A theoretical approach to understanding population dynamics with seasonal developmental durations [*]

Yijun Lou[1] and Xiao-Qiang Zhao[2]

[1]Department of Applied Mathematics, The Hong Kong Polytechnic University, Hung Hom, Kowloon, Hong Kong. Email: yijun.lou@polyu.edu.hk
[2]Department of Mathematics and Statistics, Memorial University of Newfoundland, St. Johns, NL A1C 5S7, Canada. Email: zhao@mun.ca

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Abstract

There is a growing body of biological investigations to understand impacts of seasonally changing environmental conditions on population dynamics in various research fields such as single population growth and disease transmission. On the other side, understanding the population dynamics subject to seasonally changing weather conditions plays a fundamental role in predicting the trends of population patterns and disease transmission risks under the scenarios of climate change. With the host-macroparasite interaction as a motivating example, we propose a synthesised approach for investigating the population dynamics subject to seasonal environmental variations from theoretical point of view, where the model development, basic reproduction ratio formulation and computation, and rigorous mathematical analysis are involved. The resultant model with periodic delay presents a novel term related to the rate of change of the developmental duration, bringing new challenges to dynamics analysis. By investigating a periodic semiflow on a suitably chosen phase space, the global dynamics of a threshold type is established: all solutions either go to zero when basic reproduction ratio is less than one, or stabilise at a positive periodic state when the reproduction ratio is greater than one. The synthesised approach developed here is applicable to broader contexts of investigating biological systems with seasonal developmental durations.

Keywords: Functional differential equation; periodic delay; seasonal developmental duration; host-parasite interaction; basic reproduction ratio; threshold dynamics
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1 Introduction

The rhythm of life on earth, occurring on daily or annual scales, is driven by seasonal changes in the environment [32] which regulate various physiological and behavioural processes, as well as the population dynamics of species. Many plant and animal species have demonstrated seasonal population dynamics in response to seasonal environmental changes, in particular, the weather conditions.

Mosquito species *Culex pipiens* and *Culex restuans*, main vectors of West Nile virus transmission, are very sensitive to long-term variations in climate and short-term variations in weather [34], in particular, temperature condition affects the rates of immature mosquito development and activity of adults, and precipitation determines the amount and quality of larval habitats. Temperature also affects the host-seeking activity of ticks and their rates from one life stage to the next one, as a result, it is proposed as a statistically significant determinant and possible driver of emergence of the tick in Canada [20]. Seasonal forcing in host and parasite biology also determines the risk of infectious diseases through the following aspects [2]: (a) host social behaviour and aggregation; (b) vector population and activity; (c) parasite stages in the environment; (d) timing of reproduction and pulses of susceptible hosts; and (e) host susceptibility and immune defences.

Given the significant roles that seasonal environment factors play in population growth, disease transmission and other life systems, theoretical models have been formulated to incorporate the seasonality of parameters in phenomenological ways, such as those reported in [2]. Many model parameters in ecosystems are influenced by the environmental conditions in a nonlinear way [19], and in previous models, it is well-accepted to assume the parameters subject to seasonal factors change periodically. For example, a sinusoidal form with period one year

$$\beta(t) = \beta_0(1 + \beta_1 \cos(2\pi t))$$

can be fitted to describe the seasonal transmission term [2]. A growing body of literature reported that the developmental duration can be driven by seasonal forcing, and thus be periodic. For example, the developmental duration of mosquito species *Culex pipiens* and *Culex restuans* is affected by temperature conditions. In the transmission cycle of malaria, the extrinsic incubation period (EIP) of the parasite within the mosquito is one of the most critical parameters to evaluate the disease risk. During EIP, malaria parasites go through various developmental stages and distinct replication cycles before migrating to the salivary glands where they can be transmitted to humans. The speed of this development depends on host, parasite and environmental factors with estimate order of 10-14 days in areas of high malaria transmission. However, 90% of the female mosquitoes die within 12 days and are therefore unlikely to contribute to malaria transmission. On the other side, the extrinsic incubation period is extremely temperature sensitive [21], and hence, it is pivotal to incorporate this seasonally forced incubation period on describing malaria transmission. For these two aforementioned scenarios, the developmental durations for immature mosquitoes and incubation period for parasites are periodic functions of time, which brings new challenges into model formulation where careful mathematical derivation and biological justification are needed. Usually, a delay τ is used to describe the developmental duration from one stage I to another stage M, see, e.g., the following single population growth model with a time-independent developmental duration τ introduced in [1]:

$$\begin{aligned} I'(t) &= bM(t) - \mu I(t) - bM(t-\tau)e^{-\mu\tau}, \\ M'(t) &= bM(t-\tau)e^{-\mu\tau} - dM^2(t). \end{aligned} \quad (1.1)$$

In this model, the term $\mu I(t)$ is the death rate term for stage I and $dM^2(t)$ is the death term for stage M, $bM(t)$ is the birth term to stage I. However, this model can not be directly extended to incorporate the seasonal developmental delay term by simply changing τ into a time-dependent delay $\tau(t)$ to formulate models when the developmental duration $\tau(t)$ varies seasonally. The reader may get surprised to find that the model system involves a term, $1 - \tau'(t)$, related to the rate of change of $\tau(t)$ (see the model system (2.2) in the next section). Moreover, the model system becomes a periodic delay differential system with periodic delays, which adds challenges into theoretical analysis. The purpose of this paper is to propose a synthesised mathematical approach to the study

of biological systems with seasonal forcing, in particular, with seasonal variations on developmental duration.

To present our approach, we use the host-macroparasite interaction as a motivating example. The host-parasite interaction has attracted great attention since the pioneering work of Anderson and May [3], with most models aiming to figure out the basic reproduction number R_0 of parasite (measuring "the expected lifetime reproductive output of a new born larva" for macroparasite [19]). Here we develop a theoretical framework to investigate the population dynamics with time-dependent developmental duration for the parasitic nematodes with a direct life cycle and endotherm hosts [19], but we should point out that this framework can be extended to broader contexts in life science, such as single species population growth, pathogen transmission and in-host viral dynamics, where the developmental duration has various definitions such as the maturation time for species, pathogen incubation duration in epidemiology, the duration for immune system development in immunology, and so on.

This paper is organized as follows. The model is formulated in the next section through careful arguments. Then the basic reproduction ratio R_0 is introduced and the long-term behavior of solutions is investigated in section 3. Numerical simulations are presented in section 4, and a brief discussion section finishes the paper. In the appendix, we show how to write the next generation operator into the integral form in [22] so that the numerical algorithm in that paper remains applicable to R_0 computation here.

2 Model formulation

Before introducing the whole model system for host-parasite interaction, we investigate a two-stage single population growth scenario as a toy example, in the hope of presenting the modelling idea through a simpler case.

2.1 A two-stage population growth model

We start with a two-stage model, with population containing first stage $I(t)$ and second stage $M(t)$ defined, respectively, as those of age less than, and greater than, some threshold age $\tau(t)$ (the maturation time for the cohort that matures at time t), which is assumed to be seasonal due to the seasonal variations of weather conditions. That is, at time t, the individuals with age greater (less) than $\tau(t)$ are in the second stage (remaining in the first stage). Within each age group, all individuals have the same age-independent birth and death rates. Let $\rho(t,a)$ be the population density of age a at time t, then the numbers $I(t)$ and $M(t)$ of individuals in the first and second stages, respectively, are given by

$$I(t) = \int_0^{\tau(t)} \rho(t,a)\,da \quad \text{and} \quad M(t) = \int_{\tau(t)}^{\infty} \rho(t,a)\,da.$$

The age density $\rho(t,a)$ satisfies the following McKendrick von-Foerster type equation [9, 36]

$$\frac{\partial \rho(t,a)}{\partial t} + \frac{\partial \rho(t,a)}{\partial a} = -\mu(a,t)\rho(t,a), \tag{2.1}$$

with the age-dependent death rates

$$\mu(a,t) = \mu_1(t) \text{ if } a \leq \tau(t) \quad \text{and} \quad \mu(a,t) = \mu_2(t) \text{ if } a > \tau(t).$$

Taking the derivatives of $I(t)$ and $M(t)$, and using (2.1), we obtain

$$
\begin{array}{rcl}
\frac{dI(t)}{dt} & = & \rho(t,0) - (1 - \tau'(t))\rho(t,\tau(t)) - \mu_1(t)I(t), \\
\frac{dM(t)}{dt} & = & (1 - \tau'(t))\rho(t,\tau(t)) - \mu_2(t)M(t) - \rho(t,\infty).
\end{array}
$$

Since no individual can live forever, $\rho(t,\infty)$ is taken as zero. The term $\rho(t,0)$ represents the flow in rate to the first stage at time t, supposed to be $\rho(t,0) = b(t) = B(t,M(t))$, a function of time t and population density $M(t)$. Mathematically, we also assume the delay $\tau(t)$ involved is continuously differentiable in $[0,\infty)$ and bounded away from zero and infinity. To close the system, we calculate $\rho(t,\tau(t))$ in terms of $\rho(t-\tau(t),0) = b(t-\tau(t)) = B(t-\tau(t),M(t-\tau(t)))$ which is achieved by the technique of integration along characteristics with the aid of the variable $V^s(t) = \rho(t, t-s)$. By direct calculations, we arrive at

$$
\frac{d}{dt}V^s(t) = -\mu_1(t)V^s(t)
$$

for $t - s \le \tau(t)$, with $V^s(s) = \rho(s,0) = b(s)$. It follows that

$$
V^s(t) = V^s(s)e^{-\int_s^t \mu_1(\xi)\,d\xi} = B(s,M(s))e^{-\int_s^t \mu_1(\xi)\,d\xi}.
$$

Setting $s = t - \tau(t)$, we have, for $t \ge \hat{\tau}$ with $\hat{\tau} = \max\{\tau(t)\}$,

$$
\rho(t,\tau(t)) = V^{t-\tau(t)}(t) = B(t-\tau(t),M(t-\tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi)\,d\xi}.
$$

Hence, we obtain a closed system to describe two age groups subject to seasonal effects when $t \ge \hat{\tau}$:

$$
\begin{array}{rcl}
\frac{dI(t)}{dt} & = & B(t,M(t)) - (1 - \tau'(t))B(t-\tau(t),M(t-\tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi)\,d\xi} \\
 & & -\mu_1(t)I(t), \\
\frac{dM(t)}{dt} & = & (1 - \tau'(t))B(t-\tau(t),M(t-\tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi)\,d\xi} - \mu_2(t)M(t).
\end{array}
\tag{2.2}
$$

This model turns out to be a differential system with periodic time delay, which is different from previous work without seasonal effects (see, e.g., system (1.1) and those models in [29]) in the sense that the term $1 - \tau'(t)$ is included in the development rate from the first stage to the next one

$$
(1 - \tau'(t))B(t-\tau(t),M(t-\tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi)\,d\xi}.
\tag{2.3}
$$

An alternative approach, more biologically oriented, to describe the population growth of two stages (especially the maturation term (2.3)) is also feasible. The first stage population size $I(t)$ at time t counts all accumulation of individuals born at moment ξ with rate $b(\xi)$ between $t - \tau(t)$ to t but remain alive with the survival probability $e^{-\int_\xi^t \mu_1(s)\,ds}$. Intuitively, the size $I(t)$ depends on the duration of $\tau(t)$ for individuals staying in the first stage. Motivated by these biological inductions, we can represent $I(t)$ into an integral form

$$
I(t) = \int_{t-\tau(t)}^t b(\xi)e^{-\int_\xi^t \mu_1(s)\,ds}\,d\xi.
$$

Taking the derivative of $I(t)$, we get the differential equation version of this variable in the first equation of (2.2). The maturation rate should be the birth rate at time $t - \tau(t)$, $b(t - \tau(t))$, multiplied with survival probability to time t, $e^{-\int_{t-\tau(t)}^t \mu_1(s)\,ds}$ and corrected with the rate of change for $t - \tau(t)$.

In parameterizing the delay $\tau(t)$, the developmental proportion $r(\xi)$ at time ξ is taken into consideration (see [38] and subsection 4.1 for estimation of the developmental proportion) such that the accumulative proportion from $t - \tau(t)$ to t reaches unity when the individual moves to the next stage. Theoretically, we use the following relation to determine $\tau(t)$

$$1 = \int_{t-\tau(t)}^{t} r(\xi)d\xi, \tag{2.4}$$

where $r(\xi)$ is the time-periodic development proportion at moment ξ. The periodicity of $r(\xi)$ in ξ implies the periodicity of the delay $\tau(t)$ in time variable t. Taking the derivative with respect to t, we have

$$0 = r(t) - (1 - \tau'(t))r(t - \tau(t))$$

from which we can get

$$1 - \tau'(t) = \frac{r(t)}{r(t - \tau(t))},$$

and hence, the conversion rate in (2.3) can be expressed as

$$\frac{r(t)}{r(t - \tau(t))}b(t - \tau(t))e^{-\int_{t-\tau(t)}^{t} \mu_1(\xi)\,d\xi}.$$

Thanks to this relation, we can always assume that $1 - \tau'(t) > 0$ for any biologically reasonable developmental delay. One interesting scenario for the relationship $1 - \tau'(t) > 0$ in plain language is addressed in [8] to project this inherent relationship to a real life situation. A similar term has been derived in a state-dependent delay system in the recent work by Kloosterman, Campbell and Poulin [15].

A similar term was formulated in models proposed by Barbarossa, Hadeler and Kuttler [8] and Wu et al. [39] as well as some others, see, e.g., [18] and references therein, to describe the population growth with threshold age τ depending on time t. The introduction of the term $1 - \tau'(t)$ is due to the incorporation of state-dependent delay in [8, 15]. Another biologically motivated approach to get the similar term can be derived by following the idea in [18]. We reformulate the similar terms here as a part of modelling process to develop the whole model system. In the next subsection, we extend the two-stage model (2.2) to describe host-parasite interaction, where the parasite developmental duration is dependent on time.

2.2   The model for host-parasite interaction

We extend the fundamental modelling frameworks proposed by Anderson and May [3] and Dobson and Hudson [10] by considering four stages (see Fig 1): Free living larvae not infective $X(t)$, free living larvae infective $L(t)$, arrested larvae in the host $Y(t)$ and adult parasites $P(t)$. We are concerned with two delays in the parasite life cycle, one in the free-living stage and the other within the host population: (i) the developmental delay $\tau_L(t)$ between the moment when newly shed parasites enter the environment and the moment they reach the infective larval stage and (ii) the time period $\tau_P(t)$ needed for the arrested larvae infecting the host to develop to pathogenic adults [10]. Since the development time to the infectivity stage depends on metabolic rate, and hence the temperature condition, we assume the developmental duration is a time-periodic parameter with period one year (365 days) as temperature changes seasonally [19]. Much attention should be paid to estimate these time-dependent delays and we will employ a theoretically rigorous and well-accepted approach as shown in the equation (4.2) in Section 4. Other life cycle components may also be temperature-dependent, and therefore, be periodic in time t.
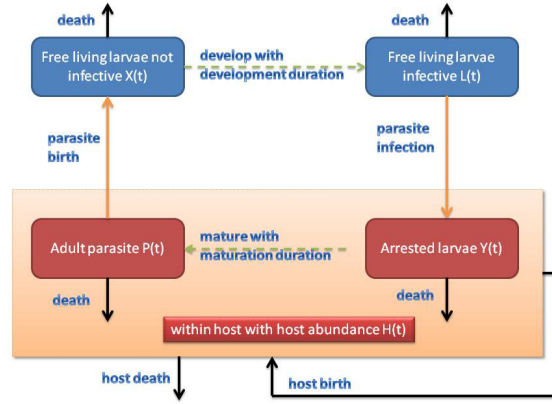
Figure 1: Schematic diagram for the parasite life cycle. Arrows show the rates for host $H(t)$ and parasite in four distinct stages. Solid arrows indicate the rates for gains and losses to respective compartment while dashed arrows represent developmental time delays for development from new born to infective larvae $\tau_L(t)$ in the free living stage and the length of prepatent period $\tau_P(t)$ within the host.

Host population dynamics may be regulated by parasites, which is a crucial assumption for some host-parasite models [24]. However, in the current project we are more concerned with the reproduction ratio analysis, and therefore, we ignore the host survival or fecundity affected by the arrested parasite since the metabolic activity in arrested larvae is very low [10]. This assumption becomes much more reasonable for farmed animal hosts, which density is largely controlled by the farm owner [24]. Therefore, the host population $H(t)$ is considered to be seasonal, analogous to those constant host population assumptions in notable papers [25, 26] and recent work [31]. We defer inclusion of the host abundance dynamics to the discussion section, which justifies that the analytic results remain valid under such an assumption.

Based on the diagram (Fig 1) and conversion rate on incorporating the periodic delays (2.3), we can write down the model system as follows:

$$\frac{dX(t)}{dt} = \lambda P(t) - \mu_X(t)X(t) - \lambda(1-\tau_L'(t))P(t-\tau_L(t))e^{-\int_{t-\tau_L(t)}^{t}\mu_X(\xi)\,d\xi}, \tag{2.5a}$$

$$\frac{dL(t)}{dt} = \lambda(1-\tau_L'(t))P(t-\tau_L(t))e^{-\int_{t-\tau_L(t)}^{t}\mu_X(\xi)\,d\xi} - \mu_L(t)L(t) - \beta(t)H(t)L(t), \tag{2.5b}$$

$$\frac{dY(t)}{dt} = \beta(t)H(t)L(t) - (\mu_Y(t)+\mu_H(t))Y(t) \tag{2.5c}$$

$$\qquad -(1-\tau_P'(t))\beta(t-\tau_P(t))H(t-\tau_P(t))e^{-\int_{t-\tau_P(t)}^{t}(\mu_Y(\xi)+\mu_H(\xi))\,d\xi}L(t-\tau_P(t)),$$

$$\frac{dP(t)}{dt} = (1-\tau_P'(t))\beta(t-\tau_P(t))H(t-\tau_P(t))e^{-\int_{t-\tau_P(t)}^{t}(\mu_Y(\xi)+\mu_H(\xi))\,d\xi}L(t-\tau_P(t))$$

$$\qquad -(\mu_P(t)+\mu_H(t))P(t) - \alpha_H\left(1+\frac{P(t)}{H(t)}\frac{k+1}{k}\right)P(t). \tag{2.5d}$$

System (2.5) describes the change of densities for the four compartments: (i) The free living larvae $X(t)$ are regained though the birth of adult parasite at rate λ, lost by either mortality (at rate $\mu_X(t)$) or development to free living infected larvae (the last term of equation (2.5a)); (ii) The density of free living infected larvae $L(t)$ increases from the development of non infected larvae (the first term of equation (2.5b)) and decreases with the death rate $\mu_L(t)$ and host uptake at rate $\beta(t)H(t)$, which is dependent on the host population $H(t)$; (iii) Ingested larvae $Y(t)$ enter the host population with rate $\beta(t)H(t)$. They stay in the host for $\tau_P(t)$ unit time, which is the developmental duration from infecting larvae to adult parasite. The development rate to adult

parasite is described in the last term of equation (2.5c). Their density decreases due to the natural death rate $\mu_Y(t)$ and host death rate $\mu_H(t)$ as the larvae will also die when hosts die; (iv) The density of adult parasites $P(t)$ increases with the development from larvae (first term of (2.5d)), decreases with the mortality, both the natural death at rate $\mu_P(t)$ and host death at rate $\mu_H(t)$. The burden of adult parasite also decreases due to the aggregated distribution of parasites in the host population, by assuming the distribution of parasites within the host population to be negative binomial with exponent k (also known as aggregation parameter) [3]. As argued previously, we can replace $(1 - \tau_L'(t))$ and $(1 - \tau_P'(t))$, respectively, with the developmental proportions

$$1 - \tau_L'(t) = \frac{r_L(t)}{r_L(t - \tau_L(t))} \text{ and } 1 - \tau_P'(t) = \frac{r_P(t)}{r_P(t - \tau_P(t))},$$

where $r_L(t)$ and $r_P(t)$ are the corresponding developmental proportions.

3   The threshold dynamics

In this section, we first introduce the basic reproduction ratio R_0 for model (2.5), and then establish a threshold type result on its global dynamics. We postpone the numerical algorithm for the computation of R_0 to the Appendix.

3.1   The basic reproduction ratio R_0

In system (2.5), the equations (2.5a) and (2.5c) can be decoupled since variables X and Y do not appear in the other two equations. Therefore, we start with the decoupled system:

$$\begin{aligned}
\frac{dL}{dt} &= \lambda(1 - \tau_L'(t))e^{-\int_{t-\tau_L(t)}^{t} \mu_X(\xi)\,d\xi} P(t - \tau_L(t)) - \mu_L(t)L(t) - \beta(t)H(t)L(t), \\
\frac{dP}{dt} &= (1 - \tau_P'(t))\beta(t - \tau_P(t))H(t - \tau_P(t))e^{-\int_{t-\tau_P(t)}^{t} (\mu_Y(\xi) + \mu_H(\xi))\,d\xi} L(t - \tau_P(t)) \\
&\quad - (\mu_P(t) + \mu_H(t))P(t) - \alpha_H\left(1 + \frac{P(t)}{H(t)}\frac{k+1}{k}\right)P(t).
\end{aligned} \tag{3.1}$$

Note that system (3.1) is the model[1] proposed in [19], which motivated us to work on the analysis from mathematical point of view. Actually, we can rewrite the other two variables into integral forms:

$$\begin{aligned}
X(t) &= \int_{t-\tau_L(t)}^{t} \lambda P(\xi)e^{-\int_{\xi}^{t} \mu_X(s)\,ds}\,d\xi, \\
Y(t) &= \int_{t-\tau_P(t)}^{t} \beta(\xi)H(\xi)L(\xi)e^{-\int_{\xi}^{t}(\mu_Y(s) + \mu_H(s))\,ds}\,d\xi.
\end{aligned} \tag{3.2}$$

Once the dynamics of two variables $L(t)$ and $P(t)$ are obtained, that of $X(t)$ and $Y(t)$ can be deduced naturally. The dynamics of the full system (2.5) will be discussed in the next subsection.

To address the well-posedness of system (3.1), we introduce some notations. Let $\hat{\tau} = \max\{\max_{t\in[0,\omega]} \tau_L(t), \max_{t\in}$ and $\mathcal{X} := C([-\hat{\tau}, 0], \mathbb{R}^2)$ equipped with the maximum norm. For a function $x(\cdot) \in C([-\hat{\tau}, \infty), \mathbb{R}^2)$, we can define $x_t \in \mathcal{X}$ as $x_t(\theta) = x(t + \theta), \forall \theta \in [-\hat{\tau}, 0]$. For any $\phi \in \mathcal{X}$, we define $f(t, \phi) = (f_1(t, \phi), f_2(t, \phi))$ with

$$f_1(t, \phi) = \lambda(1 - \tau_L'(t))e^{-\int_{t-\tau_L(t)}^{t} \mu_X(\xi)\,d\xi}\phi_2(-\tau_L(t)) - \mu_L(t)\phi_1(0) - \beta(t)H(t)\phi_1(0),$$

$$\begin{aligned}
f_2(t, \phi) = \ &(1 - \tau_P'(t))\beta(t - \tau_P(t))H(t - \tau_P(t))e^{-\int_{t-\tau_P(t)}^{t}(\mu_Y(\xi) + \mu_H(\xi))\,d\xi}\phi_1(-\tau_P(t)) \\
&- (\mu_P(t) + \mu_H(t) + \alpha_H)\phi_2(0) - \frac{k+1}{k}\frac{\alpha_H}{H(t)}\phi_2^2(0).
\end{aligned}$$

---

[1]In the model system of [19], L should be $L(t - \tau_P)$ in the equation (8b), as well as in (1b).

Due to the ω-periodicity of $\tau_L(t)$, $\mu_L(t)$, $\beta(t)$, $H(t)$, $\tau_P(t)$, $\mu_P(t)$, and $\mu_H(t)$, it is easy to see that $f(t + \omega, \phi) = f(t, \phi)$. Thus, (3.1) is an ω- periodic functional differential system. For notational simplicity, we rewrite system (3.1) into

$$
\begin{aligned}
\frac{dL}{dt} &= b_L(t)P(t - \tau_L(t)) - d_L(t)L(t), \\
\frac{dP}{dt} &= b_P(t)L(t - \tau_P(t)) - d_P(t)P(t) - \alpha(t)P^2(t),
\end{aligned}
\tag{3.3}
$$

with the following combinations

$$
b_L(t) = \lambda(1 - \tau_L'(t))e^{-\int_{t-\tau_L(t)}^{t} \mu_X(\xi)\, d\xi}, \quad d_L(t) = \mu_L(t) + \beta(t)H(t),
$$

$$
b_P(t) = (1 - \tau_P'(t))\beta(t - \tau_P(t))H(t - \tau_P(t))e^{-\int_{t-\tau_P(t)}^{t}(\mu_Y(\xi)+\mu_H(\xi))\, d\xi},
$$

$$
d_P(t) = \mu_P(t) + \mu_H(t) + \alpha_H, \quad \text{and} \quad \alpha(t) = \frac{\alpha_H(k+1)}{kH(t)}.
$$

Clearly, all these coefficients are positive ω-periodic functions.

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

$$
\hat{g} = \max_{t \in [0,\omega]} g(t), \qquad \overline{g} = \min_{t \in [0,\omega]} g(t).
$$

The following result shows that system (3.1) is well-posed on

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

and hence, the derived model system is also biologically reasonable.

Lemma 3.1. *For any $\phi = (\phi_1, \phi_2) \in \mathcal{X}_+$, system (3.1) has a unique nonnegative and bounded solution $v(t, \phi)$ with $v_0 = \phi$ on $[0, \infty)$.*

Proof. Note that $f(t, \phi)$ is continuous and Lipschitzian in ϕ in each compact subset of $\mathcal{X}_+$. It follows that for any $\phi \in \mathcal{X}_+$, system (3.1) admits a unique solution $u(t, \phi)$ with $u_0 = \phi$ on its maximal interval of existence. Let $x^* = (x_1^*, x_2^*) := \left(\frac{\hat{b}_L}{\overline{d}_L} \frac{\hat{b}_p \hat{b}_L}{\overline{\alpha} \overline{d}_L}, \frac{\hat{b}_p \hat{b}_L}{\overline{\alpha} \overline{d}_L} \right)$. For any given $\rho \geq 1$, let $[0, \rho x^*]_{\mathcal{X}}$ be the order interval in $\mathcal{X}$, that is,

$$
[0, \rho x^*]_{\mathcal{X}} := \{\phi \in \mathcal{X} : 0 \leq \phi(\theta) \leq \rho x^*, \forall \theta \in [-\hat{\tau}, 0]\}.
$$

It is easy to verify that whenever $\psi \in [0, \rho x^*]_{\mathcal{X}}$, $t \in \mathbb{R}$, and $\psi_i(0) = 0$ $(\psi_i(0) = \rho x_i^*)$ for some i, then $f_i(t, \psi) \geq 0$ $(f_i(t, \psi) \leq 0)$. By [30, Theorem 5.2.1 and Remark 5.2.1], it follows that $[0, \rho x^*]_{\mathcal{X}}$ is positively invariant for system (3.1). Since ρ can be chosen as large as we wish, this proves the positivity and boundedness of solutions in $\mathcal{X}_+$. $\qquad\square$

The basic reproduction ratio has been extensively studied over the decades for autonomous models of disease transmission, and it has been extended to various epidemic models with periodic coefficients (see, e.g., [5, 6, 7, 13, 23, 33, 35, 39, 40] and references therein). Below we will use the recent theory developed in [42] to introduce the basic reproduction ratio for our model system with periodic time delays.

The parasite free state of the system is $(0,0)$ and the corresponding linearized system for system (3.3) is

$$
\begin{aligned}
\frac{dL}{dt} &= b_L(t)P(t - \tau_L(t)) - d_L(t)L(t), \\
\frac{dP}{dt} &= b_P(t)L(t - \tau_P(t)) - d_P(t)P(t).
\end{aligned}
\tag{3.4}
$$

Let

$$F(t) \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} = \begin{pmatrix} b_L(t)\phi_2(-\tau_L(t)) \\ b_P(t)\phi_1(-\tau_P(t)) \end{pmatrix} \text{ and } V(t) = \begin{pmatrix} d_L(t) & 0 \\ 0 & d_P(t) \end{pmatrix}.$$

Then the linear system (3.4) can be written as

$$\frac{du(t)}{dt} = F(t)u_t - V(t)u(t), \quad \forall t \geq 0.$$

Note that $F(t)$ and $V(t)$ are ω-periodic in t and the newly "birth" parasites is described by $F(t)$ while the growth of the parasites except birth is described by the following evolution system

$$\frac{du(t)}{dt} = -V(t)u(t).$$

Let $Z(t,s)$, $t \geq s$, be the evolution matrix of the above linear system. That is, for each $s \in \mathbb{R}$, the 2×2 matrix $Z(t,s)$ satisfies

$$\frac{d}{dt}Z(t,s) = -V(t)Z(t,s), \quad \forall t \geq s, \quad Z(s,s) = I,$$

where I is the 2×2 identity matrix. Clearly, we have

$$Z(t,s) = \begin{pmatrix} e^{-\int_s^t d_L(\xi)d\xi} & 0 \\ 0 & e^{-\int_s^t d_P(\xi)d\xi} \end{pmatrix}.$$

Recall that the exponential growth bound of $Z(t,s)$ is defined as

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

It is easy to see that $\Omega(Z) \leq -\min\{\overline{d}_L, \overline{d}_P\}$. Therefore, $F(t)$ and $V(t)$ satisfy the following assumptions in [42]:

(H1) $F(t) : \mathcal{X} \to \mathbb{R}^2$ is positive in the sense that $F(t)\mathcal{X}_+ \subseteq \mathbb{R}_+^2$;

(H2) The periodic matrix $-V(t)$ is cooperative, and $\Omega(Z) < 0$.

Let C_ω be the Banach space of all ω-periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$, equipped with the maximum norm and the positive cone $C_\omega^+ := \{u \in C_\omega : u(t) \geq 0, \ \forall t \in \mathbb{R}\}$. Suppose $v \in C_\omega$ is the initial distribution of larval and adult parasites in this periodic environment, then $F(t-s)v_{t-s}$ is the distribution of newly born parasites at time $t - s$ with $t \geq s \geq 0$, and $Z(t, t-s)F(t-s)v_{t-s}$ represents the distribution of those parasites who were newly reproduced at time $t - s$ and still survive in the environment at time t for $t \geq s$. Hence,

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

gives the distribution of accumulative parasite burden at time t produced by those parasites introduced at all previous time.

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

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

According to [42], the basic reproduction ratio is $R_0 := r(L)$, the spectral radius of L.

For any given $t \geq 0$, let $W(t)$ be the time-t map of the linear periodic system (3.4) on $\mathcal{X}$, that is, $W(t)\phi = w_t(\phi)$, where $w(t, \phi)$ is the unique solution of (3.4) with $w_0 = \phi \in \mathcal{X}$. By [42, Theorem 2.1], we have the following result, which indicates that $R_0 - 1$ is a threshold value for the stability of the zero solution of system (3.4).

Lemma 3.2. $R_0 - 1$ *has the same sign as* $r(W(\omega)) - 1$.

Based on this lemma, we can characterise the global dynamics of the model system by R_0, which will be investigated in the next subsection.

3.2 The global dynamics in terms of R_0

To study the global dynamics of the model system in terms of R_0, our strategy is to use the theory of monotone and subhomogeneous semiflows (see, e.g., [41, Section 2.3]). We start with a new phase space on which system (3.1) generates an eventually strongly monotone periodic semiflow.

Let
$$\mathcal{Y} := C([-\tau_P(0), 0], \mathbb{R}) \times C([-\tau_L(0), 0], \mathbb{R}),$$
and
$$\mathcal{Y}_+ := C([-\tau_P(0), 0], \mathbb{R}_+) \times C([-\tau_L(0), 0], \mathbb{R}_+).$$

Then $(\mathcal{Y}, \mathcal{Y}_+)$ is an ordered Banach space. For a continuous function $u : [-\tau_P(0), +\infty) \times [-\tau_L(0), +\infty) \to \mathbb{R}^2$ and $t \geq 0$, we define $u_t \in \mathcal{Y}$ by

$$(u_t)_1(\theta) = u_1(t + \theta), \ \forall \theta \in [-\tau_P(0), 0], \quad (u_t)_2(\eta) = u_2(t + \eta), \ \forall \eta \in [-\tau_L(0), 0].$$

Lemma 3.3. *For any* $\phi \in \mathcal{Y}_+$, *system* (3.3) *admits a unique nonnegative solution* $u(t, \phi)$ *on* $[0, \infty)$ *with* $u_0 = \phi$.

Proof. Let $\bar{\tau} = \min\{\bar{\tau}_L, \bar{\tau}_P\}$. For any $t \in [0, \bar{\tau}]$, since $t - \tau_L(t)$ is strictly increasing, we have

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

and hence
$$P(t - \tau_L(t)) = \phi_2(t - \tau_L(t)).$$
Similarly,
$$L(t - \tau_P(t)) = \phi_1(t - \tau_P(t)).$$

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

$$\frac{dL}{dt} = b_L(t)\phi_2(t - \tau_L(t)) - d_L(t)L(t),$$
$$\frac{dP}{dt} = b_P(t)\phi_1(t - \tau_P(t)) - d_P(t)P(t) - \alpha(t)P^2(t).$$

Given $\phi \in \mathcal{Y}_+$, the solution $(L(t), P(t))$ of the above system exists for $t \in [0, \bar{\tau}]$. In other words, we obtain the values of $u_1(\theta) = L(\theta)$ for $\theta \in [-\tau_P(0), \bar{\tau}]$ and $u_2(\eta) = P(\eta)$ for $\eta \in [-\tau_L(0), \bar{\tau}]$.

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

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

and hence, $P(t - \tau_L(t)) = u_2(t - \tau_L(t))$ is known. Similarly, $L(t - \tau_P(t)) = u_1(t - \tau_P(t))$ is also given from the previous step. Solving the following ordinary differential system for $t \in [\bar{\tau}, 2\bar{\tau}]$ with $L(\bar{\tau}) = u_1(\bar{\tau})$ and $P(\bar{\tau}) = u_2(\bar{\tau})$:

$$\frac{dL}{dt} = b_L(t)u_2(t - \tau_L(t)) - d_L(t)L(t),$$
$$\frac{dP}{dt} = b_P(t)u_1(t - \tau_P(t)) - d_P(t)P(t) - \alpha(t)P^2(t),$$

we then get the solution $(L(t), P(t))$ on the interval $[\bar{\tau}, 2\bar{\tau}]$.

We can extend this procedure to $[n\bar{\tau}, (n+1)\bar{\tau}]$ for all $n \in \mathbb{N}$. It then follows that for any initial data $\phi \in \mathcal{Y}_+$, the solution $(L(t), P(t))$ exists uniquely for all $t \geq 0$. $\qquad \square$

Remark 3.4. *By the uniqueness of solutions in Lemmas 3.1 and 3.3, it follows that for any $\psi \in \mathcal{X}_+$ and $\phi \in \mathcal{Y}_+$ with $\psi_1(\theta) = \phi_1(\theta), \forall \theta \in [-\tau_P(0), 0]$ and $\psi_2(\eta) = \phi_2(\eta), \forall \eta \in [-\tau_L(0), 0]$, then $u(t, \phi) = v(t, \psi), \forall t \geq 0$, where $u(t, \phi)$ and $v(t, \psi)$ are solutions of system (3.3) satisfying $u_0 = \phi$ and $v_0 = \psi$, respectively.*

Lemma 3.5. *Let $Q_t(\phi) = u_t(\phi), t \geq 0$. Then Q_t is an ω-periodic semiflow on $\mathcal{Y}_+$ in the sense that (i) $Q_0 = I$; (ii) $Q_{t+\omega} = Q_t \circ Q_\omega, \forall t \geq 0$; and (iii) $Q_t(\phi)$ is continuous in $(t, \phi) \in [0, \infty) \times \mathcal{Y}_+$.*

Proof. Clearly, property (i) holds true, and property (iii) follows from a standard argument. It suffices to prove (ii). Denote $v(t) = u(t + \omega, \phi)$, we need to show that $v(t) = u(t, u_\omega\phi), \forall t \geq 0$. To do this, we first check

$$\begin{aligned}
\frac{dv_1(t)}{dt} &= \frac{du_1(t + \omega, \phi)}{dt} \\
&= b_L(t + \omega)u_2(t + \omega - \tau_L(t + \omega), \phi) - d_L(t + \omega)u_1(t + \omega, \phi) \\
&= b_L(t)u_2(t + \omega - \tau_L(t + \omega), \phi) - d_L(t)u_1(t + \omega, \phi) \\
&= b_L(t)v_2(t - \tau_L(t), \phi) - d_L(t)v_1(t, \phi).
\end{aligned}$$

Similarly, we have

$$\frac{dv_2(t)}{dt} = b_P(t)v_1(t - \tau_P(t), \phi) - d_P(t)v_2(t, \phi) - \alpha(t)(v_2(t, \phi))^2.$$

This shows that $v(t)$ is also a solution of system (3.3). Moreover, we have $v_1(\theta) = u_1(\theta + \omega, \phi)$ for $\theta \in [-\tau_P(0), 0]$ and $v_2(\eta) = u_2(\eta + \omega, \phi)$ for $\eta \in [-\tau_L(0), 0]$. On the other side, let $w(t) = u(t, u_\omega\phi)$, then $w(t)$ is also a solution of system (3.3), and $w_1(\theta) = u_1(\theta, u_\omega\phi) = u_\omega(\phi)_1(\theta) = u_1(\theta + \omega, \phi)$ for $\theta \in [-\tau_P(0), 0]$ and $w_2(\eta) = u_2(\eta, u_\omega\phi) = u_\omega(\phi)_2(\eta) = u_2(\eta + \omega, \phi)$ for $\eta \in [-\tau_L(0), 0]$. Thus, $v(t)$ and $w(t)$ are solutions of system (3.3) with the same initial data. By the uniqueness of solutions, we see that $v(t) = w(t), \forall t \geq 0$, that is,

$$u(t + \omega, \phi) = u(t, u_\omega\phi), \quad \forall t \geq 0.$$

For any $t \geq 0$ and $\theta \in [-\tau_P(0), 0]$, if $t + \theta \geq 0$, we have $u_1(t + \theta + \omega, \phi) = u_1(t + \theta, u_\omega\phi)$, that is, $u_{t+\omega}(\phi)_1(\theta) = u_t \circ u_\omega(\phi)_1(\theta)$; if $t + \theta < 0$, then $u_1(t + \theta, u_\omega\phi) = u_\omega(\phi)_1(t + \theta) = u_1(t + \theta + \omega, \phi)$, which also implies $u_t \circ u_\omega(\phi)_1(\theta) = u_{t+\omega}(\phi)_1(\theta)$. Similarly, we can show that $u_t \circ u_\omega(\phi)_2(\eta) = u_{t+\omega}(\phi)_2(\eta)$ for all $\eta \in [-\tau_L(0), 0]$ and $t \geq 0$. It then follows that $u_t \circ u_\omega(\phi) = u_{t+\omega}(\phi)$, and hence, $Q_{t+\omega}(\phi) = Q_t \circ Q_\omega(\phi)$ for all $\phi \in \mathcal{Y}_+$ and $t \geq 0$. $\qquad \square$

The following two lemmas indicate that the periodic semiflow Q_t is eventually strongly monotone and strictly subhomogeneous.

Lemma 3.6. *For any ϕ and ψ in $\mathcal{Y}_+$ with $\phi > \psi$ (that is, $\phi \geq \psi$ but $\phi \neq \psi$), the solutions $u(t)$ and $v(t)$ of system (3.3) with $u_0 = \phi$ and $v_0 = \psi$, respectively, satisfy $u_i(t) > v_i(t)$ for all $t > 2\hat{\tau}$, $i = 1, 2$, and hence, $Q_t(\phi) \gg Q_t(\psi)$ in $\mathcal{Y}$ for all $t > 3\hat{\tau}$.*

Proof. As in the proof of Lemma 3.3, a simple comparison argument on each interval $[n\bar{\tau}, (n+1)\bar{\tau}]$, $n \in \mathbb{N}$, implies that $u_i(t) \geq v_i(t)$ for all $t \geq 0$. By Lemma 3.1 and Remark 3.4, both $u(t)$ and $v(t)$ are bounded on $[0, \infty)$, and hence, there exists a real number $b > 0$ such that u_t and v_t are in the order interval $[(0, 0), (b, b)]_{\mathcal{Y}}$ for all $t \geq 0$. Thus, we can choose a large number $M > 0$ such that for each $t \in \mathbb{R}$, $g_1(t, L) := -d_L(t)L + ML$ is increasing in $L \in [0, b]$ and $g_2(t, P) := -d_P(t)P - \alpha(t)P^2 + MP$ is increasing in $P \in [0, b]$. It then follows that both $u(t)$ and $v(t)$ satisfy the following system of integral equations:

$$
\begin{aligned}
L(t) &= e^{-Mt}L(0) + \int_0^t e^{-M(t-s)}g_1(s, L(s))ds + \int_0^t e^{-M(t-s)}b_L(s)P(s - \tau_L(s))ds, \\
P(t) &= e^{-Mt}P(0) + \int_0^t e^{-M(t-s)}g_2(s, P(s))ds + \int_0^t e^{-M(t-s)}b_P(s)L(s - \tau_P(s))ds,
\end{aligned}
\tag{3.5}
$$

for all $t \geq 0$. Since both $m_L(t) := t - \tau_L(t)$ and $m_P(t) := t - \tau_P(t)$ are increasing in $t \in \mathbb{R}$, it easily follows that $[-\tau_L(0), 0] \subseteq m_L([0, \hat{\tau}])$ and $[-\tau_P(0), 0] \subseteq m_P([0, \hat{\tau}])$. Without loss of generality, we assume that $\phi_2 > \psi_2$. Then there exists an $\eta \in [-\tau_L(0), 0]$ such that $u_2(\eta) > v_2(\eta)$. In view of the first equation of (3.5), we have $u_1(t) > v_1(t)$ for all $t > \hat{\tau}$. Note that if $s > 2\hat{\tau}$, then $s - \tau_P(s) > 2\hat{\tau} - \hat{\tau} = \hat{\tau}$. By the second equation of (3.5), it follows that $u_2(t) > v_2(t)$ for all $t > 2\hat{\tau}$. This shows that $u_i(t) > v_i(t)$ for all $t > 2\hat{\tau}$, $i = 1, 2$, and hence, the solution map Q_t is strongly monotone whenever $t > 3\hat{\tau}$. $\qquad\square$

Lemma 3.7. *For any $\phi \gg 0$ in $\mathcal{Y}$ and any $\gamma \in (0, 1)$, we have $u_i(t, \gamma\phi) > \gamma u_i(t, \phi)$ for all $t > \hat{\tau}$, $i = 1, 2$, and hence, $Q_\omega^n(\gamma\phi) \gg \gamma Q_\omega^n(\phi)$ in $\mathcal{Y}$ for all integers n with $n\omega > 2\hat{\tau}$.*

Proof. Let $w(t) = u(t, \gamma\phi)$ and $v(t) = \gamma u(t, \phi)$, where $u(t, \phi)$ is the unique solution of system (3.3) with $u_0 = \phi \gg 0$ in $\mathcal{Y}$. As in the proof of Lemma 3.3, we see that $u(t) > 0$ and $v(t) > 0$ for all $t \geq 0$. Moreover, for all $\theta \in [-\tau_P(0), 0]$ and $\eta \in [-\tau_L(0), 0]$, we have

$$w_1(\theta) = \gamma\phi_1(\theta) = v_1(\theta) \quad \text{and} \quad w_2(\eta) = \gamma\phi_2(\eta) = v_2(\eta).$$

It is easy to see that $v(t)$ satisfies the following system:

$$
\begin{aligned}
\frac{dv_1(t)}{dt} &= b_L(t)v_2(t - \tau_L(t)) - d_L(t)v_1(t), \\
\frac{dv_2(t)}{dt} &= b_P(t)v_1(t - \tau_P(t)) - d_P(t)v_2(t) - \frac{\alpha(t)}{\gamma}v_2^2(t),
\end{aligned}
$$

and hence,

$$
v_1(t) = \left[v_1(0) + \int_0^t b_L(\xi)v_2(\xi - \tau_L(\xi)) \exp\left(\int_0^\xi d_L(\eta)d\eta\right)d\xi\right] \exp\left(-\int_0^t d_L(\eta)d\eta\right), \forall t \geq 0.
$$

For any $0 \leq t \leq \bar{\tau}$, we have $-\tau_L(0) \leq t - \tau_L(t) \leq \bar{\tau} - \tau_L(\bar{\tau}) \leq 0$ and

$$
\begin{aligned}
w_1&(t) \\
&= \left[w_1(0) + \int_0^t b_L(\xi)w_2(\xi - \tau_L(\xi)) \exp\left(\int_0^\xi d_L(\eta)d\eta\right)d\xi\right] \exp\left(-\int_0^t d_L(\eta)d\eta\right) \\
&= \left[v_1(0) + \int_0^t b_L(\xi)v_2(\xi - \tau_L(\xi)) \exp\left(\int_0^\xi d_L(\eta)d\eta\right)d\xi\right] \exp\left(-\int_0^t d_L(\eta)d\eta\right) \\
&= v_1(t).
\end{aligned}
$$

On the other side, the derivative of $v_2(t)$ at $t = 0$:

$$\frac{dv_2(t)}{dt}\bigg|_{t=0} = b_P(0)v_1(0 - \tau_P(0)) - d_P(0)v_2(0) - \frac{\alpha(0)}{\gamma}v_2^2(0)$$

$$< b_P(0)v_1(0 - \tau_P(0)) - d_P(0)v_2(0) - \alpha(0)v_2^2(0)$$

$$= b_P(0)w_1(-\tau_P(0)) - d_P(0)w_2(0) - \alpha(0)w_2^2(0)$$

$$= \frac{dw_2(t)}{dt}\bigg|_{t=0}.$$

Since $v_2(0) = w_2(0) > 0$, it follows that there exists an $\epsilon \in (0, \bar{\tau})$ such that $0 < v_2(t) < w_2(t)$ for all $0 < t < \epsilon$. We claim that $v_2(t) < w_2(t)$ for all $0 < t \leq \bar{\tau}$. Assume not, then there exists $t_0 \in (0, \bar{\tau}]$ such that $v_2(t) < w_2(t)$ for all $0 < t < t_0$ while $v_2(t_0) = w_2(t_0)$, which implies $v_2'(t_0) \geq w_2'(t_0)$. However, we have

$$\frac{dv_2(t)}{dt}\bigg|_{t=t_0} = b_P(t_0)v_1(t_0 - \tau_P(t_0)) - d_P(t_0)v_2(t_0) - \frac{\alpha(t_0)}{\gamma}v_2^2(t_0)$$

$$< b_P(t_0)v_1(t_0 - \tau_P(t_0)) - d_P(t_0)v_2(t_0) - \alpha(t_0)v_2^2(t_0)$$

$$= b_P(t_0)w_1(t_0 - \tau_P(t_0)) - d_P(t_0)w_2(t_0) - \alpha(t_0)w_2^2(t_0)$$

$$= \frac{dw_2(t)}{dt}\bigg|_{t=t_0},$$

a contradiction. This shows that $v_2(t) < w_2(t)$ for all $0 < t \leq \bar{\tau}$.

Similar arguments for any interval $(n\bar{\tau}, (n+1)\bar{\tau}]$ imply that $v_1(t) \leq w_1(t)$ and $v_2(t) < w_2(t)$ for all $t \in (n\bar{\tau}, (n+1)\bar{\tau}]$ with $n \in \mathbb{N}$. In particular, $\xi - \tau_L(\xi) > \hat{\tau} - \hat{\tau} = 0$ and $w_2(\xi - \tau_L(\xi)) > v_2(\xi - \tau_L(\xi))$ for all $\xi > \hat{\tau}$. Therefore, for any $t > \hat{\tau}$, we have

$$w_1(t) = \left[w_1(0) + \int_0^t b_L(\xi)w_2(\xi - \tau_L(\xi))\exp\left(\int_0^\xi d_L(\eta)d\eta\right)d\xi \right]\exp\left(-\int_0^t d_L(\eta)d\eta\right)$$

$$> \left[v_1(0) + \int_0^t b_L(\xi)v_2(\xi - \tau_L(\xi))\exp\left(\int_0^\xi d_L(\eta)d\eta\right)d\xi \right]\exp\left(-\int_0^t d_L(\eta)d\eta\right)$$

$$= v_1(t).$$

It follows that $v_1(t) < w_1(t)$ and $v_2(t) < w_2(t)$ for all $t > \hat{\tau}$, that is, $u_i(t, \gamma\phi) > \gamma u_i(t, \phi)$ for all $t > \hat{\tau}$, $i = 1, 2$. Thus, $Q_\omega^n(\gamma\phi) = Q_{n\omega}(\gamma\phi) \gg \gamma Q_{n\omega}(\phi) = \gamma Q_\omega^n(\phi)$ for all integer n with $n\omega > 2\hat{\tau}$. $\square$

For any given $t \geq 0$, let $G(t)$ be the time-t map of the linear periodic system (3.4) on $\mathcal{Y}$, that is, $G(t)\phi = z_t(\phi)$, where $z(t, \phi)$ is the unique solution of (3.4) with $z_0 = \phi \in \mathcal{Y}$. The subsequent result shows that the stability of the zero solution for system (3.4) on $\mathcal{X}$ is equivalent to that on $\mathcal{Y}$.

Lemma 3.8. *Two Poincaré maps $W(\omega) : \mathcal{X} \to \mathcal{X}$ and $G(\omega) : \mathcal{Y} \to \mathcal{Y}$ have the same spectral radius, that is, $r(W(\omega)) = r(G(\omega))$.*

Proof. We fix an integer n_0 such that $n_0\omega > 3\hat{\tau}$. By the proof of Lemma 3.6, we see that $G(\omega)^{n_0} = G(n_0\omega)$ is strongly positive on $\mathcal{Y}$. Further, [11, Theorem 3.6.1] implies that $G(\omega)^{n_0}$ is compact. Then $r(G(\omega)) > 0$ according to the Krein-Rutmann theorem, as applied to the linear operator $(G(\omega))^{n_0}$, together with the fact that $r(G(\omega)^{n_0}) = (r(G(\omega)))^{n_0}$. For any given $\phi = (\phi_1, \phi_2) \in \mathcal{Y}$, we define $\tilde{\phi} = (\tilde{\phi}_1, \tilde{\phi}_2) \in \mathcal{X}$ by

$$\tilde{\phi}_1(\theta) = \begin{cases} \phi_1(-\tau_P(0)) & \text{if } \theta \in [-\hat{\tau}, -\tau_P(0)], \\ \phi_1(\theta) & \text{if } \theta \in [-\tau_P(0), 0]; \end{cases}$$

and

$$\tilde{\phi}_2(\theta) = \begin{cases} \phi_2(-\tau_L(0)) & \text{if } \theta \in [-\hat{\tau}, -\tau_L(0)], \\ \phi_2(\theta) & \text{if } \theta \in [-\tau_L(0), 0]. \end{cases}$$

Clearly, $\|\phi\|_{\mathcal{Y}} = \|\tilde{\phi}\|_{\mathcal{X}}$. By Remark 3.4, it follows that for all integer n with $n\omega > \hat{\tau}$,

$$\|G(n\omega)\phi\|_{\mathcal{Y}} \leq \|W(n\omega)\tilde{\phi}\|_{\mathcal{X}} \leq \|W(n\omega)\|_{\mathcal{X}} \cdot \|\tilde{\phi}\|_{\mathcal{X}} = \|W(n\omega)\|_{\mathcal{X}} \cdot \|\phi\|_{\mathcal{Y}}, \ \forall \phi \in \mathcal{Y},$$

and hence, $\|G(n\omega)\|_{\mathcal{Y}} \leq \|W(n\omega)\|_{\mathcal{X}}$. Since

$$r(G(\omega)) = \lim_{n\to\infty} \|G(\omega)^n\|_{\mathcal{Y}}^{\frac{1}{n}} = \lim_{n\to\infty} \|G(n\omega)\|_{\mathcal{Y}}^{\frac{1}{n}}$$

and

$$r(W(\omega)) = \lim_{n\to\infty} \|W(\omega)^n\|_{\mathcal{X}}^{\frac{1}{n}} = \lim_{n\to\infty} \|W(n\omega)\|_{\mathcal{X}}^{\frac{1}{n}},$$

we then have $r(W(\omega)) \geq r(G(\omega)) > 0$.

It remains to prove that $r(W(\omega)) \leq r(G(\omega))$. In view of [30, Theorem 5.1.1] and [11, Theorem 3.6.1], we see that the linear operator $W(\omega)^{n_0} = W(n_0\omega)$ is positive and compact on $\mathcal{X}$. By the Krein-Rutmann theorem (see, e.g., [12, Theorem 7.1]), $r(W(\omega)^{n_0})$ is an eigenvalue of $W(\omega)^{n_0}$ with an eigenvector $\phi^* > 0$ in $\mathcal{X}$. For any $\phi \in \mathcal{X}$, we define $\underline{\phi} \in \mathcal{Y}$ as

$$\underline{\phi}_1(\theta) = \phi_1(\theta), \ \forall \theta \in [-\tau_P(0), 0], \ \text{and} \ \underline{\phi}_2(\eta) = \phi_2(\eta), \ \forall \eta \in [-\tau_L(0), 0].$$

By Remark 3.4, we have $u(t, \phi) = v(t, \underline{\phi}), \forall t \geq 0$, where $u(t, \phi)$ and $v(t, \underline{\phi})$ are the unique solutions of system (3.4) with $u_0 = \phi \in \mathcal{X}$ and $v_0 = \underline{\phi} \in \mathcal{Y}$, respectively. We further claim that $\underline{\phi^*} > 0$ in $\mathcal{Y}$. Otherwise, $\underline{\phi^*} = 0$, and hence, $u(t, \phi^*) = v(t, \underline{\phi^*}) = 0, \forall t \geq 0$. This implies that

$$(r(W(\omega)))^{n_0}\phi^* = r(W(\omega)^{n_0})\phi^* = W(\omega)^{n_0}\phi^* = W(n_0\omega)\phi^* = 0,$$

and hence, $\phi^* = 0$ in $\mathcal{X}$, which is a contradiction. Since

$$G(\omega)^{n_0}\underline{\phi^*} = \underline{W(\omega)^{n_0}\phi^*} = \underline{r(W(\omega))^{n_0})\phi^*} = (r(W(\omega)))^{n_0}\underline{\phi^*},$$

$(r(W(\omega)))^{n_0}$ is a positive eigenvalue of $G(\omega)^{n_0}$ with $\underline{\phi^*}$ being a positive eigenvector in $\mathcal{Y}$. It then follows that $(r(W(\omega)))^{n_0} \leq r(G(\omega)^{n_0}) = (r(G(\omega)))^{n_0}$, and hence $r(W(\omega)) \leq r(G(\omega))$. Consequently, we have $r(W(\omega)) = r(G(\omega))$. $\square$

Now we are in a position to prove the main result of this section.

Theorem 3.9. *The following statements are valid:*

  (i) *If $R_0 \leq 1$, then $(0, 0)$ is globally asymptotically stable for system (3.3) in $\mathcal{Y}_+$.*

  (ii) *If $R_0 > 1$, then system (3.3) admits a unique positive ω-periodic solution $(L^*(t), P^*(t))$, and it is globally asymptotically stable for system (3.3) in $\mathcal{Y}_+ \setminus \{(0, 0)\}$.*

Proof. We fix an integer n_0 such that $n_0\omega > 3\hat{\tau}$. In view of Lemma 3.5, Q_t can be regarded as an $n_0\omega$-periodic semiflow on $\mathcal{Y}_+$. By Lemmas 3.6 and 3.7, $Q_{n_0\omega}$ is a strongly monotone and strictly subhomogeneous map on $\mathcal{Y}_+$. Applying [41, Theorem 2.3.4] to the map $Q_{n_0\omega}$, we have the following threshold type result:

  (a) *If $r(DQ_{n_0\omega}(0)) \leq 1$, then $(0, 0)$ is globally asymptotically stable for system (3.3) in $\mathcal{Y}_+$.*

(b) If $r(DQ_{n_0\omega}(0)) > 1$, then system (3.3) admits a unique positive $n_0\omega$-periodic solution $(L^*(t), P^*(t))$, and it is globally asymptotically stable for system (3.3) in $\mathcal{Y}_+ \setminus \{(0,0)\}$.

Note that $r(DQ_{n_0\omega}(0)) = r(G(n_0\omega)) = (r(G(\omega)))^{n_0}$. By Lemmas 3.2 and 3.8, we then see that $sign(R_0 - 1) = sign(r(DQ_{n_0\omega}(0)) - 1)$. Thus, it suffices to show that in case (b), $(L^*(t), P^*(t))$ is also ω-periodic. Let $\psi^* = v_0^* \in \mathcal{Y}$ with $v^*(t) = (L^*(t), P^*(t))$. Then $Q_{n_0\omega}\psi^* = \psi^*$. Note that

$$Q_\omega^{n_0}(Q_\omega\psi^*) = Q_\omega(Q_\omega^{n_0}\psi^*) = Q_\omega(Q_{n_0\omega}\psi^*) = Q_\omega(\psi^*).$$

By the uniqueness of the positive fixed point of $Q_\omega^{n_0} = Q_{n_0\omega}$, it follows that $Q_\omega\psi^* = \psi^*$, which implies that $(L^*(t), P^*(t)) = u(t, \psi^*)$ is an ω-periodic solution of system (3.3). $\qquad\square$

In the rest of this section, we deduce the dynamics for the other two variables $X(t)$ and $Y(t)$ in system (2.5), which do not appear in system (3.1). In the case where $R_0 > 1$, we have

$$\lim_{t\to\infty} [(L(t), P(t)) - (L^*(t), P^*(t))] = 0$$

for any solution of system (3.1) through nonzero initial data. By using the integral form for the free living non-infected larvae $X(t)$ and arrested larvae $Y(t)$ in (3.2), we obtain

$$\lim_{t\to\infty} \left[X(t) - \int_{t-\tau_L(t)}^t \lambda P^*(\xi) e^{-\int_\xi^t \mu_X(s)\, ds} d\xi \right] = 0, \text{ and}$$

$$\lim_{t\to\infty} \left[Y(t) - \int_{t-\tau_P(t)}^t \beta(\xi) H(\xi) L^*(\xi) e^{-\int_\xi^t (\mu_Y(s)+\mu_H(s))\, ds} d\xi \right] = 0.$$

Moreover, it is easy to verify that both

$$X^*(t) := \int_{t-\tau_L(t)}^t \lambda P^*(\xi) e^{-\int_\xi^t \mu_X(s)\, ds} d\xi$$

and

$$Y^*(t) := \int_{t-\tau_P(t)}^t \beta(\xi) H(\xi) L^*(\xi) e^{-\int_\xi^t (\mu_Y(s)+\mu_H(s))\, ds} d\xi$$

are positive ω-periodic functions. In the case where $R_0 \leq 1$, we have

$$\lim_{t\to\infty} (L(t), P(t)) = (0,0).$$

By using the integral form in (3.2) again, we obtain

$$\lim_{t\to\infty} (X(t), Y(t)) = (0,0).$$

In summary, we have the following result on the global dynamics of the full model system.

Theorem 3.10. *The following statements hold for system (2.5):*

(i) If $R_0 \leq 1$, then $(0,0,0,0)$ is globally asymptotically stable.

(ii) If $R_0 > 1$, then there exists a positive ω-periodic solution

$$(X^*(t), L^*(t), Y^*(t), P^*(t)),$$

and it is globally asymptotically stable for all nontrivial solutions.

4 Numerical simulations

In this section, we present numerical simulation results to validate our analytic results on the global dynamics and investigate the temperature impacts on model prediction.

4.1 Parameters

Most parameters are taken from [19], which justifies the metabolic approach to investigate the climate change impact on host-macroparasite dynamics. In particular, the authors employed Shape-Schoolfield models to parameterize the temperature-dependent coefficients, such as the development time and mortality rate. Interested readers may find more details in this extraordinary reference. For reader's convenience, we restate the parameters here. The temperature data (in degrees $^\circ C$) is taken as a function of time t (in day) in the following form

$$T(t) = c_K + d_K \times \sin\left(\frac{2\pi}{365} \times (t - t_0)\right). \tag{4.1}$$

However, we should use the temperature in $^\circ K$ on each day of the year to parameterize the temperature-dependent coefficients in the model system. The immature death rate under the temperature $T = T(t)$ (in $^\circ K$ of day t) can be described by the following Shape-Schoolfield models [19]:

$$\mu_L(T) = \mu_0 \times \exp(-\frac{E_\mu}{k_B}(\frac{1}{T} - \frac{1}{T_0})) \times (1 + \exp(\frac{E_\mu^L}{k_B}(\frac{1}{T} - \frac{1}{T_\mu^L})) + \frac{E_\mu^H}{k_B}(-\frac{1}{T} + \frac{1}{T_\mu^H}))$$

For simplicity, we assume $\mu_X(t) = \mu_L(t)$ in the model system. To determine the maturation time $\tau(t)$ for the cohort that matures at time t, as shown in equation (2.4), we need to get the development proportion $r(\xi)$ on the interval $\xi \in [t - \tau(t), t]$, which can be evaluated as the reciprocal of the maturation time $\widetilde{\tau}_L(T(\xi))$ needed under temperature $T(\xi)$ of day ξ, that is

$$r(\xi) = \frac{1}{\widetilde{\tau}_L(T(\xi))}.$$

The development duration $\widetilde{\tau}_L(T)$ can be estimated through the Shape-Schoolfield formula [19]:

$$\widetilde{\tau}_L(T) = \tau_0 \times \exp(-\frac{E_\tau}{k_B}(\frac{1}{T} - \frac{1}{T_0})) \times (1 + \exp(\frac{E_\tau^L}{k_B}(\frac{1}{T} - \frac{1}{T_\tau^L})) + \frac{E_\tau^H}{k_B}(-\frac{1}{T} + \frac{1}{T_\tau^H})).$$

In summary, the accumulative development proportions in previous $\tau_L(t)$ days $t - 1$, $t - 2$, $\cdots$, $t - \tau_L(t)$ should be unity, that is

$$\int_{t-\tau_L(t)}^{t} \frac{1}{\widetilde{\tau}_L(T(\xi))} d\xi = 1. \tag{4.2}$$

with $T(\xi)$ being the mean temperature at day ξ. The maturation time $\tau_L(t)$ can be estimated from the above relation (4.2).

For numerical computation, we take the constant parameters from other biological literature. In the model system, the instantaneous birth rate λ is assumed to be a variable, dependent on the parasite and host species [14] . The outflow rate $\mu_P(t) + \mu_H(t) + \alpha_H = d_P(t)$ is taken as 14.9/365 per day, to be consistent with the report [14]. The survival probability $e^{-\int_{t-\tau_P(t)}^{t}(\mu_Y(\xi) + \mu_H(\xi))\, d\xi}$ is 0.655 [14]. The uptake rate βH is assumed to be 1, to keep consistent with the work [19]. Moreover, we assume $k=2$ as that reported in [3] and the prepatent period for the matured individuals is $\tau_P=18$ days, in align with previous work [37]. All related parameters with their biological/metabolic explanations are summarised in Table 1 in the last page.

4.2 Curves of time-dependent parameters

Based on the default parameters, the temperature in one year varies in the pattern of Fig 2(a). Then the metabolic theory in ecology [19] gives the developmental time $\widetilde{\tau}_L(t)$ required corresponding to the temperature of day t, immature death rate $d_L(t)$ and survival probability $\exp(-\int_{t-\tau_L(t)}^{t} \mu_X(\xi)\,d\xi)$, respectively, in Figs 2(b), (c) and (d). Comparing Figs 2(a) and (b), the relationship between the developmental time required under the specific temperature $\widetilde{\tau}_L(t)$ on the specific day and temperature is highly nonlinear, neither positively nor negatively correlated. There is one peak temperature in one year (at around day 210), while there are roughly two valleys (at around day 100 and day 320) for $\widetilde{\tau}_L(t)$ when the temperature is mild, neither too high, nor too low. These results are consistent with Fig 2 of the previous work [19], which shows that too high, or too low temperatures will prolong the development time. Similar results are reported for the death rate (Fig 2(c)) and immature survival probability to adult (Fig 2(d)). All these three temperature dependent parameters exhibit totally distinct patterns from the temperature variation, which call for accurate measurements of the metabolic relationship between biological parameters and temperature conditions.
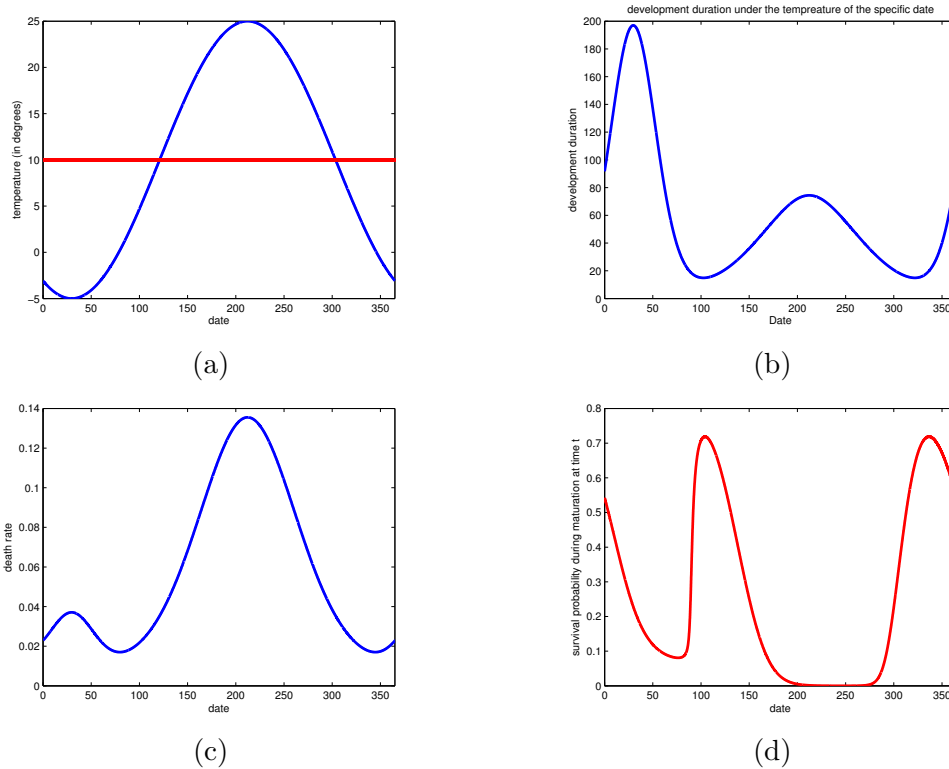

(a)

(b)

(c)

(d)

Figure 2: Temperature data and seasonal parameters: development time $\widetilde{\tau}_L(t)$ required under temperature at day t, immature death rate $d_L(t)$ and survival probability $\exp(-\int_{t-\tau_L(t)}^{t} \mu_X(\xi)\,d\xi)$.

There are two valleys and two local peaks on the developmental duration $\tau_L(t)$ as shown in Fig 3(a), which can also be observed from four points where its derivative is zero in Fig 3(b). The temperatures for the period before the valley date should be mild to produce a smaller developmental duration $\tau_L(t)$. Moreover, it is clear that the peaks and valleys of Fig 2(b) and Fig 3(a) are shifted, since it is the accumulating environmental condition that should be evaluated in Fig 3(a) (as in the formula (4.2) to estimate the developmental duration for adults maturing on day t). Fig 3(b) shows the derivative of $\tau_L(t)$ versus time t (with maximum value being 0.9052), which

numerically validates the inequality $1 - \tau'_L(t) > 0$, as argued in the previous section. It can also be observed that the parasite maturing at time t during day 200 and 270 survive through tough time as very small survival probability is observed (Fig 2(d)), due to the joint effect of a relatively longer developmental duration (shown in Fig 3(a)) and larger death rate during that period (Fig 2(c)). One can further claim from Fig 2(b) that the largest duration $\tilde{\tau}_L(t)$ required under the temperature of a specific date is around 200 days because of the extreme (too low) weather condition in the 45-th day, however, in reality, the largest developmental duration $\tau_L(t)$ is less than 100 days (Fig 3(a)), due to the accumulative effect that the weather condition before the worst weather condition date is mild. Moreover, the peaking time of Figs 2(b) and 3(a) is observed to be totally different.
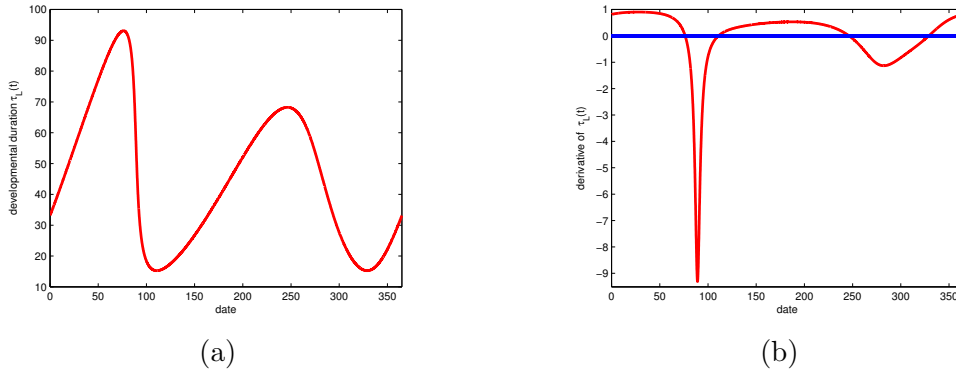

(a)   (b)

Figure 3: The time-dependent developmental delay $\tau_L(t)$ and its derivative. It is clear from the simulation that the derivative is always smaller than one and therefore $1 - \tau'_L(t) > 0$ for all t.

4.3   Simulation results

Using parameters presented in previous subsections, we can run simulations for the solutions as shown in Fig 4 fed with two different initial values, where the instantaneous birth rate is variable, with $\lambda = 100$ (top two figures), 10 (middle figures) and 0.6 (bottom figures). The corresponding basic reproduction ratio R_0 takes the values of 15.2 ($\lambda = 100$), 4.8 ($\lambda = 10$), and 0.9 ($\lambda = 0.6$) respectively. The solutions always stabilize at a positive seasonal state at a high level (when $\lambda = 100$) or a lower level (when $\lambda = 10$), while go to zero when $\lambda = 0.6$ (the result can be shown when more than 100 years simulation is performed). This figure is consistent with theoretical results in Theorem 3.9, that is, all solutions starting from various initial values either go to zero when $R_0 < 1$ or stabilize at a periodic state when $R_0 > 1$. When changing the aggregation parameter k of the model system (2.5) while keeping the basic reproduction number $R_0 > 1$ unchanged, numerical simulations show that the positive periodic states with different k share almost similar patterns (figures are not provided here).

The impact of variations in seasonal temperature on population dynamics is predicted in Fig 5, with the scenario that the annual mean temperature c_K changes (two top figures) or the amplitude d_K of annual temperature varies (two bottom figures). The minimum value of the density when $R_0 > 1$ is very small compared with the maximum density. The relationship between the annual temperature and maximum population density is neither increasing nor decreasing for both free living infective larvae $L(t)$ and adult parasites $P(t)$. For instance, when annual temperature is very small (at around $6°C$), increasing the annual temperature may decrease the maximum density, while increasing the annual temperature can increase the maximum density when the annual temperature is relatively high (for example, at around $10°C$). However, when checking the relationship between
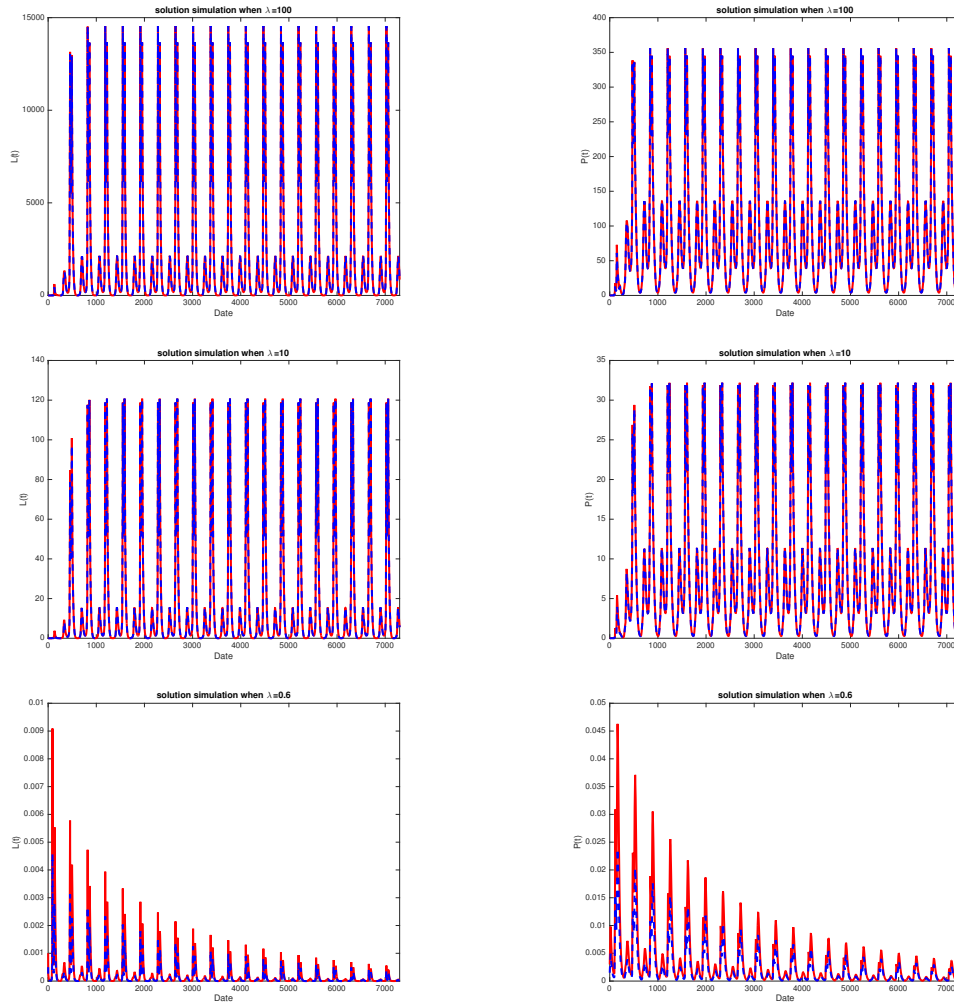
Figure 4: Solution simulations in different birth rates λ show that either the positive periodic state or the zero solution is globally asymptotically stable.

minimum densities and temperature amplitude, we observed a negative correlation (two bottom graphs of Fig 5), which implies larger temperature variation amplitudes decrease the minimum population densities.

5 Discussion

In this paper, with the reference to the host-parasite interaction subject to temperature conditions, we present a mathematical approach to analyzing the temperature impact on the pathogen transmission in a synthesised way from following components: model development with careful mathematical reasoning and biological justification, basic reproduction ratio formulation and computation, and global dynamics analysis for the model system. Mathematically, we start with the widely used age-structured PDE model with periodic parameters, based on the McKendrick von-Foerster model [9, 36]. Since a direct dynamics analysis is very difficult for this kind of PDE models, we reduce the PDE equation into a periodic system of delay differential equations with periodic
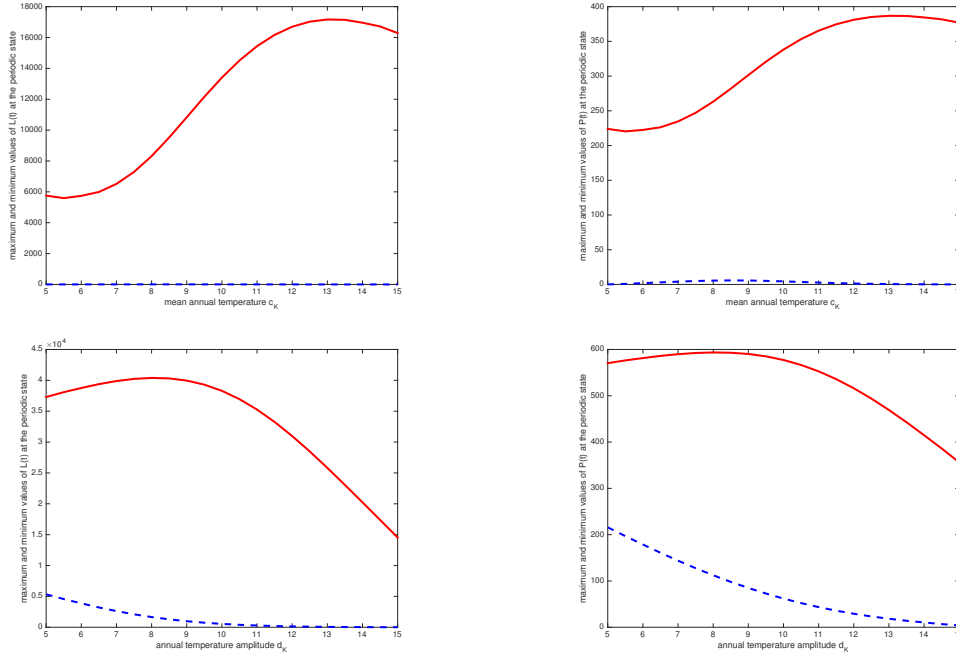
Figure 5: The impact of c_K and d_K in the temperature formula (4.1) on the maximum and minimum values of the population densities.

delay. Due to the seasonality of developmental duration, the model system involves a term related to the rate of change for the developmental duration, which becomes zero and disappears when the developmental duration is independent of time. At first glance, it is a bit surprising to have this term in the age-structured model. However, a reasonable biological argument, with the help of an integral equation, justifies the model system. We further show analytically and numerically that the derivative of this developmental duration must be smaller than one, which is also required to guarantee the positivity of solutions. The basic reproduction ratio R_0 is formulated for the resultant periodic delay differential system with seasonal delay by using the approach in [42], which also illustrates that the stability of the linearized system is solely determined by the sign of $R_0 - 1$. Furthermore, we study the population dynamics, which is challenging due to the incorporation of the periodic delay. By constructing a periodic semiflow on a special functional space and applying the theory of monotone dynamical systems, we successfully establish the global stability of zero or the positive periodic state, dependent on the sign of $R_0 - 1$. Here we remark that the general definition of R_0 proposed in [6] has been employed in [7, 23, 39] to introduce the basic reproduction number for some specific periodic epidemic models with time delays. For example, R_0 was successfully evaluated in [39] for the Nicholson blowflies equation and four stage *Aedes aegypti* mosquito population with temporally periodic delays. However, the global dynamics was not investigated in [39], which motivates us to use the theory developed in [42] for the current research.

In the model system (2.5), we assume that the host density remains at a stable state $H(t)$. Normally the host population dynamics $N(t)$ follows a growth model such as that in [17], which has a globally asymptotically stable periodic solution $H(t)$, that is,

$$\lim_{t \to \infty} (N(t) - H(t)) = 0.$$

As such, the theory of asymptotically periodic semiflows [41] can be employed to establish the

global dynamics of the biological system, as illustrated in [17]. In the host-parasite model (2.5), we describe the host immunity against parasite indirectly by an additional adult parasite death rate, that is, the level of immunity is determined solely by the adult parasite density, which is different from some notable efforts in this field [26, 27]. Some other factors [14, 27, 28], such as the host heterogeneity, multiple host species, host movement, competition between parasite species in the case where hosts harbour more than one single parasite species, are not included either. We hope to incorporate the complexity of these aspects in our future work.

Since the constant coefficients, as well as periodic parameters, can affect the basic reproduction ratio in the biological system, accurate model parameter estimation is necessary. In the current paper, we employ the metabolic approach [19] to parameterize the periodic coefficients. Other approaches may also be applicable to the problem in study, for example, the parameterization approach used in [20, 38] where the relationship between the development components and temperature is obtained via fitting experimental datasets. However, further field and laboratory investigations are needed to improve the accuracy of our parameter estimates.

Beyond the host-parasite systems, our framework also applies to other ecosystems, with appropriate modifications to the terminology of developmental duration in the study and we hope this general approach can be applied to broader contexts than examined here, such as the population growth where the time needed for development from one stage to the next is periodic, disease transmission where the incubation period of the pathogen in the host is seasonal, and in-host immunology where the time duration required for immune system development is dependent on time. Moreover, this approach remains valid to explore potential impacts of climate change on biodiversity, as climate change is regarded as a major threat to biodiversity. Furthermore, the framework is expected to investigate the climate effect on species habitat change [16], such as range expansion, shift or contraction, by incorporating spatial and temporal heterogeneity of environmental conditions, as well as the species movement. Further extensions are also possible to predict the risk redistribution of emerging and reemerging infectious diseases. However, the extension of the current approach to these fields is challenging, but worth further investigation.

Appendix

To numerically compute the basic reproduction ratio, we are going to rewrite the linear operator L into the form of equation (3) in [22], where an algorithm is proposed for R_0 computation of periodic ordinary differential systems. We should also note that other algorithms have been proposed, such as [4], for periodic growth models with time delay. However, here the delay is periodic and therefore, we first fit our computation into other algorithms. Since

$$F(t-s)\begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} = \begin{pmatrix} b_L(t-s)\phi_2(-\tau_L(t-s)) \\ b_P(t-s)\phi_1(-\tau_P(t-s)) \end{pmatrix},$$

we have

$$
\begin{aligned}
& [Lv](t) \\
= {} & \int_0^\infty Z(t, t-s) F(t-s) v(t-s+\cdot) ds \\
= {} & \int_0^\infty \begin{pmatrix} e^{-\int_{t-s}^t d_L(\xi)d\xi} & 0 \\ 0 & e^{-\int_{t-s}^t d_P(\xi)d\xi} \end{pmatrix} \begin{pmatrix} b_L(t-s) v_2(t-s-\tau_L(t-s)) \\ b_P(t-s) v_1(t-s-\tau_P(t-s)) \end{pmatrix} ds \\
= {} & \begin{pmatrix} \int_0^\infty e^{-\int_{t-s}^t d_L(\xi)d\xi} b_L(t-s) v_2(t-s-\tau_L(t-s)) ds \\ \int_0^\infty e^{-\int_{t-s}^t d_P(\xi)d\xi} b_P(t-s) v_1(t-s-\tau_P(t-s)) ds \end{pmatrix}.
\end{aligned}
$$

Let $t - s - \tau_L(t-s) = t - s_1$. Since the function $y = x - \tau_L(x)$ is strictly increasing, the inverse function exists and we can solve $x = h_L(y)$. Hence, we obtain $t - s = h_L(t - s_1)$, that is, $s = t - h_L(t - s_1)$, $ds_1 = d(s + \tau_L(t-s)) = (1 - \tau_L'(t-s))ds$ and $ds = \frac{1}{1-\tau_L'(h_L(t-s_1))}ds_1$. Therefore,

$$
\begin{aligned}
& \int_0^\infty e^{-\int_{t-s}^t d_L(\xi)d\xi} b_L(t-s) v_2(t-s-\tau_L(t-s)) ds \\
= {} & \int_{\tau_L(t)}^\infty \frac{e^{-\int_{h_L(t-s_1)}^t d_L(\xi)d\xi} b_L(h_L(t-s_1))}{1-\tau_L'(h_L(t-s_1))} v_2(t-s_1) ds_1 \\
= {} & \int_{\tau_L(t)}^\infty \frac{e^{-\int_{h_L(t-s)}^t d_L(\xi)d\xi} b_L(h_L(t-s))}{1-\tau_L'(h_L(t-s))} v_2(t-s) ds.
\end{aligned}
$$

Similarly, let $t - s - \tau_P(t-s) = t - s_2$. Assume the inverse function of $y = x - \tau_P(x)$ is $y = h_P(x)$. Solving $t - s = h_P(t - s_2)$, we get

$$
s = t - h_P(t - s_2), ds_2 = (1 - \tau_P'(t-s))ds \text{ and } ds = \frac{1}{1 - \tau_P'(h_P(t - s_2))}ds_2.
$$

Therefore,

$$
\begin{aligned}
& \int_0^\infty e^{-\int_{t-s}^t d_P(\xi)d\xi} b_P(t-s) v_1(t-s-\tau_P(t-s)) ds \\
= {} & \int_{\tau_P(t)}^\infty \frac{e^{-\int_{h_P(t-s_2)}^t d_P(\xi)d\xi} b_P(h_P(t-s_2))}{1-\tau_P'(h_P(t-s_2))} v_1(t-s_2) ds_2 \\
= {} & \int_{\tau_P(t)}^\infty \frac{e^{-\int_{h_P(t-s)}^t d_P(\xi)d\xi} b_P(h_P(t-s))}{1-\tau_P'(h_P(t-s))} v_1(t-s) ds.
\end{aligned}
$$

Define

$$
K_{12}(t, s) = \begin{cases} 0, & s < \tau_L(t) \\ \frac{e^{-\int_{h_L(t-s)}^t d_L(\xi)d\xi} b_L(h_L(t-s))}{1-\tau_L'(h_L(t-s))}, & s \geq \tau_L(t) \end{cases}
$$

and

$$
K_{21}(t, s) = \begin{cases} 0, & s < \tau_P(t) \\ \frac{e^{-\int_{h_P(t-s)}^t d_P(\xi)d\xi} b_P(h_P(t-s))}{1-\tau_P'(h_P(t-s))}, & s \geq \tau_P(t) \end{cases}
$$

while $K_{11}(t, s) = K_{22}(t, s) = 0$. Then we can rewrite

$$
\begin{aligned}
[Lv](t) & = \int_0^\infty K(t, s) v(t-s) ds \\
& = \sum_{j=0}^\infty \int_{j\omega}^{(j+1)\omega} K(t, s) v(t-s) ds \\
& = \sum_{j=0}^\infty \int_0^\omega K(t, j\omega + s) v(t-s-j\omega) ds \\
& = \int_0^\omega G(t, s) v(t-s) ds
\end{aligned}
$$

with

$$G(t,s) = \sum_{j=0}^{\infty} K(t, j\omega + s),$$

which is of the integral form in [22]. Thus, the numerical algorithm in [22] can be used to compute the basic reproduction ratio for our model system.

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Symbol	Description	Baseline Value	Resource
c_K	mean annual temperature	$10°C$	[19]
d_K	the amplitude of temperature variation	$15°C$	[19]
t_0	day of the year when temperature increases to its annual mean	121	[19]
T_0	the reference temperature	$15°C$	[19]
τ_0	the scaling factor for development time at temperature T_0	29.6 days	[19]
μ_0	the scaling factor for mortality rate at temperature T_0	0.056 per day	[19]
T_τ^L	lower temperature threshold for development	$2.5°C$	[19]
T_τ^H	upper temperature threshold for development	$32.5°C$	[19]
T_μ^L	lower temperature threshold where abruptly mortality increases	$-2.5°C$	[19]
T_μ^H	upper temperature threshold where abruptly mortality increases	$37.5°C$	[19]
E_τ, E_μ	average activation energy	0.65eV	[19]
E_τ^L	inactivation energy for lower temperature threshold	$5 \times E_\tau$	[19]
E_τ^H	inactivation energy for upper temperature threshold	$5 \times E_\tau$	[19]
E_μ^L	an index analogous to the inactivation energy	$5 \times E_\mu$	[19]
E_μ^H	an index analogous to the inactivation energy	$5 \times E_\mu$	[19]
k_B	Boltzmann's constant	8.62×10^{-5}	[19]
$d_P(t)$	the summarised outflow rate $\mu_P + \mu_H + \alpha_H$	$\frac{14.9}{365}$ per day	[14]
D_p	survival probability $e^{-\int_{t-\tau_P(t)}^{t}(\mu_Y(\xi)+\mu_H(\xi))\,d\xi}$	0.655	[14]
$\beta(t)$	uptake rate per host	5	assumed
$H(t)$	host density	0.2	assumed
λ	instantaneous rate of parasite birth per day	variable	
k	aggregation parameter	2	[3]
α_H	instaneous host death rate caused by the parasite	0.01	assumed
τ_P	the prepatent period for the matured individuals	18 days	[37]

Table 1: Parameter definitions (daily) with baseline values. Temperature are reported in degrees $°C$ in the table. However, the parameterizations are performed for temperature in $°K$. Please note that β and H are chosen such that the uptake rate is $\beta H=1$ as in [19].