

Research Article

A Periodic West Nile Virus Transmission Model with Stage-Structured Host Population

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Received 8 November 2019; Revised 25 December 2019; Accepted 7 January 2020; Published 29 January 2020

Academic Editor: Eric Campos

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In this paper, we study an avian (host) stage-structured West Nile virus model, which incorporates seasonality as well as stage-specific mosquito biting rates. We first introduce the basic reproduction number R_0 for this model and then show that the disease-free periodic solution is globally asymptotically stable when $R_0 < 1$, while there exists at least one positive periodic solution and that the disease is uniformly persistent if $R_0 > 1$. In the case where all coefficients are constants, for a special case, we obtain the global stability of the disease-free equilibrium, the uniqueness of the endemic equilibrium, and the permanence of the disease in terms of the basic reproduction number R_0 . Numerical simulations are carried out to verify the analytic result. Some sensitivity analysis of R_0 is performed. Our finding shows that an increase in juvenile exposure will lead to more severe transmission. Moreover, we find that the ignorance of the seasonality may result in underestimation of the basic reproduction number R_0 .

1. Introduction

West Nile virus (WNV) is a flavivirus commonly found in Africa, West Asia, and the Middle East. The virus can infect humans, birds, mosquitoes, horses, and some other mammals. It was believed that WNV is maintained in nature in a mosquito-bird-mosquito transmission cycle [1–4]. Since the first outbreak in New York in 1999, West Nile virus remains an annual public health concern. Therefore, it is important to understand the transmission dynamics of WNV in the mosquito-bird population.

Mathematical models have played a significant role in understanding and analyzing the WNV transmission dynamics. Wonham et al. [5] presented a single-season susceptible-infectious-removed (SIR) model for WNV transmission in the mosquito-bird population. Lewis et al. [6] developed a reaction-diffusion model for the spatial spread of WNV, established the existence of traveling waves, and calculated the spatial spread rate of infection. Liu et al. [7] formulated a patchy model and studied the impact of directional dispersal of birds on the spatial spreading of WNV. Cruz-Pacheco et al. [8] studied the

impact of seasonal variations on the dynamics of WNV infection. Seasonality of WNV has also been discussed in [9, 10]. In a more recent work by Fan et al. [11], they formulated and analyzed a single-season model for the transmission of WNV between vector mosquitoes and avian hosts, and their model incorporated maturation delay for mosquitoes. Further work has also been carried out to model the WNV transmission dynamics; see, e.g., Jiang et al. [12], Bergsman et al. [13], Zhang et al. [14], Xu et al. [15], Lin and Zhu [16], Chen et al. [17], and the references therein.

Though mathematical modelling for the transmission of WNV has been studied extensively, the effect of within-species variability, such as differences among host age groups, along with species-specific host feeding preferences of vectors seem to have received little attention. It is obvious that since newly hatched, or nestlings, have little feather coverage, are largely immobile, and have more exposure to mosquito bites relative to older birds. The fledglings that have left the nest have nearly complete feather coverage and exhibit some antimosquito defensive behaviors. The fledglings are more exposed to vectors than mature adult birds,

but less than nestlings [18]. Also, the climate effect on the dynamics of vector population and the biting rate from mosquitoes to birds cannot be neglected. Transmission of WNV in most regions of the United States is highly seasonal. Seasonality is strongly influenced by climatic factors. Due to these reason, in [18], Robertson and Caillouët [18] developed a host-vector model for WNV transmission dynamics across a single season, which incorporated the host stage-structure as well as stage-specific biting rates of vectors on avian hosts. They mainly studied the model from the numerical simulation point of view.

In this paper, by taking into account the seasonality, the avian stage-structure and within-species heterogeneity, we derive a periodic model to describe the dynamics of WNV transmission. The rest of the paper is organized as follows. In Section 2, we present the model rigorously and study its well-posedness, and then we introduce the basic reproduction number R_0 . In Section 3, we study the threshold dynamics in terms of R_0 . In Section 4, for a special case, we study the autonomous case of the periodic model and prove the global stability of the disease-free equilibrium and the permanence of the system. In Section 5, we carry out numerical simulations to illustrate the obtained results. A brief discussion section completes the paper.

2. Model Formulation

Our model was built on the framework of [18]. The host population is divided into three stages, nestlings, fledglings, and adults. Each stage the birds are classified into three categories: the susceptible class (N_S, F_S, A_S), infectious class (N_I, F_I, A_I), and recovered class (N_R, F_R, A_R). The total number of nestlings, fledglings, and adults are denoted by $N_T = N_S + N_I + N_R$, $F_T = F_S + F_I + F_R$, and $A_T = A_S + A_I + A_R$, respectively. The mosquito population is divided into three epidemiological classes: the susceptible class M_S , exposed class M_L , and infectious class M_I . The total number of mosquito population is denoted by M , and then $M = M_S + M_L + M_I$.

Susceptible nestlings are produced at rate $b(t)$, mosquito bites are distributed among the avian stage classes. The

fraction of bites going to nestlings, fledglings, and adults is given by $\alpha_N(t)$, $\alpha_F(t)$, and $\alpha_A(t)$, respectively:

$$\begin{aligned}\alpha_N(t) &= \frac{a_N(t)N_T(t)}{a_N(t)N_T(t) + a_F(t)F_T(t) + a_A(t)A_T(t)}, \\ \alpha_F(t) &= \frac{a_F(t)F_T(t)}{a_N(t)N_T(t) + a_F(t)F_T(t) + a_A(t)A_T(t)}, \\ \alpha_A(t) &= \frac{a_A(t)A_T(t)}{a_N(t)N_T(t) + a_F(t)F_T(t) + a_A(t)A_T(t)},\end{aligned}\quad (1)$$

where $a_N(t)$, $a_F(t)$, and $a_A(t)$ are the exposure coefficients for each stage.

Susceptible nestlings, fledglings, and adults can move into the infectious nestling, fledgling, and adult class, respectively, upon being bitten by an infectious mosquito. The probability of mosquito to bird transmission per bite are assumed to be stage-dependent and is given by $\beta_i(t)$, $i = N, F, A$. The stage-dependent disease-induced death rate is given by $\gamma_i(t)$, $i = N, F, A$, and each stage recovers at rate $\gamma_i(t)$, $i = N, F, A$. Nestlings mature into fledglings at rate $m_N(t)$ and fledglings mature into adults at rate $m_F(t)$. Natural mortality rates are given by $\mu_i(t)$, $i = N, F, A$. The probability of bird-mosquito transmission per bite is also assumed to be stage-dependent and is denoted by $\delta_i(t)$, $i = N, F, A$. Latent mosquitoes transition to infectious mosquitoes at rate $k(t)$. Due to their relatively short life-cycle, we assume that mosquitoes never recover from infection after they are infected, and their infective period ends with their death. We assume all mosquitoes are born into the susceptible class. A density-dependent logistic-type birth rate (due to competition for environmentally limited breeding sites) with intrinsic per capita birth rate $r(t)$ and carrying capacity $K(t)$ is assumed, and the death rate for the mosquito population is denoted by $\mu_M(t)$. We assume the biting rate on competent avian hosts is $a(t)$, then the force of infection at time t for the susceptible nestlings, fledglings, adults, and susceptible mosquitoes are, respectively, given by

$$\begin{aligned}\lambda_1(t) &:= a(t)\alpha_N(t)\beta_N(t)M_I(t)\frac{N_S(t)}{N_T(t)} = \frac{a(t)a_N(t)\beta_N(t)M_I(t)N_S(t)}{a_N(t)N_T(t) + a_F(t)F_T(t) + a_A(t)A_T(t)}, \\ \lambda_2(t) &:= a(t)\alpha_F(t)\beta_F(t)M_I(t)\frac{F_S(t)}{F_T(t)} = \frac{a(t)a_F(t)\beta_F(t)M_I(t)F_S(t)}{a_N(t)N_T(t) + a_F(t)F_T(t) + a_A(t)A_T(t)}, \\ \lambda_3(t) &:= a(t)\alpha_A(t)\beta_A(t)M_I(t)\frac{A_S(t)}{A_T(t)} = \frac{a(t)a_A(t)\beta_A(t)M_I(t)A_S(t)}{a_N(t)N_T(t) + a_F(t)F_T(t) + a_A(t)A_T(t)}, \\ \lambda_4(t) &:= a(t)\left(\alpha_N(t)\delta_N(t)\frac{N_I(t)}{N_T(t)} + \alpha_F(t)\delta_F(t)\frac{F_I(t)}{F_T(t)} + \alpha_A(t)\delta_A(t)\frac{A_I(t)}{A_T(t)}\right)M_S(t) \\ &= a(t)\left(\frac{a_N(t)\delta_N(t)N_I(t) + a_F(t)\delta_F(t)F_I(t) + a_A(t)\delta_A(t)A_I(t)}{a_N(t)N_T(t) + a_F(t)F_T(t) + a_A(t)A_T(t)}\right)M_S(t).\end{aligned}\quad (2)$$

Consequently, we propose the following model of West Nile virus:

$$\left\{ \begin{aligned}
 \frac{dN_S(t)}{dt} &= b(t) - \lambda_1(t) - \sigma_N(t)N_S(t), \\
 \frac{dN_I(t)}{dt} &= \lambda_1(t) - (\sigma_N(t) + \eta_N(t))N_I(t), \\
 \frac{dN_R(t)}{dt} &= \gamma_N(t)N_I(t) - \sigma_N(t)N_R(t), \\
 \frac{dF_S(t)}{dt} &= m_N(t)N_S(t) - \lambda_2(t) - \sigma_F(t)F_S(t), \\
 \frac{dF_I(t)}{dt} &= \lambda_2(t) + m_N(t)N_I(t) - (\sigma_F(t) + \eta_F(t))F_I(t), \\
 \frac{dF_R(t)}{dt} &= \gamma_F(t)F_I(t) + m_N(t)N_R(t) - \sigma_F(t)F_R(t), \\
 \frac{dA_S(t)}{dt} &= m_F(t)F_S(t) - \lambda_3(t) - \mu_A(t)A_S(t), \\
 \frac{dA_I(t)}{dt} &= \lambda_3(t) + m_F(t)F_I(t) - \sigma_A(t)A_I(t), \\
 \frac{dA_R(t)}{dt} &= \gamma_A(t)A_I(t) + m_F(t)F_R(t) - \mu_A(t)A_R(t), \\
 \frac{dM_S(t)}{dt} &= r(t)M(t) \left(1 - \frac{M(t)}{K(t)} \right) - \lambda_4(t) - \mu_M(t)M_S(t), \\
 \frac{dM_L(t)}{dt} &= \lambda_4(t) - k(t)M_L(t) - \mu_M(t)M_L(t), \\
 \frac{dM_I(t)}{dt} &= k(t)M_L(t) - \mu_M(t)M_I(t),
 \end{aligned} \right. \quad (3)$$

where

$$\begin{aligned}
 \sigma_N(t) &= m_N(t) + \mu_N(t), \\
 \sigma_F(t) &= m_F(t) + \mu_F(t), \\
 \sigma_A(t) &= \gamma_A(t) + \mu_A(t) + \nu_A(t), \\
 \eta_N(t) &= \gamma_N(t) + \nu_N(t), \\
 \eta_F(t) &= \gamma_F(t) + \nu_F(t).
 \end{aligned} \quad (4)$$

Note that if all the parameters in (3) are positive constants except for that $b(t)$ and $\mu_M(t)$ are time-dependent, then this system has the same form as equation (3) in [18].

We assume that $\nu_i(t) \geq 0$, $i = N, F, A$, are continuous ω -periodic functions, and all the other parameters are continuous and positive ω -periodic functions for some $\omega > 0$. All parameters and their biological interpretations are given in Table 1.

In order to avoid the extinction of the mosquito population, we make the following assumption throughout this paper:

$$(A1) r(t) > \mu_M(t), \quad \forall t \geq 0. \quad (5)$$

Since the carrying capacity of the mosquito population $K(t)$ is time-dependent, to prove the well-posedness of system (3), we need to impose a condition on this function. Throughout this paper, we require the following condition:

$$\frac{dK(t)}{dt} \geq -\mu_M(t)K(t). \quad (6)$$

For the whole mosquito population, we have

$$\frac{dM(t)}{dt} = r(t)M(t) \left(1 - \frac{M(t)}{K(t)} \right) - \mu_M(t)M(t). \quad (7)$$

Then, $K(t)$ is an upper solution of (7), which means that if $M(0) \leq K(0)$, then $M(t) \leq K(t)$ for all $t \geq 0$.

For continuous positive ω -periodic function $g(t)$, let

$$\begin{aligned}
 g^u &= \max_{t \in [0, \omega]} g(t), \\
 g^l &= \min_{t \in [0, \omega]} g(t).
 \end{aligned} \quad (8)$$

Model (3) is mathematically and epidemiologically well posed on the region $D(t)$ given by

$$\begin{aligned}
 D(t) &= \left\{ (N_S, N_I, N_R, F_S, F_I, F_R, A_S, A_I, A_R, M_S, M_I, M_R) \right. \\
 &\quad \left. \in \mathbb{R}_+^{12} \mid 0 < N_T + F_T + A_T \leq \frac{b^u}{\mu}, M_S + M_L + M_I \leq K(t) \right\},
 \end{aligned} \quad (9)$$

where $\bar{\mu} = \min\{\mu_N^l, \mu_F^l, \mu_A^l\}$.

Theorem 1. *For any initial value z in $D(t)$, system (3) has a unique nonnegative solution through z for all $t \geq 0$, and all solutions are ultimately bounded and uniformly bounded.*

Proof. Let $G(t, z)$ be the vector field described by (3) with $z \in D(t)$. Then, $G(t, z)$ is continuous and Lipschitzian in z on each compact subset of $\mathbb{R}^1 \times D(t)$. Clearly, $G_i(t, z) \geq 0$ whenever $z \geq 0$ and $z_i = 0, i = 1, \dots, 12$. It follows from Theorem 5.2.1 in Smith [19] that there exists a unique nonnegative solution for system (3) through $z \in D(t)$ in its maximal interval of existence. The total numbers for birds satisfies

TABLE 1: Parameters of model (3) and their interpretations.

| Parameter | Description |
|---|---|
| $b(t)$ | Nestling recruitment rate |
| $a(t)$ | Biting rate on competent avian hosts |
| $a_N(t), a_F(t), a_A(t)$ | Exposure coefficients of nestling, fledgling and adult |
| $r(t)$ | Mosquito per capita birth rate |
| $K(t)$ | Mosquito carrying capacity |
| $\mu_M(t)$ | Vector mortality rate |
| $1/k(t)$ | Virus extrinsic incubation period |
| $m_N(t), m_F(t)$ | Maturation rates of nestling and fledgling |
| $\gamma_N(t), \gamma_F(t), \gamma_A(t)$ | Recovery rates of nestling, fledgling, and adult |
| $\mu_N(t), \mu_F(t), \mu_A(t)$ | Natural mortality rates of nestling, fledgling, and adult |
| $\beta_N(t), \beta_F(t), \beta_A(t)$ | Susceptibility of nestling, fledgling and adult |
| $\delta_N(t), \delta_F(t), \delta_A(t)$ | Infectivity of nestling, fledgling, and adult |
| $\nu_N(t), \nu_F(t), \nu_A(t)$ | Disease-induced death rates of nestling, fledgling, and adult |

$$\begin{aligned} \frac{d(N_T + F_T + A_T)}{dt} &= b(t) - \mu_N(t)N_T - \mu_F(t)F_T - \mu_A(t)A_T \\ &\quad - \nu_N(t)N_I - \nu_F(t)F_I - \nu_A(t)A_I, \end{aligned} \quad (10)$$

and it follows that

$$\begin{aligned} b^l - (\hat{\mu} + \hat{\nu})(N_T + F_T + A_T) &\leq \frac{d(N_T + F_T + A_T)}{dt} \leq b^u \\ &\quad - \bar{\mu}(N_T + F_T + A_T), \end{aligned} \quad (11)$$

where $\hat{\mu} = \max\{\mu_N^u, \mu_F^u, \mu_A^u\}$ and $\hat{\nu} = \max\{\nu_N^u, \nu_F^u, \nu_A^u\}$. Thus, we have

$$0 < N_T(t) + F_T(t) + A_T(t) \leq \frac{b^u}{\hat{\mu}}, \quad (12)$$

for each $z \in D(t)$, $t \geq 0$.

By Lemma 1 in Teng et al. [20], (7) has a unique positive ω -periodic solution $M^*(t)$ which is globally asymptotically stable with respect to $M(0) > 0$, that is,

$$\lim_{t \rightarrow \infty} (M(t) - M^*(t)) = 0, \quad \text{for } M(0) > 0. \quad (13)$$

It follows that the solutions are ultimately bounded. Hence, every solution of (3) exists for all $t \geq 0$. Since $M(t) \leq K(t)$, for all $t \geq 0$, and $K(t)$ is a positive ω -periodic function, this implies that all solutions are uniformly bounded.

From the proof of Theorem 1, we know that any solution of (3) with initial condition in $D(t)$ will remain in $D(t)$ for all $t \geq 0$, then $D(t)$ is positively invariant.

We define the diseased classes as the birds or mosquito populations that are either exposed or infectious, i.e.,

N_I, F_I, A_I, M_L , and M_I . To find the disease-free state, letting $N_I = F_I = A_I = M_L = M_I = 0$, we then obtain

$$\begin{cases} \frac{dN_S(t)}{dt} = b(t) - \sigma_N(t)N_S(t), \\ \frac{dN_R(t)}{dt} = -\sigma_N(t)N_R(t), \\ \frac{dF_S(t)}{dt} = m_N(t)N_S(t) - \sigma_F(t)F_S(t), \\ \frac{dF_R(t)}{dt} = m_N(t)N_R(t) - \sigma_F(t)F_R(t), \\ \frac{dA_S(t)}{dt} = m_F(t)F_S(t) - \mu_A(t)A_S(t), \\ \frac{dA_R(t)}{dt} = m_F(t)F_R(t) - \mu_A(t)A_R(t), \\ \frac{dM_S(t)}{dt} = r(t)M_S(t) \left(1 - \frac{M_S(t)}{K(t)}\right) - \mu_M(t)M_S(t). \end{cases} \quad (14)$$

It is easy to see that the ordinary differential system $dN_S(t)/dt = b(t) - \sigma_N(t)N_S(t)$ has a globally attractive positive ω -periodic solution $N_S^*(t)$, that is, $\lim_{t \rightarrow \infty} (N_S(t) - N_S^*(t)) = 0$. Then, by the third and fifth equations in (14), there exist positive ω -periodic solutions $F_S^*(t)$ and $A_S^*(t)$ such that $\lim_{t \rightarrow \infty} (F_S(t) - F_S^*(t)) = 0$ and $\lim_{t \rightarrow \infty} (A_S(t) - A_S^*(t)) = 0$. Hence, there is only one disease-free state,

$E_0(t) = (N_S^*(t), 0, 0, F_S^*(t), 0, 0, A_S^*(t), 0, 0, M^*(t), 0, 0)$, where $M^*(t)$ is the positive periodic solution of (7). There exists another trivial periodic solution, $E_{00}(t) = (N_S^*(t), 0, 0, F_S^*(t), 0, 0, A_S^*(t), 0, 0, 0, 0, 0)$.

Let $(\mathbb{R}^n, \mathbb{R}_+^n)$ be the standard ordered n -dimensional Euclidean space with a norm $\|\cdot\|$. For $u, v \in \mathbb{R}^n$, we denote $u \geq v$, if $u - v \in \mathbb{R}_+^n$; $u > v$, if $u - v \in \mathbb{R}_+^n \setminus \{0\}$; $u \gg v$, if $u - v \in \text{Int}(\mathbb{R}_+^n)$.

Let $A(t)$ be a continuous, cooperative, irreducible, and periodic $n \times n$ matrix function with period $\omega > 0$ and $\Phi_A(t)$ be the fundamental solution matrix of the linear ordinary differential equation:

$$\dot{x} = A(t)x. \quad (15)$$

Let $r(\Phi_A(\omega))$ be the spectral radius of $\Phi_A(\omega)$. By Perron-Frobenius theorem, $r(\Phi_A(\omega))$ is the principle eigenvalue of $\Phi_A(\omega)$, in the sense that it is simple and admits an eigenvector $v^* \gg 0$. The following lemma is useful for our discussion in the Section 3.

Lemma 1 (see [21], Lemma 1). *Let $p = 1/\omega \ln r(\Phi_A(\omega))$. Then, there exists a positive ω -periodic function $v(t)$ such that $e^{pt}v(t)$ is a solution of (15).*

Now we introduce the basic reproduction number of (3), by applying the theory in Wang and Zhao [22] with

$$F(t) = \begin{pmatrix} 0 & 0 & 0 & 0 & \frac{b_N(t)N_S^*(t)}{\Theta} \\ 0 & 0 & 0 & 0 & \frac{b_F(t)F_S^*(t)}{\Theta} \\ 0 & 0 & 0 & 0 & \frac{b_A(t)A_S^*(t)}{\Theta} \\ \frac{c_N(t)M^*(t)}{\Theta} & \frac{c_F(t)M^*(t)}{\Theta} & \frac{c_A(t)M^*(t)}{\Theta} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix}, \quad (16)$$

$$V(t) = \begin{pmatrix} \sigma_N(t) + \eta_N(t) & 0 & 0 & 0 & 0 \\ -\mu_N(t) & \sigma_F(t) + \eta_F(t) & 0 & 0 & 0 \\ 0 & -m_F(t) & \sigma_A(t) & 0 & 0 \\ 0 & 0 & 0 & k(t) + \mu_M(t) & 0 \\ 0 & 0 & 0 & -k(t) & \mu_M(t) \end{pmatrix},$$

where $b_x(t) = a(t)a_x(t)\beta_x(t)$, $c_x(t) = a(t)a_x(t)\delta_x(t)$ ($x = N, F$ or A), and $\Theta = a_N(t)N_S^*(t) + a_F(t)F_S^*(t) + a_A(t)A_S^*(t)$.

Let $Y(t, s)$ be a 5×5 matrix solution of the system:

$$\frac{\partial}{\partial t} Y(t, s) = -V(t)Y(t, s), \quad \text{for any } t \geq s, Y(s, s) = I, \quad (17)$$

where I is a 5×5 identity matrix.

Let C_ω be the ordered Banach space of all ω -periodic function from $\mathbb{R} \rightarrow \mathbb{R}^5$, which is equipped with maximum norm $\|\cdot\|_\infty$ and the positive cone $C_\omega^+ = \{\phi \in C_\omega: \phi(t) \geq 0, \text{ for any } t \in \mathbb{R}\}$. Consider the following linear operator $L: C_\omega \rightarrow C_\omega$ by

$$(L\phi)(t) = \int_0^{+\infty} Y(t, t-a)F(t-a)\phi(t-a)da, \quad (18)$$

for any $t \in \mathbb{R}, \phi \in C_\omega$.

Finally, we can define the spectral radius of L as the basic reproduction number R_0 of (3) as follows:

$$R_0 = r(L). \quad (19)$$

From the abovementioned discussion, we obtain the following results for the local asymptotic stability of the disease-free periodic solution $E_0(t) = (N_S^*(t), 0, 0, F_S^*(t), 0, 0, A_S^*(t), 0, 0, M^*(t), 0, 0)$.

Lemma 2 (see [22], Theorem 2.2). *The following statements are valid:*

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

Thus, the disease-free periodic solution $E_0(t) = (N_S^*(t), 0, 0, F_S^*(t), 0, 0, A_S^*(t), 0, 0, M^*(t), 0, 0)$ of (3) is asymptotically stable if $R_0 < 1$ and unstable if $R_0 > 1$.

Let $W(t, \lambda)$ be the monodromy matrix of the following linear ω -periodic system:

$$\frac{dW(t)}{dt} = \left(-V(t) + \frac{F(t)}{\lambda} \right) W(t), \quad t \in \mathbb{R}, \quad (20)$$

with parameter $\lambda \in (0, \infty)$. Since $F(t)$ is nonnegative and $-V(t)$ is cooperative, it follows that $r(W(\omega, \lambda))$ is continuous and nonincreasing for $\lambda \in (0, \infty)$ and $\lim_{\lambda \rightarrow \infty} r(W(\omega, \lambda)) < 1$. Then, we have the following result, which will be used in our numerical calculation of the basic reproduction number in Section 5.

Lemma 3 (see [22], Theorem 1). *The following statements are valid:*

- (i) If $r(W(\omega, \lambda)) = 1$ has a positive solution λ_0 , then λ_0 is an eigenvalue of L , and hence $R_0 > 0$
- (ii) If $R_0 > 0$, then $\lambda = R_0$ is the unique solution of $r(W(\omega, \lambda)) = 1$
- (iii) $R_0 = 0$ if and only if $r(W(\omega, \lambda)) < 1$ for all $\lambda > 0$.

3. Threshold Dynamics

In this section, we study the global dynamics of system (3) in terms of the basic reproduction number. The following theorem shows that when the disease-induced death rates are equal to zero, and then the disease will be cleared from the populations if $R_0 < 1$.

Theorem 2. Let (A1) hold. If $R_0 < 1$ and $\nu_N(t) = \nu_F(t) = \nu_A(t) = 0$, then the disease-free periodic solution $E_0(t) = (N_S^*(t), 0, 0, F_S^*(t), 0, 0, A_S^*(t), 0, 0, M^*(t), 0, 0)$ is globally asymptotically stable in the sense that for any $u(0) = x^0 \in D(t)$ with $u_{10}(0) + u_{11}(0) + u_{12}(0) > 0$, and the solution $u(t, x^0)$ of system (3) through x^0 at $t = 0$ satisfies

$$\lim_{t \rightarrow \infty} (u(t, x^0) - (N_S^*(t), 0, 0, F_S^*(t), 0, 0, A_S^*(t), 0, 0, M^*(t), 0, 0)) = 0. \quad (21)$$

If $R_0 > 1$, $E_0(t) = (N_S^*(t), 0, 0, F_S^*(t), 0, 0, A_S^*(t), 0, 0, M^*(t), 0, 0)$ is unstable.

Proof. By Lemma 2, we know that $E_0(t)$ is unstable if $R_0 > 1$, and if $R_0 < 1$, then $E_0(t)$ is locally stable. Hence, it is sufficient to show the global attractivity of $E_0(t)$ for $R_0 < 1$.

Let $M_\varepsilon(t) = F_\varepsilon(t) - V(t)$, with

$$F_\varepsilon(t) = \begin{pmatrix} 0 & 0 & 0 & 0 & \frac{b_N(t)(N_S^*(t) + \varepsilon)}{\Theta_\varepsilon} \\ 0 & 0 & 0 & 0 & \frac{b_F(t)(F_S^*(t) + \varepsilon)}{\Theta_\varepsilon} \\ 0 & 0 & 0 & 0 & \frac{b_A(t)(A_S^*(t) + \varepsilon)}{\Theta_\varepsilon} \\ \frac{c_N(t)(M^*(t) + \varepsilon)}{\Theta_\varepsilon} & \frac{c_F(t)(M^*(t) + \varepsilon)}{\Theta_\varepsilon} & \frac{c_A(t)(M^*(t) + \varepsilon)}{\Theta_\varepsilon} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix}, \quad (22)$$

where $\Theta_\varepsilon = a_N(t)(N_S^*(t) - \varepsilon) + a_F(t)(F_S^*(t) - \varepsilon) + a_A(t)(A_S^*(t) - \varepsilon)$. By Lemma 2, if $R_0 < 1$, we have $r(\Phi_{F-V}(\omega)) < 1$, and we can restrict $\varepsilon > 0$ small enough such that $r(\Phi_{M_\varepsilon}(\omega)) < 1$.

Since $\nu_N(t) = \nu_F(t) = \nu_A(t) = 0$, we then get the following equations:

$$\begin{cases} \frac{dN_T(t)}{dt} = b(t) - \sigma_N(t)N_T(t), \\ \frac{dF_T(t)}{dt} = m_N(t)N_T(t) - \sigma_F(t)F_T(t), \\ \frac{dA_T(t)}{dt} = m_F(t)F_T(t) - \mu_A(t)A_T(t). \end{cases} \quad (23)$$

It is easy to see that system (23) has a globally attractive ω -periodic solution $(N_S^*(t), F_S^*(t), A_S^*(t))$, that is, $\lim_{t \rightarrow \infty} (N_T(t) - N_S^*(t)) = 0$, $\lim_{t \rightarrow \infty} (F_T(t) - F_S^*(t)) = 0$, and $\lim_{t \rightarrow \infty} (A_T(t) - A_S^*(t)) = 0$. Therefore, there exists an $\varepsilon > 0$ and a $T_1 > 0$ such that, for any $t \geq T_1$, we have

$$\begin{aligned} N_S^*(t) - \varepsilon &< N_T(t) < N_S^*(t) + \varepsilon, \\ F_S^*(t) - \varepsilon &< F_T(t) < F_S^*(t) + \varepsilon, \\ A_S^*(t) - \varepsilon &< A_T(t) < A_S^*(t) + \varepsilon. \end{aligned} \quad (24)$$

Thus, when $t \geq T_1$, we have

$$\begin{cases} \frac{dN_I(t)}{dt} \leq \frac{b_N(t)(N_S^*(t) + \varepsilon)}{\Theta_\varepsilon} M_I(t) - (\sigma_N(t) + \eta_N(t))N_I(t), \\ \frac{dF_I(t)}{dt} \leq \frac{b_F(t)(F_S^*(t) + \varepsilon)}{\Theta_\varepsilon} M_I(t) + m_N(t)N_I(t) - (\sigma_F(t) + \eta_F(t))F_I(t), \\ \frac{dA_I(t)}{dt} \leq \frac{b_A(t)(A_S^*(t) + \varepsilon)}{\Theta_\varepsilon} M_I(t) + m_F(t)F_I(t) - \sigma_A(t)A_I(t), \\ \frac{dM_L(t)}{dt} \leq (c_N(t)N_I(t) + c_F(t)F_I(t) + c_A(t)A_I(t)) \frac{M^*(t) + \varepsilon}{\Theta_\varepsilon}, \\ \frac{dM_I(t)}{dt} = k(t)M_L(t) - \mu_M(t)M_I(t). \end{cases} \quad (25)$$

By Lemma 1, there exists a positive ω -periodic function $v(t)$ such that $u(t) = e^{pt}v(t)$ is a solution of $u'(t) = M_\varepsilon(t)u(t)$, where $p = 1/\omega \ln(r(\Phi_{M_\varepsilon}(\omega))) < 0$. We see that $u(t) \rightarrow 0$ as $t \rightarrow \infty$. Using the standard comparison principle, we have

$$\lim_{t \rightarrow \infty} (N_I(t), F_I(t), A_I(t), M_L(t), M_I(t)) = (0, 0, 0, 0, 0). \quad (26)$$

It then follows from the theory of asymptotically periodic semiflow (see [23], Theorem 3.2.1) that

$$\begin{aligned} \lim_{t \rightarrow \infty} (N_R(t), F_R(t), A_R(t)) &= (0, 0, 0), \\ \lim_{t \rightarrow \infty} (N_S(t) - N_S^*(t), F_S(t) - F_S^*(t), A_S(t) \\ &\quad - A_S^*(t), M_S(t) - M^*(t)) = (0, 0, 0, 0). \end{aligned} \quad (27)$$

This completes the proof.

The following result shows the uniform persistence of the disease if $R_0 > 1$.

Theorem 3. *Let (A1) hold. If $R_0 > 1$, then system (3) admits at least one positive periodic solution, and there exists a positive constant $\eta > 0$ such that any solution $(N_S(t), N_I(t), N_R(t), F_S(t), F_I(t), F_R(t), A_S(t), A_I(t), A_R(t), M_S(t), M_L(t), M_I(t))$ of (3) in $D(t)$ with $N_I(0) > 0$, $F_I(0) > 0$, $A_I(0) > 0$, $M_L(0) > 0$, and $M_I(0) > 0$ satisfies*

$$\liminf_{t \rightarrow \infty} (N_I(t), F_I(t), A_I(t), M_L(t), M_I(t)) \geq (\eta, \eta, \eta, \eta, \eta). \quad (28)$$

Proof. Define

$$\begin{aligned} X &:= \mathbb{R}_+^{12}, \\ X_0 &:= \{(N_S, N_I, N_R, F_S, F_I, F_R, A_S, A_I, A_R, M_S, M_L, M_I) \\ &\quad \in X: N_I > 0, F_I > 0, A_I > 0, M_L > 0, M_I > 0\}, \\ \partial X_0 &:= X \setminus X_0. \end{aligned} \quad (29)$$

Let P be the Poincaré' map associated with (3), i.e.,

$$P(x_0) = u(\omega, x_0), \quad \text{for } x_0 \in \mathbb{R}_+^{12}, \quad (30)$$

where $u(t, x_0)$ is the unique solution of (3) with $u(0, x_0) = x_0$.

It then suffices to show that (3) is uniformly persistent with respect to $(X_0, \partial X_0)$. Note that both X and X_0 are positively invariant. Further, Theorem 1 means that (3) is

point dissipative. It is apparent that ∂X_0 is relatively closed in X .

Set $x_0 = (N_S^0, N_I^0, N_R^0, F_S^0, F_I^0, F_R^0, A_S^0, A_I^0, A_R^0, M_S^0, M_L^0, M_I^0) \in X_0$. Let $u(t, x_0) = (N_S(t, x_0), N_I(t, x_0), N_R(t, x_0), F_S(t, x_0), F_I(t, x_0), F_R(t, x_0), A_S(t, x_0), A_I(t, x_0), A_R(t, x_0), M_S(t, x_0), M_L(t, x_0), M_I(t, x_0))$ be the solution of (3) through x_0 at $t = 0$. Let $M_1 = (N_{S_0}^*, 0, 0, F_{S_0}^*, 0, 0, A_{S_0}^*, 0, 0, M_{S_0}^*, 0, 0)$, and $M_2 = (N_{S_0}^*, 0, 0, F_{S_0}^*, 0, 0, A_{S_0}^*, 0, 0, 0, 0, 0)$, where $N_{S_0}^*(0) = N_S^*(0)$, $F_{S_0}^*(0) = F_S^*(0)$, $A_{S_0}^*(0) = A_S^*(0)$, and $M_{S_0}^*(0) = M_S^*(0)$.

Since $\lim_{x_0 \rightarrow M_1} (u(t, x_0) - u(t, M_1)) = 0$ uniformly for $t \in [0, \omega]$, then for any $\varepsilon > 0$, there exists $\delta_1 > 0$ such that

$$\|u(t, x_0) - u(t, M_1)\| \leq \varepsilon, \quad \forall t \in [0, \omega], \|x_0 - M_1\| \leq \delta_1. \quad (31)$$

Then, we have the following claim.

Claim 1. $\limsup_{m \rightarrow \infty} d(P^m(x_0), M_1) \geq \delta_1$, for all $x_0 \in X_0$.
If not, then

$$\limsup_{m \rightarrow \infty} d(P^m(x_0), M_1) < \delta_1, \quad (32)$$

for some $x_0 \in X_0$. Without loss of generality, we can assume that

$$d(P^m(x_0), M_1) < \delta_1, \quad (33)$$

for all $m > 0$. Then, we know that

$$\|u(t, P^m(x_0)) - u(t, M_1)\| \leq \varepsilon, \quad \forall t \in [0, \omega], \quad \text{for any } m > 0. \quad (34)$$

For any $t \geq 0$, let $t = m\omega + t_1$, where $t_1 \in [0, \omega)$ and $m = [t/\omega]$, which is the greatest integer less than or equal to t/ω . Then, we have

$$\|u(t, x_0) - u(t, M_1)\| = \|u(t_1, P^m(x_0)) - u(t_1, M_1)\| \leq \varepsilon, \quad \forall t \geq 0. \quad (35)$$

It follows that $N_S^*(t) - \varepsilon \leq N_S(t) \leq N_S^*(t) + \varepsilon$, $0 < N_I(t) \leq \varepsilon$, $0 \leq N_R(t) \leq \varepsilon$, $F_S^*(t) - \varepsilon \leq F_S(t) \leq F_S^*(t) + \varepsilon$, $0 < F_I(t) \leq \varepsilon$, $0 \leq F_R(t) \leq \varepsilon$, $A_S^*(t) - \varepsilon \leq A_S(t) \leq A_S^*(t) + \varepsilon$, $0 < A_I(t) \leq \varepsilon$, $0 \leq A_R(t) \leq \varepsilon$, and $M^*(t) - \varepsilon \leq M_S(t) \leq M^*(t) + \varepsilon$, $0 < M_L(t) \leq \varepsilon$, $0 < M_I(t) \leq \varepsilon$, and this, together with (3), implies

$$J'(t) \geq (A_\varepsilon(t) - V(t))J(t), \quad (36)$$

where $J(t) = (N_I(t), F_I(t), A_I(t), M_L(t), M_I(t))^T$ and

$$A_\varepsilon(t) = \begin{pmatrix} 0 & 0 & 0 & 0 & \frac{b_N(t)(N_S^*(t) - \varepsilon)}{\Delta_\varepsilon} \\ 0 & 0 & 0 & 0 & \frac{b_F(t)(F_S^*(t) - \varepsilon)}{\Delta_\varepsilon} \\ 0 & 0 & 0 & 0 & \frac{b_A(t)(A_S^*(t) - \varepsilon)}{\Delta_\varepsilon} \\ \frac{c_N(t)(M^*(t) - \varepsilon)}{\Delta_\varepsilon} & \frac{c_F(t)(M^*(t) - \varepsilon)}{\Delta_\varepsilon} & \frac{c_A(t)(M^*(t) - \varepsilon)}{\Delta_\varepsilon} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix}, \quad (37)$$

where $\Delta_\varepsilon = a_N(t)(N_S^*(t) + 3\varepsilon) + a_F(t)(F_S^*(t) + 3\varepsilon) + a_A(t)(A_S^*(t) + 3\varepsilon)$. By Lemma 2, we know that $r(\Phi_{F-V}(\omega)) > 1$, then we can choose $\varepsilon > 0$ small enough, such that $r(\Phi_{A_\varepsilon-V}(\omega)) > 1$. Again by Lemma 1 and the standard comparison principle, there exists a positive ω -periodic function $\tilde{v}(t)$ such that $J(t) \geq e^{\mu t} \tilde{v}(t)$, where $\mu = 1/\omega \ln r(\Phi_{A_\varepsilon-V}(\omega)) > 0$, which implies that $N_I(t) \rightarrow \infty, F_I(t) \rightarrow \infty, A_I(t) \rightarrow \infty, M_L(t) \rightarrow \infty, M_I(t) \rightarrow \infty$, which leads to a contradiction.

Since $M^*(t)$ is a positive periodic solution, we can choose a small positive number δ_2 such that

$$3\delta_2 < \inf_{t \geq 0} M^*(t). \quad (38)$$

Since $\lim_{x_0 \rightarrow M_2} (u(t, x_0) - M_2) = 0$ uniformly for $t \in [0, \omega]$, there exists $\eta_1 > 0$ such that

$$\|u(t, x_0) - M_2\| \leq \delta_2, \quad \text{for all } t \in [0, \omega], \|x_0 - M_2\| \leq \eta_1. \quad (39)$$

Claim 2. $\limsup_{n \rightarrow \infty} d(P^n(x_0), M_2) \geq \eta_1$, for all $x_0 \in X_0$.

Suppose, by contradiction, that $\limsup_{n \rightarrow \infty} d(P^n(x_0), M_2) < \eta_1$, for some $x_0 \in X_0$, without loss of generality, we can assume that

$$d(P^n(x_0), M_2) < \eta_1, \quad \text{for all } n > 0. \quad (40)$$

For any $t \geq 0$, let $t = n\omega + t_2$, where $t_2 \in [0, \omega]$ and $n = [t/\omega]$. Then, we have

$$\|u(t, x_0) - M_2\| = \|u(t_2, P^n(x_0)) - M_2\| \leq \delta_2, \quad \forall t \geq 0. \quad (41)$$

Hence, $M_S(t) \leq \delta_2, M_L(t) \leq \delta_2, M_I(t) \leq \delta_2$, and $M(t) \leq 3\delta_2$ when $t \geq 0$. Since $M(0) = M_S(0) + M_L(0) + M_I(0) > 0$, we have $\lim_{t \rightarrow \infty} (M(t) - M^*(t)) = 0$, a contradiction.

Then, we define

$$\begin{aligned} M_\partial &:= \{(\tilde{N}_S, \tilde{N}_I, \tilde{N}_R, \tilde{F}_S, \tilde{F}_I, \tilde{F}_R, \tilde{A}_S, \tilde{A}_I, \tilde{A}_R, \tilde{M}_S, \tilde{M}_L, \tilde{M}_I) \\ &\in \partial X_0: P^m(\tilde{N}_S, \tilde{N}_I, \tilde{N}_R, \tilde{F}_S, \tilde{F}_I, \tilde{F}_R, \tilde{A}_S, \tilde{A}_I, \tilde{A}_R, \tilde{M}_S, \\ &\tilde{M}_L, \tilde{M}_I) \in \partial X_0, \forall m \geq 0\}, \\ D_1 &:= \{u \in X: u_i(0, x_0) = 0, \quad \forall i \in \{2, 5, 8, 11, 12\}\}, \\ D_2 &:= \{u \in X: u_i(0, x_0) = 0, \quad \forall i = 10, 11, 12\}. \end{aligned} \quad (42)$$

We claim that $M_\partial = D_1 \cup D_2$. We first prove that $M_\partial \subset D_1 \cup D_2$. For any $u(t, x_0) \in D_2$, it is easy to see that $u_i(t, x_0) = 0, i = 10, 11, 12$. Hence, $D_2 \subset M_\partial$. For any $u(t, x_0) \in D_1$, we can define $\tilde{V}(t) \geq 0$ such that $\tilde{V}_i(t) \equiv 0$ for all $t \geq 0$ and $i = 2, 5, 8, 11, 12$. Let $\tilde{V}_i(t)$ ($i = 1, 3, 4, 6, 7, 9, 10$) satisfy the following equations:

$$\begin{cases} \frac{d\tilde{V}_1(t)}{dt} = b(t) - \sigma_N(t)\tilde{V}_1(t), \\ \frac{d\tilde{V}_3(t)}{dt} = -\sigma_N(t)\tilde{V}_3(t), \\ \frac{d\tilde{V}_4(t)}{dt} = m_N(t)\tilde{V}_1(t) - \sigma_F(t)\tilde{V}_4(t), \\ \frac{d\tilde{V}_6(t)}{dt} = m_N(t)\tilde{V}_3(t) - \sigma_F(t)\tilde{V}_6(t), \\ \frac{d\tilde{V}_7(t)}{dt} = m_F(t)\tilde{V}_4(t) - \mu_A(t)\tilde{V}_7(t), \\ \frac{d\tilde{V}_9(t)}{dt} = m_F(t)\tilde{V}_6(t) - \mu_A(t)\tilde{V}_9(t), \\ \frac{d\tilde{V}_{10}(t)}{dt} = r(t)\tilde{V}_{10}(t) \left(1 - \frac{\tilde{V}_{10}(t)}{K(t)}\right) - \mu_M(t)\tilde{V}_{10}(t), \end{cases} \quad (43)$$

with $\tilde{V}_i(0) = u_i(0, x_0)$, $i = 1, 3, 4, 6, 7, 9, 10$. Then, $\tilde{V}(t)$ is a solution of (3) through x_0 . By the uniqueness of the solution, we have $u(t, x_0) = \tilde{V}(t)$ for all $t \geq 0$, and hence $D_1 \subset M_\partial$. To prove the claim, it then suffices to show that $M_\partial \subset D_1 \cup D_2$. For any $u(t, x_0) \in \partial X_0 \setminus (D_1 \cup D_2)$, we have $\sum_{i=10}^{12} u_i(0, x_0) > 0$, and hence $\lim_{t \rightarrow \infty} |\sum_{i=10}^{12} u_i(t, x_0) - M^*(t)| = 0$. From the first, fourth, seventh, and tenth of (3), we have $u_1(t, x_0) > 0$, $u_4(t, x_0) > 0$, $u_7(t, x_0) > 0$, and $u_{10}(t, x_0) > 0$ for all $t > 0$. If $u_2(0, x_0) > 0$, by (3), we get $u_j(t, x_0) > 0$ for all $t > 0$ and $j \in \{2, 3, 5, 6, 8, 9, 11, 12\}$. If $u_5(0, x_0) > 0$, by the fifth and sixth equations of (3), we have $u_5(t, x_0) > 0$ and $u_6(t, x_0) > 0$ for all $t > 0$. Then, by the eighth and ninth equation of (3), we have $u_8(t, x_0) > 0$ and $u_9(t, x_0) > 0$ for all $t > 0$. Then, we have $u_{11}(t, x_0) > 0$ and $u_{12}(t, x_0) > 0$ and $u_2(t, x_0) > 0$ and $u_3(t, x_0) > 0$ for all $t > 0$. For the case $u_8(0, x_0) > 0$ or $u_{11}(0, x_0) > 0$ or $u_{12}(0, x_0) > 0$, we can similarly prove that $u_i(t, x_0) > 0$ for $i \in \{1, 2, \dots, 12\}$. Therefore, we have $u(t, x_0) \in X_0$ for all $t > 0$. This implies that for any $x_0 \in \partial X_0 \setminus (D_1 \cup D_2)$, we have $P(u(t, x_0)) \notin \partial X_0$ for all $t > 0$, and hence $M_\partial \subset D_1 \cup D_2$. It then follows that M_1 and M_2 are disjoint, compact, and isolated invariant sets for P in M_∂ , and $\cup_{u \in M_j} \omega(u) = \{M_1, M_2\}$. Furthermore, no subset of M_1 and M_2 forms a cycle in M_∂ (and hence in ∂X_0). In view of the two claims above, we see that M_1 and M_2 are isolated invariant sets for P in X , and $W^s(M_i) \cap X_0 = \emptyset$ for all $i = 1, 2$, where $W^s(M_i)$ is the stable set of M_i for P .

Applying the acyclicity theory on uniform persistence for maps (see [23], Theorem 1.3.1 and Remark 1.3.1), we see that $P: X \rightarrow X$ is uniformly persistent with respect to $(X_0, \partial X_0)$. It follows from [23], Theorem 3.1.1, that the solution of (3) is uniformly persistent.

Furthermore, by [23], Theorem 1.3.6, P has a fixed point $(\overline{N}_S(0), \overline{N}_I(0), \overline{N}_R(0), \overline{F}_S(0), \overline{F}_I(0), \overline{F}_R(0), \overline{A}_S(0), \overline{A}_I(0), \overline{A}_R(0), \overline{M}_S(0), \overline{M}_L(0), \overline{M}_I(0)) \in X_0$. Then, we see that $\overline{N}_S(0), \overline{N}_R(0), \overline{F}_S(0), \overline{F}_R(0), \overline{A}_S(0), \overline{A}_R(0), \overline{M}_S(0)$ are all nonnegative, and $\overline{N}_I(0), \overline{F}_I(0), \overline{A}_I(0), \overline{M}_L(0)$, and $\overline{M}_I(0)$ are all positive. We further prove that $\overline{N}_S(0), \overline{N}_R(0), \overline{F}_S(0), \overline{F}_R(0), \overline{A}_S(0), \overline{A}_R(0)$, and $\overline{M}_S(0)$ are all positive. Suppose not, if $\overline{N}_S(0) = 0$, then from the first equation of (3), we obtain

$$\frac{d\overline{N}(t)}{dt} = b(t) - a_1(t)\overline{N}(t), \quad (44)$$

with $\overline{N}_S(0) = \overline{N}_S(n\omega) = 0$, $n = 1, 2, 3, \dots$, where $a_1(t) = b_N(t) \overline{M}_I(t) / a_N(t) \overline{N}_T(t) + a_F(t) \overline{F}_T(t) + a_A(t) \overline{A}_T(t) + \sigma_N(t)$. Then, we obtain

$$\overline{N}_S(t) = \left[\overline{N}_S(0) + \int_0^t b(\rho) e^{\int_0^\rho a_1(s) ds} d\rho \right] e^{-\int_0^t a_1(s) ds}, \quad (45)$$

a contradiction. Thus $\overline{N}_S(0) > 0$. Similarly, we can prove that $\overline{N}_R(0) > 0$, $\overline{F}_S(0) > 0$, $\overline{F}_R(0) > 0$, $\overline{A}_S(0) > 0$, $\overline{A}_R(0) > 0$, and $\overline{M}_S(0) > 0$. Thus, $u(t, (\overline{N}_S(0), \overline{N}_I(0), \overline{N}_R(0), \overline{F}_S(0), \overline{F}_I(0), \overline{F}_R(0), \overline{A}_S(0), \overline{A}_I(0), \overline{A}_R(0), \overline{M}_S(0), \overline{M}_L(0), \overline{M}_I(0))) \in \text{Int}(\mathbb{R}_+^{12})$ and $(\overline{N}_S(t), \overline{N}_I(t), \overline{N}_R(t), \overline{F}_S(t), \overline{F}_I(t), \overline{F}_R(t), \overline{A}_S(t), \overline{A}_I(t), \overline{A}_R(t), \overline{M}_S(t), \overline{M}_L(t), \overline{M}_I(t))$ is a positive

ω -periodic solution of (3) due to the definition of semiflow P . Hence, the proof is complete.

4. Autonomous Case of System (3)

In this section, we study the corresponding autonomous system of system (3), that is, all the coefficients of system (3) are constants, and also we assume that the disease-induced death rates of infected birds are zero. Based on the references and also mathematical tractability, we also make the following assumptions: $a_N = a_F = a_A := \tilde{a}$, $\beta_N = \beta_F = \beta_A := \beta$ [4, 24, 25] $\delta_N = \delta_F = \delta_A := \delta$, $m_N = m_F := m$, $\gamma_N = \gamma_F = \gamma_A := \gamma$, and $\mu_N = \mu_F = \mu_A := \mu$. In this case, system (3) becomes

$$\left\{ \begin{aligned} \frac{dN_S(t)}{dt} &= b - \lambda_1(t) - (m + \mu)N_S(t), \\ \frac{dN_I(t)}{dt} &= \lambda_1(t) - (m + \mu + \gamma)N_I(t), \\ \frac{dN_R(t)}{dt} &= \gamma N_I(t) - (m + \mu)N_R(t), \\ \frac{dF_S(t)}{dt} &= mN_S(t) - \lambda_2(t) - (m + \mu)F_S(t), \\ \frac{dF_I(t)}{dt} &= \lambda_2(t) + mN_I(t) - (m + \mu + \gamma)F_I(t), \\ \frac{dF_R(t)}{dt} &= \gamma F_I(t) + mN_R(t) - (m + \mu)F_R(t), \\ \frac{dA_S(t)}{dt} &= mF_S(t) - \lambda_3(t) - \mu A_S(t), \\ \frac{dA_I(t)}{dt} &= \lambda_3(t) + mF_I(t) - (\mu + \gamma)A_I(t), \\ \frac{dA_R(t)}{dt} &= \gamma A_I(t) + mF_R - \mu A_R(t), \\ \frac{dM_S(t)}{dt} &= rM(t) \left(1 - \frac{M(t)}{K} \right) - \lambda_4(t) - \mu_M M_S(t), \\ \frac{dM_L(t)}{dt} &= \lambda_4(t) - kM_L(t) - \mu_M M_L(t), \\ \frac{dM_I(t)}{dt} &= kM_L(t) - \mu_M M_I(t), \end{aligned} \right. \quad (46)$$

with $\lambda_1(t) = (a\beta M_I(t)N_S(t))/(N_T(t) + F_T(t) + A_T(t))$, $\lambda_2(t) = a\beta M_I(t)F_S(t)/(N_T(t) + F_T(t) + A_T(t))$, $\lambda_3(t) = a\beta M_I(t)A_S(t)/(N_T(t) + F_T(t) + A_T(t))$, $\lambda_4(t) = (a\delta(N_I(t) + F_I(t) + A_I(t))M_S(t))/(N_T(t) + F_T(t) + A_T(t))$.

It is easy to show that

$$\Omega = \left\{ (N_S, N_I, N_R, F_S, F_I, F_R, A_S, A_I, A_R, M_S, M_I, M_R) \right. \\ \left. \in \mathbb{R}_+^{12} \mid 0 < N_T + F_T + A_T \leq \frac{b}{\mu}, M_S + M_L + M_I \leq K \right\}, \quad (47)$$

is the positive invariant set for system (46).

Corresponding to (A1), we also need the following assumption:

$$(A2) r > \mu_M. \quad (48)$$

It is clear that system (46) always has two equilibria $P_0 = (N_T^*, 0, 0, F_T^*, 0, 0, A_T^*, 0, 0, 0, 0, 0)$ and $P_1 = (N_T^*, 0, 0, F_T^*, 0, 0, A_T^*, 0, 0, M^*, 0, 0)$, where $N_T^* = b/(m + \mu)$, $F_T^* = bm/(m + \mu)^2$, $A_T^* = bm^2/(\mu(m + \mu)^2)$, and $M^* = (K(r - \mu_M))/r$.

In order to find any endemic equilibrium of system (46), we introduce the basic reproduction number R_0 . According to the concepts of the next generation matrix and reproduction number presented in [26, 27], R_0 is given by the following expression:

$$R_0 = \frac{ka^2\beta\mu\delta K(r - \mu_M)}{rb\mu_M(k + \mu_M)(\mu + \gamma)}. \quad (49)$$

Let the right-hand sides be zero, then system (46) admits another equilibrium: $P^* = (N_S^*, N_I^*, N_R^*, F_S^*, F_I^*, F_R^*, A_S^*, A_I^*, A_R^*, M_S^*, M_I^*, M_R^*)$, where

$$\begin{aligned} N_S^* &= \frac{b^2}{a\beta\mu M_I^* + b(m + \mu)}, \\ N_I^* &= \frac{ab\beta\mu M_I^*}{(a\beta\mu M_I^* + b(m + \mu))(m + \mu + \gamma)}, \\ N_R^* &= \frac{\gamma N_I^*}{m + \mu}, \\ F_S^* &= \frac{mbN_S^*}{a\beta\mu M_I^* + b(m + \mu)}, \\ F_I^* &= \frac{a\beta\mu M_I^* F_S^* + bmN_I^*}{b(m + \mu + \gamma)}, \\ F_R^* &= \frac{\gamma F_I^* + mN_R^*}{m + \mu}, \\ A_S^* &= \frac{mbF_S^*}{\mu(a\beta\mu M_I^* + b)}, \\ A_I^* &= \frac{a\beta\mu M_I^* A_S^* + bmF_I^*}{b(\mu + \gamma)}, \\ A_R^* &= \frac{\gamma A_I^* + mF_R^*}{\mu}, \\ M_S^* &= \frac{\mu_M K(r - \mu_M)}{r(a\delta + \mu_M)}, \\ M_R^* &= \frac{\mu_M M_I^*}{k}, \end{aligned} \quad (50)$$

and M_I^* satisfies equation $f_1(M_I^*) = f_2(M_I^*)$, where

$$\begin{aligned} f_1(M_I^*) &= \frac{bm}{a\beta\mu M_I^* + b(m + \mu)} \\ &+ \frac{b^2 m^2}{[a\beta\mu M_I^* + b(m + \mu)](a\beta\mu M_I^* + b\mu)} + 1, \\ f_2(M_I^*) &= \frac{\mu_M(k + \mu_M)(\mu + \gamma)[a\beta\mu M_I^* + b(m + \mu)]}{\beta\delta a^2 \mu^2 (kM^* - (k + \mu_M)M_I^*)}. \end{aligned} \quad (51)$$

Note that $f_1(0) = (m + \mu)/\mu$, $f_1(x)$ is decreasing with respect to $x > 0$ and $\lim_{x \rightarrow +\infty} f_1(x) = 1$. Also, $f_2(0) = (\mu_M(k + \mu_M)(\mu + \gamma)b(m + \mu))/k\beta\delta a^2 \mu^2 M^*$ and $f_2'(x) = (\mu_M(k + \mu_M)(\mu + \gamma)[a\beta\mu k M^* + b(m + \mu)(k + \mu_M)])/(\beta\delta a^2 \mu^2 (kM^* - (k + \mu_M)x)^2) > 0$ for $M_I^* \in (0, kM^*/(k + \mu_M))$, and $\lim_{x \rightarrow (kM^*/(k + \mu_M))} f_2(x) = +\infty$. Then, $f_1(x) = f_2(x)$ has a unique positive root in $(0, kM^*/(k + \mu_M))$, if and only if $f_1(0) > f_2(0)$, which is equivalent to $R_0 > 1$. Therefore, if $R_0 > 1$, system (46) has a unique endemic equilibrium P^* .

It is easy to show that P_0 is a saddle and is unstable. By Theorem 2, we know that P_1 is globally asymptotically stable in $\Omega \setminus \{P_0\}$ if $R_0 < 1$ and is unstable for $R_0 > 1$. Also, by Theorem 3, if $R_0 > 1$, there exists a positive constant $\eta_1 > 0$ such that any solution $(N_S(t), N_I(t), N_R(t), F_S(t), F_I(t), F_R(t), M_S(t), M_L(t), M_I(t))$ of (46) with $N_I(0) > 0$, $F_I(0) > 0$, $A_I(0) > 0$, $M_L(0) > 0$, and $M_I(0) > 0$ satisfies

$$\liminf_{t \rightarrow \infty} (N_I(t), F_I(t), A_I(t), M_L(t), M_I(t)) \geq (\eta_1, \eta_1, \eta_1, \eta_1, \eta_1). \quad (52)$$

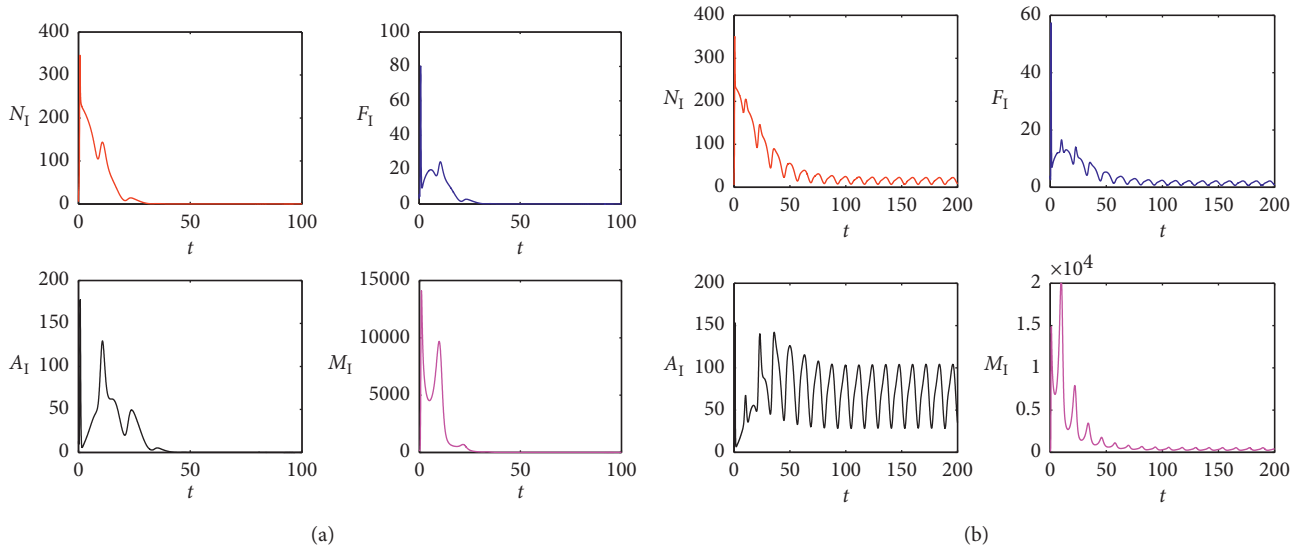
5. Numerical Simulations

In this section, we will perform some numerical simulations to illustrate the results of previous sections and explore the effects of some parameters on the WNV transmission. First from [18], we can determine some realistically feasible constant parameters. We assume that the disease-induced death rates of nestling, fledgling, and adult are zero. The time unit is taken as month. Baseline parameters are listed in Table 2.

5.1. Long Term Behavior. We take $a(t) = 30.4(0.133 + 0.1 \sin \pi t/6)$, $r(t) = 30.4(0.537 + 0.5 \sin \pi t/6)$, $\mu_M(t) = 30.4(0.096 + 0.09 \sin \pi t/6)$, $b = 3040$, $K = 5 \times 10^5$, $a_N = 5$, and $a_F = a_A = 1$, which are chosen or adapted from Robertson and Caillouët [18]. Using Lemma 3, we can numerically compute the basic reproduction number R_0 . With this set of parameters, we have $R_0 = 0.8644 < 1$, and the infection is extinct in host and mosquito populations. If the nestling exposure coefficient increases to $a_N = 10$, then $R_0 = 1.0832 > 1$, and then the infection is persistent in host and mosquito populations. Figure 1 shows the long-term behavior of the infectious birds and mosquitoes when $R_0 < 1$

TABLE 2: Parameters of model (3) and their interpretations.

| Parameter | Value | Reference |
|--------------------------------|----------------------|-----------|
| b | Varies | |
| a_N, a_F, a_A | Varies | |
| K | Varies | |
| $1/k$ | 0.106×30.4 | [5] |
| m_N, m_F | $30.4/14$ | [24] |
| $\gamma_N, \gamma_F, \gamma_A$ | $30.4/3$ | [4] |
| μ_N, μ_F, μ_A | 0.0014×30.4 | [25] |
| $\beta_N, \beta_F, \beta_A$ | 1 | [4] |
| $\delta_N, \delta_F, \delta_A$ | 0.36 | [4] |

FIGURE 1: Long-term behavior of the infectious host and vector populations. (a) $R_0 < 1$ and (b) $R_0 > 1$.

and $R_0 > 1$. These simulations are consistent with our theoretical results in Section 3.

5.2. Sensitivity Analysis of R_0 . In order to provide some effective control measures about mosquitoes, in this section, we will perform some sensitivity analyses of the basic reproduction number R_0 in terms of some coefficients in our model (3).

We first discuss four important factors to control the disease: the mosquito carrying capacity K ; the biting rate of mosquitoes on birds $a(t)$; the death rate of mosquitoes $\mu_M(t)$; and the recruitment rate of mosquitoes $r(t)$. Obviously the biting rate of mosquitoes on birds can be reduced if the population size of mosquitoes decreases. Let $\underline{a}_N = \underline{a}_F = \underline{a}_A = 1$, by replacing $a(t)$, $\mu_M(t)$, and $r(t)$ with $\underline{a}(t) = (1 - c)a(t)$, $\underline{\mu}_M(t) = l\mu_M(t)$, and $\underline{r}(t) = (1 - f)r(t)$, respectively, and keeping the other parameter values the same as those in Figure 1. Figure 2 reflects the relationship between R_0 and these parameters. Our numerical analysis shows that R_0 is a decreasing function of c, l , and f and an increasing function of K ; to reduce the basic reproduction number below 1, we should at least decrease the recruitment rate of mosquitoes by 32% or increase the death rate of mosquitoes by 50% from the current level.

Figure 2(b) shows that we should keep $c > 0.273$ to control WNV transmission. Hence, we may take some vector control measures to control WNV, such as using products to kill mosquito larvae and adult mosquitoes, and we can also reduce mosquito breeding sites by eliminating standing pools of water, such as in old tires, buckets, gutters, and swimming pools.

Secondly, we explore the effect of host stage exposure heterogeneity. We take parameter values as those in Figure 1. Figure 3 shows that the larger the exposure coefficients, the larger the basic reproduction number R_0 becomes. Moreover, this figure shows that juvenile (nestling or fledgling) exposure has a larger impact on the WNV transmission than that of the adult.

Thirdly, Figure 4 compares R_0 of the periodic system and the autonomous system. For the periodic system, the parameters are the same as those in Figure 2(b); for the autonomous system, the parameters are the average values of those in the periodic system. We can see that the basic reproduction number of the autonomous one is always less than that of the periodic one when c varies ranging from 0 to 1. This implies that, without seasonality, the risk of infection will be underestimated. Therefore, considering the influence of temperature, we should make more efforts to control the spread of WNV.

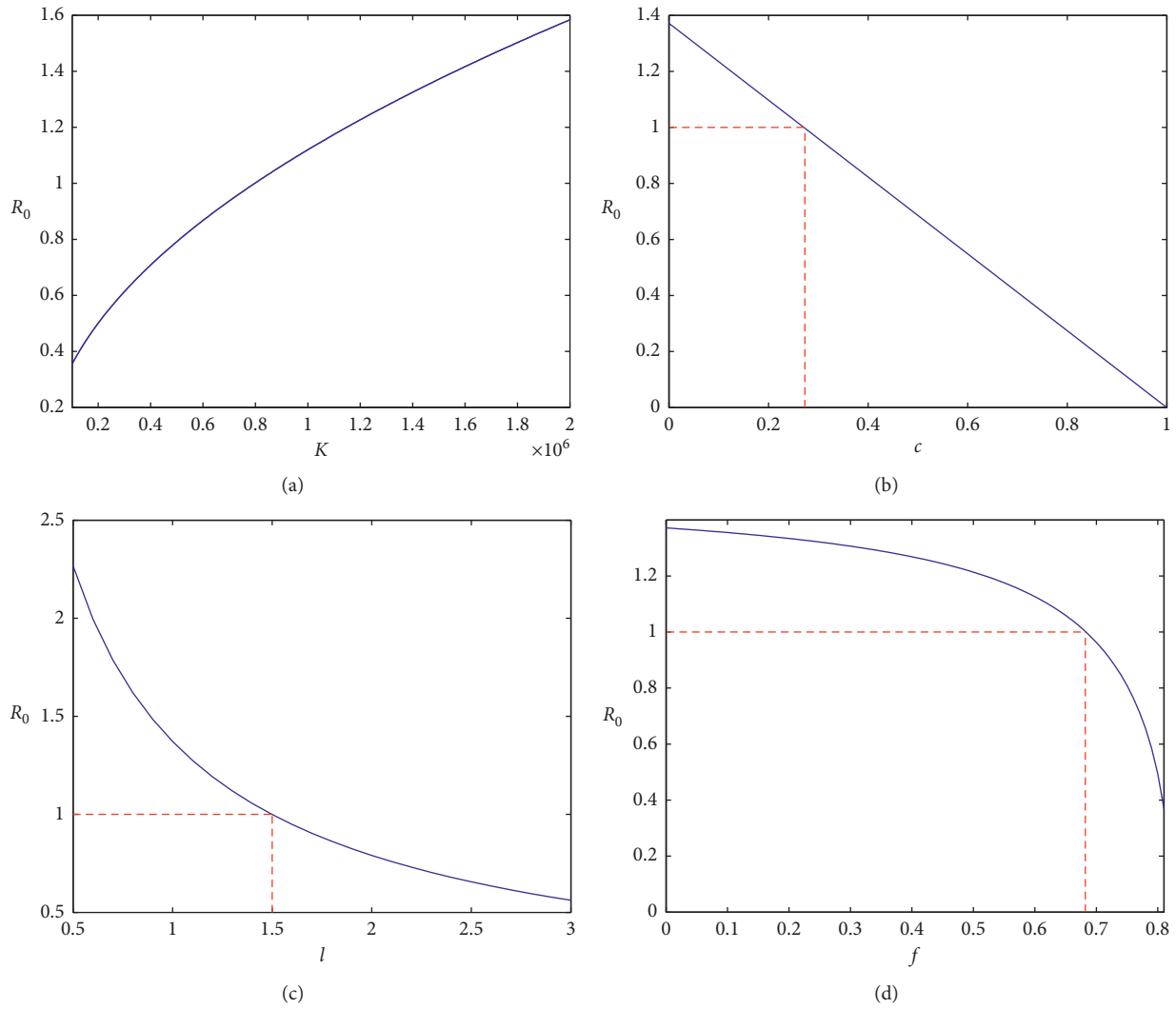


FIGURE 2: R_0 vs K , c , l , and f . (a) Relationship between R_0 and K . (b) Relationship between R_0 and c . (c) Relationship between R_0 and l . (d) Relationship between R_0 and f . In (b, c, and d), we fix $K = 1.5 \times 10^6$.

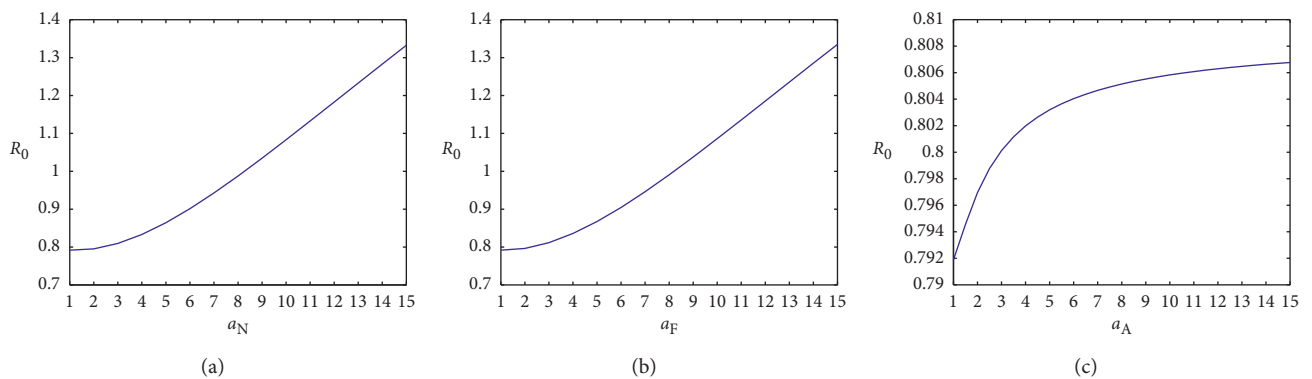


FIGURE 3: Effect of host stage exposure on the basic reproduction number R_0 .

6. Discussion

In this paper, we have analyzed a mathematical WNV model, which was presented in Robertson and Caillouët [18]. The

model incorporates the stage structure of avian, host stage exposure heterogeneity, and the seasonal climate effects on WNV transmission. We have obtained the basic reproduction number and showed that the disease-free periodic

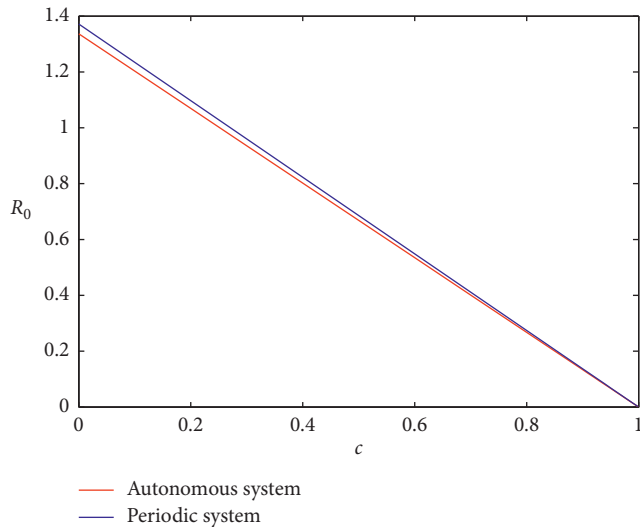


FIGURE 4: The curves of the basic reproduction numbers versus c .

state is globally asymptotically stable if the disease-induced death rates are zero and $R_0 < 1$, and the disease will persist if $R_0 > 1$. For the corresponding autonomous system, for a special case, we establish a threshold result in terms of the basic reproduction number R_0 .

The numerical simulations about the long-term behavior of the model solutions are consistent with the obtained analytic result. In order to seek for effective control measures to prevent outbreaks of WNV, we performed sensitive analysis of the basic reproduction number in terms of the mosquito carrying capacity, the recruitment rate of mosquitoes, the death rate of mosquitoes, and the biting rate of mosquitoes on birds. It is clear that if the mosquito population size decreases, then the biting rate of mosquitoes on birds can be reduced. Hence, the key to control the spread of WNV is to increase the death rate and decrease the recruitment rate of mosquitoes. To do this, we can reduce mosquito breeding sites, kill adult mosquitoes by adulticides, and kill mosquito larvae by larvicides. Furthermore, we compare the effect of host stage exposure heterogeneity, and Figure 3 shows that increased exposure of all stages increases transmission. Moreover, this figure shows that the juvenile stage exposure has a larger impact on WNV transmission than that of the adult stage. Our numerical simulations also show that the risk of the disease will be underestimated if we do not consider the seasonality. Thus, it is necessary to include the seasonality and stage-dependent host differences in mosquito exposure in the models.

Data Availability

All data generated or analyzed during this study are included in this article.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (11801431 and 11801432), Natural Science Basic Research Plan in Shaanxi Province of China (2018JM1011), Fundamental Research Funds for the Central Universities (300102129202), and China Scholarship Council.

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