a) i_h^*(a), \\ \frac{di_v^*(a)}{da} = -\mu_v i_v^*(a), \\ i_h^*(0) = \varphi(S_h^*, \int_0^\infty k(a) i_v^*(a) da), \\ i_v^*(0) = \psi(N_v - \int_0^\infty i_v^*(a) da, \int_0^\infty \beta(a) i_h^*(a) da). \end{cases}$$
(3.2)

Solving the second and third equations of (3.2) gives us

$$i_h^*(a) = i_h^*(0)\sigma(a)$$
 and $i_v^*(a) = i_v^*(0)\pi(a)$.

These, together with the first equation of (3.2), yield

$$\lambda - \mu_h S_h^* - \varphi(S_h^*, \xi i_v^*(0)) = 0.$$

By the property of φ and the implicit function theorem, there exists a function $f : R \to R$ such that

$$S_h^* = f(i_v^*(0))$$

with $f(0) = S_h^0$ and $f'(i_v^*(0)) = -\frac{\xi\varphi_2(f(i_v^*(0)),\xi i_v^*(0))}{\mu_h + \varphi_1(f(i_v^*(0)),\xi i_v^*(0))}$. By the last two equations of (3.2), we get

$$\begin{split} i_{h}^{*}(0) &= \varphi \left(S_{h}^{*}, \int_{0}^{\infty} k(a) i_{v}^{*}(a) \mathrm{d}a \right) \\ &= \varphi (f(i_{v}^{*}(0)), \xi i_{v}^{*}(0)), \\ i_{v}^{*}(0) &= \psi \left(N_{v} - \frac{1}{\mu_{v}} i_{v}^{*}(0), \eta i_{h}^{*}(0) \right) \\ &= \psi \left(N_{v} - \frac{1}{\mu_{v}} i_{v}^{*}(0), \varphi (f(i_{v}^{*}(0)), \xi i_{v}^{*}(0)) \eta \right) \end{split}$$

Clearly, $i_h^*(0) = 0$ if and only if $i_v^*(0) = 0$. This tells us that an equilibrium is endemic if it is not the disease-free equilibrium E^0 . From the above discussion, we see that an equilibrium (S_h^*, i_h^*, i_v^*) is an endemic equilibrium if and only if $i_v^*(0)$ is a positive zero of F, where

$$F(y) = y - \psi \left(N_v - \frac{1}{\mu_v} y, \varphi(f(y), \xi y) \eta \right).$$
(3.3)

First, assume $\mathcal{R}_0 \leq 1$. Then, for y > 0, by (H₂) and (H₃),

$$F(y) > y - \psi(N_{v}, \varphi(S_{h}^{0}, \xi y)\eta) \geq y - \psi_{2}(N_{v}, 0)\varphi(S_{h}^{0}, \xi y)\eta \geq y - \psi_{2}(N_{v}, 0)\varphi_{2}(S_{h}^{0}, \xi y)\xi\eta y = (1 - \mathcal{R}_{0})y \geq 0.$$

This implies that there is no endemic equilibrium when $\mathcal{R}_0 \leq 1$.

Next, suppose $\mathcal{R}_0 > 1$. Note that

$$F(0) = -\psi(N_v, 0) = 0$$
 and $F(\mu_v N_v) = \mu_v N_v > 0$.

Moreover,

Then, F(y) < 0 if y > 0 and is close enough to 0. By the Intermediate Value Theorem, F has at least one positive zero and hence there is at least one endemic equilibrium. Now, we prove that (2.1) has a unique endemic equilibrium. By way of contracdiction, we assume that there exists another endemic equilibrium $(\overline{S}_h, \overline{i}_h, \overline{i}_v)$. Without loss of generality, we assume $\overline{i}_v > i_v^*$. Denote $b = \frac{\overline{i}_v}{\overline{i}_v^*} (> 1)$. Then by (H₂) and concavity of φ in (H₃), we get

$$\begin{split} i_{h}^{*}(0) &= \varphi(f(i_{v}^{*}(0)), i_{v}^{*}(0)\xi) \\ &= \varphi\left(f(i_{v}^{*}(0)), \frac{1}{b}\bar{i}_{v}(0)\xi\right) \\ &> \varphi\left(f(\bar{i}_{v}(0)), \frac{1}{b}\bar{i}_{v}(0)\xi\right) \\ &\geq \frac{1}{b}\varphi(\overline{S}_{h}, \overline{i}_{v}(0)\xi) \\ &= \frac{1}{b}\bar{i}_{h}(0). \end{split}$$

Then

$$\begin{split} i_{v}^{*}(0) &= \psi \left(N_{v} - \frac{1}{\mu_{v}} i_{v}^{*}(0), \eta i_{h}^{*}(0) \right) \\ &> \psi \left(N_{v} - \frac{1}{\mu_{v}} \overline{i_{v}}^{*}(0), \frac{1}{b} \eta \overline{i}_{h}(0) \right) \\ &\geq \frac{1}{b} \psi \left(N_{v} - \frac{1}{\mu_{v}} \overline{i_{v}}^{*}(0), \eta \overline{i}_{h}(0) \right) \\ &= \frac{1}{b} \overline{i}_{v}(0), \end{split}$$

which is a contradiction.

To summarize, we have obtained the following results.

Theorem 3.1 (i) If $\mathcal{R}_0 \leq 1$, then (2.1) only has the disease-free equilibrium E^0 . (ii) If $\mathcal{R}_0 > 1$, then besides E^0 , (2.1) also has a unique endemic equilibrium, denoted $E^* = (S_h^*, i_h^*, i_v^*)$, where $S_h^* = f(i_v^*(0)), i_h^*(a) = \varphi(S_h^*, \xi i_v^*(0))\sigma(a), i_v^*(a) = i_v^*(0)\pi(a)$ with $i_v^*(0)$ being the unique positive zero of F defined by (3.3).

In the following, we study the local stability of the equilibria of (2.1) by the technique of linearization. For the details on the theory, we refer to Iannelli (1995).

Theorem 3.2 (i) The disease-free equilibrium E^0 of (2.1) is locally asymptotically stable if $\mathcal{R}_0 < 1$ and it is unstable if $\mathcal{R}_0 > 1$.

(ii) The endemic equilibrium E^* of (2.1) is locally asymptotically stable if $\mathcal{R}_0 > 1$.

Proof (i) Note that $\varphi_1(S_h^0, 0) = \psi_1(N_v, 0) = 0$. Then, the characteristic equation at the disease-free equilibrium E^0 is

$$\begin{vmatrix} \tau + \mu_h & 0 & \varphi_2(S_h^0, 0) \int_0^\infty k(a)\pi(a)e^{-\tau a} da \\ 0 & -1 & \varphi_2(S_h^0, 0) \int_0^\infty k(a)\pi(a)e^{-\tau a} da \\ 0 & \psi_2(N_v, 0) \int_0^\infty \beta(a)\sigma(a)e^{-\tau a} da & -1 \end{vmatrix} = 0.$$

Clearly, the stability of E^0 is determined by the roots of the following equation:

$$g_1(\tau) \stackrel{\Delta}{=} 1 - \varphi_2(S_h^0, 0) \int_0^\infty k(a) \pi(a) e^{-\tau a} \mathrm{d}a \cdot \psi_2(N_v, 0) \int_0^\infty \beta(a) \sigma(a) e^{-\tau a} \mathrm{d}a = 0.$$

If $\mathcal{R}_0 > 1$, then $g_1(0) = 1 - \mathcal{R}_0 < 0$. Noting that $\lim_{\tau \to \infty} g_1(\tau) = 1 > 0$, by the Intermediate Value Theorem, we know that g_1 has a positive zero and hence E^0 is unstable.

Now, suppose $\mathcal{R}_0 < 1$. It suffices to show that all zeros of $g_1 = 0$ have negative real parts. Otherwise, let τ_0 be a zero of $g_1(\tau)$ with $Re(\tau_0) \ge 0$. Then, we have

$$1 = \left| \varphi_2(S_h^0, 0) \int_0^\infty k(a) \pi(a) e^{-\tau_0 a} \mathrm{d}a \cdot \psi_2(N_v, 0) \int_0^\infty \beta(a) \sigma(a) e^{-\tau_0 a} \mathrm{d}a \right|$$

$$\leq \varphi_2(S_h^0, 0) \psi(N_v, 0) \int_0^\infty k(a) \pi(a) \mathrm{d}a \int_0^\infty \beta(a) \sigma(a) \mathrm{d}a$$

$$= \mathcal{R}_0 < 1,$$

which is a contradiction.

(ii) For E^* , the characteristic equation is

$$0 = (\tau + \mu_h + \varphi_1(S_h^*, \int_0^\infty k(a)i_v^*(a)da)\Gamma_2(\tau) - (\tau + \mu_h)(\varphi_2(S_h^*, \int_0^\infty k(a)i_v^*(a)da)\int_0^\infty k(a)\pi(a)e^{-\tau a}da)\Gamma_1(\tau),$$
(3.4)

where

$$\Gamma_1(\tau) = \psi_2 \left(N_v - \int_0^\infty i_v^*(a) \mathrm{d}a, \int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a \right) \int_0^\infty \beta(a) \sigma(a) e^{-\tau a} \mathrm{d}a,$$

$$\Gamma_2(\tau) = 1 + \psi_1 \left(N_v - \int_0^\infty i_v^*(a) \mathrm{d}a, \int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a \right) \int_0^\infty \pi(a) e^{-\tau a} \mathrm{d}a.$$

We claim that (3.4) has no root with a nonnegative real part. Otherwise, suppose that it has a root τ^0 with $Re(\tau^0) \ge 0$. Then

$$1 = \frac{|(\tau^0 + \mu_h)(\varphi_2(S_h^*, \int_0^\infty k(a)i_v^*(a)da) \int_0^\infty k(a)\pi(a)e^{-\tau^0 a}da\Gamma_1(\tau^0)|}{|(\tau^0 + \mu_h + \varphi_1(S_h^*, \int_0^\infty k(a)i_v^*(a)da))\Gamma_2(\tau^0)|}$$

It follows from (H_3) that

$$\varphi_2\left(S_h^*, \int_0^\infty k(a)i_v^*(a)\mathrm{d}a\right) \le \frac{\varphi(S_h^*, \int_0^\infty k(a)i_v^*(a)\mathrm{d}a)}{\int_0^\infty k(a)i_v^*(a)\mathrm{d}a},$$
$$\psi_2\left(N_v - \int_0^\infty i_v^*(a)\mathrm{d}a, \int_0^\infty \beta(a)i_h^*(a)\mathrm{d}a\right) \le \frac{\psi(N_v - \int_0^\infty i_v^*(a)\mathrm{d}a, \int_0^\infty \beta(a)i_h^*(a)\mathrm{d}a)}{\int_0^\infty \beta(a)i_h^*(a)\mathrm{d}a}.$$

Thus

$$\begin{split} &\int_{0}^{\infty} k(a)i_{v}^{*}(a)da \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)da \\ &\leq \frac{|(\tau^{0} + \mu_{h})\varphi(S_{h}^{*}, \int_{0}^{\infty} k(a)i_{v}^{*}(a)da) \int_{0}^{\infty} k(a)\pi(a)e^{-\tau^{0}a}da\psi(N_{v} - \int_{0}^{\infty} i_{v}^{*}(a)da, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)da) \int_{0}^{\infty} \beta(a)\sigma(a)e^{-\tau^{0}a}da|}{|(\tau^{0} + \mu_{h} + \varphi_{1}(S_{h}^{*}, \int_{0}^{\infty} k(a)i_{v}^{*}(a)da))(1 + \psi_{1}(N_{v} - \int_{0}^{\infty} i_{v}^{*}(a)da, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)da) \int_{0}^{\infty} \pi(a)e^{-\tau^{0}a}da|} \\ &< \frac{|(\tau^{0} + \mu_{h})i_{v}^{*}(0) \int_{0}^{\infty} k(a)\pi(a)da \cdot i_{h}^{*}(0) \int_{0}^{\infty} \beta(a)\sigma(a)da|}{|\tau^{0} + \mu_{h}|} \\ &= \int_{0}^{\infty} k(a)i_{v}^{*}(a)da \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)da, \end{split}$$

a contradiction. This completes the proof.

4 The global dynamics

In this section, we first prove the global stability of the disease-free equilibrium E^0 using the Fluctuation Lemma.



For any function $f : R_+ \to R$, we set

$$f_{\infty} = \liminf_{t \to \infty} f(t), \quad f^{\infty} = \limsup_{t \to \infty} f(t).$$

Lemma 4.1 (Fluctuation Lemma Hirsch et al. 1985) Let $f : R_+ \to R$ be a bounded and continuously differentiable function. Then, there exist two sequences $\{s_n\}$ and $\{t_n\}$ such that $s_n \to \infty, t_n \to \infty, f(s_n) \to f_\infty, f'(s_n) \to 0, f(t_n) \to f^\infty \text{ and } f'(t_n) \to 0 \text{ as } n \to \infty.$

The following estimate is useful in the coming discussion.

Lemma 4.2 (Iannelli 1995) Suppose $k \in L^1_+(0, \infty)$ and $B : R_+ \to R$ is a bounded function. Then

$$\limsup_{t\to\infty}\int_0^t k(\theta)B(t-\theta)d\theta \le B^\infty ||k||_1.$$

Theorem 4.3 If $\mathcal{R}_0 < 1$, then the disease-free equilibrium E^0 of (2.1) is globally asymptotically stable.

Proof By Theorem 3.2, we only need to show that E^0 is globally attractive in Ω . To this end, let $(S_h(t), i_h(t, \cdot), i_v(t, \cdot))$ be a solution of (2.1) with initial value $(S_{h0}, i_{h0}, i_{v0}) \in \Omega$. Recall that

$$i_{h}(t,a) = \begin{cases} \sigma(a)B_{\varphi}(t-a), & 0 \le a < t\\ \frac{\sigma(a)}{\sigma(a-t)}i_{h0}(a-t), & a \ge t > 0 \end{cases}$$
(4.1)

and

$$i_{v}(t,a) = \begin{cases} \pi(a)B_{\psi}(t-a), & 0 \le a < t, \\ \frac{\pi(a)}{\pi(a-t)}i_{v0}(a-t), & a \ge t > 0, \end{cases}$$
(4.2)

where

$$B_{\varphi}(t) = i_h(t, 0) = \varphi\left(S_h(t), \int_0^\infty k(a)i_v(t, a)da\right),$$

$$B_{\psi}(t) = i_v(t, 0) = \psi\left(N_v - \int_0^\infty i_v(t, a)da, \int_0^\infty \beta(a)i_h(t, a)da\right).$$

Obviously, B_{φ} and B_{ψ} are nonnegative, bounded, and differentiable.

Firstly, we show $B_{\varphi}^{\infty} = B_{\psi}^{\infty} = 0$. Note that



$$\begin{split} B_{\varphi}(t) &\leq \varphi \left(S_{h}^{0}, \int_{0}^{\infty} k(a)i_{v}(t, a)da \right) \\ &\leq \varphi_{2} \left(S_{h}^{0}, 0 \right) \int_{0}^{\infty} k(a)i_{v}(t, a)da \\ &= \varphi_{2} \left(S_{h}^{0}, 0 \right) \left[\int_{0}^{t} k(a)\pi(a)B_{\psi}(t-a)da + \int_{t}^{\infty} k(a)\frac{\pi(a)}{\pi(a-t)}i_{v0}(a-t)da \right] \\ &\leq \varphi_{2} \left(S_{h}^{0}, 0 \right) \left[\int_{0}^{t} k(a)\pi(a)\psi \left(N_{v}, \int_{0}^{\infty} \beta(s)i_{h}(t-a, s)ds \right) + e^{-\mu_{v}t} \|k\|_{\infty} \|i_{v0}\|_{1} \right] \\ &\leq \varphi_{2} \left(S_{h}^{0}, 0 \right) \left[\int_{0}^{t} k(a)\pi(a) \left(\psi_{2}(N_{v}, 0) \int_{0}^{\infty} \beta(s)i_{h}(t-a, s)ds \right) da + e^{-\mu_{v}t} \|k\|_{\infty} \|i_{v0}\|_{1} \right] \\ &= \varphi_{2} \left(S_{h}^{0}, 0 \right) \left[\psi_{2}(N_{v}, 0) \int_{0}^{t} k(a)\pi(a) \left[\int_{0}^{t-a} \beta(s)\sigma(s)B_{\varphi}(t-a-s)ds \right. \\ &+ \int_{t-a}^{\infty} \beta(s) \frac{\sigma(s)}{\sigma(s-t+a)} i_{h0}(s-t+a)ds \right] da + e^{-\mu_{v}t} \|k\|_{\infty} \|i_{v0}\|_{1} \right] \\ &\leq \varphi_{2} \left(S_{h}^{0}, 0 \right) \left[\psi_{2}(N_{v}, 0) \int_{0}^{t} k(a)\pi(a) \left[\int_{0}^{t-a} \beta(s)\sigma(s)B_{\varphi}(t-a-s)ds \right. \\ &+ e^{-\mu_{h}(t-a)} \|\beta\|_{\infty} \|i_{h0}\|_{1}] da + e^{-\mu_{v}t} \|k\|_{\infty} \|i_{v0}\|_{1} \right]. \end{split}$$

Applying Lemma 4.2 twice, we get

$$B_{\varphi}^{\infty} \leq \varphi_2(S_h^0, 0)\psi_2(N_v, 0)\xi \limsup_{t \to \infty} \int_0^t \beta(s)\sigma(s)B_{\varphi}(t-s)ds$$

$$\leq \varphi_2(S_h^0, 0)\psi_2(N_v, 0)\xi\eta B_{\varphi}^{\infty}$$

$$= \mathcal{R}_0 B_{\varphi}^{\infty},$$

which implies that $B_{\varphi}^{\infty} = 0$ since $\mathcal{R}_0 < 1$. Similarly, one can show that $B_{\psi}^{\infty} = 0$. Next, we show $\lim_{t\to\infty} \|i_h(t, \cdot)\|_1 = \lim_{t\to\infty} \|i_v(t, \cdot)\|_1 = 0$. In fact, using (4.1), we get

$$\begin{aligned} \|i_h(t,\cdot)\|_1 &= \int_0^t B_{\varphi}(t-a)\sigma(a)\mathrm{d}a + \int_t^\infty i_{h0}(a-t)\frac{\sigma(a)}{\sigma(a-t)}\mathrm{d}a \\ &\leq \int_0^t B_{\varphi}(t-a)\sigma(a)\mathrm{d}a + e^{-\mu_h t}\|i_{h0}\|_1. \end{aligned}$$

By Lemma 4.2,

$$\limsup_{t \to \infty} \|i_h(t, \cdot)\|_1 \le B_{\varphi}^{\infty} \|\sigma\|_1 = 0$$

and hence $\lim_{t\to\infty} \|i_h(t,\cdot)\|_1 = 0$. Similarly, we have $\lim_{t\to\infty} \|i_v(t,\cdot)\|_1 = 0$. Finally, we show $\lim_{t\to\infty} S_h(t) = S_h^0$. It suffices to show $(S_h)_\infty \ge S_h^0$ since $(S_h)^\infty \le S_h^0$. According to Lemma 4.1, there exists a sequence $\{t_n\}$ such that $t_n \to \infty$, $S_h(t_n) \to (S_h)_\infty$, and $\frac{dS_h(t_n)}{dt} \to 0$ as $n \to \infty$. Note that

$$\frac{\mathrm{d}S_h(t_n)}{\mathrm{d}t} = \lambda - \mu_h S_h(t_n) - \varphi\left(S_h(t_n), \int_0^\infty k(a)i_v(t_n, a)\mathrm{d}a\right)$$

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and $\lim_{t\to\infty} \int_0^\infty k(a)i_v(t,a)da = 0$ since k is bounded and $\lim_{t\to\infty} ||i_v(t,\cdot)||_1 = 0$. Then, we get

$$0 = \lambda - \mu_h(S_h)_{\infty}$$

and hence $(S_h)_{\infty} = S_h^0$.

In summary, we have shown that $\lim_{t\to\infty} (S_h(t), i_h(t, \cdot), i_v(t, \cdot)) = E^0$. This completes the proof.

In the following, we establish the global stability of the endemic equilibrium E^* . We start with the permanence of (2.1) using uniform persistence theory for infinite dimensional system developed by Smith and Thieme (2011).

By Theorem 2.1, there is a continuous solution semiflow of (2.1), denoted by $\Phi : R_+ \times X_+ \to X_+$, where

$$\Phi(t, (S_{h0}, i_{h0}, i_{v0})) = (S_h(t), i_h(t, \cdot), i_v(t, \cdot)) \quad \text{for } (t, (S_{h0}, i_{h0}, i_{v0})) \in R_+ \times X_+,$$

where $(S_h(t), i_h(t, \cdot), i_v(t, \cdot))$ is the solution of (2.1) with the initial value (S_{h0}, i_{h0}, i_{v0}) . The semiflow is also written as $\{\Phi(t)\}_{t \in R_{\perp}}$.

Define $\rho: X_+ \to R_+$ by

$$\rho(S_h, i_h, i_v) = \int_0^\infty k(a)i_v(a)da \quad \text{for } (S_h, i_h, i_v) \in X_+.$$

Let

 $\Omega_0 = \{ (S_{h0}, i_{h0}, i_{v0}) \in \Omega | \text{ there exists } t_0 \in R_+ \text{ such that } \rho(\Phi(t_0, (S_{h0}, i_{h0}, i_{v0}))) > 0 \}.$

If $(S_{h0}, i_{h0}, i_{v0}) \in \Omega \setminus \Omega_0$, then $\lim_{t\to\infty} S_h(t) = S_h^0$ and a little modification of the proof of Theorem 4.3 will yield $\lim_{t\to\infty} \Phi(t, (S_{h0}, i_{h0}, i_{v0})) = E^0$.

Definition 4.1 System (2.1) is uniformly weakly ρ -persistent (respectively, uniformly strongly ρ -persistent) if there exists an r > 0, independent of the initial conditions, such that

 $\limsup_{t \to \infty} \rho(\Phi(t, (S_{h0}, i_{h0}, i_{v0}))) > r \text{ (respectively, } \liminf_{t \to \infty} \rho(\Phi(t, (S_{h0}, i_{h0}, i_{v0}))) > r)$

for $(S_{h0}, i_{h0}, i_{v0}) \in \Omega_0$.

Proposition 4.4 If $\mathcal{R}_0 > 1$, then system (2.1) is uniformly weakly ρ -persistent.

Proof By way of contradiction, for any $\varepsilon > 0$, there exists an $x^{\varepsilon} = (S_{h0}^{\varepsilon}, i_{h0}^{\varepsilon}, i_{v0}^{\varepsilon}) \in \Omega_0$ such that

$$\limsup_{t\to\infty}\int_0^\infty k(a)i_v^\varepsilon(t,a)\mathrm{d}a\leq\varepsilon.$$

Since $\mathcal{R}_0 > 1$, we can choose $\varepsilon_0 > 0$ such that

$$\varepsilon_{1} = \frac{\lambda - L_{v}\varepsilon_{0}}{\mu_{h}} - \varepsilon_{0} > 0,$$

$$1 < \varphi_{2}(\varepsilon_{1}, \varepsilon_{0})\psi_{2}(N_{v} - \varepsilon_{3}, \|\beta\|_{\infty}\varepsilon_{2})\int_{0}^{\infty} k(a)\pi(a)e^{-\varepsilon_{0}a}da \int_{0}^{\infty}\beta(a)\sigma(a)e^{-\varepsilon_{0}a}da,$$

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where $\varepsilon_2 = (\varphi_2(S_h^0, 0) \|\sigma\|_1 + 1)\varepsilon_0$ and $\varepsilon_3 = \frac{\psi_2(N_v, 0) \|\beta\|_{\infty}\varepsilon_2}{\mu_v} + \varepsilon_0$. For $\frac{\varepsilon_0}{2}$, there exists $x^{\frac{\varepsilon_0}{2}}$, for simplicity of notation denoted by $x = (S_{h0}, i_{h0}, i_{v0})$, such that

$$\limsup_{t\to\infty}\int_0^\infty k(a)i_v(t,a)\mathrm{d}a\leq\frac{\varepsilon_0}{2}.$$

In the following, we shall use Laplace transforms to get a contradiction.

On the one hand, there exists $t_0 \in R_+$ such that

$$\int_0^\infty k(a)i_v(t,a)\mathrm{d}a \le \varepsilon_0 \quad \text{for } t \ge t_0.$$

Without loss of generality, we can assume $t_0 = 0$ since we can replace x with $\Phi(t_0, x)$. These, together with the first equation of (2.1), (H₂), and (H₄), give us

$$\begin{aligned} \frac{\mathrm{d}S_h(t)}{\mathrm{d}t} &= \lambda - \mu_h S_h(t) - \left(\varphi(S_h(t), \int_0^\infty k(a)i_v(t, a)\mathrm{d}a) - \varphi(S_h(t), 0)\right) \\ &\geq \lambda - \mu_h S_h(t) - L_v \int_0^\infty k(a)i_v(t, a)\mathrm{d}a \\ &\geq \lambda - L_v \varepsilon_0 - \mu_h S_h(t), \end{aligned}$$

which implies that $\liminf_{t\to\infty} S_h(t) \ge \frac{\lambda - L_v \varepsilon_0}{\mu_h}$. Again, without loss of generality, we assume $S_h(t) \ge \varepsilon_1$ for $t \in R_+$. On the other hand, for $t \in R_+$,

$$B_{\varphi}(t) \le \varphi(S_h^0, \varepsilon_0) \le \varphi_2(S_h^0, 0)\varepsilon_0.$$
(4.3)

Then, from (4.3) and the arguments in the proof of Theorem 4.3, $\limsup_{t\to\infty} ||i_h(t, \cdot)||_1 \le \varphi_2(S_h^0, 0)\varepsilon_0||\sigma||_1$. Again, without loss of generality, we assume that $||i_h(t, \cdot)||_1 \le \varepsilon_2$ for $t \in R_+$. It follows that

$$i_{v}(t,0) \leq \psi(N_{v}, \|\beta\|_{\infty} \|i_{h}(t,\cdot)\|_{1}) \leq \psi_{2}(N_{v},0) \|\beta\|_{\infty} \|i_{h}(t,\cdot)\|_{1} \leq \psi_{2}(N_{v},0) \|\beta\|_{\infty} \varepsilon_{2}$$

for $t \in R_+$. Similarly as before, we have $\limsup_{t\to\infty} \|i_v(t,\cdot)\|_1 \leq \frac{\psi_2(N_v,0)\|\beta\|_{\infty}\varepsilon_2}{\mu_v}$. Again, without loss of generality, we assume that $\|i_v(t,\cdot)\|_1 \leq \varepsilon_3$ for $t \in R_+$.

Now, under assumptions (H_2) and (H_3) , with the help of (4.1) and (4.2), we get

$$B_{\varphi}(t) \geq \varphi\left(\varepsilon_{1}, \int_{0}^{\infty} k(a)i_{v}(t, a)\right) \geq \varphi_{2}(\varepsilon_{1}, \varepsilon_{0}) \int_{0}^{\infty} k(a)i_{v}(t, a)da$$

$$\geq \varphi_{2}(\varepsilon_{1}, \varepsilon_{0}) \int_{0}^{t} k(a)i_{v}(t, a)da$$

$$= \varphi_{2}(\varepsilon_{1}, \varepsilon_{0}) \int_{0}^{t} k(a)\pi(a) \left(\psi(N_{v} - \int_{0}^{\infty} i_{v}(t - a, s)ds, \int_{0}^{\infty} \beta(s)i_{h}(t - a, s)ds\right) da$$

$$\geq \varphi_{2}(\varepsilon_{1}, \varepsilon_{0}) \int_{0}^{t} k(a)\pi(a) \left(\psi(N_{v} - \varepsilon_{3}, \int_{0}^{\infty} \beta(s)i_{h}(t - a, s)ds\right) da$$

$$\geq \varphi_{2}(\varepsilon_{1}, \varepsilon_{0})\psi_{2}(N_{v} - \varepsilon_{3}, \|\beta\|_{\infty}\varepsilon_{2}) \int_{0}^{t} k(a)\pi(a) \left(\int_{0}^{t - a} \beta(s)i_{h}(t - a, s)ds\right) da$$

$$\geq \varphi_{2}(\varepsilon_{1}, \varepsilon_{0})\psi_{2}(N_{v} - \varepsilon_{3}, \|\beta\|_{\infty}\varepsilon_{2}) \int_{0}^{t} k(a)\pi(a) \left(\int_{0}^{t - a} \beta(s)i_{h}(t - a, s)ds\right) da$$

$$= \varphi_{2}(\varepsilon_{1}, \varepsilon_{0})\psi_{2}(N_{v} - \varepsilon_{3}, \|\beta\|_{\infty}\varepsilon_{2}) \int_{0}^{t} k(a)\pi(a) \left(\int_{0}^{t - a} \beta(s)\sigma(s)B_{\varphi}(t - a - s)ds\right) da$$

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for $t \in R_+$. Taking Laplace transforms of the both sides of the above inequality produces

$$\widehat{B}_{\varphi}(\theta) \geq \varphi_{2}(\varepsilon_{1}, \varepsilon_{0})\psi_{2}(N_{\upsilon} - \varepsilon_{3}, \|\beta\|_{\infty}\varepsilon_{2})\widehat{B}_{\varphi}(\theta)\widehat{k\pi}(\theta)\widehat{\beta\sigma}(\theta) \quad \text{for } \theta > 0,$$

where $\widehat{\cdot}$ denotes the Laplace transform of a function. As $B_{\varphi}(\cdot)$ is not identically zero on R_+ , we have $\widehat{B}_{\varphi}(\theta) > 0$ for $\theta > 0$. Therefore, in particular,

$$\varphi_2(\varepsilon_1,\varepsilon_0)\psi_2(N_v-\varepsilon_3,\|\beta\|_{\infty}\varepsilon_2)\widehat{k\pi}(\varepsilon_0)\widehat{\beta\sigma}(\varepsilon_0)\leq 1,$$

a contradiction with the choice of ε_0 .

Now, we consider the uniform strong ρ -persistence of (2.1). To this end, we only need to show that Φ has a global compactor in Ω_0 . A global compact attractor \mathcal{A} is a maximal compact invariant set in Ω_0 such that for any open set that contains \mathcal{A} , all solutions of (2.1) that start at zero from a bounded set, are contained in that open set, at least for sufficiently large time. The existence of a global attractor is established by applying the following two results.

Lemma 4.5 (Hale 1988) If $\Phi(t) : X \to X$, $t \in R_+$ is asymptotically smooth, point dissipative and orbits of bounded sets are bounded, then there exists a global attractor.

Definition 4.2 (Smith and Thieme 2011) A semiflow is asymptotically smooth if each forward invariant bounded closed set is attracted by a non-empty compact set.

Lemma 4.6 (Hale 1988) For each $t \in R_+$, suppose $\Phi(t) = \Phi_1(t) + \Phi_2(t) : X \to X$ has the property that $\Phi_2(t)$ is complete continuous and there is a continuous function \tilde{f} : $R_+ \times R_+ \to R_+$ such that $\tilde{f}(t, \tilde{r}) \to 0$ as $t \to \infty$ and $|\Phi_1(t)x| \le \tilde{f}(t, \tilde{r})$ if $|x| < \tilde{r}$. Then, $\Phi(t), t \in R_+$ is asymptotically smooth.

Lemma 4.7 For any $\varepsilon > 0$, there exists $\delta > 0$ such that

$$|B_i(t+h) - B_i(t)| \le \varepsilon_1$$
 for $t \in R_+, h \in (0, \delta), (S_{h0}, i_{h0}, i_{v0}) \in \Omega_0$,

where $i = \varphi, \psi$.

Proof We only show the case where $i = \varphi$ as the other can be dealt with similarity.

Obviously,

$$B_{\varphi}(t) \leq \varphi \left(S_{h}^{0}, \int_{0}^{\infty} k(a)i_{v}(t, a)da \right)$$
$$\leq \varphi_{2}(S_{h}^{0}, 0) \int_{0}^{\infty} k(a)i_{v}(t, a)da$$
$$\leq \varphi_{2}(S_{h}^{0}, 0) ||k||_{\infty} N_{v} \triangleq M_{\varphi}.$$

It follows that

$$\left|\frac{\mathrm{d}S_h(t)}{\mathrm{d}t}\right| \leq \lambda + \mu_h \cdot S_h^0 + B_\varphi(t) \leq 2\lambda + M_\varphi \triangleq M_S.$$

Moreover, $B_{\psi}(t) \leq \psi(N_v, \|\beta\|_{\infty}S_h^0) \triangleq M_{\psi}$. Note that M_{φ}, M_S , and M_{ψ} all are independent of *t* and the initial values.



Now, for $t \in R_+$ and h > 0, we have

$$\begin{split} |B_{\varphi}(t+h) - B_{\varphi}(t)| \\ &= \left| \varphi \left(S_{h}(t+h), \int_{0}^{\infty} k(a)i_{v}(t+h,a)da \right) - \varphi \left(S_{h}(t), \int_{0}^{\infty} k(a)i_{v}(t,a)da \right) \right| \\ &\leq \left| \varphi \left(S_{h}(t+h), \int_{0}^{\infty} k(a)i_{v}(t+h,a)da \right) - \varphi \left(S_{h}(t), \int_{0}^{\infty} k(a)i_{v}(t+h,a)da \right) \right| \\ &+ \left| \varphi \left(S_{h}(t), \int_{0}^{\infty} k(a)i_{v}(t+h,a)da \right) - \varphi \left(S_{h}(t), \int_{0}^{\infty} k(a)i_{v}(t,a)da \right) \right| \\ &\leq L_{u}|S_{h}(t+h) - S_{h}(t)| + L_{v} \left| \int_{0}^{\infty} k(a)i_{v}(t+h,a)da - \int_{0}^{\infty} k(a)i_{v}(t,a)da \right| \\ &\leq L_{u}M_{S}h + L_{v} \int_{0}^{h} k(a)i_{v}(t+h,a)da \\ &+ L_{v} \left| \int_{h}^{\infty} k(a)i_{v}(t+h,a)da - \int_{0}^{\infty} k(a)i_{v}(t,a)da \right|. \end{split}$$

Note that

$$L_{v} \int_{0}^{h} k(a) i_{v}(t+h,a) \mathrm{d}a = L_{v} \int_{0}^{h} k(a) \pi(a) B_{\psi}(t+h-a) \mathrm{d}a \le L_{v} \|k\|_{\infty} M_{\psi} h$$

and

$$\left|\int_{h}^{\infty} k(a)i_{v}(t+h,a)\mathrm{d}a - \int_{0}^{\infty} k(a)i_{v}(t,a)\mathrm{d}a\right|$$
$$= \left|\int_{0}^{\infty} k(a+h)i_{v}(t+h,a+h)\mathrm{d}a - \int_{0}^{\infty} k(a)i_{v}(t,a)\mathrm{d}a\right|.$$

It follows from (4.2) that $i_v(t+h, a+h) = \frac{\pi(a+h)}{\pi(a)}i_v(t, a)$. Therefore,

$$\begin{split} \left| \int_{h}^{\infty} k(a)i_{v}(t+h,a)da - \int_{0}^{\infty} k(a)i_{v}(t,a)da \right| \\ &= \left| \int_{0}^{\infty} k(a+h)\frac{\pi(a+h)}{\pi(a)}i_{v}(t,a)da - \int_{0}^{\infty} k(a)i_{v}(t,a)da \right| \\ &\leq \left| \int_{0}^{\infty} k(a+h)\Big(\frac{\pi(a+h)}{\pi(a)} - 1\Big)i_{v}(t,a)da \Big| + \int_{0}^{\infty} |k(a+h) - k(a)|i_{v}(t,a)da \right| \\ &= \left| \int_{0}^{\infty} k(a+h)\Big(e^{-\mu_{v}h} - 1\Big)i_{v}(t,a)da \right| + \int_{0}^{\infty} |k(a+h) - k(a)|i_{v}(t,a)da \\ &\leq \mu_{v}h \|k\|_{\infty}N_{v} + \int_{0}^{\infty} |k(a+h) - k(a)|i_{v}(t,a)da \end{split}$$

since $0 \le 1 - e^{-\mu_v h} - 1 \le \mu_v h$. In summary,

$$|B_{\varphi}(t+h) - B_{\varphi}(t)| \leq (L_u M_S + L_v M_{\psi} ||k||_{\infty} + L_v \mu_v ||k||_{\infty} N_v)h$$
$$+ L_v \int_0^\infty |k(a+h) - k(a)|i_v(t,a)da.$$

It is easy to see that conclusion holds since k is uniformly continuous.

Proposition 4.8 If $\mathcal{R}_0 > 1$, then there exists a global attractor \mathcal{A} for the solution semiflow Φ of (2.1) in Ω_0 .

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Proof By Lemma 4.5, we only need to show that the induced semiflow on Ω_0 is asymptotically smooth. To apply Lemma 4.6, for any $t \in R_+$ and $x = (S_{h0}, i_{h0}, i_{v0}) \in \Omega_0$, we denote $\Phi = \Phi_1 + \Phi_2$ with

$$\Phi_1(t, x) = (0, \hat{i}_h(t, \cdot), \hat{i}_v(t, \cdot)) \text{ and } \Phi_2(t, x) = (S_h(t), \hat{i}_h(t, \cdot), \hat{i}_v(t, \cdot)),$$

where

$$\widehat{i}_{h}(t,a) = \begin{cases} 0, & 0 \le a \le t, \\ \frac{\sigma(a)}{\sigma(a-t)} i_{h0}(a-t), & 0 < t < a, \end{cases}$$

$$\widehat{i}_{v}(t,a) = \begin{cases} 0, & 0 \le a \le t, \\ \frac{\pi(a)}{\pi(a-t)} i_{v0}(a-t), & 0 < t < a, \end{cases}$$

and

$$\widetilde{i}_{h}(t,a) = i_{h}(t,a) - \widehat{i}_{h}(t,a) = \begin{cases} \sigma(a)B_{\varphi}(t-a), & 0 \le a \le t, \\ 0, & 0 < t < a, \end{cases}$$
$$\widetilde{i}_{v}(t,a) = i_{v}(t,a) - \widehat{i}_{v}(t,a) = \begin{cases} \pi(a)B_{\psi}(t-a), & 0 \le a \le t, \\ 0, & 0 < t < a. \end{cases}$$

It is obvious that $\hat{i}_h, \hat{i}_v, \hat{i}_h$ and \tilde{i}_v are nonnegative.

First,

$$\begin{split} \|\Phi_{1}(t,x)\| &= \|\widehat{i}_{h}(t,\cdot)\|_{1} + \|\widehat{i}_{v}(t,\cdot)\|_{1} \\ &= \int_{t}^{\infty} i_{h0}(a-t) \frac{\sigma(a)}{\sigma(a-t)} \mathrm{d}a + \int_{t}^{\infty} i_{v0}(a-t) \frac{\pi(a)}{\pi(a-t)} \mathrm{d}a \\ &= \int_{0}^{\infty} i_{h0}(a) \frac{\sigma(a+t)}{\sigma(a)} \mathrm{d}a + \int_{0}^{\infty} i_{v0}(a) \frac{\pi(a+t)}{\pi(a)} \mathrm{d}a \\ &\leq e^{-\mu_{h}t} \|i_{h0}\|_{1} + e^{-\mu_{v}t} \|i_{v0}\|_{1} \\ &\leq e^{-\widetilde{\mu}t} \|x\|, \end{split}$$

where $\tilde{\mu} = \min\{\mu_h, \mu_v\}$. This means that Φ_1 satisfies the condition of Lemma 4.6.

Next, we show that Φ_2 is completely continuous, that is, for any fixed $t \in R_+$ and any bounded set $\Omega_1 \subseteq \Omega_0$, the set

$$\Omega_t \triangleq \left\{ \Phi_2(t, x) : x = (S_{h0}, i_{h0}, i_{v0}) \in \Omega_1 \right\}$$

is precompact. It is enough to show that

$$\Omega_t(i_h, i_v) = \left\{ (\widetilde{i}_h(t, \cdot), \widetilde{i}_v(t, \cdot)) : (S_h(t), \widetilde{i}_h(t, \cdot), \widetilde{i}_v(t, \cdot)) \in \Omega_t \right\}$$

is precompact.

According to similar arguments in Chen et al. (2016), we only need to verify the second condition of the Fréchet–Kolmogrov Theorem, that is, the translation operator $\Omega_t(i_h, i_v)$ is uniformly continuous or

$$\lim_{h \to 0^+} \|\tilde{i}_h(t, \cdot) - \tilde{i}_h(t, \cdot + h)\|_1 = \lim_{h \to 0^+} \|\tilde{i}_v(t, \cdot) - \tilde{i}_v(t, \cdot + h)\|_1 = 0$$
(4.4)

uniformly in $\Omega_t(i_h, i_v)$.



It is obvious that (4.4) holds when t = 0 since $\tilde{i}_h(0, \cdot) = 0$ and $\tilde{i}_v(0, \cdot) = 0$. Therefore, we only need to consider the case when t > 0. Concerning with the limit as $h \to 0^+$, we assume that $h \in (0, t)$. Then

$$\begin{split} \widetilde{i}_{h}^{t}(t,\cdot) &- \widetilde{i}_{h}^{t}(t,\cdot+h) \|_{1} \\ &= \int_{0}^{\infty} |\widetilde{i}_{h}^{t}(t,a) - \widetilde{i}_{h}^{t}(t,a+h)| \mathrm{d}a \\ &= \int_{0}^{t-h} |B_{\varphi}(t-a-h)\sigma(a+h) - B_{\varphi}(t-a)\sigma(a)| \mathrm{d}a + \int_{t-h}^{t} B_{\varphi}(t-a)\sigma(a) \mathrm{d}a \\ &\leq \int_{0}^{t-h} B_{\varphi}(t-a-h)|\sigma(a+h) - \sigma(a)| \mathrm{d}a \\ &+ \int_{0}^{t-h} |B_{\varphi}(t-a-h) - B_{\varphi}(t-a)|\sigma(a)\mathrm{d}a + hM_{\varphi} \\ &\leq M_{\varphi}t \|\delta\|_{\infty}h + \int_{0}^{t-h} |B_{\varphi}(t-a-h) - B_{\varphi}(t-a)|\sigma(a)\mathrm{d}a + hM_{\varphi} \end{split}$$

as $B_{\varphi}(t) \leq M_{\varphi}$ for $t \in R_+$ and $|\sigma(a+h) - \sigma(a)| \leq h \|\delta\|_{\infty}$. This, combined with Lemma 4.7, gives us

$$\lim_{h \to 0^+} \|\widetilde{i}_h(t, \cdot) - \widetilde{i}_h(t, \cdot + h)\|_1 = 0.$$

Similarly, we can show that $\lim_{h\to 0^+} \|\widetilde{i}_v(t,\cdot) - \widetilde{i}_v(t,\cdot+h)\|_1 = 0.$

Now the uniform strong ρ -persistence follows from (Thieme 2000, Theorem 2.3) and Propositions 4.4 and 4.8.

Theorem 4.9 Suppose $\mathcal{R}_0 > 1$. Then, (2.1) is uniformly strongly ρ -persistent.

We know that the global attractor \mathcal{A} only can contain points with total trajectories through them since it must be invariant. A *total trajectory* of Φ is a function $x : R \to X_+$ such that $\Phi(s, x(t)) = x(s + t)$ for all $t \in R$ and all $s \in R_+$. For a total trajectory, $i_h(t, a) =$ $i_h(t - a, 0)\sigma(a)$ and $i_v(t, a) = i_v(t - a, 0)\pi(a)$ for all $t \in R$ and $a \in R_+$. The alpha limit of a total trajectory x(t) passing through $x(0) = x_0$ is

$$\alpha(x_0) = \bigcap_{t \le 0} \bigcup_{s \le t} \{x(s)\} \subseteq \mathcal{A} \bigcap \Omega_0.$$

Theorem 4.10 Suppose $\mathcal{R}_0 > 1$. Then there exists $\varepsilon_0 > 0$ such that $S_h(t)$, $i_h(t, 0)$, $i_v(t, 0) \ge \varepsilon_0$ for all $t \in R$, where $(S_h(t), i_h(t, \cdot), i_v(t, \cdot))$ is any total trajectory in \mathcal{A} .

Proof Firstly, it follows from

$$\frac{\mathrm{d}S_h(t)}{\mathrm{d}t} \ge \lambda - (\mu_h + L_u)S_h(t)$$

that $\liminf_{t\to\infty} S_h(t) \ge \frac{\lambda}{\mu_h + L_u} \triangleq \varepsilon_h$. By invariance, $S_h(t) \ge \varepsilon_h$ for $t \in R$.

Secondly, by Theorem 4.9 and invariance, there exists $\varepsilon_1 > 0$ such that

$$\int_0^\infty k(a)i_v(t,a)\mathrm{d}a \ge \varepsilon_1 \quad \text{ for } t \in R$$

Then, $i_h(t, 0) = \varphi(S_h(t), \int_0^\infty k(a)i_v(t, a) da \ge \varphi(\varepsilon_h, \varepsilon_1) \triangleq \varepsilon_2$ for $t \in \mathbb{R}$.

Thirdly,

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t} \left(N_v - \int_0^\infty i_v(t,a) \mathrm{d}a \right) &= -\int_0^\infty \frac{\partial i_v(t,a)}{\partial t} \mathrm{d}a = \int_0^\infty \left(\mu_v + \frac{\partial i_v(t,a)}{\partial a} \right) \mathrm{d}a \\ &= \mu_v \int_0^\infty i_v(t,a) \mathrm{d}a + i_v(t,\infty) - i_v(t,0) \\ &\geq \mu_v \int_0^\infty i_v(t,a) \mathrm{d}a - \psi \left(N_v - \int_0^\infty i_v(t,a) \mathrm{d}a, \int_0^\infty \beta(a) i_h(t,a) \mathrm{d}a \right) \\ &\geq \mu_v \int_0^\infty i_v(t,a) \mathrm{d}a - K_u \left(N_v - \int_0^\infty i_v(t,a) \mathrm{d}a \right) \\ &= \mu_v N_v - (\mu_v + K_u) \left(N_v - \int_0^\infty i_v(t,a) \mathrm{d}a \right), \end{aligned}$$

which implies that $\liminf_{t\to\infty} (N_v - \int_0^\infty i_v(t, a) da) \ge \frac{\mu_v N_v}{\mu_v + K_u} \triangleq \varepsilon_v$. By invariance, $N_v - \int_0^\infty i_v(t, a) da \ge \varepsilon_v$ for $t \in R$. Then, for $t \in R$,

$$i_{v}(t,0) = \psi \left(N_{v} - \int_{0}^{\infty} i_{v}(t,a) \mathrm{d}a, \int_{0}^{\infty} \beta(a) i_{h}(t,a) \mathrm{d}a \right)$$
$$\geq \psi \left(\varepsilon_{v}, \int_{0}^{\infty} \beta(a) i_{h}(t-a,0) \sigma(a) \mathrm{d}a \right) \geq \psi(\varepsilon_{v}, \varepsilon_{2}\eta) \triangleq \varepsilon_{3}.$$

Letting $\varepsilon_0 = \min{\{\varepsilon_h, \varepsilon_2, \varepsilon_3\}}$ immediately completes the proof.

Now, we are ready to establish the global stability of E^* with the approach of Lyapunov functionals.

Theorem 4.11 If $\mathcal{R}_0 > 1$, then the endemic equilibrium E^* of (2.1) is globally asymptotically stable in Ω_0 .

Proof By Theorem 3.2, it suffices to show that $\mathcal{A} = \{E^*\}$. To construct a Lypunov functional, we introduce $g : (0, \infty) \to R$ defined as $g(u) = u - 1 - \ln u$ for $u \in (0, \infty)$. It is easy to see that $g(u) \ge 0$ for $u \in (0, \infty)$ and g(u) = 0 if and only if u = 1.

Let $x(t) = (S_h(t), i_h(t, \cdot), i_v(t, \cdot))$ be a total trajectory in \mathcal{A} . Note that all $S_h(t), i_h(t, 0)$, and $i_v(t, 0)$ are bounded above. Furthermore, by Theorem 4.10, they are also bounded below by a positive number. Therefore, there exists $r_0 > 0$ such that $0 \le g(z) \le r_0$ with $z = \frac{S_h(t)}{S_h^*}$, $\frac{i_h(t,a)}{i_h^*(a)}$, or $\frac{i_v(t,a)}{i_v^*(a)}$ for any $t \in R$ and $a \in R_+$ as $\frac{i_h(t,a)}{i_h^*(t,a)} = \frac{i_h(t-a,0)}{i_h^*(0)}$ and $\frac{i_v(t,a)}{i_v^*(a)} = \frac{i_v(t-a,0)}{i_v^*(0)}$.

We now define a Lyapunov functional

$$W(t) = W(x(t)) = W_1(t) + W_2(t) + W_3(t) + W_4(t),$$

where

$$\begin{split} W_{1}(t) &= \frac{\int_{0}^{\infty} k(a) i_{v}^{*}(a) \mathrm{d}a}{\varphi(S_{h}^{*}, \int_{0}^{\infty} k(a) i_{v}^{*}(a) \mathrm{d}a)} \left(S_{h}(t) - S_{h}^{*} - \int_{S_{h}^{*}}^{S_{h}(t)} \frac{\varphi(S_{h}^{*}, \int_{0}^{\infty} k(a) i_{v}^{*}(a) \mathrm{d}a)}{\varphi(\theta, \int_{0}^{\infty} k(a) i_{v}^{*}(a) \mathrm{d}a)} d\theta \right), \\ W_{2}(t) &= \frac{\int_{0}^{\infty} k(a) i_{v}^{*}(a) \mathrm{d}a}{\eta\varphi(S_{h}^{*}, \int_{0}^{\infty} k(a) i_{v}^{*}(a) \mathrm{d}a)} \int_{0}^{\infty} \eta(a) i_{h}^{*}(a) g\left(\frac{i_{h}(t, a)}{i_{h}^{*}(a)}\right) \mathrm{d}a, \\ W_{3}(t) &= \xi\left(S_{v}(t) - S_{v}^{*} - \int_{S_{v}^{*}}^{S_{v}(t)} \frac{\psi(S_{v}^{*}, \int_{0}^{\infty} \beta(a) i_{h}^{*}(a) \mathrm{d}a)}{\psi(\theta, \int_{0}^{\infty} \beta(a) i_{h}^{*}(a) \mathrm{d}a)} d\theta \right), \\ W_{4}(t) &= \int_{0}^{\infty} \xi(a) i_{v}^{*}(a) g\left(\frac{i_{v}(t, a)}{i_{v}^{*}(a)}\right) \mathrm{d}a, \end{split}$$

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and

$$S_{v}(t) = N_{v} - \int_{0}^{\infty} i_{v}(t, a) da,$$

$$S_{v}^{*} = N_{v} - \int_{0}^{\infty} i_{v}^{*}(a) da = N_{v} - \frac{i_{v}^{*}(0)}{\mu_{v}},$$

$$\eta(a) = \int_{a}^{\infty} \beta(\theta) e^{-\int_{a}^{\theta} \delta(s) ds} d\theta,$$

$$\xi(a) = \int_{a}^{\infty} k(\theta) e^{-\int_{a}^{\theta} \mu_{v} ds} d\theta.$$

Then, W(t) is bounded on the solution $x(t) = (S_h(t), i_h(t, \cdot), S_v(t), i_v(t, \cdot))$. Now we calculate the time derivatives of W one by one as follows.

Firstly,

$$\begin{aligned} \frac{\mathrm{d}W_{1}(t)}{\mathrm{d}t} &= \frac{\int_{0}^{\infty} k(a)i_{v}^{*}(a)\mathrm{d}a}{\varphi(S_{h}^{*},\int_{0}^{\infty} k(a)i_{v}^{*}(a)\mathrm{d}a)} \left(1 - \frac{\varphi(S_{h}^{*},\int_{0}^{\infty} k(a)i_{v}^{*}(a)\mathrm{d}a)}{\varphi(S_{h}(t),\int_{0}^{\infty} k(a)i_{v}^{*}(a)\mathrm{d}a)}\right) \frac{\mathrm{d}S_{h}(t)}{\mathrm{d}t} \\ &= \frac{\int_{0}^{\infty} k(a)i_{v}^{*}(a)\mathrm{d}a}{\varphi(S_{h}^{*},\int_{0}^{\infty} k(a)i_{v}^{*}(a)\mathrm{d}a)} \left(1 - \frac{\varphi(S_{h}^{*},\int_{0}^{\infty} k(a)i_{v}^{*}(a)\mathrm{d}a)}{\varphi(S_{h}(t),\int_{0}^{\infty} k(a)i_{v}^{*}(a)\mathrm{d}a)}\right) \\ &\times \left(\lambda - \mu_{h}S_{h}(t) - \varphi(S_{h}(t),\int_{0}^{\infty} k(a)i_{v}(t,a)\mathrm{d}a)\right).\end{aligned}$$

Since $\lambda = \mu_h S_h^* + \varphi(S_h^*, \int_0^\infty k(a) i_v^*(a) da)$ and $\varphi(S_h^*, \int_0^\infty k(a) i_v^*(a) da) = i_h^*(0)$, we obtain

$$\begin{aligned} \frac{\mathrm{d}W_{1}(t)}{\mathrm{d}t} &= \frac{\mu_{h}S_{h}(t)\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a}{\varphi(S_{h}^{*},\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a)} \left(\frac{S_{h}^{*}}{S_{h}(t)} - 1\right) \left(1 - \frac{\varphi(S_{h}^{*},\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a)}{\varphi(S_{h}(t),\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a}\right) \\ &+ \int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a \left(1 - \frac{\varphi(S_{h}^{*},\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a)}{\varphi(S_{h}(t),\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a}\right) \\ &- \frac{\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a\varphi(S_{h}(t),\int_{0}^{\infty}k(a)i_{v}(a)\mathrm{d}a)}{\varphi(S_{h}^{*},\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a} \\ &\times \left(1 - \frac{\varphi(S_{h}^{*},\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a}{\varphi(S_{h}(t),\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a}\right) \right) \\ &= \mu_{h}S_{h}(t)\frac{\xi i_{v}^{*}(0)}{i_{h}^{*}(0)} \left(\frac{S_{h}^{*}}{S_{h}(t)} - 1\right) \left(1 - \frac{\varphi(S_{h}^{*},\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a}{\varphi(S_{h}(t),\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a}\right) \\ &- g\left(\frac{\varphi(S_{h}^{*},\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a}{\varphi(S_{h}(t),\int_{0}^{\infty}k(a)i_{v}(a)\mathrm{d}a}\right) \int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a} \\ &- \int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a\left[\frac{\varphi(S_{h}(t),\int_{0}^{\infty}k(a)i_{v}(t,a)\mathrm{d}a}{\varphi(S_{h}^{*},\int_{0}^{\infty}k(a)i_{v}(a)\mathrm{d}a} + \ln\frac{\varphi(S_{h}^{*},\int_{0}^{\infty}k(a)i_{v}^{*}(a)\mathrm{d}a}{\varphi(S_{h}(t),\int_{0}^{\infty}k(a)i_{v}(a)\mathrm{d}a}\right] \right]. \end{aligned}$$

4074

Secondly,

$$\begin{aligned} \frac{\mathrm{d}W_2(t)}{\mathrm{d}t} &= \frac{\int_0^\infty k(a)i_v^*(a)\mathrm{d}a}{\eta\varphi(S_h^*,\int_0^\infty k(a)i_v^*(a)\mathrm{d}a)} \int_0^\infty \eta(a) \left(1 - \frac{i_h^*(a)}{i_h(t,a)}\right) \frac{\partial i_h(t,a)}{\partial t} \mathrm{d}a \\ &= \frac{\xi i_v^*(0)}{\eta i_h^*(0)} \int_0^\infty \eta(a) \left(1 - \frac{i_h^*(a)}{i_h(t,a)}\right) \left(-\frac{\partial i_h(t,a)}{\partial a} - \delta(a)i_h(t,a)\right) \mathrm{d}a. \end{aligned}$$

Note that

$$i_{h}^{*}(a)\frac{\partial}{\partial a}\left(g\left(\frac{i_{h}(t,a)}{i_{h}^{*}(a)}\right)\right) = \left(1 - \frac{i_{h}^{*}(a)}{i_{h}(t,a)}\right)\frac{\partial i_{h}(t,a)}{\partial a} + \left(1 - \frac{i_{h}^{*}(a)}{i_{h}(t,a)}\right)\delta(a)i_{h}(t,a).$$

Thus

$$\begin{split} \frac{\mathrm{d}W_{2}(t)}{\mathrm{d}t} &= -\frac{\xi i_{v}^{*}(0)}{\eta i_{h}^{*}(0)} \int_{0}^{\infty} \eta(a) i_{h}^{*}(a) \frac{\partial}{\partial a} \left(g\left(\frac{i_{h}(t,a)}{i_{h}^{*}(a)}\right) \right) \mathrm{d}a \\ &= -\frac{\xi i_{v}^{*}(0)}{\eta i_{h}^{*}(0)} \eta(a) i_{h}^{*}(a) g\left(\frac{i_{h}(t,a)}{i_{h}^{*}(a)}\right) \Big|_{a=0}^{\infty} \\ &+ \frac{\xi i_{v}^{*}(0)}{\eta i_{h}^{*}(0)} \int_{0}^{\infty} g\left(\frac{i_{h}(t,a)}{i_{h}^{*}(a)}\right) (\eta'(a) - \delta(a)\eta(a)) i_{h}^{*}(a) \mathrm{d}a \\ &= \xi i_{v}^{*}(0) g\left(\frac{i_{h}(t,0)}{i_{h}^{*}(0)}\right) - \frac{\xi i_{v}^{*}(0)}{\eta i_{h}^{*}(0)} \int_{0}^{\infty} \beta(a) i_{h}^{*}(a) g\left(\frac{i_{h}(t,a)}{i_{h}^{*}(a)}\right) \mathrm{d}a. \end{split}$$

Then

$$\begin{aligned} \frac{\mathrm{d}W_{1}(t)}{\mathrm{d}t} + \frac{\mathrm{d}W_{2}(t)}{\mathrm{d}t} &= \frac{\mu_{h}S_{h}(t)\xi i_{v}^{*}(0)}{i_{h}^{*}(0)} \left(\frac{S_{h}^{*}}{S_{h}(t)} - 1\right) \left(1 - \frac{\varphi(S_{h}^{*}, \int_{0}^{\infty}k(a)i_{v}^{*}(a)da)}{\varphi(S_{h}(t), \int_{0}^{\infty}k(a)i_{v}^{*}(a)da)}\right) \\ &- g\left(\frac{\varphi(S_{h}^{*}, \int_{0}^{\infty}k(a)i_{v}^{*}(a)da)}{\varphi(S_{h}, \int_{0}^{\infty}k(a)i_{v}^{*}(a)da)}\right) \int_{0}^{\infty}k(a)i_{v}^{*}(a)da \\ &+ \int_{0}^{\infty}k(a)i_{v}^{*}(a)da \cdot g\left(\frac{\varphi(S_{h}(t), \int_{0}^{\infty}k(a)i_{v}(t, a)da)}{\varphi(S_{h}(t), \int_{0}^{\infty}k(a)i_{v}^{*}(a)da)}\right) \\ &- \frac{\xi i_{v}^{*}(0)}{\eta i_{h}^{*}(0)} \int_{0}^{\infty}\beta(a)i_{h}^{*}(a)g\left(\frac{i_{h}(t, a)}{i_{h}^{*}(a)}\right) \mathrm{d}a. \end{aligned}$$

Similarly, noting $\frac{dS_v(t)}{dt} = \mu_v N_v - \mu_v S_v(t) - \psi(S_v(t), \int_0^\infty \beta(a)i_h(t, a)da)$, we can obtain

$$\begin{aligned} \frac{\mathrm{d}W_{3}(t)}{\mathrm{d}t} &= \xi \mu_{v} S_{v}(t) \left(\frac{S_{v}^{*}}{S_{v}(t)} - 1 \right) \left(1 - \frac{\psi(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)}{\psi(S_{v}(t), \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)} \right) \\ &+ \xi \psi(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a) \left(1 - \frac{\psi(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)}{\psi(S_{v}(t), \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)} \right) \\ &- \xi \psi(S_{v}(t), \int_{0}^{\infty} \beta(a)i_{h}(t, a)\mathrm{d}a) \left(1 - \frac{\psi(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)}{\psi(S_{v}(t), \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)} \right) \\ &= \xi \mu_{v} S_{v}(t) \left(\frac{S_{v}^{*}}{S_{v}(t)} - 1 \right) \left(1 - \frac{\psi(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)}{\psi(S_{v}(t), \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)} \right) \\ &- \xi \psi \left(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a \right) g \left(\frac{\psi(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)}{\psi(S_{v}(t), \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)} \right) \end{aligned}$$

$$-\xi\psi(S_{v}^{*},\int_{0}^{\infty}\beta(a)i_{h}^{*}(a)\mathrm{d}a)\left[\frac{\psi(S_{v}(t),\int_{0}^{\infty}\beta(a)i_{h}(t,a)\mathrm{d}a)}{\psi(S_{v}^{*},\int_{0}^{\infty}\beta(a)i_{h}^{*}(a)\mathrm{d}a)} -\frac{\psi(S_{v}(t),\int_{0}^{\infty}\beta(a)i_{h}(t,a)\mathrm{d}a)}{\psi(S_{v}(t),\int_{0}^{\infty}\beta(a)i_{h}^{*}(a)\mathrm{d}a)} +\ln\frac{\psi(S_{v}^{*},\int_{0}^{\infty}\beta(a)i_{h}^{*}(a)\mathrm{d}a)}{\psi(S_{v}(t),\int_{0}^{\infty}\beta(a)i_{h}^{*}(a)\mathrm{d}a)}\right]$$

and

$$\frac{\mathrm{d}W_4(t)}{\mathrm{d}t} = \xi \psi \Big(S_v^*, \int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a \Big) g \Big(\frac{\psi(S_v(t), \int_0^\infty \beta(a) i_h(t, a) \mathrm{d}a)}{\psi(S_v^*, \int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a)} \Big) \\ - \int_0^\infty k(a) i_v^*(a) g \Big(\frac{i_v(t, a)}{i_v^*(a)} \Big) \mathrm{d}a.$$

It follows that

$$\begin{aligned} \frac{\mathrm{d}W_{3}(t)}{\mathrm{d}t} + \frac{\mathrm{d}W_{4}(t)}{\mathrm{d}t} &= \xi \mu_{v} S_{v}(t) \left(\frac{S_{v}^{*}}{S_{v}(t)} - 1 \right) \left(1 - \frac{\psi(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)}{\psi(S_{v}(t), \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)} \right) \\ &- \xi \psi \left(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a \right) g \left(\frac{\psi(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)}{\psi(S_{v}(t), \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a)} \right) \\ &+ \xi \psi \left(S_{v}^{*}, \int_{0}^{\infty} \beta(a)i_{h}^{*}(a)\mathrm{d}a \right) g \left(\frac{\psi(S_{v}(t), \int_{0}^{\infty} \beta(a)i_{h}(a)\mathrm{d}a)}{\psi(S_{v}(t), \int_{0}^{\infty} \beta(a)i_{h}(a)\mathrm{d}a)} \right) \\ &- \int_{0}^{\infty} k(a)i_{v}^{*}(a)g \left(\frac{i_{v}(t, a)}{i_{v}^{*}(a)} \right) \mathrm{d}a. \end{aligned}$$

From the concavity and monotonicity of the functions $\varphi(u, v)$ and $\psi(u, v)$ on v, we have the following inequalities:

$$\begin{cases} \frac{v}{v^*} \le \frac{\varphi(u,v)}{\varphi(u,v^*)}, \frac{\psi(u,v)}{\psi(u,v^*)} \le 1, \qquad 0 < v \le v^*, \\ 1 \le \frac{\varphi(u,v)}{\varphi(u,v^*)}, \frac{\psi(u,v)}{\psi(u,v^*)} \le \frac{v}{v^*}, \qquad v \ge v^* > 0. \end{cases}$$

Then, $g\left(\frac{\varphi(u,v)}{\varphi(u,v^*)}\right) \leq g\left(\frac{v}{v^*}\right)$ and $g\left(\frac{\psi(u,v)}{\psi(u,v^*)}\right) \leq g\left(\frac{v}{v^*}\right)$ for any u > 0, v > 0, and $v^* > 0$. This, combined with the Jensen's Inequality, yields

$$\begin{split} &\int_0^\infty k(a)i_v^*(a)\mathrm{d}a \cdot g\left(\frac{\varphi(S_h(t),\int_0^\infty k(a)i_v(t,a)\mathrm{d}a)}{\varphi(S_h(t),\int_0^\infty k(a)i_v^*(a)\mathrm{d}a)}\right) \\ &\leq \int_0^\infty k(a)i_v^*(a)\mathrm{d}a \cdot g\left(\frac{\int_0^\infty k(a)i_v(t,a)\mathrm{d}a}{\int_0^\infty k(a)i_v^*(a)\mathrm{d}a}\right) \\ &= \int_0^\infty k(a)i_v^*(a)\mathrm{d}a \cdot g\left(\frac{\int_0^\infty k(a)i_v^*(a) \cdot \frac{i_v(t,a)}{i_v^*(a)}\mathrm{d}a}{\int_0^\infty k(a)i_v^*(a)\mathrm{d}a}\right) \\ &\leq \int_0^\infty k(a)i_v^*(a)g\left(\frac{i_v(t,a)}{i_v^*(a)}\right)\mathrm{d}a \end{split}$$

and similarly

$$\begin{split} &\xi\psi(S_v^*, \int_0^\infty \beta(a)i_h^*(a)\mathrm{d}a)g\bigg(\frac{\psi(S_v(t), \int_0^\infty \beta(a)i_h(t, a)\mathrm{d}a)}{\psi(S_v(t), \int_0^\infty \beta(a)i_h^*(a)\mathrm{d}a)}\bigg) \\ &\leq \frac{\xi i_v^*(0)}{\eta i_h^*(0)} \int_0^\infty \beta(a)i_h^*(a)g\bigg(\frac{i_h(t, a)}{i_h^*(a)}\bigg)\mathrm{d}a. \end{split}$$

Moreover, by the monotonicity of $\varphi(u, v)$ and $\psi(u, v)$ on u, we have

$$\left(\frac{S_h^*}{S_h(t)} - 1\right) \left(1 - \frac{\varphi(S_h^*, \int_0^\infty k(a)i_v^*(a)da)}{\varphi(S_h(t), \int_0^\infty k(a)i_v^*(a)da)}\right) \le 0,$$
$$\left(\frac{S_v^*}{S_v(t)} - 1\right) \left(1 - \frac{\psi(S_v^*, \int_0^\infty \beta(a)i_h^*(a)da)}{\varphi(S_v(t), \int_0^\infty \beta(a)i_h^*(a)da)}\right) \le 0,$$

and, using the equilibrium equations, one gets

$$\frac{\xi\psi(S_v^*,\int_0^\infty\beta(a)i_h^*(a)\mathrm{d}a)}{\int_0^\infty\beta(a)i_h^*(a)\mathrm{d}a} - \frac{\xi i_v^*(0)}{\eta i_h^*(0)} = 0.$$

Therefore,

$$\begin{split} \frac{\mathrm{d}W(t)}{\mathrm{d}t} &\leq \mu_h S_h(t) \frac{\xi i_v^*(0)}{i_h^*(0)} \left(\frac{S_h^*}{S_h(t)} - 1 \right) \left(1 - \frac{\varphi(S_h^*, \int_0^\infty k(a) i_v^*(a) \mathrm{d}a)}{\varphi(S_h(t), \int_0^\infty k(a) i_v^*(a) \mathrm{d}a)} \right) \\ &\quad - \int_0^\infty k(a) i_v^*(a) \mathrm{d}a \cdot g \left(\frac{\varphi(S_h^*, \int_0^\infty k(a) i_v^*(a) \mathrm{d}a)}{\varphi(S_h(t), \int_0^\infty k(a) i_v^*(a) \mathrm{d}a)} \right) \\ &\quad + \xi \mu_v S_v(t) \left(\frac{S_v^*}{S_v(t)} - 1 \right) \left(1 - \frac{\psi(S_v^*, \int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a)}{\psi(S_v(t), \int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a)} \right) \\ &\quad - \xi \psi \left(S_v^*, \int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a \right) g \left(\frac{\psi(S_v^*, \int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a)}{\psi(S_v(t), \int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a)} \right) \\ &\quad + \left(\frac{\xi \psi(S_v^*, \int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a}{\int_0^\infty \beta(a) i_h^*(a) \mathrm{d}a} - \frac{\xi i_v^*(0)}{\eta i_h^*(0)} \right) \int_0^\infty \beta(a) i_h^*(a) g \left(\frac{i_h(t, a)}{i_h^*(a)} \right) \mathrm{d}a \\ &\leq 0, \end{split}$$

which implies that W is non-increasing. Since W is bounded on $x(\cdot)$, the alpha limit set of $x(\cdot)$ must be contained in the largest invariant subset \mathcal{M} in $\{\frac{dW(t)}{dt} = 0\}$. It is easy to see that $\mathcal{M} = \{E^*\}$. From the above discussion, we find that $\alpha(x_0) = \{E^*\}$ and hence $W(x(t)) \leq W(E^*)$ for all $t \in R$. This yields $x(t) = E^*$ and hence $\mathcal{A} = \{E^*\}$, which completes the proof.

5 Conclusions

Infection age is a very important factor in malaria disease transmission. In this paper, we incorporated infection ages into both infected hosts and infected vectors in our model (2.1). The vector population size is assumed to be a constant. The incidence between susceptible hosts and infectious vectors takes a general nonlinear form $\varphi(S_h, \int_0^\infty k(a)i_v(t, a)da)$, where k(a) is the age-dependent biting rate of a susceptible host by an infected vector; while that between susceptible vectors and infected hosts takes another general nonlinear form $\psi(S_v, \int_0^\infty \beta(a)i_h(t, a)da)$, which is the probability of a susceptible vector becoming infected

in a unit of time. Here, $\beta(a)$ is the age-dependent biting rate of an infected host by a susceptible vector. By employing some recently developed techniques on global analysis in Magal et al. (2010) and Melnik and Korobeinikov (2013), we have successfully coped with the great challenge brought by the introduction of infection ages and general nonlinear incidence rates. With the applications of the fluctuation lemma and Lyapunov functionals, a global threshold dynamics is established, which is completely determined by the basic reproduction number \mathcal{R}_0 . Precisely, the disease-free equilibrium is globally asymptotically stable if $\mathcal{R}_0 > 1$ (Theorem 4.3) while the endemic equilibrium is globally asymptotically stable if $\mathcal{R}_0 > 1$ (Theorem 4.11).

From the expression (3.1) for the basic reproduction number \mathcal{R}_0 , we see that the nonlinear incidence rates φ and ψ as well as infection ages have combined effects on \mathcal{R}_0 . This, in turn, indicates that these factors introduced in this paper have profound impact on the dynamics of vector-borne disease models. In this paper, we established rigorous results on the qualitative dynamics of (2.1). However, how the nonlinear incidence rates as well as infection age change the quantitative behaviors of (2.1) remains open, which we leave as our future work.

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References

- Altizer S, Dobson A, Hosseini P et al (2006) Seasonality and the dynamics of infectious diseases. Ecol Lett 9(4):467–484
- Anderson RM, May RM (1978) Regulation and stability of host-parasite population interactions: I. Regulatory processes. J Anim Ecol 47:219–247
- Antonovics J, Iwasa Y, Hassell MP (1995) A generalized model of parasitoid, venereal, and vector-based transmission processes. Am Nat 145(5):661–675
- Avila-Vales E, Buonomo B (2015) Analysis of a mosquito-borne disease transmission model with vector stages and nonlinear forces of infection. Ricerche di Matematica. 64(2):377–390
- Aron JL (1988) Mathematical modelling of immunity to malaria. Math Biosci 90(1):385-396
- Barlow ND (2000) Non-linear transmission and simple models for bovine tuberculosis. J Anim Ecol 69(4):703– 713
- Begon M, Hazel SM, Baxby D et al (1999) Transmission dynamics of a zoonotic pathogen within and between wildlife host species. Proc R Soc Lond B Biol Sci 266(1432):1939–1945
- Bhatt S, Gething PW, Brady OJ, Messina JP et al (2013) The global distribution and burden of dengue. Nature 496:504–507
- Bowman C, Gumel AB, Van den Driessche P et al (2005) A mathematical model for assessing control strategies against West Nile virus. Bull Math Biol 67(5):1107–1133
- Brand SPC, Rock KS, Keeling MJ (2016) The interaction between vector life history and short vector life in vector-borne disease transmission and control. PLoS Comput Biol 12(4):e1004837
- Briggs CJ, Godfray HCJ (1995) The dynamics of insect-pathogen interactions in stage-structured populations. Am Nat 145(6):855–887
- Browne CJ, Pilyugin SS (2013) Global analysis of age-structured within-host virus model. Discret Contin Dyn Syst Ser B 18(8):1999–2017
- Capasso V, Grosso E, Serio G (1977) I modelli matematici nella indagine epidemiologica. Applicazione all'epidemia di colera verificatasi in Bari nel 1973 (italian). Annali Sclavo. 1977(19):193–208
- Capasso V, Serio G (1978) A generalization of the Kermack-Mc Kendrick deterministic epidemic model. Math Biosci 42:41–61
- Caminade C, McIntyre MK, Jones AE (2016) Climate change and vector-borne diseases: where are we next heading? J Infect Dis 214(9):1300–1301

- Centers for Disease Control and Prevention (2002) Provisional surveillance summary of the West Nile virus epidemic-United States, January–November 2002. MMWR. Morbid Mortality Week Rep 51(50):1129–1133
- Chen Y, Zou S, Yang J (2016) Global analysis of an SIR epidemic model with infection age and saturated incidence. Nonlinear Anal Real World Appl 30:16–31
- Diekmann O, Kretzschmar M (1991) Patterns in the effects of infectious diseases on population growth. J Math Biol 29(6):539–570
- Dietz K, Molineaux, L, Thomas A (1974) A malaria model tested in the African savannah. Bull World Health Org 50(3–4):347
- Feng X, Ruan S, Teng Z, Wang K (2015) Stability and backward bifurcation in a malaria transmission model with applications to the control of malaria in China. Math Biosci 266:52–64
- Feng Z, Velasco-Hernández JX (1997) Competitive exclusion in a vector-host model for the dengue fever. J Math Biol 35(5):523–544
- Forouzannia F, Gumel AB (2014) Mathematical analysis of an age-structured model for malaria transmission dynamics. Math Biosci 247(2):80–94
- Georgescu P, Hsieh YH (2006) Global stability for a virus dynamics model with nonlinear incidence of infection and removal. SIAM J Appl Math 67:337–353
- Hale JK (1988) Asymptotic behavior of dissipative systems. Am. Math. Soc, Providence, RI
- Hethcote HW (2000) The mathematics of infectious diseases. SIAM Rev 42(4):599-653
- Hirsch WM, Hanisch H, Gabriel J-P (1985) Differential equation models of some parasitic infections: methods for the study of asymptotic behavior. Commun Pure Appl Math 38:733–753
- Hochberg ME (1991) Non-linear transmission rates and the dynamics of infectious disease. J Theoret Biol 153(3):301–321
- Hollingsworth TD, Pulliam JRC, Funk S et al (2015) Seven challenges for modelling indirect transmission: vector-borne diseases, macroparasites and neglected tropical diseases. Epidemics 10:16–20
- Iannelli M (1995) Mathematical theory of age-structured population dynamics. In: Applied mathematics monographs, vol 7, comitato Nazionale per le Scienze Matematiche, Consiglio Nazionale delle Ricerche (C.N.R.), Giardini, Pisa
- Inaba H, Sekine H (2004) A mathematical model for Chagas disease with infection-age-dependent infectivity. Math Biosci 190(1):39–69
- Knell RJ, Begon M, Thompson DJ (1996) Transmission dynamics of Bacillus thuringiensis infecting Plodia interpunctella: a test of the mass action assumption with an insect pathogen. Proc R Soc Lond B Biol Sci 263(1366):75–81
- Korobeinikov A (2009) Global asymptotic properties of virus dynamics models with dose-dependent parasite reproduction and virulence and nonlinear incidence rate. Math Med Biol 26:225–239
- Korobeinikov A (2007) Global properties of infectious disease models with nonlinear incidence. Bull Math Biol 69:1871–1886
- Kuniya T (2014) Existence of a nontrivial periodic solution in an age-structured SIR epidemic model with time periodic coefficients. Appl Math Lett 27:15–20
- Kuniya T, Oizumi R (2015) Existence result for an age-structured SIS epidemic model with spatial diffusion. Nonlinear Anal Real World Appl 23:196–208
- Lutambi AM, Penny MA, Smith T, Chitnis N (2013) Mathematical modelling of mosquito dispersal in a heterogeneous environment. Math Biosci 241:198–216
- Lashari AA, Zaman G (2011) Global dynamics of vector-borne diseases with horizontal transmission in host population. Comput Math Appl 61(4):745–754
- Liu H, Yu J, Zhu G (2006) Analysis of a vector-host malaria model with impulsive effect and infection-age. Adv Comp Syst 9(3):237–248
- Mandal S, Sarkar RR, Sinha S (2011) Mathematical models of malaria-a review. Malaria J 10(1):202
- Macdonald G (1952) The analysis of equilibrium in malaria. Trop Dis Bull 49(9):813–829
- Maidana NA, Yang HM (2008) Describing the geographic spread of dengue disease by traveling waves. Math Biosci 215(1):64–77
- Magal P, McCluskey CC, Webb GF (2010) Lyapunov functional and global asymptotic stability for an infectionage model. Appl Anal 89(7):1109–1140
- Anderson RM, May RM (1978) Regulation and stability of host-parasite population interactions: II. Destabilizing processes. J Anim Ecol 47:249–267
- McCallum H, Barlow N, Hone J (2001) How should pathogen transmission be modelled? Trends Ecol Evol 16(6):295–300
- Melnik AV, Korobeinikov A (2013) Lyapunov functions and global stability for SIR and SEIR models with age-dependent susceptibility. Math Biosci Eng 10(2):369–378



- Nash D, Mostashari F, Fine A et al (2001) The outbreak of West Nile virus infection in the New York City area in 1999. N Engl J Med 344(24):1807–1814
- Ngwa GA, Shu WS (2000) A mathematical model for endemic malaria with variable human and mosquito populations. Math Comput Model 32:747–763
- Novoseltsev VN, Michalski AI, Novoseltseva JA et al (2012) An age-structured extension to the vectorial capacity model. PloS One 7(6):e39479
- Park TR (2004) Age-dependence in epidemic models of vector-borne infections. The University of Alabama in Huntsville, Thesis
- Qiu Z (2008) Dynamical behavior of a vector-host epidemic model with demographic structure. Comput Math Appl 56(12):3118–3129
- Rock KS, Wood DA, Keeling MJ (2015) Age-and bite-structured models for vector-borne diseases. Epidemics 12:20–29
- Roop-O P, Chinviriyasit W, Chinviriyasit S (2015) The effect of incidence function in backward bifurcation for malaria model with temporary immunity. Math Biosci 265:47–64
- Ross R (1910) The prevention of malaria. J. Murray, London
- Ross R (1911) Some quantitative studies in epidemiology. Nature 87:466–467
- Ruan S, Xiao D, Beier JC (2008) On the delayed Ross-Macdonald model for malaria transmission. Bull Math Biol 70(4):1098–1114
- Smith HL, Thieme HR (2011) Dynamical systems and population persistence. American Mathematical Society, Providence, RI
- Tahir MT (2017) Incidence of dengue haemorrhagic fever in local population of Lahore. Pak Biomed 25(2):93– 96
- Thieme HR (2000) Uniform persistence and permanence for non-autonomous semiflows in population biology. Math Biosci 166:173–201
- Tumwiine J, Mugisha JYT, Luboobi LS (2007) A mathematical model for the dynamics of malaria in a human host and mosquito vector with temporary immunity. Appl Math Comput 189(2):1953–1965
- Saul A (1996) Transmission dynamics of Plasmodium falciparum. Parasitol Today 12:74–79
- Soufiane B, Touaoula TM (2016) Global analysis of an infection age model with a class of nonlinear incidence rates. J Math Anal Appl 434:1211–1239
- Vargas-De-León C (2012) Global analysis of a delayed vector-bias model for malaria transmission with incubation period in mosquitoes. Math Biosci Eng 9(1):165–174
- Vargas-De-León C, Esteva L, Korobeinikov A (2014) Age-dependency in host-vector models: the global analysis. Appl Math Comput 243:969–981
- Wang X, Lou Y, Song X (2017a) Age-structured within-host hiv dynamics with multiple target cells. Stud Appl Math 138(1):43–76
- Wang X, Chen, Y, Liu S (2017b) Dynamics of an age-structured host-vector model for malaria transmission. Math Methods Appl Sci. https://doi.org/10.1002/mma.4723
- Wang X, Chen Y, Martcheva M, Rong L (2017c) Threshold dynamics of an age-structured vector-borne disease model with general nonlinear incidence rates. Nonlinear Anal Real World Appl (Submitted)
- Wang J, Guo M, Liu S (2017d) SVIR epidemic model with age structure in susceptibility, vaccination effects and relapse. IMA J Appl Math 82(5):945–970
- Wang J, Zhang R, Kuniya T (2015) The dynamics of an SVIR epidemiological model with infection age. IMA J Appl Math 81(2):321–343
- World Health Organization: (2016) Fact sheet: world malaria report 2016. http://www.who.int/malaria/media/ world-malaria-report-2016/en/. Accessed Dec 2016
- Yang J, Chen Y, Kuniya T (2017) Threshold dynamics of an age-structured epidemic model with relapse and nonlinear incidence. IMA J Appl Math 82(3):629–655