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Threshold and stability results in a periodic model for malaria transmission with partial immunity in humans

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ABSTRACT

We develop a periodic compartmental population model for the spread of malaria, dividing the human population into two classes: non-immune and semi-immune. The effect of seasonal changes in weather on the malaria transmission is considered by applying a non-autonomous model where mosquito birth, death and biting rates are time-dependent. We show that the global dynamics of the system is determined by the basic reproduction number, which we define as the spectral radius of a linear integral operator. For values of the basic reproduction number less than unity, the disease-free periodic solution is globally asymptotically stable, while if $\mathcal{R}_0 > 1$, then the disease remains endemic in the population. We show simulations in accordance with the analytic results. Finally, we show that the time-average reproduction rate gives an underestimation for malaria transmission risk.

1. Introduction

Malaria is an acute febrile illness caused by *Plasmodium* microorganisms spread to humans by female *Anopheles* mosquitoes. Out of the five *Plasmodium* species, most of the lethal malaria cases can be attributed to *P. falciparum*. The latest malaria report of WHO from December 2019 estimated around 230 million malaria cases and more than 400,000 deaths in both of the preceding two years [1].

Fig. 1 shows the malaria transmission cycle.

In a person without immunity, symptoms usually appear ten to fifteen days after infection. The symptoms of the disease, including fever, headache, and chills are often mild, making malaria difficult to recognize at early stages. *P. falciparum* malaria can develop to a serious, often lethal illness if not treated within one day. Children suffering from severe malaria often show severe anemia, respiratory distress or cerebral malaria [1,2], while multi-organ failure is frequent in infected adults. In regions where the disease is endemic, several years of exposure may contribute to a partial immunity, making asymptomatic infections are possible. Partial immunity does not provide a complete protection, though it reduces the risk of a severe disease due to malaria infection. Hence, most malaria-related death cases in Africa affect young children, while in regions

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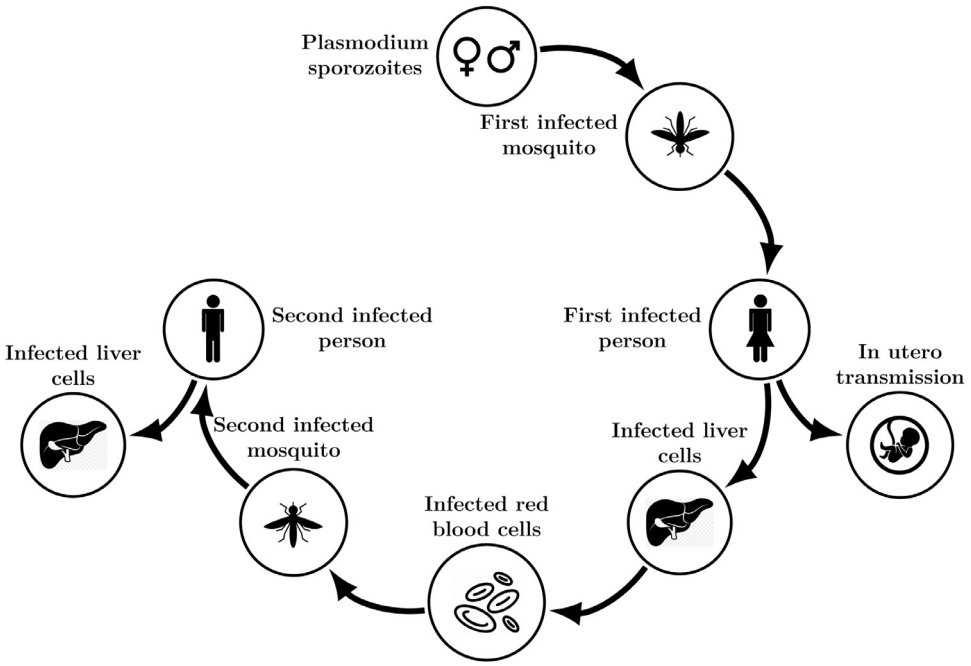


Fig. 1. Malaria transmission cycle.

with lower transmission and immunity, every age group has an equal threat. It is important to note that heterozygotes for the sickle gene (AS) also have a partial protection against malaria [3].

Several sophisticated mathematical models of malaria transmission have been previously established, the first one by Ronald Ross [4], later extended by Macdonald [5]. Ducrot et al. [6] presented a deterministic model for malaria transmission in which the population of humans is divided into two host types: non-immunes who are especially vulnerable to malaria and semi-immunes who are less vulnerable because of an earlier malaria infection providing partial immunity. Further works also (see e.g. [7,8]) study the transmission of malaria with the human population divided into two types of hosts.

Periodicity of weather and climate change are very important factors in the life cycle of the parasites and the mosquitoes transmitting them. Hence, it is of crucial importance to understand how changes in weather affect the spread of malaria [9]. Mordecai et al. [10] formulated a nonlinear thermal-response model to explain the role of temperature changes in the spread of malaria. Other works [7,11–19] have discussed the impacts of weather on mosquito populations and malaria transmission.

In the case of a disease like malaria, which depends on the abundance of mosquitoes, which, in turn, is highly dependent on the periodically changing weather, it is especially important to include this seasonality in our models.

For periodic epidemic compartmental models, Bacäer and Guernaoui [20] provided a definition of the basic reproduction number as the spectral radius of an integral operator acting on the space of continuous periodic functions. Later, Wang and Zhao [21] characterized the basic reproduction number for such models and proved that it serves as a threshold parameter regarding the local stability properties of the disease-free periodic solution. Rebelo et al. [22] studied persistence in epidemiological models in a seasonal environment. Bacaër and Ait Dads [23] gave a more biological explanation of the reproduction number for compartmental epidemic models with periodic parameters. Several papers [7,9,24–28] study the spread of malaria transmission with periodically changing mosquito birth, death and biting rates.

In our present work, motivated by [6,7] we set up and study a compartmental population model for malaria transmission in a periodically changing environment: we extend the model given in [6] by including periodicity of the environment. Unlike [7], we consider periodic vital dynamics of mosquitoes by setting the mosquito birth rates and mosquito death rates as well as the biting rates to be periodic with one year as period, following the annual change of weather. We note, however, that the model given in [7] included a compartment for immature mosquitoes, which we do not consider. The total human population is divided into two major categories: non-immune and semi-immune. We determine the basic reproduction number $\mathcal{R}_0$ to characterize the dynamics of our model, and we show the global stability of the disease-free periodic solution or the endemicity of malaria as well as the existence of a positive ω-periodic solution, depending on the basic reproduction number. We show numerical simulations to illustrate and support the analytical results.

2. Mathematical model

In our model, human population is divided into two types based on their immunity level: the non-immune, i.e. those who have not developed any immunity against malaria, and the semi-immune, that is those who have some partial im-

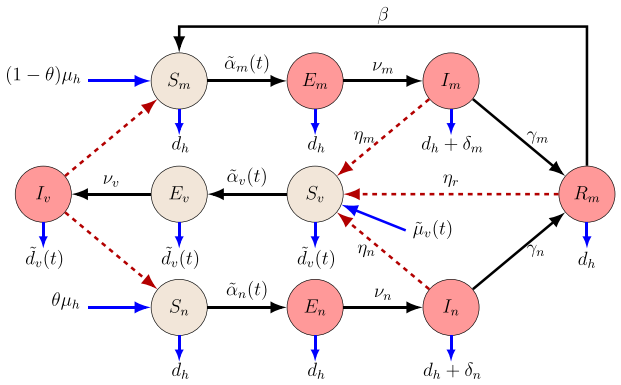


Fig. 2. Flow diagram of model (1). Red nodes are infectious and brown nodes are non-infectious. Black solid arrows show the progression of infection, while red dashed arrows show direction of transmission between humans and mosquitoes. Blue solid arrows show birth and death. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

munity due to their genetics or by contracting the disease earlier in their life. Semi-immune human, non-immune human and mosquito compartments are denoted by the lower indices m, n and v. Susceptible humans (S_m and S_n) can be infected by malaria. Following the infectious mosquito bite, susceptibles proceed to the exposed compartment (E_m, E_n). Individuals in these compartments have no symptoms yet. After the incubation time, exposed individuals proceed to the infectious class (I_m, I_n). For semi-immune, there is an additional immune compartment (R_m). Humans in the class R_m are partially immune to the disease, but their blood stream still has a low level of parasites and they are still able to infect susceptible mosquitoes [29]. We have three compartments for the mosquitoes: susceptibles (S_v), exposed (E_v) and infected (I_v).

We denote the total population of humans by $N_h(t)$ and total population of mosquitoes by $N_v(t)$. The transmission dynamics is illustrated in Fig. 2. With the above notations, our model equations can be written as

$$\begin{aligned}
S_n'(t) &= \theta\mu_h - \tilde{\alpha}_n(t)\frac{I_v(t)}{N_h(t)}S_n(t) - d_hS_n(t),\\
E_n'(t) &= \tilde{\alpha}_n(t)\frac{I_v(t)}{N_h(t)}S_n(t) - \nu_nE_n(t) - d_hE_n(t),\\
I_n'(t) &= \nu_nE_n(t) - \gamma_nI_n(t) - (d_h+\delta_n)I_n(t),\\
S_m'(t) &= (1-\theta)\mu_h - \tilde{\alpha}_m(t)\frac{I_v(t)}{N_h(t)}S_m(t) - d_hS_m(t) + \beta R_m(t),\\
E_m'(t) &= \tilde{\alpha}_m(t)\frac{I_v(t)}{N_h(t)}S_m(t) - \nu_mE_m(t) - d_hE_m(t),\\
I_m'(t) &= \nu_mE_m(t) - \gamma_mI_m(t) - (d_h+\delta_m)I_m(t),\\
R_m'(t) &= \gamma_nI_n(t) + \gamma_mI_m(t) - \beta R_m(t) - d_hR_m(t),\\
S_v'(t) &= \tilde{\mu}_v(t) - \tilde{\alpha}_v(t)\frac{\eta_nI_n(t) + \eta_mI_m(t) + \eta_rR_m(t)}{N_h(t)}S_v(t) - \tilde{d}_v(t)S_v(t),\\
E_v'(t) &= \tilde{\alpha}_v(t)\frac{\eta_nI_n(t) + \eta_mI_m(t) + \eta_rR_m(t)}{N_h(t)}S_v(t) - \nu_vE_v(t) - \tilde{d}_v(t)E_v(t),\\
I_v'(t) &= \nu_vE_v(t) - \tilde{d}_v(t)I_v(t),
\end{aligned} \tag{1}$$

where $\tilde{\mu}_v(t)$, $\tilde{\alpha}_n(t)$, $\tilde{\alpha}_m(t)$, $\tilde{\alpha}_v(t)$ and $\tilde{d}_v(t)$ are the mosquito birth rate, the rate of transmission from an infected mosquito to a non-immune susceptible human, transmission rate from an infectious mosquito to susceptible semi-immune humans, the transmission rate from infected humans to susceptible mosquitoes and mosquito death rate, respectively. In our model we assumed $\tilde{\mu}_v(t)$, $\tilde{\alpha}_n(t)$, $\tilde{\alpha}_m(t)$, $\tilde{\alpha}_v(t)$ and $\tilde{d}_v(t)$ to be continuous, positive ω-periodic functions. The explanation of the model parameters is summarized in Table 1.

We first engage in the study of the existence and uniqueness of solutions of (1). Introduce the notation

$$(S_n(0), E_n(0), I_n(0), S_m(0), E_m(0), I_m(0), R_m(0), S_v(0), E_v(0), I_v(0)) = (S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0) \in \mathbb{R}_+^{10},$$

where $\mathbb{R}_+ \coloneqq [0, \infty)$.

First, we show that (1) has a disease-free periodic solution. For the human subsystem of system (1) with a positive initial condition $(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0) \in \mathbb{R}_+^{10}$, we have the linear differential equation

$$\frac{dN_h(t)}{dt} = \mu_h - d_hN_h(t) - \delta_nI_n(t) - \delta_mI_m(t). \tag{2}$$

Table 1
Summary of parameters and notations of model (1).

Parameters	Description
μ_h	Humans birth rate
d_h	Humans death rate
θ	Probability of recruitment for humans
δ_n, δ_m	Disease mortality rate for non-immune and semi-immune humans
β	Rate of losing immunity for humans
η_n, η_m, η_r	Relative transmissibility of infectious humans to mosquitoes
γ_n, γ_m	Transfer rate of humans from I_n and I_m to R_m
ν_n, ν_m	Non-immune and semi-immune human incubation rate
ν_v	Mosquitoes incubation rate
α_n, α_m	Baseline value of mosquito-to-human transmission rate
α_v	Baseline value of human-to-mosquio transmission rate
μ_v, d_v	Baseline value of mosquito birth and death rates

If the disease is not present in the population, (2) has a unique, globally asymptotically stable equilibrium $N_h^* = \frac{\mu_h}{d_h}$, and $N_h(t)$ is bounded.

To obtain the disease-free periodic solution of (1), let us consider the equation

$$\frac{\mathrm{d}S_v(t)}{\mathrm{d}t} = \tilde{\mu}_v(t) - \tilde{d}_v(t)S_v(t), \tag{3}$$

with initial condition $S_v(0) = S_v^0 \in \mathbb{R}_+$. Eq. (3) clearly has a single positive ω-periodic solution, given by

$$S_v^*(t) = \left[\int_0^t \tilde{\mu}_v(r)e^{\int_0^r \tilde{d}_v(s)ds}dr + \frac{\int_0^\omega \tilde{\mu}_v(r)e^{\int_0^r \tilde{d}_v(s)ds}dr}{e^{\int_0^\omega \tilde{d}_v(s)ds} - 1}\right]e^{-\int_0^t \tilde{d}_v(s)ds} > 0. \tag{4}$$

This solution is globally attractive in $\mathbb{R}_+$ yielding that (1) has a single disease-free periodic solution

$$E_0 = \left(S_n^*, 0, 0, S_m^*, 0, 0, 0, S_v^*(t), 0, 0\right),$$

with $S_n^* = \theta\frac{\mu_h}{d_h}$ and $S_m^* = (1-\theta)\frac{\mu_h}{d_h}$.

To introduce the following result, we set $h^L = \sup_{t\in[0,\omega)} h(t)$ and $h^M = \inf_{t\in[0,\omega)} h(t)$ for a positive, continuous ω-periodic function $h(t)$.

Lemma 2.1. *There is $N_v^* = \frac{\mu_v^L}{d_v^M} > 0$ such that each solution in X of (1) eventually enters*

$$G_{N^*} := \left\{(S_n, E_n, I_n, S_m, E_m, I_m, R_m, S_v, E_v, I_v) \in \mathbb{R}_+^{10} : \begin{array}{l} N_h \leqslant N_h^*, \\ N_v \leqslant N_v^* \end{array}\right\},$$

and for each $N_v(t) \geqslant N_v^*$, G_N is positively invariant for system (1). Also, we have that

$$\lim_{t\to+\infty}(N_v(t) - S_v^*(t)) = 0.$$

Proof. From (1), for the mosquito subsystem we have

$$\frac{\mathrm{d}N_v(t)}{\mathrm{d}t} = \tilde{\mu}_v(t) - \tilde{d}_v(t)N_v(t) \leqslant \mu_v^L - d_v^M N_v(t) \leqslant 0, \quad \text{if } N_v(t) \geqslant N_v^*,$$

which implies that G_N, $N_v(t) \geqslant N_v^*$, is positively invariant and eventually, each forward orbit enters G_{N^*}. To finish the proof, let us assume $y(t) = N_v(t) - S_v^*(t)$, $t \geqslant 0$. Hence, we have

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

from which we have

$$\lim_{t\to+\infty} y(t) = 0.$$

Hence, the proof is complete. □

The next lemma will be needed in proving global stability of E_0 and the persistence of malaria in Section 4.

Lemma 2.2 [30, Lemma 2.1]**.** *Let $\mu = \frac{1}{\omega}\ln\rho(\Phi_{A(\cdot)}(\omega))$. Then there exists an ω-periodic positive function $v(t)$ such that $e^{\mu t}v(t)$ is a positive solution of $x' = A(t)x$.*

3. Basic reproduction numbers and local stability

In this section, following the technique introduced by Wang and Zhao [21], we will show the local stability of the disease-free periodic solution E_0 of (1). First, we identify the basic reproduction number $\mathcal{R}_0$ for system (1). Let $\mathcal{X} = (E_n, I_n, E_m, I_m, R_m, E_v, I_v, S_n, S_m, S_v)^T$ where E_n, I_n, E_m, I_m, R_m, E_v and I_v are infected compartments, and S_n, S_m and S_v are uninfected compartments with

$$\mathcal{F}(t,\mathcal{X}(t)) = \begin{bmatrix} \frac{\tilde{\alpha}_n(t)}{N_h(t)} I_v(t) S_n(t) \\ 0 \\ \frac{\tilde{\alpha}_m(t)}{N_h(t)} I_v(t) S_m(t) \\ 0 \\ 0 \\ \tilde{\alpha}_v(t) \frac{\eta_n I_n(t) + \eta_m I_m(t) + \eta_r R_m(t)}{N_h(t)} S_v(t) \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix},$$

$$\mathcal{V}^-(t,\mathcal{X}(t)) = \begin{bmatrix} (\nu_n + d_h) E_n(t) \\ (\gamma_n + d_h + \delta_n) I_n(t) \\ (\nu_m + d_h) E_m(t) \\ (\gamma_m + d_h + \delta_m) I_m(t) \\ (\beta + d_h) R_m(t) \\ (\nu_v + \tilde{d}_v(t)) E_v(t) \\ \tilde{d}_v(t) I_v(t) \\ d_h S_n(t) \\ d_h S_m(t) \\ \tilde{d}_v(t) S_v(t) \end{bmatrix}, \quad \mathcal{V}^+(t,\mathcal{X}(t)) = \begin{bmatrix} 0 \\ \nu_n E_n(t) \\ 0 \\ \nu_m E_m(t) \\ \gamma_n I_n(t) + \gamma_m I_m(t) \\ 0 \\ \nu_v E_v(t) \\ \theta \mu_h \\ (1-\theta)\mu_h \\ \tilde{\mu}_v(t) \end{bmatrix}. \tag{5}$$

We need to verify that the conditions (A1)–(A7) in [21, Section 1] are satisfied. Eq. (1) is equivalent to

$$\mathcal{X}'(t) = \mathcal{F}(t,\mathcal{X}(t)) - \mathcal{V}(t,\mathcal{X}(t)), \tag{6}$$

where we introduce the notation $\mathcal{V}(t,\mathcal{X}(t))$ for $\mathcal{V}^-(t,\mathcal{X}(t)) - \mathcal{V}^+(t,\mathcal{X}(t))$. It is straightforward to check that conditions (A1)–(A5) hold.

It is clear from the above that Eq. (6) has the disease-free periodic solution

$$\mathcal{X}^*(t) = (0,0,0,0,0,0,0,S_n^*, S_m^*, S_v^*(t)).$$

Let us introduce $f(t,\mathcal{X}(t))$ for $\mathcal{F}(t,\mathcal{X}(t)) - \mathcal{V}(t,\mathcal{X}(t))$ and the matrix function $M(t) = \left(\frac{\partial f_i(t,\mathcal{X}^*(t))}{\partial \mathcal{X}_j}\right)_{8\leqslant i,j\leqslant 10}$ where $f_i(t,\mathcal{X}(t))$ is the ith coordinate of $f(t,\mathcal{X}(t))$ and $\mathcal{X}_i$ is the ith component of $\mathcal{X}$. From (5), the matrix function $M(t)$ can be calculated as

$$M(t) = \begin{bmatrix} -d_h & 0 & 0 \\ 0 & -d_h & 0 \\ 0 & 0 & -\tilde{d}_v(t) \end{bmatrix}. \tag{7}$$

Let us denote by $\Phi_M(t)$ the monodromy matrix of $\frac{\mathrm{d}}{\mathrm{d}t} z = M(t)z$ and we will use the notation $\rho(\Phi_M(t))$ for the spectral radius of $\Phi_M(\omega)$. Hence, $\rho(\Phi_M(t)) < 1$, which implies that $\mathcal{X}^*(t)$ is a linearly asymptotically stable solution in the disease-free subspace $\mathcal{X}_s = \{(0,0,0,0,0,0,S_n,S_m,S_v) \in \mathbb{R}_+^{10}\}$. This implies that the condition (A6) holds as well.

We introduce the 7×7 matrix functions $F(t)$, $V(t)$ given as $F(t) = \left(\frac{\partial \mathcal{F}_i(t,\mathcal{X}^*(t))}{\partial \mathcal{X}_j}\right)_{1\leqslant i,j\leqslant 7}$, $V(t) = \left(\frac{\partial \mathcal{V}_i(t,\mathcal{X}^*(t))}{\partial \mathcal{X}_j}\right)_{1\leqslant i,j\leqslant 7}$ with $\mathcal{F}_i$ and $\mathcal{V}_i$ denoting the i-th coordinate of the vector functions $\mathcal{F}$ and $\mathcal{V}$, respectively. Then from (5), we have

$$F(t) = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & \tilde{\alpha}_n(t)\frac{S_n^*}{N_h^*} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \tilde{\alpha}_m(t)\frac{S_m^*}{N_h^*} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \eta_n\tilde{\alpha}_v(t)\frac{S_v^*(t)}{N_h^*} & 0 & \eta_m\tilde{\alpha}_v(t)\frac{S_v^*(t)}{N_h^*} & \eta_r\tilde{\alpha}_v(t)\frac{S_v^*(t)}{N_h^*} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix},$$

$$V(t) = \begin{bmatrix} \nu_n + d_h & 0 & 0 & 0 & 0 & 0 & 0 \\ -\nu_n & L_n & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \nu_m + d_h & 0 & 0 & 0 & 0 \\ 0 & 0 & -\nu_m & L_m & 0 & 0 & 0 \\ 0 & -\gamma_n & 0 & -\gamma_m & \beta + d_h & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \nu_v + \tilde{d}_v(t) & 0 \\ 0 & 0 & 0 & 0 & 0 & -\nu_v & \tilde{d}_v(t) \end{bmatrix}, \tag{8}$$

where $L_n = \gamma_n + d_h + \delta_n$ and $L_m = \gamma_m + d_h + \delta_m$. $F(t)$ is a non-negative matrix, and $-V(t)$ is cooperative.

Denote by $Y(t, s), t \geq s$ the evolution operator of equation

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -V(t)y, \tag{9}$$

meaning that, for any $s \in \mathbb{R}$, the 7×7 matrix function $Y(t, s)$ fulfils

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

with I being the 7×7 unit matrix. From this, $\Phi_{-V}(t)$, the monodromy matrix of (9) is equal to $Y(t, 0)$, $t \geq 0$. We have shown that condition (A7) holds.

Assume that the initial distribution of infected is given by $\phi(s)$, which is ω-periodic in s. $F(s)\phi(s)$ gives the rate of new cases due to those infected who were introduced at time s. For $t \geq s$, the formula $Y(t, s)F(s)\phi(s)$ provides the distribution of the infectious individuals who were newly infected at time s and who are still infected at time t. From this we obtain that the distribution of cumulative new infections at t, generated by all infected $\phi(s)$ introduced at any time $s \leq t$ is

$$\psi(t) \coloneqq \int_{-\infty}^{t} Y(t,s)F(s)\phi(s)ds = \int_{0}^{\infty} Y(t,t-a)F(t-a)\phi(t-a)da.$$

Let us introduce the notation C_ω for the ordered Banach space

$$\{h : \mathbb{R} \to \mathbb{R}^7 : h \text{ is } \omega\text{-periodic}\},$$

with the maximum norm $\|\cdot\|_\infty$. Consider the positive cone C_ω^+ defined as

$$C_\omega^+ \coloneqq \{\phi \in C_\omega : \phi(t) \geqslant 0,\ \forall t \in \mathbb{R}\}.$$

Then the linear next infection operator $\mathcal{L}$ from C_ω to C_ω, defined as

$$(\mathcal{L}\phi)(t) = \int_0^\infty Y(t,t-a)F(t-a)\phi(t-a)da, \qquad \forall t \in \mathbb{R},\ \phi \in C_\omega, \tag{10}$$

can be used to define the basic reproduction number of (1) as the spectral radius of the operator $\mathcal{L}$ [21].

Let $W(t, \lambda)$ denote the monodromy matrix of the ω-periodic linear equation

$$\frac{\mathrm{d}w(t)}{\mathrm{d}t} = \left(-V(t) + \frac{1}{\lambda}F(t)\right)w(t), \qquad \forall\ t \in \mathbb{R},$$

where $\lambda \in (0, \infty)$ is a parameter. $F(t)$ being non-negative and $-V(t)$ being cooperative imply that $\rho(W(\omega, \lambda))$ is continuous and non-increasing in $\lambda \in (0, \infty)$ and $\lim_{\lambda \to \infty}\rho(W(\omega, \lambda)) < 1$.

We evoke the following theorem from [21] as we will need it for the numerical calculation of the basic reproduction rate.

Theorem 3.1 [21, Theorem 2.1]**.**

(i) *If $\rho(W(\omega, \lambda)) = 1$ has a solution $\lambda_0 > 0$, then λ_0 is an eigenvalue of $\mathcal{L}$, and thus $\mathcal{R}_0 > 0$.*
(ii) *If $\mathcal{R}_0 > 0$, then $\lambda = \mathcal{R}_0$ is the only solution of $\rho(W(\omega, \lambda)) = 1$.*
(iii) *$\mathcal{R}_0 = 0$ if and only if $\rho(W(\omega, \lambda)) < 1$ for all $\lambda > 0$.*

Theorem 3.2 [21, Theorem 2.2]**.**

(i) $\mathcal{R}_0 = 1$ *is equivalent to* $\rho(\Phi_{F-V}(\omega)) = 1$.
(ii) $\mathcal{R}_0 > 1$ *is equivalent to* $\rho(\Phi_{F-V}(\omega)) > 1$.
(iii) $\mathcal{R}_0 < 1$ *is equivalent to* $\rho(\Phi_{F-V}(\omega)) < 1$.

Based on the results so far, we can formulate the following theorem concerning the local stability properties of the disease-free periodic solution E_0 of (1).

Theorem 3.3. *The disease-free periodic solution E_0 is locally asymptotically stable if $\mathcal{R}_0 < 1$, while it is unstable in the case $\mathcal{R}_0 > 1$.*

Proof. $J(t)$ is the Jacobian of (1) calculated in E_0:

$$J(t) = \begin{bmatrix} F(t) - V(t) & 0 \\ J_1(t) & M(t) \end{bmatrix},$$

with $M(t)$ defined in (7) and $J_1(t)$ is given by

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & -\theta\tilde{\alpha}_n(t) \\ 0 & 0 & 0 & 0 & \beta & 0 & -(1-\theta)\tilde{\alpha}_m(t) \\ 0 & -\eta_n\tilde{\alpha}_v(t)\frac{S_v^*(t)}{N_h^*} & 0 & -\eta_m\tilde{\alpha}_v(t)\frac{S_v^*(t)}{N_h^*} & -\eta_r\tilde{\alpha}_v(t)\frac{S_v^*(t)}{N_h^*} & 0 & 0 \end{bmatrix}.$$

By [31], E_0 is a locally asymptotically stable periodic solution if $\rho(\Phi_M(\omega)) < 1$ as well as $\rho(\Phi_{F-V}(\omega)) < 1$ hold. From condition (A6), we have $\rho(\Phi_M(\omega)) < 1$. It then follows that the stability of E_0 is determined by $\rho(\Phi_{F-V}(\omega))$. Hence, E_0 is locally asymptotically stable if $\rho(\Phi_{F-V}(\omega)) < 1$, and unstable if $\rho(\Phi_{F-V}(\omega)) > 1$. By using Theorem 3.2, we complete the proof. □

3.1. Derivation of the basic reproduction number of the autonomous model

To calculate the basic reproduction number $\mathcal{R}_0^A$ of the autonomous model which we obtain from (1) by setting the time-varying parameters mosquito birth ($\tilde{\mu}_v(t) \equiv \mu_v$) and death rates ($\tilde{d}_v(t) \equiv d_v$) and biting rates ($\tilde{\alpha}_n(t) \equiv \alpha_n$, $\tilde{\alpha}_m(t) \equiv \alpha_m$ and $\tilde{\alpha}_v(t) \equiv \alpha_v$) to constant, we follow the general approach established in [32].

Substituting the values in the disease-free equilibrium $S_v^*(t) \equiv S_v^* = \frac{\mu_v}{d_v}$ in Eq. (8), for all $t \geq 0$, we obtain the Jacobian F given by

$$F = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & \alpha_n\frac{S_n^*}{N_h^*} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \alpha_m\frac{S_m^*}{N_h^*} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \eta_n\alpha_v\frac{S_v^*}{N_h^*} & 0 & \eta_m\alpha_v\frac{S_v^*}{N_h^*} & \eta_r\alpha_v\frac{S_v^*}{N_h^*} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix},$$

and the Jacobian V given by

$$V = \begin{bmatrix} \nu_n + d_h & 0 & 0 & 0 & 0 & 0 & 0 \\ -\nu_n & L_n & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \nu_m + d_h & 0 & 0 & 0 & 0 \\ 0 & 0 & -\nu_m & L_m & 0 & 0 & 0 \\ 0 & -\gamma_n & 0 & -\gamma_m & \beta + d_h & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \nu_v + d_v & 0 \\ 0 & 0 & 0 & 0 & 0 & -\nu_v & d_v \end{bmatrix},$$

therefore the characteristic polynomial of the next generation matrix FV^{-1} is

$$\lambda^5\left(\lambda^2 - \frac{\alpha_v\nu_v S_v^*}{d_v(d_h+\beta)(\nu_v+d_v)N_h^*}\left(\mathcal{R}_{0n}^2 + \mathcal{R}_{0m}^2\right)\right) = 0,$$

where

$$\mathcal{R}_{0n}^2 = \frac{\theta\alpha_n\nu_n(\eta_n(d_h+\beta)+\gamma_n\eta_r)}{L_n(d_h+\nu_n)},$$

$$\mathcal{R}_{0m}^2 = \frac{(1-\theta)\alpha_m\nu_m(\eta_m(d_h+\beta)+\gamma_m\eta_r)}{L_m(d_h+\nu_m)}.$$

The characteristic polynomial therefore is the quadratic equation

$$\lambda^2 - \frac{\nu_v\alpha_v S_v^*}{d_v(d_h+\beta)(\nu_v+d_v)N_h^*}\left(\mathcal{R}_{0n}^2 + \mathcal{R}_{0m}^2\right) = 0. \tag{11}$$

According to [32], one obtains the basic reproduction number as the largest absolute value eigenvalue of FV^{-1}, i.e. it is given as the root of the quadratic Eq. (11)

$$\mathcal{R}_0^A = \sqrt{\frac{\nu_v \alpha_v S_v^*}{d_v(d_h+\beta)(\nu_v+d_v)N_h^*}\left(\mathcal{R}_{0n}^2+\mathcal{R}_{0m}^2\right)}. \tag{12}$$

Remark 3.4. Given an ω-periodic continuous function $h(t)$, we introduce the integral average (using the notation presented in [33]) as

$$[h] \coloneqq \frac{1}{\omega}\int_0^{\omega} h(t)\,dt.$$

Then, the time-average reproduction rate, $[\mathcal{R}_0]$, of the associated time-varying model is given by

$$[\mathcal{R}_0] = \sqrt{\frac{\nu_v[\tilde{\alpha}_v][S_v^*]}{[\tilde{d_v}](d_h+\beta)(\nu_v+[\tilde{d_v}])N_h^*}\left([\mathcal{R}_{0n}^2]+[\mathcal{R}_{0m}^2]\right)} \tag{13}$$

where

$$[\mathcal{R}_{0n}^2] = \frac{\theta[\tilde{\alpha}_n]\nu_n(\eta_n(d_h+\beta)+\gamma_n\eta_r)}{L_n(d_h+\nu_n)},$$
$$[\mathcal{R}_{0m}^2] = \frac{(1-\theta)[\tilde{\alpha}_m]\nu_m(\eta_m(d_h+\beta)+\gamma_m\eta_r)}{L_m(d_h+\nu_m)}.$$

4. Threshold dynamics

We will show the global stability of the disease-free periodic solution E_0 and the extinction of the disease if $\mathcal{R}_0$ is less than 1, as well as the persistence of malaria and the existence of a positive periodic solution of (1) if $\mathcal{R}_0$ is larger than 1.

4.1. Global stability of the disease-free periodic solution

Theorem 4.1. *If $\delta_n = 0$, $\delta_m = 0$ and $\mathcal{R}_0 < 1$, then the disease-free periodic solution E_0 of (1) is globally asymptotically stable and if $\mathcal{R}_0 > 1$, then it is unstable.*

Proof. From Theorem 3.3, we know that if $\mathcal{R}_0 > 1$, then E_0 is unstable and if $\mathcal{R}_0 < 1$, then E_0 is locally asymptotically stable. Therefore, it is only left us to show that for $\mathcal{R}_0 < 1$, E_0 is globally attractive.

If $\delta_n = 0$ and $\delta_m = 0$, we can rewrite (2) as

$$\frac{dN_h(t)}{dt} = \mu_h - d_h N_h(t),$$

and from Lemma 2.1, for any ε_1, there exists a $T_1 > 0$ such that $N_v(t) \leqslant S_v^*(t)+\varepsilon_1$ and $N_h(t) \geqslant N_h^* - \varepsilon_1$ for $t > T_1$. We obtain that

$$\frac{S_n(t)}{N_h(t)} \leqslant \frac{S_n^*}{N_h^*-\varepsilon_1}, \qquad \frac{S_m(t)}{N_h(t)} \leqslant \frac{S_m^*}{N_h^*-\varepsilon_1} \quad \text{and} \quad \frac{S_v(t)}{N_h(t)} \leqslant \frac{S_v^*(t)+\varepsilon_1}{N_h^*-\varepsilon_1}.$$

From system (1), we get

$$\begin{aligned}
E_n'(t) &\leqslant \tfrac{S_n^*}{N_h^*-\varepsilon_1}\tilde{\alpha}_n(t)I_v(t) - \nu_n E_n(t) - d_h E_n(t),\\
I_n'(t) &= \nu_n E_n(t) - \gamma_n I_n(t) - d_h I_n(t),\\
E_m'(t) &\leqslant \tfrac{S_m^*}{N_h^*-\varepsilon_1}\tilde{\alpha}_m(t)I_v(t) - \nu_m E_m(t) - d_h E_m(t),\\
I_m'(t) &= \nu_m E_m(t) - \gamma_m I_m(t) - d_h I_m(t),\\
R_m'(t) &= \gamma_n I_n(t) + \gamma_m I_m(t) - \beta R_m(t) - d_h R_m(t),\\
E_v'(t) &\leqslant \tilde{\alpha}_v(t)(\eta_n I_n(t) + \eta_m I_m(t) + \eta_r R_m(t))\tfrac{S_v^*(t)+\varepsilon_1}{N_h^*-\varepsilon_1} - (\nu_v + \tilde{d_v}(t))E_v(t),\\
I_v'(t) &= \nu_v E_v(t) - \tilde{d_v}(t)I_v(t),
\end{aligned}$$

for $t > T_1$. Let $M_{\varepsilon_1}(t)$ be the 7×7 matrix function defined by

$$\begin{bmatrix} -\nu_n - d_h & 0 & 0 & 0 & 0 & 0 & \frac{\tilde{\alpha}_n(t)S_n^*}{N_h^* - \varepsilon_1} \\ \nu_n & -\gamma_n - d_h & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -\nu_m - d_h & 0 & 0 & 0 & \frac{\tilde{\alpha}_m(t)S_m^*}{N_h^* - \varepsilon_1} \\ 0 & 0 & \nu_m & -\gamma_m - d_h & 0 & 0 & 0 \\ 0 & \gamma_n & 0 & \gamma_m & -\beta - d_h & 0 & 0 \\ 0 & \eta_n\tilde{\alpha}_v(t)\frac{S_v^*(t)+\varepsilon_1}{N_h^* - \varepsilon_1} & 0 & \eta_m\tilde{\alpha}_v(t)\frac{S_v^*(t)+\varepsilon_1}{N_h^* - \varepsilon_1} & \eta_r\tilde{\alpha}_v(t)\frac{S_v^*(t)+\varepsilon_1}{N_h^* - \varepsilon_1} & -\nu_v - \tilde{d}_v(t) & 0 \\ 0 & 0 & 0 & 0 & 0 & \nu_v & -\tilde{d}_v(t) \end{bmatrix}.$$

Consider the auxiliary equation

$$\frac{d\tilde{u}(t)}{dt} = M_{\varepsilon_1}(t)\tilde{u}(t), \tag{14}$$

with $\tilde{u}(t) = \left(\tilde{E_n}(t), \tilde{I_n}(t), \tilde{E_m}(t), \tilde{I_m}(t), \tilde{R_m}(t), \tilde{E_v}(t), \tilde{I_v}(t)\right)$.

Applying Theorem 3.2, it follows that $\mathcal{R}_0 < 1$ is equivalent to $\rho(\Phi_{F-V}(\omega))$ being less than 1. It is clear that $\lim_{\varepsilon_1 \to 0} \Phi_{M_{\varepsilon_1}}(\omega) = \Phi_{F-V}(\omega)$. As $\rho(\Phi_{F-V}(\omega))$ is continuous, we can choose a small enough $\varepsilon_1 > 0$ for which $\rho(\Phi_{M_{\varepsilon_1}}(\omega)) < 1$.

By Lemma 2.2, there is an ω-periodic positive function $p_1(t)$ s.t. $p_1(t)\exp(\xi_1 t)$ is a solution of (14) and $\xi_1 = \frac{1}{\omega}\ln\rho(\Phi_{M_{\varepsilon_1}}(\omega)) < 0$. For any $h(0) \in \mathbb{R}_+^7$, we can select $K^* \in \mathbb{R}_+$ such that $h(0) \le K^* p_1(0)$ where

$$h(t) = (E_n(t), I_n(t), E_m(t), I_m(t), R_m(t), E_v(t), I_v(t))^T.$$

Applying the comparison principle [34, Theorem B.1], we obtain $h(t) \le p_1(t)\exp(\xi_1 t)$ for $t > 0$. Hence, we get

$$\lim_{t\to\infty}(E_n(t), I_n(t), E_m(t), I_m(t), R_m(t), E_v(t), I_v(t)) = (0, 0, 0, 0, 0, 0, 0).$$

Thus, (4) and the equations for $S_n'(t)$, $S_m'(t)$ and $S_v'(t)$ in (1) yield

$$\lim_{t\to\infty} S_n(t) = S_n^*, \qquad \lim_{t\to\infty} S_m(t) = S_m^*, \quad \text{and} \quad \lim_{t\to\infty} S_v(t) = S_v^*(t),$$

and hence, the proof is complete. □

4.2. Existence of positive periodic solutions

Let us introduce the notations

$$\begin{aligned} X &:= \left\{(S_n, E_n, I_n, S_m, E_m, I_m, R_m, S_v, E_v, I_v) \in \mathbb{R}_+^{10}\right\}, \\ X_0 &:= \left\{(S_n, E_n, I_n, S_m, E_m, I_m, R_m, S_v, E_v, I_v) \in X : \begin{array}{l} E_n > 0, I_n > 0, \\ E_m > 0, I_m > 0, \\ R_m > 0, E_v > 0, \\ I_v > 0 \end{array}\right\}, \\ \partial X_0 &:= X \setminus X_0. \end{aligned} \tag{15}$$

Let $P : \mathbb{R}_+^{10} \to \mathbb{R}_+^{10}$ defined as the Poincaré map corresponding to (1), i.e. the map P is defined as

$$P(x^0) = u(\omega, x^0), \qquad x^0 \in \mathbb{R}_+^{10},$$

with $u(t, x^0)$ being the single solution of (1) started from initial condition $x^0 \in \mathbb{R}_+^{10}$. Clearly,

$$P^m(x^0) = u(m\omega, x^0), \qquad \forall m \ge 0.$$

Lemma 4.2. *If the basic reproduction number $\mathcal{R}_0$ is larger than 1, then there exists a $\sigma > 0$ such that for any $(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0) \in X_0$ with $\|\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right) - E_0\| \le \sigma$, we have*

$$\limsup_{m\to\infty} d\left(P^m\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right), E_0\right) \ge \sigma.$$

Proof. It follows from Theorem 3.2 that $\rho(\Phi_{F-V}(\omega)) > 1$ if the basic reproduction number is larger than 1. In this case, there exists an $\eta > 0$ small enough for which $\rho(\Phi_{F-V-M_\eta}(\omega)) > 1$, with $M_\eta(t)$ being the 7×7 matrix function defined by

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & \tilde{\alpha}_n(t)\eta \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \tilde{\alpha}_m(t)\eta \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \eta_n\tilde{\alpha}_v(t)\eta & 0 & \eta_m\tilde{\alpha}_v(t)\eta & \eta_r\tilde{\alpha}_v(t)\eta & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}.$$

Let us choose an arbitrary $\eta > 0$. Applying the continuous dependence of solutions on initial values, there exists a $\sigma = \sigma(\eta) > 0$ such that for any $\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right) \in X_0$ with $\|\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right) - E_0\| \leqslant \sigma$, it holds that

$$\|u(t, \left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right)) - u(t, E_0)\| \leqslant \eta, \text{ for } 0 \leqslant t \leqslant \omega.$$

We further claim that

$$\limsup_{m\to\infty} d\left(P^m\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right), E_0\right) \geqslant \sigma. \tag{16}$$

Suppose that (16) is not satisfied. Then

$$\limsup_{m\to\infty} d\left(P^m\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right), E_0\right) < \sigma \tag{17}$$

holds for some $\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right) \in X_0$.

Without loss of generality we may assume that

$$d\left(P^m\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right), E_0\right) < \sigma, \quad \forall m \geq 0.$$

Then the above discussion implies that

$$\|u(t, P^m\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right) - u(t, E_0)\| < \sigma, \ \forall m \geq 0, \ t \in [0, \omega].$$

For $t \geq 0$, we write t as $t = m\omega + t_1$ with $t_1 \in [0, \omega)$ and $m = [\frac{t}{\omega}]$, which is the greatest integer not larger than $\frac{t}{\omega}$. Then, we obtain

$$\begin{aligned}\|u\left(t, \left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right)\right) - u(t, E_0)\| \\ = \|u\left(t_1, P^m\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right)\right) - u(t_1, E_0)\| < \sigma,\end{aligned}$$

for all $t \geq 0$, which implies that

$$\frac{S_n(t)}{N_h(t)} \geqslant \frac{S_n^*}{N_h^*} - \eta, \quad \frac{S_m(t)}{N_h(t)} \geqslant \frac{S_m^*}{N_h^*} - \eta \quad \text{and} \quad \frac{S_v(t)}{N_h(t)} \geqslant \frac{S_v^*(t)}{N_h^*} - \eta.$$

Then for $\|\left(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0\right) - E_0\| \leqslant \sigma$, we obtain

$$\begin{aligned}
E_n'(t) &\geqslant \tilde{\alpha}_n(t) I_v(t)\left(\frac{S_n^*}{N_h^*} - \eta\right) - \nu_n E_n(t) - d_h E_n(t)\\
I_n'(t) &= \nu_n E_n(t) - \gamma_n I_n(t) - (d_h + \delta_n) I_n(t)\\
E_m'(t) &\geqslant \tilde{\alpha}_m(t) I_v(t)\left(\frac{S_m^*}{N_h^*} - \eta\right) - \nu_m E_m(t) - d_h E_m(t)\\
I_m'(t) &= \nu_m E_m(t) - \gamma_m I_m(t) - (d_h + \delta_m) I_m(t)\\
R_m'(t) &= \gamma_n I_n(t) + \gamma_m I_m(t) - \beta R_m(t) - d_h R_m(t)\\
E_v'(t) &\geqslant \tilde{\alpha}_v(t)(\eta_n I_n(t) + \eta_m I_m(t) + \eta_r R_m(t))\left(\frac{S_v^*(t)}{N_h^*} - \eta\right) - (\nu_v + \tilde{d_v}(t)) E_v(t)\\
I_v'(t) &= \nu_v E_v(t) - \tilde{d_v}(t) I_v(t)
\end{aligned}$$

Consider now the auxiliary linear system

$$\frac{\mathrm{d}\hat{u}(t)}{\mathrm{d}t} = (F(t) - V(t) - M_\eta(t))\hat{u}(t), \tag{18}$$

where $\hat{u}(t) = \left(\hat{E_n}(t), \hat{I_n}(t), \hat{E_m}(t), \hat{I_m}(t), \hat{R_m}(t), \hat{E_v}(t), \hat{I_v}(t)\right)$.

Now we have that $\rho(\Phi_{F-V-M_\eta}(\omega)) > 1$. Once again by Lemma 2.2, there is an ω-periodic positive function $p_2(t)$ s.t. $p_2(t)\exp(\xi_2 t)$ is a solution of (18) and $\xi_2 = \frac{1}{\omega}\ln\rho(\Phi_{F-V-M_\eta}(\omega)) > 0$. For any $h(0) \in \mathbb{R}_+^7$, we can find $K_2^* \in \mathbb{R}_+$ such that $h(0) \geqslant K_2^* p_2(0)$ where

$$h(t) = (E_n(t), I_n(t), E_m(t), I_m(t), R_m(t), E_v(t), I_v(t))^T.$$

Applying the comparison principle (see, e.g. [34, Theorem B.1]), we obtain $h(t) \geq p_2(t)\exp(\xi_2 t)$ for all $t > 0$, from which it follows that $\lim_{t\to\infty} E_n(t) = \infty$, $\lim_{t\to\infty} I_n(t) = \infty$, $\lim_{t\to\infty} E_m(t) = \infty$, $\lim_{t\to\infty} I_m(t) = \infty$, $\lim_{t\to\infty} R_m(t) = \infty$, $\lim_{t\to\infty} E_v(t) = \infty$ and $\lim_{t\to\infty} I_v(t) = \infty$. This leads to a contradiction, hence the proof is complete. □

Proposition 4.3. *X_0 and ∂X_0 defined in(15) are positively invariant w.r.t. the flow defined by (1).*

Proof. Let $(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0) \in X_0$ be an arbitrary initial condition. By solving (1), we obtain

$$\begin{aligned} S_n(t) &= e^{\int_0^t -a_1(s)\,ds}\left[S_n^0 + \theta\mu_h \int_0^t e^{\int_0^s a_1(r)\,dr}\,ds\right] \\ &\geqslant \theta\mu_h e^{\int_0^t -a_1(s)\,ds}\left[\int_0^t e^{\int_0^s a_1(r)\,dr}\,ds\right] > 0, \quad \forall t > 0, \end{aligned} \tag{19}$$

$$\begin{aligned} E_n(t) &= e^{-(\nu_n+d_h)t}\left[E_n^0 + \int_0^t \frac{\tilde{\alpha}_n(s)}{N_h(s)} I_v(s) S_n(s) e^{(\nu_n+d_h)s}\,ds\right] \\ &\geqslant e^{-(\nu_n+d_h)t}\left[\int_0^t \frac{\tilde{\alpha}_n(s)}{N_h(s)} I_v(s) S_n(s) e^{(\nu_n+d_h)s}\,ds\right] > 0, \quad \forall t > 0, \end{aligned} \tag{20}$$

$$\begin{aligned} I_n(t) &= e^{-L_n t}\left[I_n^0 + \nu_n \int_0^t E_n(s) e^{L_n s}\,ds\right] \\ &\geqslant e^{-L_n t}\left[\nu_n \int_0^t E_n(s) e^{L_n s}\,ds\right] > 0, \quad \forall t > 0, \end{aligned} \tag{21}$$

$$\begin{aligned} S_m(t) &= e^{\int_0^t -a_2(s)\,ds}\left[S_m^0 + \int_0^t ((1-\theta)\mu_h + \beta R_m(s)) e^{\int_0^s a_2(r)\,dr}\,ds\right] \\ &\geqslant e^{\int_0^t -a_2(s)\,ds}\left[\int_0^t ((1-\theta)\mu_h + \beta R_m(s)) e^{\int_0^s a_2(r)\,dr}\,ds\right] \\ &> 0, \quad \forall t > 0, \end{aligned} \tag{22}$$

$$\begin{aligned} E_m(t) &= e^{-(\nu_m+d_h)t}\left[E_m^0 + \int_0^t \frac{\tilde{\alpha}_m(s)}{N_h(s)} I_v(s) S_m(s) e^{(\nu_m+d_h)s}\,ds\right] \\ &\geqslant e^{-(\nu_m+d_h)t}\left[\int_0^t \frac{\tilde{\alpha}_m(s)}{N_h(s)} I_v(s) S_m(s) e^{(\nu_m+d_h)s}\,ds\right] > 0, \quad \forall t > 0, \end{aligned} \tag{23}$$

$$\begin{aligned} I_m(t) &= e^{-L_m t}\left[I_m^0 + \nu_m \int_0^t E_m(s) e^{L_m s}\,ds\right] \\ &\geqslant e^{-L_m t}\left[\nu_m \int_0^t E_m(s) e^{L_m s}\,ds\right] > 0, \quad \forall t > 0, \end{aligned} \tag{24}$$

$$\begin{aligned} R_m(t) &= e^{-(\beta+d_h)t}\left[R_m^0 + \int_0^t (\gamma_n I_n(s) + \gamma_m I_m(s)) e^{(\beta+d_h)s}\,ds\right] \\ &\geqslant e^{-(\beta+d_h)t}\left[\int_0^t (\gamma_n I_n(s) + \gamma_m I_m(s)) e^{(\beta+d_h)s}\,ds\right] > 0, \quad \forall t > 0, \end{aligned} \tag{25}$$

$$\begin{aligned} S_v(t) &= e^{\int_0^t -(a_3(s)+\tilde{d}_v(s))\,ds}\left[S_v^0 + \int_0^t \tilde{\mu}_v(s) e^{\int_0^s (a_3(r)+\tilde{d}_v(r))\,dr}\,ds\right] \\ &\geqslant e^{\int_0^t -(a_3(s)+\tilde{d}_v(s))\,ds}\left[\int_0^t \tilde{\mu}_v(s) e^{\int_0^s (a_3(r)+\tilde{d}_v(r))\,dr}\,ds\right] > 0, \quad \forall t > 0, \end{aligned} \tag{26}$$

$$\begin{aligned} E_v(t) &= e^{-\int_0^t (\nu_v+\tilde{d}_v(s))\,ds}\left[E_v^0 + \int_0^t a_3(s) S_v(s) e^{\int_0^s (\nu_v+\tilde{d}_v(r))\,dr}\,ds\right] \\ &\geqslant e^{-\int_0^t (\nu_v+\tilde{d}_v(s))\,ds}\left[\int_0^t a_3(s) S_v(s) e^{\int_0^s (\nu_v+\tilde{d}_v(r))\,dr}\,ds\right] > 0, \quad \forall t > 0, \end{aligned} \tag{27}$$

$$\begin{aligned} I_v(t) &= e^{-\int_0^t \tilde{d}_v(s)\,ds}\left[I_v^0 + \nu_v \int_0^t E_v(s) e^{\int_0^s \tilde{d}_v(r)\,dr}\,ds\right] \\ &\geqslant \nu_v e^{-\int_0^t \tilde{d}_v(s)\,ds}\left[\int_0^t E_v(s) e^{\int_0^s \tilde{d}_v(r)\,dr}\,ds\right] > 0, \quad \forall t > 0, \end{aligned} \tag{28}$$

where

$$a_1(t) = \frac{\tilde{\alpha}_n(t)}{N_h(t)} I_v(t) + d_h,$$
$$a_2(t) = \frac{\tilde{\alpha}_m(t)}{N_h(t)} I_v(t) + d_h,$$
$$a_3(t) = \tilde{\alpha}_v(t) \frac{\eta_n I_n(t) + \eta_m I_m(t) + \eta_r R_m(t)}{N_h(t)}.$$

Hence we obtain the positive invariance of X_0. The positive invariance of X and the fact that ∂X_0 is relatively closed in X implies the positive invariance of ∂X_0. □

Theorem 4.4. *Assume $\mathcal{R}_0 > 1$. Then (1) admits at least one positive periodic solution and there is an $\varepsilon > 0$ s.t.*

$$\begin{array}{llllllll} \liminf_{t\to\infty} E_n(t) & \geqslant \varepsilon, & \liminf_{t\to\infty} I_n(t) & \geqslant \varepsilon, & \liminf_{t\to\infty} E_m(t) & \geqslant \varepsilon, & \liminf_{t\to\infty} I_m(t) & \geqslant \varepsilon, \\ \liminf_{t\to\infty} R_m(t) & \geqslant \varepsilon, & \liminf_{t\to\infty} E_v(t) & \geqslant \varepsilon, & \liminf_{t\to\infty} I_v(t) & \geqslant \varepsilon, & & \end{array}$$

for all $(S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0) \in X_0$.

Proof. First, we prove the uniform persistence of P w.r.t. $(X_0, \partial X_0)$, as from this, applying [35, Theorem 3.1.1], we obtain the uniform persistence of the solution of (1) w.r.t. $(X_0, \partial X_0)$.

From Proposition 4.3, we have the positive invariance of both X and X_0 and that ∂X_0 is relatively closed in X. Then, from Lemma 2.1 the point dissipativity of system (1) follows. Let us introduce

$$M_\partial = \left\{x^0 \in \partial X_0 : P^m(x^0) \in \partial X_0, \ \forall m \geqslant 0\right\}.$$

where $x^0 = (S_n^0, E_n^0, I_n^0, S_m^0, E_m^0, I_m^0, R_m^0, S_v^0, E_v^0, I_v^0)$. We will apply the theory of uniform persistence [35] (see also [30, Theorem 2.3]). In order to do this, we first show that

$$M_\partial = \{(S_n, 0, 0, S_m, 0, 0, 0, S_v, 0, 0) : S_n \geqslant 0, \ S_m \geqslant 0, \ S_v \geqslant 0\}. \tag{29}$$

Let us note that $M_\partial \supseteq \{(S_n, 0, 0, S_m, 0, 0, 0, S_v, 0, 0): S_n \geq 0, S_m \geq 0, S_v \geq 0\}$. It is enough to prove that $M_\partial \subset \{(S_n, 0, 0, S_m, 0, 0, 0, S_v, 0, 0): S_n \geq 0, S_m \geq 0, S_v \geq 0\}$, namely, for an arbitrary initial value $\phi \in \partial X_0$, $E_n(n\omega)$ or $I_n(n\omega)$ or $E_m(n\omega)$ or $I_m(n\omega)$ or $I_m(n\omega)$ or $E_v(n\omega)$ or $I_v(n\omega)$ is equal to 0, for any $n \geq 0$.

By contradiction assume there is a non-negative integer n_1 for which $E_n(n_1\omega)$, $I_n(n_1\omega)$, $E_m(n_1\omega)$, $I_m(n_1\omega)$, $I_m(n_1\omega)$, $E_v(n_1\omega)$ and $I_v(n_1\omega)$ are all positive. Then, by changing $t = 0$ to $t = n_1\omega$ in (19)–(28), one gets that $S_n(t)$, $E_n(t)$, $I_n(t)$, $S_m(t)$, $E_m(t)$, $I_m(t)$, $R_m(t)$, $S_v(t)$, $E_v(t)$, $I_v(t)$ are all positive. However, this contradicts the positive invariance of ∂X_0.

We know the weak uniform persistence of P w.r.t. $(X_0, \partial X_0)$ using Lemma 4.2. Then, Lemma 2.1 yields P has a global attractor. Then we can see E_0 is an isolated invariant subset of X and $W^s(E_0) \cap X_0 = \emptyset$. Each solution in M_∂ tends to E_0 and E_0 is acyclic in M_∂. Applying [35, Theorem 1.3.1, Remark 1.3.1], we obtain the uniform persistence of P w.r.t. $(X_0, \partial X_0)$. From this, there is an $\varepsilon > 0$ for which

$$\begin{array}{llllllll} \liminf_{t\to\infty} E_n(t) & \geqslant \varepsilon, & \liminf_{t\to\infty} I_n(t) & \geqslant \varepsilon, & \liminf_{t\to\infty} E_m(t) & \geqslant \varepsilon, & \liminf_{t\to\infty} I_m(t) & \geqslant \varepsilon, \\ \liminf_{t\to\infty} R_m(t) & \geqslant \varepsilon, & \liminf_{t\to\infty} E_v(t) & \geqslant \varepsilon, & \liminf_{t\to\infty} I_v(t) & \geqslant \varepsilon. & & \end{array}$$

By [35, Theorem 1.3.6], P has an equilibrium $\bar{\phi} \in X_0$, and thus at least one periodic solution $u(t, \bar{\phi})$ of system (1) exists, where

$$\bar{\phi} = \left(\bar{S}_n(0), \bar{E}_n(0), \bar{I}_n(0), \bar{S}_m(0), \bar{E}_m(0), \bar{I}_m(0), \bar{R}_m(0), \bar{S}_v(0), \bar{E}_v(0), \bar{I}_v(0)\right) \in X_0.$$

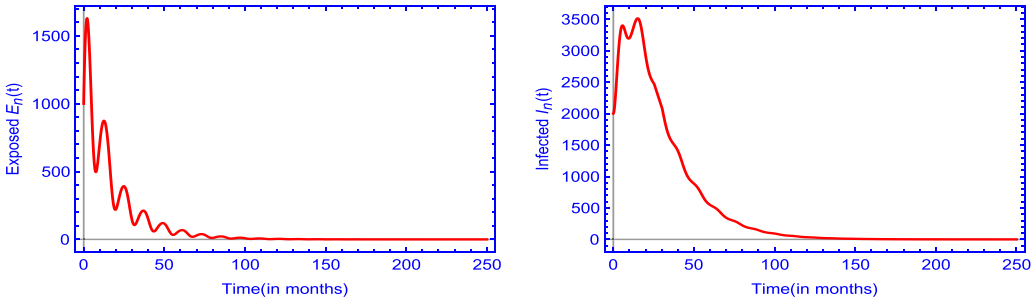
We show that $\bar{S}_n(0)$, $\bar{S}_m(0)$ and $\bar{S}_v(0)$ are positive. Suppose $\bar{S}_n(0) = \bar{S}_m(0) = \bar{S}_v(0) = 0$, then $\bar{S}_n(0) \geqslant 0$, $\bar{S}_m(0) > 0$ and $\bar{S}_v(0) > 0$ for all $t > 0$. However, applying that the solution is periodic, we have $\bar{S}_n(0) = \bar{S}_n(n\omega) = 0$, $\bar{S}_m(0) = \bar{S}_m(n\omega) = 0$ and $\bar{S}_v(0) = \bar{S}_v(n\omega) = 0$, hence, we have arrived at a contradiction. □

5. Numerical simulations

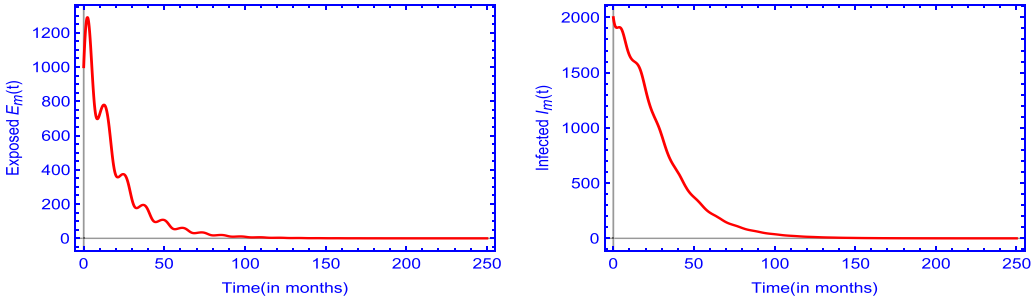
Here we show numerical simulations regarding our model to illustrate and support the theoretical results of the previous sections. From Section 4, we see that $\mathcal{R}_0$ serves as a threshold parameter concerning the persistence of the disease in the population (see Theorems 4.1 and 4.4). We show some simulations to demonstrate that our time-periodic model is in accordance with seasonally fluctuation. The functions $\tilde{\mu}_v(t)$, $\tilde{\alpha}_n(t)$, $\tilde{\alpha}_m(t)$, $\tilde{\alpha}_v(t)$ and $\tilde{d}_v(t)$ are time-periodic with one year as a period and, following e.g. [7], they are assumed to be of the form

$$\begin{array}{lll} \tilde{\alpha}_i(t) = & \alpha_i \cdot \left(\sin\left(\frac{2\pi}{p}t + b\right) + a\right), & i = n, m, v \\ \tilde{\mu}_v(t) = & \mu_v \cdot \left(\sin\left(\frac{2\pi}{p}t + b\right) + a\right), & \tilde{d}_v(t) = d_v \cdot \left(\cos\left(\frac{2\pi}{p}t + b\right) + a\right), \end{array}$$

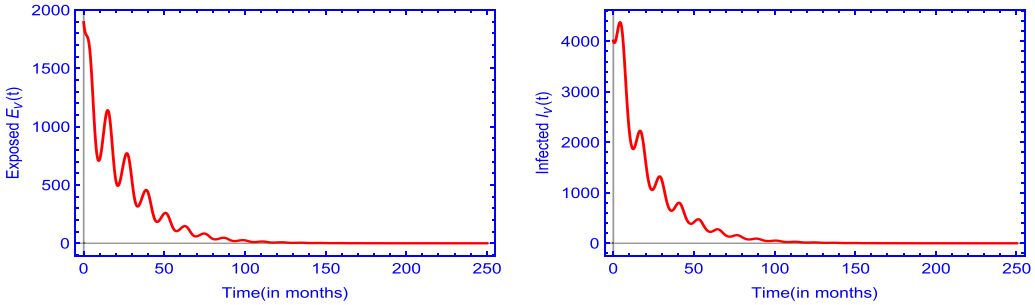
where p is period length (given in months), a, b are free adjustment parameters and μ_v, α_n, α_m, α_v and d_v are the (constant) baseline values of the corresponding time-dependent parameters.



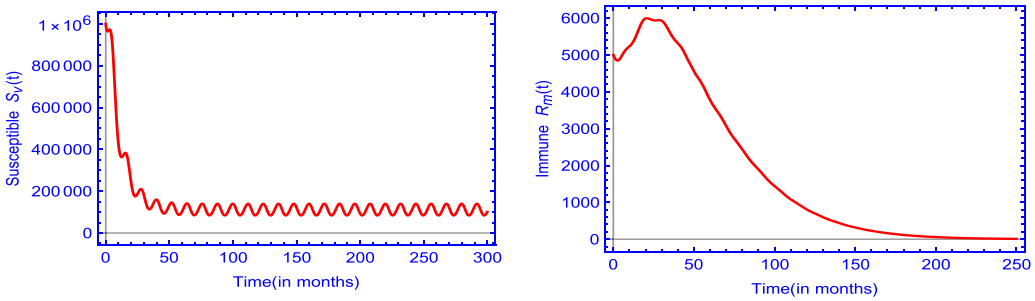
(a) Non-immune.



(b) Semi-immune.



(c) Mosquitoes.



(d) Mosquitoes and semi-immune.

Fig. 3. Extinction of malaria when $\mathcal{R}_0 = 0.625 < 1$ with parameters given in Table 2 (see Example 1).

Table 2
Parameters, values for extinction and persistence of model (1).

Parameter	Value for extinction		Value for persistence	Source
	Example 1	Example 2		
μ_h	1600	1000	2000	Assumed
d_h	0.00167	0.00167	0.00167	Assumed
α_n	0.293	0.657	0.595	[6,8]
α_m	0.17	0.42	0.348	[6,8]
α_v	0.544	0.281	0.796	[36]
β	0.0901	0.0778	0.0731	[6,8]
θ	0.19	0.4	0.756	[6,8]
η_n	0.275	0.2	0.275	[6,8]
η_m	0.219	0.2	0.219	[6,8]
η_r	0.002	0.0021	0.002	[6,8]
γ_n	0.088	0.35	0.0568	[6,8]
γ_m	0.096	0.25	0.083	[6,8]
δ_n	0	0	0.0026	[6,8]
δ_m	0	0	0.0005	[6,8]
ν_n	0.366	0.706	0.366	[6,8]
ν_m	0.168	0.549	0.168	[6,8]
ν_v	0.094	0.1	0.094	[36]
μ_v	10000	15000	2000	[36]
$1/d_v$	10	15	27	[36]
a	1.1	1.3	1.5	Assumed
b	1.83	9.43	5.9	Assumed

In order to show that the single disease-free periodic solution E_0 is globally asymptotically stable if the basic reproduction number is less than unity, we provide a couple of examples. Our first example (see Fig. 3), was created with the set of parameters given in Table 2 (see Example 1). We can calculate numerically the basic reproduction number $\mathcal{R}_0 = 0.625 < 1$. In our second example (see Fig. 4), was created with another set of parameters given in Table 2 (see Example 2). Again, we can calculate numerically the basic reproduction number $\mathcal{R}_0 = 0.913 < 1$.

Figs. 3 and 4, show that solution of our model in accordance with the analytic results stating that the unique disease-free periodic solution E_0 is globally asymptotically stable when $\mathcal{R}_0 < 1$.

By Theorem 4.4, system (1) has a positive ω-periodic solution if $\mathcal{R}_0 > 1$. Fig. 5 illustrates the uniform persistence of malaria when $\mathcal{R}_0 = 1.721 > 1$. Accordingly, one can see that, the disease compartments are persistent and the epidemic becomes endemic in the population recurring periodically every year.

5.1. Reproduction numbers

Substituting the (time-changing) parameter values into formulas (12) and (13) provide the reproduction numbers $(\mathcal{R}_0^A, [\mathcal{R}_0])$, respectively, for any time instant.

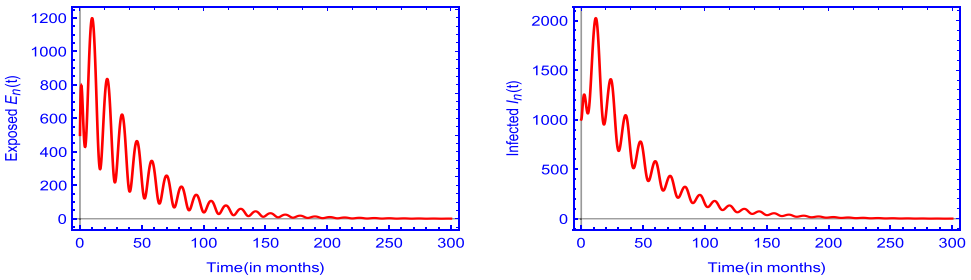
In Figs. 6 and 7, we show the reproduction rate, $\mathcal{R}_0^A$, of the corresponding time-constant system (see Figs. 6(a) and 7(a)) and the time-average basic reproduction rate, $[\mathcal{R}_0]$, of the time-dependent system (see Figs. 6(b) and 7(b)), depending on mosquito birth and death rates, respectively, as well as transmission rates from humans to mosquitoes and mosquitoes to humans. The figures suggest that mosquito control, especially the control of mosquito births, highly influences the transmission of malaria and that control of the mosquito population may be sufficient to control the disease. At the same time, decreasing the mosquito-to-human transmission rates can also efficiently contribute to reduce the basic reproduction number. Fig. 7 (in accordance with Ross' fundamental work [4]) suggests that above a certain level, killing mosquitoes has only a reduced effect.

Numerically, we can plot the reproduction ratio $\mathcal{R}_0$, the time-average reproduction number $[\mathcal{R}_0]$, and the reproduction number $\mathcal{R}_0^A$ of the constant model with respect to mosquito birth rate (μ_v), mosquito-to-human transmission rates (α_n, α_m) and human-to-mosquito transmission rate (α_v), respectively, in Fig. 8.

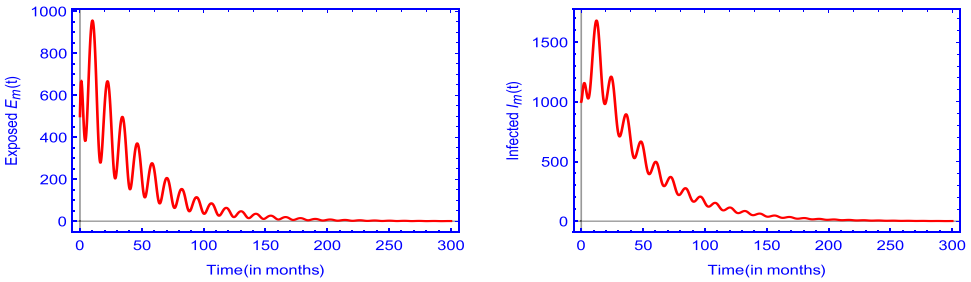
The calculations show that the time-averaged reproduction number $[\mathcal{R}_0]$ is less than the reproduction ratio $\mathcal{R}_0$, suggesting that the time-averaged reproduction number provides an underestimation of the risk of disease transmission. From this aspect, our results are similar to the those in [21] and [37]. We note that various papers present different results on under- and overestimation of the average basic reproduction number. In [38] the authors gave an approximate formula of the reproduction number for a class of epidemic models with vectorial transmission in a seasonal environment with a small perturbation parameter.

6. Discussion

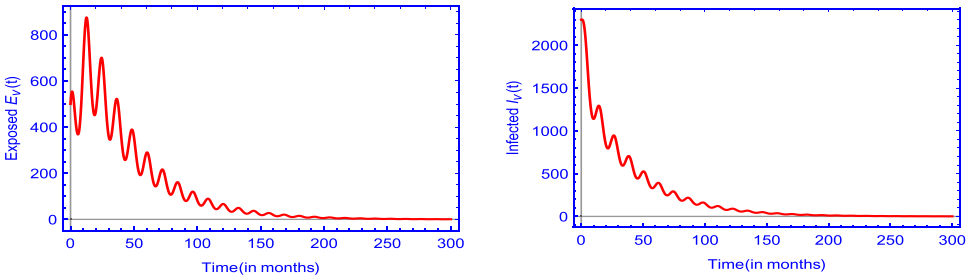
We have established a compartmental model to describe malaria transmission in a seasonal environment with periodic mosquito birth, death and biting rates, where human hosts are divided into two classes: those who do not have any immu-



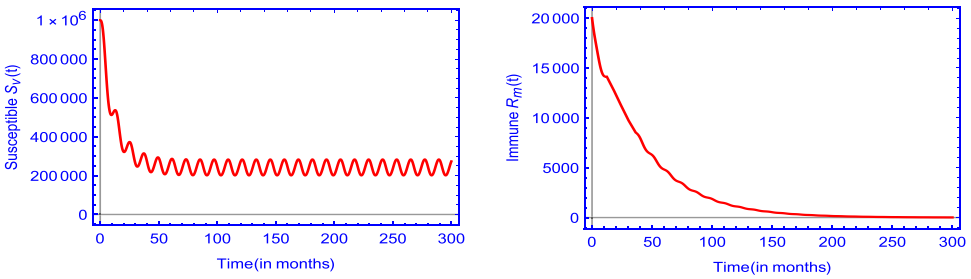
(a) Non-immune.



(b) Semi-immune.

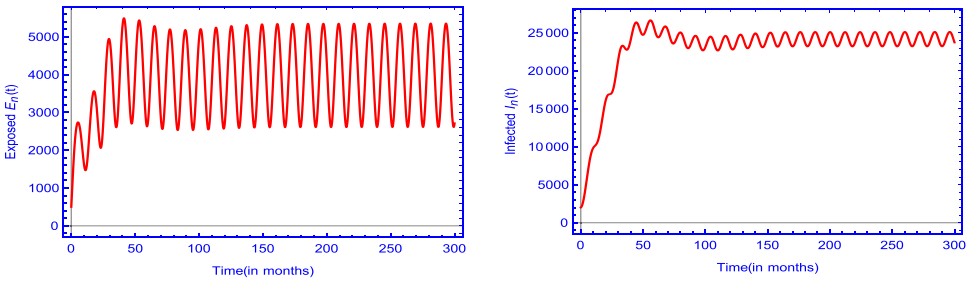


(c) Mosquitoes.

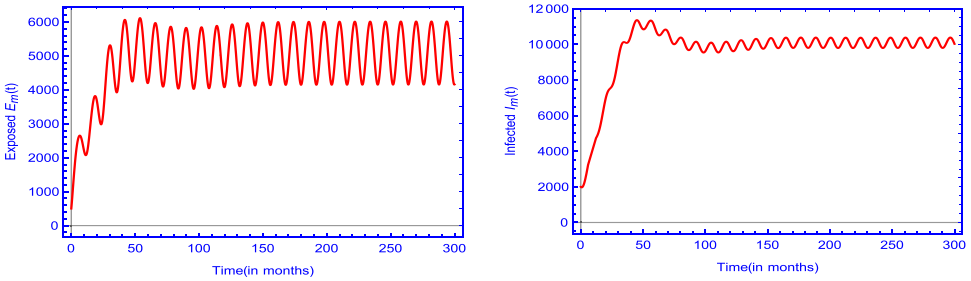


(d) Mosquitoes and semi-immune.

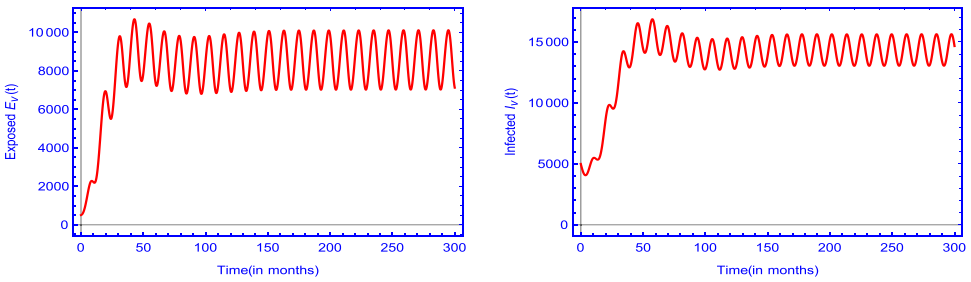
Fig. 4. Extinction of malaria when $\mathcal{R}_0 = 0.913 < 1$ with parameters given in Table 2 (see Example 2).



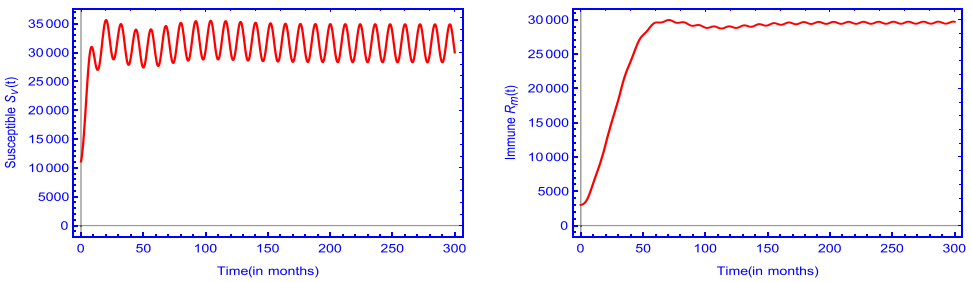
(a) Non-immune.



(b) Semi-immune.

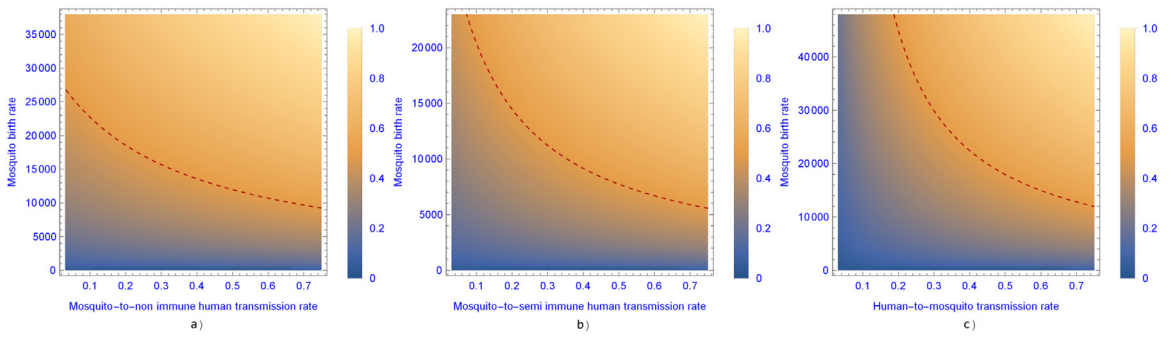


(c) Mosquitoes.

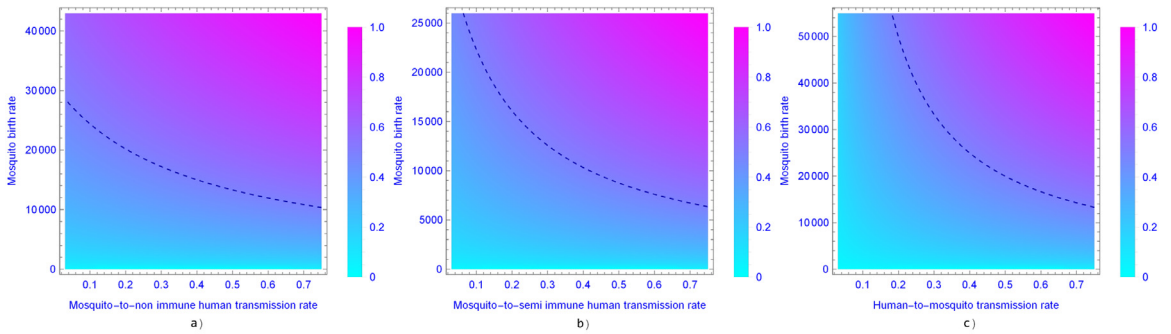


(d) Mosquitoes and semi-immune.

Fig. 5. Persistence of malaria when $\mathcal{R}_0 = 1.721 > 1$ with parameters given in Table 2.



(a)



(b)

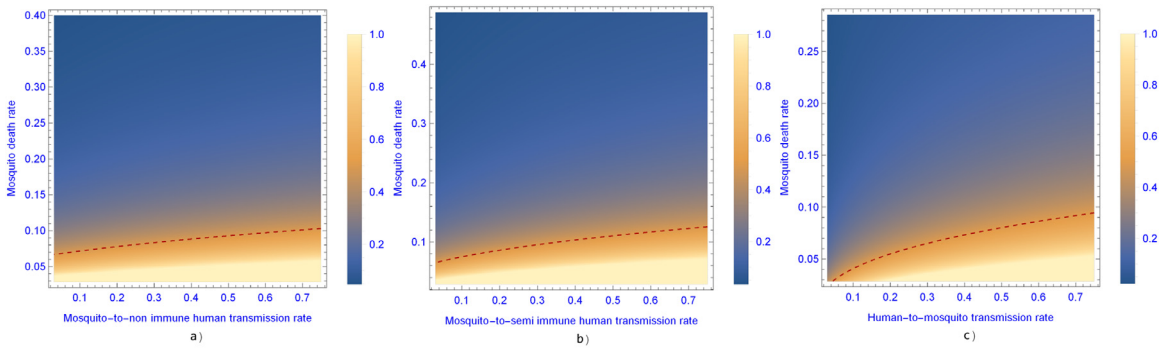
Fig. 6. Contour plot of the basic reproduction number, $\mathcal{R}_0^A$ in (a) and the time-average basic reproduction number, $[\mathcal{R}_0]$ in (b), depending on mosquito birth rate (μ_v) and (a) mosquito-to-non-immune human transmission rate (α_n), (b) mosquito-to-semi-immune human transmission rate (α_m) and (c) human-to-mosquito transmission rate (α_v). The dashed curve is the contour of $\mathcal{R}_0^A = 0.5$ in (a), and $[\mathcal{R}_0] = 0.5$ in (b). Parameter values are given in Table 2 (see Example 1).

nity and those who have a partial immunity due an earlier malaria infection or due to their genetics. Although mathematical modelling of malaria transmission has a quite extensive literature, up to our knowledge, the present one is the first paper to include both partial immunity of humans and periodicity in mosquito vital dynamics. For a disease like malaria, the spread of which is strongly correlated with the size of mosquito populations, it is of special importance to include weather seasonality which highly affects the abundance of vectors. Determining the variance between groups with different level of immunity and applying the more realistic periodic setting might help to understand the different levels of risk the different groups to establish intervention strategies applied to these groups.

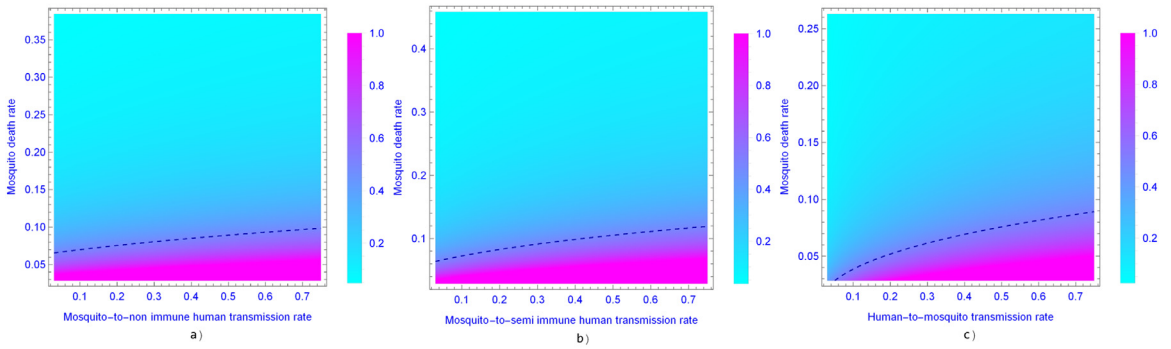
We have shown that the global dynamics of the system is characterized by the reproduction number: if $\mathcal{R}_0 < 1$, we have shown the global asymptotic stability of the disease-free periodic solution E_0, in this case the disease goes extinct. If $\mathcal{R}_0 > 1$, malaria becomes endemic in the population and the existence of at least one positive periodic solution is proved. We have also shown numerical simulations in accordance with these theoretical results (see Figs. 3–5).

The reproduction numbers were calculated as a function of the parameters α_n, α_m, α_v, μ_v and d_v. Our simulations suggest that vector control is an important factor in malaria transmission and that mosquito control, above all the control of mosquito births, may prove to be sufficient in controlling the disease (see Figs. 6 and 7). At the same time, personal protection resulting in a decrease of transmission rates is also an important tool to reduce the basic reproduction number. As is observed, the time-averaged reproduction number $[\mathcal{R}_0]$ is smaller than the reproduction number $\mathcal{R}_0$ (see Fig. 8). This implies that the time-average basic reproduction number provides an underestimation of the risk of disease transmission, while the risk is overestimated in case the basic reproduction number is applied.

Our model has several possibilities for further development. As mentioned above, in regions with high transmission, the most vulnerable are young children, hence an age-structured model could be applied. To incorporate extrinsic incubation period, i.e. the length of the development of the malaria parasite within the mosquito, a time-delayed model could be formulated. Although currently there is no available vaccine against malaria, there are several vaccine constructs under evaluated in clinical trials or in advanced development. Furthermore, there are several medications used to prevent malaria. The (possibly temporary) effect of these currently used medicines or future vaccines can also be incorporated in our model, either by a direct movement from the non-immune to the semi-immune compartment, or by introducing new compartments



(a)



(b)

Fig. 7. Contour plot of the basic reproduction number, $\mathcal{R}_0^A$ in (a) and the time-average basic reproduction number, $[\mathcal{R}_0]$ in (b), depending on mosquito death rate (d_v) and a) mosquito-to-non-immune human transmission rate (α_n), (b) mosquito-to-semi-immune human transmission rate (α_m) and (c) human-to-mosquito transmission rate (α_v). The dashed curve is the contour of $\mathcal{R}_0^A = 0.5$ in (a), and $[\mathcal{R}_0] = 0.5$ in (b). Parameter values are given in Table 2 (see Example 1).

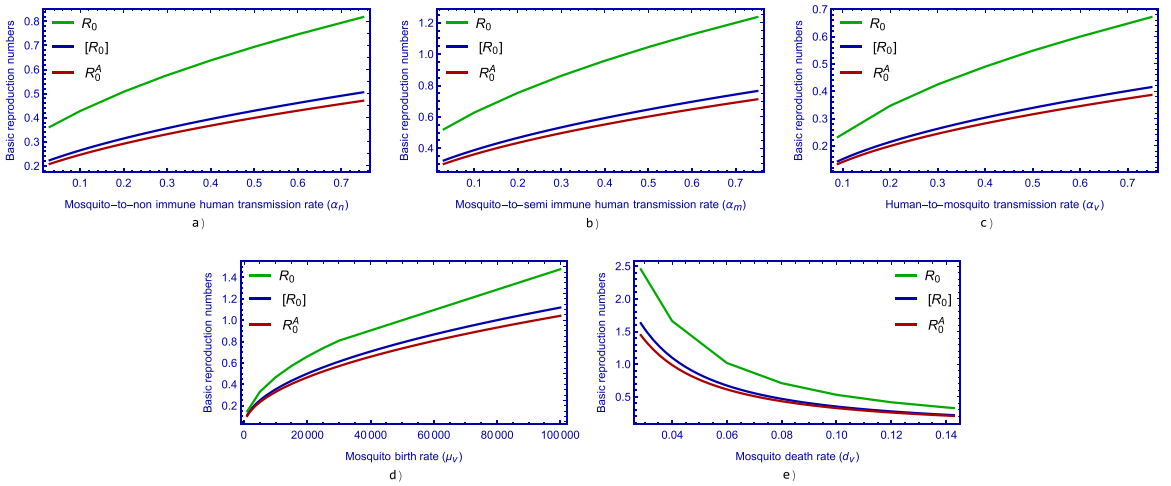


Fig. 8. The curves of the reproduction ratio $\mathcal{R}_0$, the time–averaged reproduction number $[\mathcal{R}_0]$ and the reproduction number of the constant model $\mathcal{R}_0^A$ versus in (a) mosquito-to-non-immune human transmission rate (α_n), (b) mosquito-to-semi-immune human transmission rate (α_m), (c) human-to-mosquito transmission rate (α_v), (d) mosquito birth rate (μ_v) and (e) mosquito death rate (d_v). Parameter values are given in Table 2 (see Example 1).

for the temporary protection obtained by using medication or for the vaccinated population. To make the model more realistic, one could also consider different phases of the mosquitoes' life cycle. These questions might be topics of future research.

Acknowledgments

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