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Global dynamics of a stage-structured hantavirus infection model with seasonality*

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Abstract. In this paper, we study a time-periodic model, which incorporates seasonality and host stage-structure. This model describes the propagation of Puumala hantavirus within the bank vole population of Clethrionomys glareolus. The basic reproduction number R_0 is obtained. By appealing to the theory of monotone dynamical systems and chain transitive sets, we establish a threshold-type result on the global dynamics in terms of R_0, that is, the virus-free periodic solution is globally attractive, and the virus dies out if $R_0 \leqslant 1$, while there exists a unique positive periodic solution, which is globally attractive, and the virus persists if $R_0 > 1$. Numerical simulations are given to confirm our theoretical results and to show that cleaning environment and controlling the grow of mice population are essential control strategies to reduce hantavirus infection.

Keywords: hantavirus, seasonality, basic reproduction number, global attractivity, threshold dynamics.

1 Introduction

Hantaviruses are a family of viruses spread mainly by rodents and can cause serious disease syndromes in people worldwide. Infection with any hantavirus can produce hantavirus disease in people. It causes a rare but extremely serious lung disease called hantavirus pulmonary syndrome (HPS), about 40% of the people who get the disease die, it may also causes hemorrhagic fever with renal syndrome (HFRS). As of January 2017, 728 cases of hantavirus disease have been reported since surveillance in the United States began in 1993. These are all laboratory-confirmed cases and include HPS and nonpulmonary hantavirus infection [21]. Worldwide, approximately 150,000 to 200,000 people

are hospitalized with HFRS each year. Different hantaviruses tend to cause mild, moderate or severe cases of HFRS; the mortality rate can vary from 0.1 to 3% for Puumala virus infections, to approximately 5 to 15% for Hantaan and Dobrava virus infections. Hantaviruses are found naturally in various species of rodents. Infections do not appear to be pathogenic to their rodent hosts and may be carried lifelong [22]. There is no specific treatment, cure, or vaccine for hantavirus infection. However, if infected individuals are recognized early and receive medical care in an intensive care unit, they may do better. Infected people may be given medication for fever and pain and oxygen therapy [20].

In recent years, mathematical models have shown great values in understanding and control of infectious disease. Gedeon et al. [6] developed a compartmental model for hantavirus infection in deer mice (Peromyscus maniculatus) with the goal of comparing relative importance of direct (contacts between individuals) and indirect transmission (through the environment) in sylvan and peridomestic environments. Their model predicted that direct transmission dominates in the sylvan environment, while both pathways are important in peridomestic environments. Kenkre et al. [8] proposed a stage-structured hantavirus epidemic model, they considered two types of mice, stationary (adults) and itinerant (juveniles). They assumed that adult mice remain largely confined to locations near their home ranges and itinerant juvenile mice that are not so confined, they will search for their own homes, move and infect both other juveniles and adults that they meet during their movement. The dynamics of mean field equations was analyzed. Wolf [16] analyzed a mathematical model for the propagation of Puumala hantavirus, within a population of bank voles (Clethrionomys glareolus), both chronological age and infection-age of individuals are included. A weakly coupled system of hyperbolic equations was formulated, the global existence and uniqueness of solutions were established.

Mathematical models were also proposed in [1, 2, 4, 5] to include diffusion of rodents to investigate influence of host movement on the transmission dynamics. More recently, a deterministic hantavirus epidemic model has been developed and analyzed in Wolf et al. [17]. This model described the hantavirus spread within the bank vole population. The adult mice move within their home ranges and do not stray far from the burrow, while the juvenile mice must leave to find their own home ranges. Because of different behaviors between juvenile and adult individuals, thus two types of mice are considered, adults and juveniles. The host population is divided into four classes: susceptible juveniles, infected juveniles, susceptible adults and infected adults, their densities are denoted respectively by $J_s(t)$, $J_i(t)$, $A_s(t)$ and $A_i(t)$. Then the density of juveniles is $J(t) = J_s(t) + J_i(t)$, the density of adults is $A(t) = A_s(t) + A_i(t)$, and the total population density reads $P(t) = J(t) + A(t)$. The density of infected individuals is denoted as $I(t) = J_i(t) + A_i(t)$. Population densities may oscillate due to climate variability, so demographic parameters are supposed to be time periodic. Let $\beta(t)$ be the adult fertility rate, $\tau(t, A)$ be the juvenile maturation rate depending on the density of adults. Let $\mu_J(t)$ and $\mu_A(t)$ be the natural death rates of juveniles and adults, respectively. They considered the population competition for food and shelters against predators and assumed that the density dependent effects on mortality rates $k_J(t)$ for juveniles and $k_A(t)$ for adults, respectively. Since infected mice release excreta to the local environment, hence the environment becomes contaminated, and susceptible individuals can be infected

by indirect contact with the contaminated environment. Assume that $G(t)$, $0 \leqslant G(t) \leqslant 1$ for $t \geqslant 0$, is the proportion of contaminated environment, and $G(t)$ is described by the equation $G'(t) = \alpha(t)(1 - G(t)) - \delta(t)G(t)$ [3, 11], wherein $\alpha(t)$ is the contamination rate of the environment by infected individuals, and $\delta(t)$ is a decontamination rate. Let $\sigma_J(t)$ and $\sigma_A(t)$ be the direct transmission rates for the juveniles and adults; $\gamma_J(t)$ and $\gamma_A(t)$ be the indirect contamination rates for the juveniles and adults.

In [17], the existence, nonnegativity of solutions, as well as stability of the autonomous case, were investigated. They further studied the existence of periodic solutions for small periodic perturbations of the constant coefficients. Numerical simulations and extensive discussions of modeling are also given in [17]. Motivated by this model, the purpose of the current paper is to study the global dynamics of periodic system in [17]. We assume that the available territories where mice live are large enough so that the juveniles will not experience difficulties to mate, therefore, we neglect the adult density dependence in juvenile maturation rate, that is, $\tau(t, A) = \tau(t)$. Then we obtain the following model:

$$
\begin{aligned}
\frac{\mathrm{d}J_s(t)}{\mathrm{d}t} &= \beta(t)A(t) - \big(\mu_J(t) + \tau(t) + k_J(t)P(t)\big)J_s(t) \\
&\quad - \big(\gamma_J(t)G(t) + \sigma_J(t)I(t)\big)J_s(t), \\
\frac{\mathrm{d}J_i(t)}{\mathrm{d}t} &= \big(\gamma_J(t)G(t) + \sigma_J(t)I(t)\big)J_s(t) \\
&\quad - \big(\mu_J(t) + \tau(t) + k_J(t)P(t)\big)J_i(t), \\
\frac{\mathrm{d}A_s(t)}{\mathrm{d}t} &= \tau(t)J_s(t) - \big(\mu_A(t) + k_A(t)P(t)\big)A_s(t) \\
&\quad - \big(\gamma_A(t)G(t) + \sigma_A(t)I(t)\big)A_s(t), \\
\frac{\mathrm{d}A_i(t)}{\mathrm{d}t} &= \tau(t)J_i(t) + \big(\gamma_A(t)G(t) + \sigma_A(t)I(t)\big)A_s(t) \\
&\quad - \big(\mu_A(t) + k_A(t)P(t)\big)A_i(t), \\
\frac{\mathrm{d}G(t)}{\mathrm{d}t} &= \alpha(t)I(t)\big(1 - G(t)\big) - \delta(t)G(t),
\end{aligned}
\tag{1}
$$

where all the parameters are positive, continuous and T-periodic functions for some $T > 0$.

The rest of this paper is organized as follows. In Section 2, we introduce the basic reproduction number R_0 and then obtain a threshold result on the global dynamics of system (1) by the theory of monotone dynamical systems and chain transitive sets. The last section gives some numerical simulations and a brief discussion.

2   Global dynamics

This section is devoted to study the global dynamics of system (1). We first show the existence, uniqueness of solutions to system (1). For convenience, we define the time-average of a T-periodic function $x(t)$ as $\langle x(t) \rangle := (1/T) \int_0^T x(t) \, \mathrm{d}t$, $\mu := \min\{\mu_J, \mu_A\}$

and $k := \min\{k_J, k_A\}$. For $x, y \in \mathbb{R}^n$, we write $x \geqslant y$ if $x - y \in \mathbb{R}^n_+$, $x > y$ if $x - y \in \mathbb{R}^n_+$ and $x \neq y$, and $x \gg y$ if $x - y \in \text{int}(\mathbb{R}^n_+)$.

To avoid the extinction of the population, we need the following assumption:

(A1) $\langle \beta(t) \rangle > \langle \mu(t) \rangle$.

First, we consider the equation

$$\frac{\mathrm{d}y(t)}{\mathrm{d}t} = \big(b(t) - a(t)y(t)\big)y(t), \qquad y(0) > 0, \tag{2}$$

where $a(t)$ is positive, $a(t)$ and $b(t)$ are continuous and T-periodic functions. By [13, Lemma 1] we have the following result.

Lemma 1. *System* (2) *has a unique nonnegative T-periodic solution $y^*(t)$, and $y(t) - y^*(t) \to 0$ as $t \to \infty$. Moreover,*

   (i) *if $\langle b(t) \rangle > 0$, then $y^*(t) > 0$ for all $t \geqslant 0$;*
   (ii) *if $\langle b(t) \rangle \leqslant 0$, then $y^*(t) \equiv 0$ for all $t \geqslant 0$.*

Lemma 2. *System* (1) *has a unique and bounded nonnegative solution with initial value*

$$\big(J_s(0), J_i(0), A_s(0), A_i(0), G(0)\big) \in \Omega := \big\{\big(J_s, J_i, A_s, A_i, G\big) \in \mathbb{R}^5_+ \colon 0 \leqslant G \leqslant 1\big\}.$$

Further, let (A1) *hold, then all the solutions of system* (1) *with initial values in Ω ultimately go into region $D(t) := \{(J_s, J_i, A_s, A_i, G) \in \mathbb{R}^5_+ \colon J_s + J_i + A_s + A_i \leqslant x^*(t), 0 \leqslant G \leqslant 1\}$, where $x^*(t)$ will be given in the proof.*

Proof. For any $z \in \Omega$, define $H(t, z) = (H_1(t, z), H_2(t, z), H_3(t, z), H_4(t, z), H_5(t, z))$ with

$$\begin{aligned}
H_1(t, z) &= \beta(t)(z_3 + z_4) \\
&\quad - \big(\mu_J(t) + \tau(t) + k_J(t)(z_1 + z_2 + z_3 + z_4)\big)z_1 \\
&\quad - \big(\gamma_J(t)z_5 + \sigma_J(t)(z_2 + z_4)\big)z_1, \\
H_2(t, z) &= \big(\gamma_J(t)z_5 + \sigma_J(t)(z_2 + z_4)\big)z_1 \\
&\quad - \big(\mu_J(t) + \tau(t) + k_J(t)(z_1 + z_2 + z_3 + z_4)\big)z_2, \\
H_3(t, z) &= \tau(t)z_1 - \big(\mu_A(t) + k_A(t)(z_1 + z_2 + z_3 + z_4)\big)z_3 \\
&\quad - \big(\gamma_A(t)z_5 + \sigma_A(t)(z_2 + z_4)\big)z_3, \\
H_4(t, z) &= \tau(t)z_2 + \big(\gamma_A(t)z_5 + \sigma_A(t)(z_2 + z_4)\big)z_3 \\
&\quad - \big(\mu_A(t) + k_A(t)(z_1 + z_2 + z_3 + z_4)\big)z_4, \\
H_5(t, z) &= \alpha(t)(z_2 + z_4)(1 - z_5) - \delta(t)z_5.
\end{aligned}$$

Then $H(t, z)$ is continuous and Lipschitizian in z on each compact subset of $\mathbb{R} \times \Omega$. Clearly, $H_i(t, z) \geqslant 0$ whenever $z \geqslant 0$ and $z_i = 0$, $i = 1, \ldots, 5$, if $z_5 = 1$, then

$H_5(t, z) \leqslant 0$. It follows from [12, Thm. 5.2.1] that there exists a unique nonnegative solution for system (1) through $z \in \Omega$ in its maximal interval of existence. The total host population satisfies

$$\frac{\mathrm{d}P(t)}{\mathrm{d}t} = \beta(t)A(t) - \mu_J(t)J(t) - \mu_A(t)A(t) - k_J(t)P(t)J(t) - k_A(t)P(t)A(t)$$

$$\leqslant \beta(t)P(t) - \mu(t)P(t) - k(t)P^2(t).$$

By Lemma 1(i), if (A1) holds, then

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = \big(\beta(t) - \mu(t) - k(t)x(t)\big)x(t), \qquad x(0) > 0$$

has a positive T-periodic solution $x^*(t)$, which is globally attractive. The standard comparison theorem implies that $P(t)$ is ultimately bounded. Thus, the solution of system (1) exists globally on the interval $[0, \infty)$. Further, $D(t)$ is positively invariant and attracts all positive orbits in Ω.

The density of juveniles $J(t) = J_s(t) + J_i(t)$ and the density of adults $A(t) = A_s(t) + A_i(t)$ satisfy the following coupled differential equations:

$$\begin{aligned}
\frac{\mathrm{d}J(t)}{\mathrm{d}t} &= \beta(t)A(t) - \big(\mu_J(t) + \tau(t) + k_J(t)\big(J(t) + A(t)\big)\big)J(t), \\
\frac{\mathrm{d}A(t)}{\mathrm{d}t} &= \tau(t)J(t) - \big(\mu_A(t) + k_A(t)\big(J(t) + A(t)\big)\big)A(t).
\end{aligned} \tag{3}$$

From the biological view of point the feasible domain for (3) should be

$$\Lambda(t) = \big\{(J, A) \in \mathbb{R}_+^2 \colon J + A \leqslant x^*(t)\big\}.$$

It is not hard to see that for any $(J_0, A_0) \in \Lambda(0)$, system (3) has a unique solution $(J(t), A(t))$ with $(J(0), A(0)) = (J_0, A_0)$ and $(J(t), A(t)) \in \Lambda(t)$ for all $t \geqslant 0$. □

To obtain Lemma 3, we need to impose the following condition:

(A2 $\beta(t) > k_J(t)x^*(t)$, $\tau(t) > k_A(t)x^*(t)$.

Lemma 3. *Assume that* (A1) *and* (A2) *hold. Let* $\Pi_t(u_0)$ *be the solution of system* (3) *with initial value* $u_0 \in X := \Lambda(0)$. *Then the following statements are valid*:

  (i) *For each* $t \geqslant 0$, *the map* Π_t *is monotone in the sense that* $\Pi_t(u) \geqslant \Pi_t(v)$ *whenever* $u \geqslant v$ *in* X.
  (ii) *For each* $t > 0$, *the map* Π_t *is strongly subhomogeneous in the sense that* $\Pi_t(\theta u_0) \gg \theta \Pi_t(u_0)$ *for all* $u_0 \gg 0$ *in* X *and* $\theta \in (0, 1)$.

Proof. Let $(u_1, u_2) := (J, A)$ and rewrite (3) as follows:

$$\begin{aligned}
\frac{\mathrm{d}u_1}{\mathrm{d}t} &= \beta(t)u_2 - \big(\mu_J(t) + \tau(t) + k_J(t)(u_1 + u_2)\big)u_1 := R_1(t, u_1, u_2), \\
\frac{\mathrm{d}u_2}{\mathrm{d}t} &= \tau(t)u_1 - \big(\mu_A(t) + k_A(t)(u_1 + u_2)\big)u_2 := R_2(t, u_1, u_2).
\end{aligned} \tag{4}$$

For any $(u_1, u_2) \geqslant (v_1, v_2)$ with $u_i = v_i$, we can show that

$$R_i(t, u_1, u_2) \geqslant R_i(t, v_1, v_2).$$

In fact, when $(u_1, u_2) \geqslant (v_1, v_2)$ with $u_1 = v_1$, we have

$$
\begin{aligned}
R_1(t, u_1, u_2) &= \big(\beta(t) - k_J(t)u_1\big)u_2 - \big(\mu_J(t) + \tau(t) + k_J(t)u_1\big)u_1 \\
&\geqslant \big(\beta(t) - k_J(t)u_1\big)v_2 - \big(\mu_J(t) + \tau(t) + k_J(t)u_1\big)u_1 \\
&= \big(\beta(t) - k_J(t)v_1\big)v_2 - \big(\mu_J(t) + \tau(t) + k_J(t)v_1\big)v_1 \\
&= R_1(t, v_1, v_2).
\end{aligned}
$$

Similarly, we see that $R_2(t, u_1, u_2) \geqslant R_2(t, v_1, v_2)$ for $(u_1, u_2) \geqslant (v_1, v_2)$ with $u_2 = v_2$. Then system (4) satisfies the Kamke condition. By [12, Prop. 3.1.1] it follows that the map Π_t is monotone. This proves statement (i).

Given $u_0 \gg 0$ in X and $\theta \in (0, 1)$. We set $W(t) := (W_1(t), W_2(t)) = \Pi_t(\theta u_0)$ and $V(t) := (V_1(t), V_2(t)) = \theta \Pi_t(u_0)$. Then we have

$$
\begin{aligned}
\frac{\mathrm{d}W_1}{\mathrm{d}t} &= \beta(t)W_2 - \big(\mu_J(t) + \tau(t) + k_J(t)(W_1 + W_2)\big)W_1, \\
\frac{\mathrm{d}W_2}{\mathrm{d}t} &= \tau(t)W_1 - \big(\mu_A(t) + k_A(t)(W_1 + W_2)\big)W_2, \\
W(0) &= \theta u_0
\end{aligned}
\tag{5}
$$

and

$$
\begin{aligned}
\frac{\mathrm{d}V_1}{\mathrm{d}t} &< \beta(t)V_2 - \big(\mu_J(t) + \tau(t) + k_J(t)(V_1 + V_2)\big)V_1, \\
\frac{\mathrm{d}V_2}{\mathrm{d}t} &< \tau(t)V_1 - \big(\mu_A(t) + k_A(t)(V_1 + V_2)\big)V_2, \\
V(0) &= \theta u_0.
\end{aligned}
\tag{6}
$$

It then follows from (5), (6) and the comparison theorem that

$$W_i(t) > V_i(t) \quad \forall t > 0, \ i = 1, 2.$$

That is, we have $\Pi_t(\theta u_0) \gg \theta \Pi_t(u_0)$ for all $t > 0$. This proves statement (ii). $\qquad\square$

Here we would like to emphasize that if the juvenile maturation rate depends on the density of adults, then system (4) does not satisfy the Kamke condition, that is, for any $(u_1, u_2) \geqslant (v_1, v_2)$, $R_1(t, u_1, u_2) \geqslant R_1(t, v_1, v_2)$ with $u_1 = v_1$ and $R_2(t, u_1, u_2) \geqslant R_2(t, v_1, v_2)$ with $u_2 = v_2$ cannot be true at the same time. So the conclusion in Lemma 3 may not hold.

Let E be an ordered Banach space with positive cone P such that $\mathrm{int}(P) \neq \emptyset$. For $x, y \in E$, if $a < b$, we define $[a, b] := \{x \in E : a \leqslant x \leqslant b\}$. Assume that $U \subset P$ is a nonempty, closed and order convex set, and $f : U \to U$ is a continuous map. We first give the following two conditions:

(C1) $f : U \to U$ is monotone and strongly subhomogeneous.

(C2) $f : U \to U$ is strongly monotone and strictly subhomogeneous.

Lemma 4. (*See* [19, *Thm. 2.3.4*].) *Let either* $V = [0, b]_E$ *with* $b \gg 0$ *or* $V = P$. *Assume that*

(i) $f : V \to V$ *satisfies either* (C1) *or* (C3).

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

(iii) $f(0) = 0$, *and* $DF(0)$ *is compact and strongly positive.*

Then there exist threshold dynamics:

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

(b) *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^*.

Let $P_1 : X \to X$ be the Poincaré map associated with system (3), that is,

$$P_1\big(J(0), A(0)\big) = \big(J(T), A(T)\big) \quad \forall x := \big(J(0), A(0)\big) \in X,$$

where $(J(t), A(t))$ is the unique solution of system (3). Let $r(DP_1(0, 0))$ be the spectral radius of the Fréchet derivative of P_1 at $(0, 0)$, that is, the largest-amplitude eigenvalue of the Jacobian matrix $DP_1(0, 0)$. Then we have the following threshold type result for system (3).

Lemma 5. *Let* (A1) *and* (A2) *hold. Then the following statements are valid*:

(i) *If* $r(DP_1(0, 0)) \leqslant 1$, *then the trivial solution* $(0, 0)$ *is globally attractive for system* (3) *in* X.

(ii) *If* $r(DP_1(0, 0)) > 1$, *then system* (3) *admits a unique positive* T-*periodic solution* $(J^*(t), A^*(t))$ *such that any solution* $(J(t), A(t))$ *of system* (3) *with* $(J(0), A(0)) \in X \setminus \{(0, 0)\}$ *satisfies*

$$\lim_{t \to \infty} \big[\big(J(t), A(t)\big) - \big(J^*(t), A^*(t)\big)\big] = (0, 0).$$

Proof. By Lemma 3, P_1 is monotone, strongly subhomogeneous in the sense that $P_1(\theta x) \gg \theta P_1(x)$ for all $x \in X$ with $x \gg 0$ and $\theta \in (0, 1)$. Moreover, we can show that $P_1(0, 0) = (0, 0)$, by Lemma 4 it follows that

(i) If $r(DP_1(0, 0)) \leqslant 1$, then every positive orbit of P_1 in X converges to $(0, 0)$.

(ii) If $r(DP_1(0, 0)) > 1$, then there exists a unique fixed point $u^* \gg 0$ in X such that every positive orbit of P_1 in $X \setminus \{(0, 0)\}$ converges to u^*.

Consequently, corresponding to the fixed point of the period map P_1, the conclusions in the lemma are true. $\square$

To give the virus-free periodic solution, we need the following additional assumption:

(A3) $r(DP_1(0, 0)) > 1$.

Letting $J_i = A_i = G = 0$ in (1), we then get the following differential equations:

$$\frac{\mathrm{d}J_s(t)}{\mathrm{d}t} = \beta(t)A_s(t) - \big(\mu_J(t) + \tau(t) + k_J(t)\big(J_s(t) + A_s(t)\big)\big)J_s(t),$$

$$\frac{\mathrm{d}A_s(t)}{\mathrm{d}t} = \tau(t)J_s(t) - \big(\mu_A(t) + k_A(t)\big(J_s(t) + A_s(t)\big)\big)A_s(t).$$

Hence, when (A1)–(A3) holds, there is only one virus-free state, $E_0(t) = (J^*(t), 0, A^*(t), 0, 0)$, where $(J^*(t), A^*(t))$ is the unique positive T-period solution of (3), and there always exists another trivial equilibrium, $(0, 0, 0, 0, 0)$.

Let $B(t)$ be a continuous, cooperative, irreducible and periodic $n \times n$-matrix function with period $T > 0$, $\Phi_B(t)$ be the fundamental solution matrix of the linear ordinary differential equation

$$\dot{x} = B(t)x. \tag{7}$$

Let $r(\Phi_B(T))$ be the spectral radius of $\Phi_B(T)$. By Perron–Frobenius theorem, $r(\Phi_B(T))$ is the principle eigenvalue of $\Phi_B(T)$ in the sense that it is simple and admits an eigenvector $v^* \gg 0$. The following lemma is useful for our discussion in this section.

Lemma 6. (*See* [18, *Lemma* 2.1].) *Let* $p = (1/T)\ln r(\Phi_B(T))$. *Then there exists a positive T-periodic function* $v(t)$ *such that* $\mathrm{e}^{pt}v(t)$ *is a solution of* (7).

In what follows, we introduce the basic reproduction number for system (1) by applying the theory in Wang and Zhao [15]. Linearizing the system at the virus-free periodic solution $E_0(t) = (J^*(t), 0, A^*(t), 0, 0)$, we then obtain the following periodic linear system for the infective variables J_i, A_i and G:

$$\frac{\mathrm{d}J_i(t)}{\mathrm{d}t} = \sigma_J(t)J^*(t)J_i(t) + \sigma_J(t)J^*(t)A_i(t) + \gamma_J(t)J^*(t)G(t)$$
$$- \big[\mu_J(t) + \tau(t) + k_J(t)\big(J^*(t) + A^*(t)\big)\big]J_i(t),$$

$$\frac{\mathrm{d}A_i(t)}{\mathrm{d}t} = \big(\tau(t) + \sigma_A(t)A^*(t)\big)J_i(t) + \sigma_A(t)A^*(t)A_i(t) \tag{8}$$
$$+ \gamma_A(t)A^*(t)G(t) - \big[\mu_A(t) + k_A(t)\big(J^*(t) + A^*(t)\big)\big]A_i(t),$$

$$\frac{\mathrm{d}G(t)}{\mathrm{d}t} = \alpha(t)J_i(t) + \alpha(t)A_i(t) - \delta(t)G(t).$$

Let

$$F(t) = \begin{pmatrix} \sigma_J(t)J^*(t) & \sigma_J(t)J^*(t) & \gamma_J(t)J^*(t) \\ \tau(t) + \sigma_A(t)A^*(t) & \sigma_A(t)A^*(t) & \gamma_A(t)A^*(t) \\ \alpha(t) & \alpha(t) & 0 \end{pmatrix}$$

and

$$V(t) = \begin{pmatrix} \mu_J(t) + \tau(t) + k_J(t)(J^*(t) + A^*(t)) & 0 & 0 \\ 0 & \mu_A(t) + k_A(t)(J^*(t) + A^*(t)) & 0 \\ 0 & 0 & \delta(t) \end{pmatrix}.$$

Then we can rewrite system (8) as

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = \big(F(t) - V(t)\big)x(t),$$

where $x(t) = (J_i(t), A_i(t), G(t))^{\mathrm{T}}$.

Let $Y(t, s)$, $t \geqslant s$, be the evolution operator of the linear periodic system

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -V(t)y,$$

that is,

$$\frac{\mathrm{d}Y(t, s)}{\mathrm{d}t} = -V(t)Y(t, s) \quad \forall t \geqslant s \quad \text{and} \quad Y(s, s) = I,$$

where I is the 3×3 identity matrix.

Let C_T be the ordered Banach space of all T-periodic functions from $\mathbb{R} \to \mathbb{R}^3$, which is equipped with maximum norm $\|\cdot\|_\infty$ and the positive cone $C_T^+ = \{\phi \in C_T : \phi(t) \geqslant 0$ for any $t \in \mathbb{R}\}$. Consider the following linear operator $L : C_T \to C_T$:

$$(L\phi)(t) = \int\limits_0^{+\infty} Y(t, t - a)F(t - a)\phi(t - a)\, \mathrm{d}a \quad \forall t \in \mathbb{R}, \ \phi \in C_T.$$

It then follows from [15] that L is the next infection operator, and define the spectral radius of L as the basic reproduction number $R_0 := r(L)$.

The following result gives the local stability of the virus-free periodic solution $E_0(t)$ for the system (1).

Lemma 7. (*See* [15, *Thm. 2.2*].) *The following statements are valid*:

  (i) $R_0 = 1$ *if and only if* $r(\Phi_{F-V}(T)) = 1$.
  (ii) $R_0 > 1$ *if and only if* $r(\Phi_{F-V}(T)) > 1$.
  (iii) $R_0 < 1$ *if and only if* $r(\Phi_{F-V}(T)) < 1$.

Thus, the virus-free periodic solution $E_0(t) = (J^*(t), 0, A^*(t), 0, 0)$ *of* (1) *is locally asymptotically stable with respect to* $(J_s(0), J_i(0), A_s(0), A_i(0), G(0)) \in \Omega \setminus \{(0, 0, 0, 0, 0)\}$ *if* $R_0 < 1$ *and unstable if* $R_0 > 1$.

Now we study the following system:

$$\begin{aligned}
\frac{\mathrm{d}J_i}{\mathrm{d}t} &= \big[\gamma_J(t)G + \sigma_J(t)(J_i + A_i)\big](J^*(t) - J_i) \\
&\quad - \big[\mu_J(t) + \tau(t) + k_J(t)\big(J^*(t) + A^*(t)\big)\big]J_i, \\
\frac{\mathrm{d}A_i}{\mathrm{d}t} &= \tau(t)J_i + \big[\gamma_A(t)G + \sigma_A(t)(J_i + A_i)\big]\big(A^*(t) - A_i\big) \\
&\quad - \big[\mu_A(t) + k_A(t)\big(J^*(t) + A^*(t)\big)\big]A_i, \\
\frac{\mathrm{d}G}{\mathrm{d}t} &= \alpha(t)(J_i + A_i)(1 - G) - \delta(t)G.
\end{aligned} \tag{9}$$

The reasonable region for (9) should be

$$\Sigma(t) = \big\{(J_i, A_i, G) \in \mathbb{R}_+^3 \colon J_i \leqslant J^*(t),\ A_i \leqslant A^*(t),\ 0 \leqslant G \leqslant 1\big\}. \qquad (10)$$

It is not hard to see that $\Sigma(t)$ is positively invariant for system (9).

By similar arguments as in Lemma 3 we obtain the following results.

Lemma 8. *Assume that* (A1), (A2) *and* (A3) *holds. Let* $\Psi_t(u_0)$ *be the solution of system* (9) *with initial value* $u_0 \in Y := \Sigma(0)$. *Then the following statements are valid*:

(i) *For each* $t \geqslant 0$, *the map* Ψ_t *is monotone in the sense that* $\Psi_t(u) \geqslant \Psi_t(v)$ *whenever* $u \geqslant v$ *in* Y.

(ii) *For each* $t > 0$, *the map* Ψ_t *is strongly subhomogeneous in the sense that* $\Psi_t(\theta u_0) \gg \theta \Psi_t(u_0)$ *for all* $u_0 \gg 0$ *in* Y *and* $\theta \in (0, 1)$.

Let $P_2 : Y \to Y$ be the Poincaré map associated with system (9), that is,

$$P_2\big(J_i(0), A_i(0), G(0)\big) = \big(J_i(T), A_i(T), G(T)\big) \quad \forall x := \big(J_i(0), A_i(0), G(0)\big) \in Y,$$

where $(J_i(t), A_i(t), G(t))$ is the unique solution to system (9). It is not hard to see that $P_2(0, 0, 0) = (0, 0, 0)$ and $DP_2(0, 0, 0) = \Phi_{F-V}(T)$, where $DP_2(0, 0, 0)$ denotes the Fréchet derivative of P_2 at $(0, 0, 0)$. From Lemmas 4 and 7 and the similar arguments as in Lemma 5 we have the following threshold type result for system (9).

Lemma 9. *Let* (A1), (A2) *and* (A3) *hold. Then the following statements are valid*:

(i) *If* $R_0 \leqslant 1$, *then the trivial solution* $(0, 0, 0)$ *is globally attractive for system* (9) *in* Y.

(ii) *If* $R_0 > 1$, *then system* (9) *admits a unique positive T-periodic solution* $(J_i^*(t), A_i^*(t), G^*(t))$ *such that any solution* $(J_i(t), A_i(t), G(t))$ *of system* (9) *with* $(J_i(0), A_i(0), G(0)) \in Y \setminus \{(0, 0, 0)\}$ *satisfies*

$$\lim_{t \to \infty} \big[\big(J_i(t), A_i(t), G(t)\big) - \big(J_i^*(t), A_i^*(t), G^*(t)\big)\big] = (0, 0, 0).$$

Let Z be a metric space with metric d and $g : Z \to Z$ a continuous map. We then have the following results.

Lemma 10. (*See* [19, *Lemma* 1.2.1′].) *Let* $\Psi(t) : Z \to Z$, $t \geqslant 0$, *be a continuous-time semiflow. Then the omega* (*alpha*) *limit set of any precompact positive* (*negative*) *orbit is internally chain transitive.*

Lemma 11. (*See* [19, *Lemma* 1.2.2].) *Assume that each fixed point of* g *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* g. *Then any compact internally chain transitive set is a fixed point of* g.

Now we are ready to prove the following result on the global dynamics of system (1).

Theorem 1. *Assume that* (A1), (A2) *and* (A3) *hold. Then the following statements are valid for system* (1):

    (i) *If $R_0 \leqslant 1$, then the virus-free periodic solution $(J^*(t), 0, A^*(t), 0, 0)$ is globally attractive for system* (1) *in $\Omega \setminus \{(0,0,0,0,0)\}$.*

    (ii) *If $R_0 > 1$, then every solution $(J_s(t), J_i(t), A_s(t), A_i(t), G(t))$ of system* (1) *with $(J_s(0), J_i(0), A_s(0), A_i(0), G(0)) \in \Omega \setminus \{(a, 0, b, 0, c): a, b, c \in \mathbb{R}_+\}$ satisfies*

$$\lim_{t \to \infty} \left[\left(J_s(t), J_i(t), A_s(t), A_i(t), G(t)\right) - \left(J_s^*(t), J_i^*(t), A_s^*(t), A_i^*(t), G^*(t)\right) \right]$$
$$= (0, 0, 0, 0, 0),$$

where $J_s^*(t) = J^*(t) - J_i^*(t)$, $A_s^*(t) = A^*(t) - A_i^*(t)$, and $(J_i^*(t), A_i^*(t), G^*(t))$ is the unique positive T-periodic solution of system (9).

Proof. Rewrite system (1) as follows:

$$\begin{aligned}
\frac{\mathrm{d}J_i}{\mathrm{d}t} &= \left[\gamma_J(t)G + \sigma_J(t)(J_i + A_i) \right](J - J_i) \\
&\quad - \left[\mu_J(t) + \tau(t) + k_J(t)(J + A) \right] J_i, \\
\frac{\mathrm{d}A_i}{\mathrm{d}t} &= \tau(t)J_i + \left[\gamma_A(t)G + \sigma_A(t)(J_i + A_i) \right](A - A_i) \\
&\quad - \left[\mu_A(t) + k_A(t)(J + A) \right] A_i(t), \\
\frac{\mathrm{d}G}{\mathrm{d}t} &= \alpha(t)(J_i + A_i)(1 - G) - \delta(t)G, \\
\frac{\mathrm{d}J}{\mathrm{d}t} &= \beta(t)A - \left[\mu_J(t) + \tau(t) + k_J(t)(J + A) \right] J, \\
\frac{\mathrm{d}A}{\mathrm{d}t} &= \tau(t)J - \left[\mu_A(t) + k_A(t)(J + A) \right] A.
\end{aligned} \tag{11}$$

Let

$$\begin{aligned}
\widetilde{X} &:= \left\{ (J_i, A_i, G, J, A) \in \mathbb{R}_+^5 \colon J_i \leqslant J,\ A_i \leqslant A,\ 0 \leqslant G \leqslant 1,\ J + A \leqslant x^*(t) \right\}, \\
\widetilde{X}_0 &:= \left\{ (J_i, A_i, G, J, A) \in \widetilde{X} \colon (J_i, A_i) \neq (0, 0) \right\}, \qquad \partial\widetilde{X}_0 := \widetilde{X} \setminus \widetilde{X}_0.
\end{aligned}$$

Claim. If $x := (J_i^0, A_i^0, G^0, J^0, A^0) \in \widetilde{X}$, then the solution of (11) through x satisfies $(J_i(t), A_i(t), G(t), J(t), A(t)) \in \widetilde{X}$ for all $t \geqslant 0$.

    To prove this claim, we let $J_s(t) = J(t) - J_i(t)$, $A_s(t) = A(t) - A_i(t)$. Then $(J_s(t), J_i(t), A_s(t), A_i(t), G(t))$ satisfies (1), $(J_s(0), J_i(0), A_s(0), A_i(0)) \geqslant (0, 0, 0, 0)$, $0 \leqslant G(0) \leqslant 1$ and $J(0) + A(0) \leqslant x^*(0)$. Then it follows that $(J_s(t), J_i(t), A_s(t), A_i(t)) \geqslant (0, 0, 0, 0)$, $0 \leqslant G(t) \leqslant 1$ and $J(t) + A(t) \leqslant x^*(t)$. Thus, the claim is true.

    By Lemma 5 we have

$$\lim_{t \to \infty} \left[\left(J(t), A(t)\right) - \left(J^*(t), A^*(t)\right) \right] = (0, 0).$$

Let $\widetilde{P} : \widetilde{X} \to \widetilde{X}$ be the Poincaré map associated with system (11) and $\omega(x)$ be the omega limit set of the orbit of $\widetilde{P}$ with initial values $x \in \widetilde{X}$. Then there exists a set $\mathcal{C} \in \mathbb{R}_+^3$ such that $\omega(x) = \mathcal{C} \times \{(J^*(0), A^*(0))\}$. For any given $(J_i^0, A_i^0, G^0) \in \mathcal{C}$, we have $(J_i^0, A_i^0, G^0, J^*(0), A^*(0)) \in \omega(x) \subset \widetilde{X}$. By the definition of $\widetilde{X}$ we have $(J_i^0, A_i^0, G^0) \in Y$, and hence, $\mathcal{C} \subset Y$, where $Y := \Sigma(0)$ is defined in (10).

By Lemma 10, $\omega(x)$ is a compact, invariant and internal chain transitive set for $\widetilde{P}$. Moreover, if $x^0 \in \mathbb{R}_+^3$ with $(x^0, J^*(0), A^*(0)) \in \omega(x)$, we can show that

$$\widetilde{P}|_{\omega(x)}\big(x^0, J^*(0), A^*(0)\big) = \big(P_2(x^0), J^*(T), A^*(T)\big),$$

where $P_2 : Y \to Y$ is the Poincaré map associated with system (9). It then follows that $\mathcal{C}$ is a compact, invariant and internal chain transitive set for P_2 on Y.

In the case where $R_0 \leqslant 1$, it follows from Lemma 9(i) that $(0, 0, 0)$ is globally attractive for P_2 in Y. This implies that the unique fixed point $(0, 0, 0)$ is an isolated invariant set in Y and no cycle connecting $(0, 0, 0)$ to itself in Y. Since $\mathcal{C}$ is a compact, invariant and internal chain transitive set for $P_2 : Y \to Y$, then by Lemma 11, $\mathcal{C}$ is a fixed point of P_2. That is, $\mathcal{C} = \{(0, 0, 0)\}$, and hence, $\omega(x) = (0, 0, 0, J^*(0), A^*(0))$. This implies that $(0, 0, 0, J^*(0), A^*(0))$ is globally attractive for $\widetilde{P}$ in $\widetilde{X}$. Clearly, $(0, 0, 0, J^*(0), A^*(0))$ is a fixed point of $\widetilde{P}$, then system (11) has a globally attractive T-periodic solution $(0, 0, 0, J^*(t), A^*(t))$ in $\widetilde{X}$. In view of $J(t) = J_s(t) + J_i(t)$ and $A(t) = A_s(t) + A_i(t)$, we see that statement (i) is valid.

In the case where $R_0 > 1$, by Lemma 7 we have $r(\Phi_{F-V}(T)) > 1$. Then we can choose $\epsilon > 0$ small enough such that $r(\Phi_{F-V-\epsilon M}(T)) > 1$, where

$$M(t) = \begin{pmatrix} 2(\sigma_J(t) + k_J(t)) & 2\sigma_J(t) & 2\gamma_J(t) \\ 2\sigma_A(t) & 2(\sigma_A(t) + k_A(t)) & 2\gamma_A(t) \\ \alpha(t) & \alpha(t) & 0 \end{pmatrix}.$$

By Lemma 9(ii) it follows that (9) admits a positive T-periodic solution $(J_i^*(t), A_i^*(t), G^*(t))$ in $Y_0 := Y \setminus \{(0, 0, 0)\}$, which is globally attractive. Note that $(0, 0, 0)$ is also a T-periodic solution of (9). This implies that the possible fixed points $(0, 0, 0)$ and $(J_i^*(0), A_i^*(0), G^*(0))$ are isolated invariant sets in Y and no subset of $\{(0, 0, 0)\} \cup \{(J_i^*(0), A_i^*(0), G^*(0))\}$ forms a cycle in Y. Since $\mathcal{C}$ is a compact, invariant and internal chain transitive set for P_2, by Lemma 11 it follows that either $\mathcal{C} = \{(0, 0, 0)\}$ or $\mathcal{C} = \{(J_i^*(0), A_i^*(0), G^*(0))\}$.

Suppose, by contradiction, that $\mathcal{C} = \{(0, 0, 0)\}$, then we have

$$\widetilde{P}^n\big(J_i(0), A_i(0), G(0), J(0), A(0)\big) := \big(J_i(nT), A_i(nT), G(nT), J(nT), A(nT)\big)$$
$$\to \big(0, 0, 0, J^*(0), A^*(0)\big) \quad \text{as } n \to \infty.$$

Thus, $\lim_{t \to \infty}[(J_i(t), A_i(t), G(t), J(t), A(t)) - (0, 0, 0, J^*(t), A^*(t))] = (0, 0, 0, 0, 0)$, and there exists a $t_0 > 0$ such that $0 \leqslant J_i(t) \leqslant \epsilon$, $0 \leqslant A_i(t) \leqslant \epsilon$, $0 \leqslant G(t) \leqslant \epsilon$, $J^*(t) - \epsilon \leqslant J(t) \leqslant J^*(t) + \epsilon$ and $A^*(t) - \epsilon \leqslant A(t) \leqslant A^*(t) + \epsilon$ for all $t \geqslant t_0$. Then

for any $t \geqslant t_0$, we have

$$\frac{\mathrm{d}J_i}{\mathrm{d}t} \geqslant \left[\gamma_J(t)G + \sigma_J(t)(J_i + A_i)\right]\left(J^*(t) - 2\epsilon\right)$$
$$- \left[\mu_J(t) + \tau(t) + k_J(t)(J^*(t) + A^*(t) + 2\epsilon)\right]J_i,$$

$$\frac{\mathrm{d}A_i}{\mathrm{d}t} \geqslant \tau(t)J_i + \left[\gamma_A(t)G + \sigma_A(t)(J_i + A_i)\right]\left(A^*(t) - 2\epsilon\right)$$
$$- \left[\mu_A(t) + k_A(t)(J^*(t) + A^*(t) + 2\epsilon)\right]A_i(t),$$

$$\frac{\mathrm{d}G}{\mathrm{d}t} \geqslant (1 - \epsilon)\alpha(t)(J_i + A_i) - \delta(t)G.$$

From $(J_i(0), A_i(0)) > (0,0)$ we can show that $(J_i(t), A_i(t), G(t)) \gg (0,0,0)$ for all $t > 0$. By Lemma 6 there exists a positive T-periodic function $\bar{v}(t)$ and $\bar{\mu} = (1/T)\ln r(\Phi_{F-V-\epsilon M}(T))$ such that $\overline{W}(t) = \bar{a}\mathrm{e}^{\bar{\mu}(t-t_0)}\bar{v}(t)$ is a solution of $\mathrm{d}W(t)/\mathrm{d}t = (F(t) - V(t) - \epsilon M(t))W(t)$, where $\bar{a}$ satisfies $\overline{W}(t_0) = \bar{a}\bar{v}(t_0) \leqslant (J_i(t_0), A_i(t_0), G(t_0))$. Since $\bar{\mu} > 0$, we see that $\overline{W}(t) \to \infty$ as $t \to \infty$. By the standard comparison theorem we have $(J_i(t), A_i(t), G(t)) \geqslant \overline{W}(t)$ for all $t \geqslant t_0$. This implies that $(J_i(t), A_i(t), G(t)) \to \infty$ as $t \to \infty$, a contraction. It then follows that $\mathcal{C} = \{(J_i^*(0), A_i^*(0), G^*(0))\}$, and hence, $\omega(x) = \mathcal{C} \times \{(J^*(0), A^*(0))\} = \{(J_i^*(0), A_i^*(0), G^*(0), J^*(0), A^*(0))\}$. This implies that

$$\lim_{t\to\infty} \left[\left(J_i(t), A_i(t), G(t), J(t), A(t)\right) - \left(J_i^*(t), A_i^*(t), G^*(t), J^*(t), A^*(t)\right)\right]$$
$$= (0, 0, 0, 0, 0).$$

In view of $J(t) = J_s(t) + J_i(t)$ and $A(t) = A_s(t) + A_i(t)$, we see that statement (ii) is valid. □

When all the coefficients are positive constants, in this case, system (1) reduces to the following autonomous one:

$$\frac{\mathrm{d}J_s(t)}{\mathrm{d}t} = \beta A(t) - \left(\mu_J + \tau + k_J P(t)\right)J_s(t) - \left(\gamma_J G(t) + \sigma_J I(t)\right)J_s(t),$$

$$\frac{\mathrm{d}J_i(t)}{\mathrm{d}t} = \left(\gamma_J G(t) + \sigma_J I(t)\right)J_s(t) - \left(\mu_J + \tau + k_J P(t)\right)J_i(t),$$

$$\frac{\mathrm{d}A_s(t)}{\mathrm{d}t} = \tau J_s(t) - \left(\mu_A + k_A P(t)\right)A_s(t) - \left(\gamma_A G(t) + \sigma_A I(t)\right)A_s(t), \qquad (12)$$

$$\frac{\mathrm{d}A_i(t)}{\mathrm{d}t} = \tau J_i(t) + \left(\gamma_A G(t) + \sigma_A I(t)\right)A_s(t) - \left(\mu_A + k_A P(t)\right)A_i(t),$$

$$\frac{\mathrm{d}G(t)}{\mathrm{d}t} = \alpha I(t)\left(1 - G(t)\right) - \delta G(t).$$

For the densities of juveniles $J(t) = J_s(t) + J_i(t)$ and adults $A(t) = A_s(t) + A_i(t)$, we have

$$\frac{\mathrm{d}J}{\mathrm{d}t} = \beta A - \left(\mu_J + \tau + k_J(J + A)\right)J, \qquad \frac{\mathrm{d}A}{\mathrm{d}t} = \tau J - \left(\mu_A + k_A(J + A)\right)A. \qquad (13)$$

Then assumptions (A1)–(A3) can be replaced by

(A1′) $\beta > \mu$;
(A2′) $\beta < k_J\mu/(k_J - k)$, $\tau > k_A(\beta - \mu)/k$;
(A3′) $C := \beta\tau/\mu_A(\mu_J + \tau) > 1$.

By Lemma 5 we have the following result.

Theorem 2. *Let* (A1′) *and* (A2′) *hold. Then the following statements are valid*:

(i) *If* $C \leqslant 1$, *then the trivial solution* $(0,0)$ *is globally asymptotically stable for system* (13) *in* $\Gamma = \{(J, A) \in \mathbb{R}_+^2 : J + A \leqslant (\beta - \mu)/k\}$.

(ii) *If* $C > 1$, *then system* (13) *admits a unique positive equilibrium* (J^*, A^*), *which is globally asymptotically stable in* $\Gamma \setminus \{(0,0)\}$.

The conclusion in Theorem 2 is consistent with that in Theorem 2.1 in [17].
For this autonomous case, the basic reproduction number is $[R_0] = r(FV^{-1})$, where

$$F = \begin{pmatrix} \sigma_J J^* & \sigma_J J^* & \gamma_J J^* \\ \tau + \sigma_A A^* & \sigma_A A^* & \gamma_A A^* \\ \alpha & \alpha & 0 \end{pmatrix},$$

$$V = \begin{pmatrix} \mu_J + \tau + k_J(J^* + A^*) & 0 & 0 \\ 0 & \mu_A + k_A(J^* + A^*) & 0 \\ 0 & 0 & \delta \end{pmatrix}.$$

Condition (A3′) is equivalent to $\beta > \mu_A\mu_J/\tau + \mu_A > \mu$, then (A3′) implies (A1′). By Theorem 1 we have the following observation for system (12).

Theorem 3. *Assume that* (A1′) *and* (A3′) *hold. Then the following statements are valid for system* (12):

(i) *If* $[R_0] \leqslant 1$, *then the virus-free equilibrium* $(J^*, 0, A^*, 0, 0)$ *is globally asymptotically stable for system* (12) *in* $\Omega \setminus \{(0,0,0,0,0)\}$.

(ii) *If* $[R_0] > 1$, *then every solution* $(J_s(t), J_i(t), A_s(t), A_i(t), G(t))$ *of system* (12) *with* $(J_s(0), J_i(0), A_s(0), A_i(0), G(0)) \in \Omega \setminus \{(a,0,b,0,c) : a, b, c \in \mathbb{R}_+\}$ *satisfies*

$$\lim_{t \to \infty} \left[\left(J_s(t), J_i(t), A_s(t), A_i(t), G(t) \right) - \left(J_s^*, J_i^*, A_s^*, A_i^*, G^* \right) \right]$$
$$= (0, 0, 0, 0, 0),$$

where $J_s^* = J^* - J_i^*$, $A_s^* = A^* - A_i^*$, *and* (J_i^*, A_i^*, G^*) *is the unique positive equilibrium of the following system*:

$$\frac{dJ_i}{dt} = \left[\gamma_J G + \sigma_J(J_i + A_i) \right](J^* - J_i) - \left[\mu_J + \tau + k_J(J^* + A^*) \right]J_i,$$
$$\frac{dA_i}{dt} = \tau J_i + \left[\gamma_A G + \sigma_A(J_i + A_i) \right](A^* - A_i) - \left[\mu_A + k_A(J^* + A^*) \right]A_i,$$
$$\frac{dG}{dt} = \alpha(J_i + A_i)(1 - G) - \delta G.$$

The authors in [17, Thm. 2.3] completed the local stability analysis for the autonomous model (12). Theorem 3 generalizes the conclusion of local stability in Theorem 2.3 of [17] and gives the global stability of the virus-free equilibrium and the positive equilibrium in terms of the basic reproduction number.

3 Discussion and simulations

Although there are many models that describe the spread of the hantavirus, there are few papers provide a thorough classification of dynamics for the model systems. In particular, if the basic reproduction number is greater than one, then a unique positive periodic solution (equilibrium) exists and is globally attractive in the feasible region, and the disease persists at a positive periodic solution (equilibrium) if it initially exists. In this paper, we have studied a deterministic mathematical model, which was proposed by Wolf et al. [17]. This model describes the propagation of Puumala hantavirus within the bank vole population of Clethrionomys glareolus. The host population is split into juvenile and adult individuals. Both direct transmission (contacts between individuals) and indirect transmission (through the environment) are considered. To incorporate the influence of seasonal temperature variations, the demographic parameters in the model systems are assumed to be time periodic. We first define the basic reproduction number, R_0, for the system (1). Then, by appealing to the theory of monotone dynamical systems and chain transitive sets, we show that R_0 is a sharp threshold, which completely determines the global dynamics and the outcome of the virus. If $R_0 \leqslant 1$, the virus-free periodic solution is globally attractive, and the virus always dies out (see Theorem 1(i)). If $R_0 > 1$, there exists a unique positive periodic solution, which is globally attractive, and the virus persists (see Theorem 1(ii)). The theory of monotone dynamical systems and chain transitive sets have also been applied in [7, 14]. Hsu et al. [7] studied a mathematical model of two species competing in a chemostat for two internally stored essential nutrients, both uniform persistence and the existence of periodic coexistence state were established. Wang et al. [14] investigated two-vessel gradostat models, which describe the dynamics of harmful algae with seasonal temperature variations, the global attractivity of positive periodic steady-state solution was obtained.

In this section, we will present some simulations, which illustrate our analytic results of the previous section and perform sensitivity analysis of the basic reproduction number R_0 in terms of system parameters. The time unit is 1 year. The parameters are taken as

$$\beta(t) = \left| 20 \sin\big(2\pi(t - 0.15)\big) \right| + 20 \sin\big(2\pi(t - 0.15)\big),$$

$$\mu_J(t) = 6, \qquad \mu_A(t) = 2, \qquad \tau(t) = 12,$$

$$k_J(t) = \frac{10 - \mu_J(t)}{K_J(t)}, \qquad K_J(t) = 3\left[10 + \cos^2 \frac{2\pi t}{3} - 9.5 \sin \frac{2\pi t}{3} \right],$$

$$k_A(t) = \frac{10 - \mu_A(t)}{K_A(t)}, \qquad K_A(t) = 6\left[10 + \cos^2 \frac{2\pi(t + 0.35)}{3} - 8 \sin \frac{2\pi(t + 0.35)}{3} \right],$$

$$\gamma_J(t) = \gamma_A(t) := \gamma = 9, \qquad \alpha(t) := \alpha = 0.3, \qquad \delta(t) := \delta = 52,$$
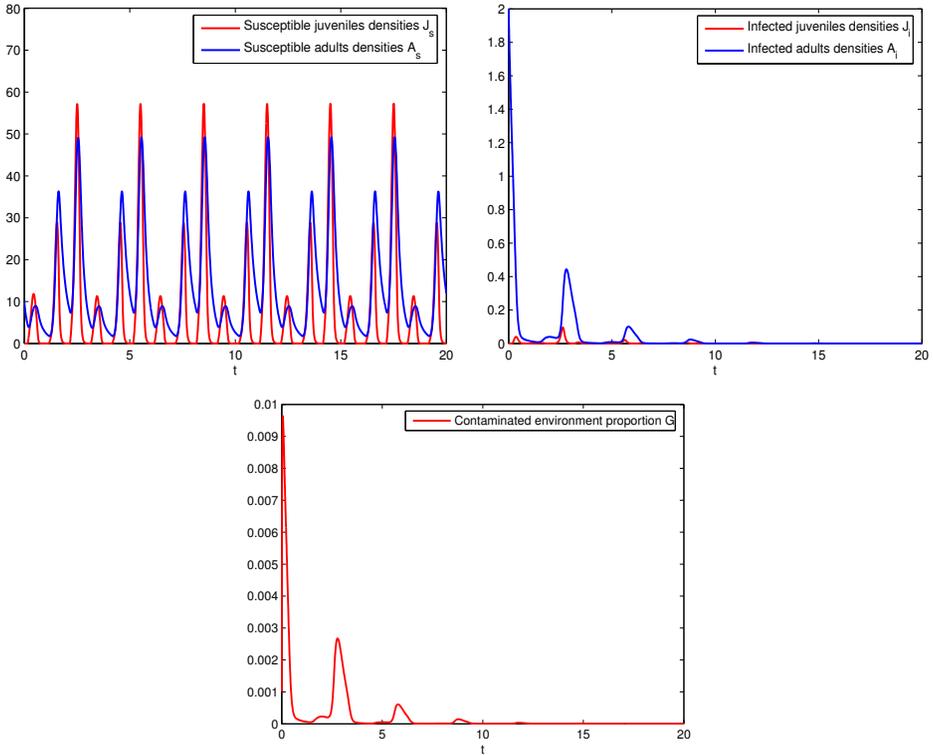
Figure 1. Dynamics for system (1) when $R_0 = 0.9215 < 1$.

which are chosen from Wolf et al. [17]. We take direct transmission rate $\sigma_J(t) = \sigma_A(t) := \sigma$ as variable.

If we choose $\sigma = 0.18$, then we get $R_0 = 0.9215 < 1$, and the virus will die out for system (1) (see Fig. 1). If we increase σ to 0.35, we have $R_0 = 1.4272 > 1$, then the virus will occur periodically for system (1), and the virus is persistent in host population and environment (see Fig. 2). These results are coincident with Theorem 1(i) and (ii), respectively.

Now we examine the sensitivity of the disease risk R_0 on system parameters. Take the direct transmission rate σ, the indirect contamination rate γ, the contamination rate of the environment α and the decontamination rate δ as examples and keep all the other parameter values the same as those in Fig. 1. This result is shown in Fig. 3, where the basic reproduction numbers are functions of σ, γ, α and δ. We plot two curves, the red one refers system (1) with time-periodic coefficients, and the blue one reflects system (12) with constant coefficients. One can observe that the red curve always lie above the blue one, which implies that the risk of hantavirus will be underestimated if periodicity is neglected. In other words, periodicity can be more favorable to the persistence of the virus. This implies that we need to make much more efforts to control the spread of hantavirus.
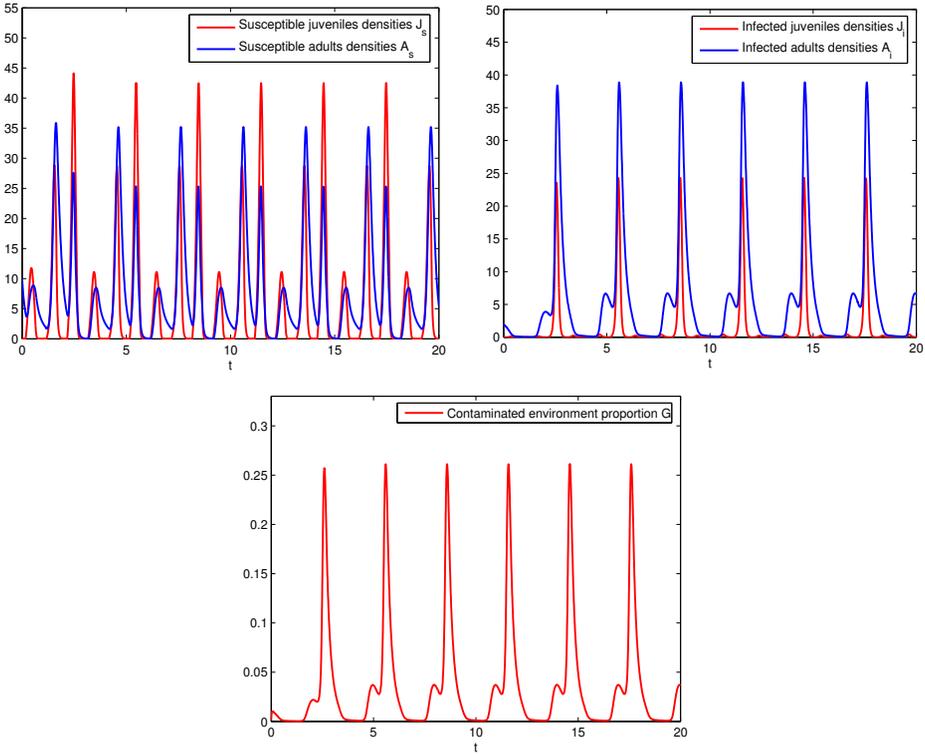
Figure 2. Dynamics for system (1) when $R_0 = 1.4272 > 1$.

Then we further do sensitivity analysis by evaluating partial rank correlation coefficients (PRCCs) [9, 10]. We assume that $\beta(t) = \beta_0(|\sin(2\pi(t - 0.15))| + \sin(2\pi \times (t - 0.15)))$, Fig. 4 reflects the impact of parameters on the basic reproduction number R_0, according to importance, they are the baseline birth rate β_0, direct transmission rate σ_A for adult mice, direct transmission rate σ_J for juvenile mice, indirect contamination rate γ_A for adult mice, the rate of environmental decontamination δ, the rate of environmental contamination α and the indirect contamination rate γ_J for juvenile mice. These results indicate that controlling the grow of mice population and enhancing environmental disinfection are important control strategies in reducing hantavirus infection.

Even though we used a general model, if more data was available, the model can be used for predictions. With the data to be collected, the parameters can be modified to fit a particular situation. Our model can be useful for epidemiologists. They can utilize the model to help predict the behavior of the hantavirus spread. For example, suppose one notices hantavirus endemic occurs, but after a period of time they notice that fewer mice are becoming infected. This periodic model will let the one know that there will be an increase in the number of infections at a later time because of the periodic oscillatory behavior of the model. This will force epidemiologists to not become relaxed in trying to combat the virus through hantavirus control methods.
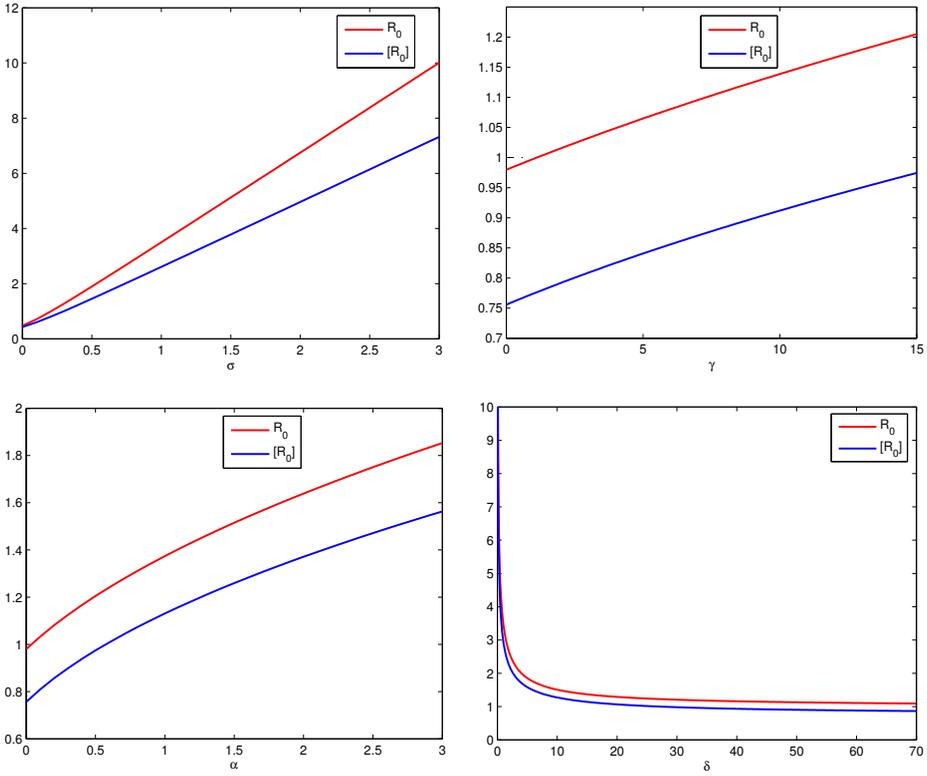
Figure 3. R_0 and $[R_0]$ vs σ, γ, α and δ.
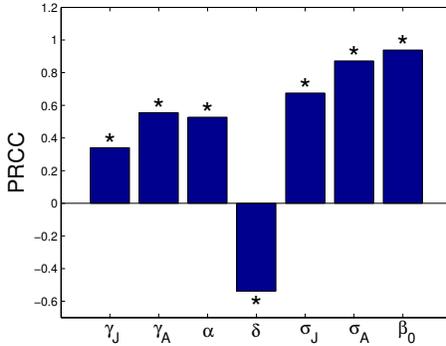
Figure 4. PRCCs results for the dependence of R_0 on parameters.

Our work generalized the results in [17], but we also did some significant simplifications in modeling and analysis. For example, the juvenile maturation rate does not depend on the density of adults, and we also assume that (A1)–(A3) hold, these assumptions make the threshold type results hold for systems (3) and (9) (see Lemmas 5 and 9). Otherwise,

the analysis will become much more complicated than those in the current paper. It will be challenging and interesting projects if we relax the aforementioned simplifications, we leave these problems for future investigation.

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