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DYNAMICS OF A PERIODIC STAGE-STRUCTURE COMPETITIVE MODEL WITH TWO MATURATION DELAYS

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Abstract. Considering that many populations are affected by seasonal fluctuations in temperature in the process of growth, and there is a general competitive relationship between populations, in this paper, a stage-structured two species competitive model with two periodic maturation delays is proposed to study the effect of temperature and maturation delays on population dynamics. Firstly, we give the formulation of the model combining with biological significance. Then, criteria on the global dynamics of the whole model are obtained based on the basic reproduction ratio R_0: when $R_0 \leq 1$, the all populations is extinction, and when $R_0 > 1$, the all populations is persistent, i.e., all solutions of system stabilize at a positive periodic state. Furthermore, we discuss the effect of temperature and length of maturation delays on the population density by numerical simulations, which implies larger temperature variation can decrease the minimum population densities and the maturation time may change the stability of the system.

Keywords: Stage-Structure, Periodic Maturation Delays, Basic Reproduction Ratio, Threshold Dynamics.

AMS Subject Classification: 92D25, 37N25, 37C35.

1. Introduction

Competition among ecological species are very prevalent phenomena in nature, which are very important central research issues for ecologists, biologists, and bio-mathematicians. The most famous one is the following Lotka-Volterra [20] competiton model given by:

$$\begin{cases} \dfrac{dx_1}{dt} = x_1(k_1 - a_{11}x_1 - a_{12}x_2), \\ \dfrac{dx_2}{dt} = x_2(k_2 - a_{21}x_1 - a_{22}x_2), \end{cases}$$

where $x_i(t)$ $(i = 1, 2)$ denote the population density (or biomasses) of species i at time t sharing a common pool of resources; k_i is the intrinsic growth rate of species i; a_{ij} $(i, j = 1, 2)$ denotes the inter (or intra) competition coefficients between species i and j. Subsequently, the Lotka-Volterra competition system has been extensively investigated in the papers [3,10,12,15,24,25,36,37,40]. However, it is assumed that each individual admits the same density-dependent rate as well as the identical ability to bear and compete with other species during the whole life cycles. In fact, all organisms have life cycles in which they go through different stages based on age. Inclusion of the stage structure is usually essential, as population responds to environmental changes with time lags that reflect individual development [22]. For example, in [1], the authors pioneered

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the following single-species model with stage-structure using a discrete time delay as:

$$\begin{cases} \dfrac{dx_1}{dt} = \alpha x_2(t) - \gamma x_1(t) - \alpha e^{-\gamma\tau} x_2(t-\tau), \\ \dfrac{dx_2}{dt} = \alpha e^{-\gamma\tau} x_2(t-\tau) - \beta x_2^2(t), \end{cases} \tag{1}$$

where $x_1(t)$ and $x_2(t)$ represent the immature (juvenile) and mature (adult) population densities, respectively; τ represents a constant time to maturity; α, β and γ are positive constants. The $\alpha x_2(t)$ term in the first equation is the birth rate, assumed proportional to the number of adults and $\gamma x_1(t)$ is juvenile mortality, the $e^{-\gamma\tau}$ term corrects for juvenile mortality. In the second equation of (1), the βx_2^2 term represents adult mortality. Subsequently, many scholars began incorporating the stage-structure into the population dynamics models [5, 16, 22, 36]. For example, in [16], the authors proposed a predator-prey model with stage-structure and Beddington-DeAngelis function and concluded that the stage-structure has influence on the population persistence and system stability, which could incur the appearance of Hopf bifurcation.

Based on the above discussion, it is natural to propose a two species competition model with stage structure. Moreover, the survival of most the immature population is almost determined by their matures and the immatures are much weaker than the matures, which leads to their competition with other individuals of whole community could be ignored. Hence, in [17], the authors proposed the following Lotka-Volterra competitive model with stage structure:

$$\begin{cases} \dfrac{dx_1}{dt} = b_1 x_2(t) - d_1 x_1(t) - b_1 e^{-d_1\tau_1} x_1(t-\tau_1), \\ \dfrac{dx_2}{dt} = b_1 e^{-d_1\tau_1} x_1(t-\tau_1) - a_{11} x_2^2(t) - a_{12} x_2(t) y_2(t), \\ \dfrac{dy_1}{dt} = b_2 y_2(t) - d_2 y_1(t) - b_2 e^{-d_2\tau_2} y_1(t-\tau_2), \\ \dfrac{dy_2}{dt} = b_2 e^{-d_2\tau_2} y_2(t-\tau_2) - a_{22} y_2^2(t) - a_{21} x_2(t) y_2(t), \end{cases}$$

$b_i, d_i, a_{ii} (i = 1, 2)$ have the same biological meaning with α, β and γ in (1), and a_{ij} represents the competition relation just exists between matures. They confirmed that stage structure has negative influence on the population permanence, meanwhile the longer duration of immature can help competitor out of elimination. Subsequently, many scholars began incorporating the stage-structure into the population dynamics models [19, 31, 35, 38, 39]. However, all the stage-structure models mentioned above are autonomous, which is not very consistent with the real ecosystem. Actually, the rhythm of life on earth usually fluctuates with seasonal alternation, e.g., plants and animals show profound annual cycles in physiology, health, morphology, behaviour and demography in response to environmental cues [30]. When winter comes the wild goose will fly to the south to seek a better habitat, whereas they do not migrate in other seasons. And in the Pacific Northwest, Larimichthys polyactis cross over deep water during the winter and migrate to the coast during the spring; then, 3-6 months after spawning, they scatter offshore and return to the depths of the sea during late autumn [23]. Considering the important roles that seasonal factors play in the dynamics of plant and animal species dynamics, it is essential to take models with periodic parameters into consideration.

Furthermore, in recent years, some works reported that the development (or maturation) durations of species are also subject to fluctuation in time due to the temperature variations [6, 21, 37, 41]. In [6], the authors claimed that the maturation rate of the malaria (Plasmodium), which parasite inside the host significantly decreases with gradually increasing temperature. However, to the best of our knowledge, almost all stage-structured models discussed above are autonomous and even if some models are non-autonomous, they do not consider the influence of temperature change on maturity at the same time, while always assumed that the development

duration τ is a positive constant. Hence, it is necessary to consider seasonal factors and the temperature-dependent maturation delays. In what follows, we will give the derivation of a stage-structure competitive model with two maturation delays driven by temperature. The outline of the work is as follows: Section 2 shows the derivation of model by rigorous arguments. The basic reproduction ratio R_0 is calculated and the global behavior of solutions is analyzed in Section 3. Numerical simulations are presented in Section 4 to validate our analytical results. Finally, a brief discussion about our results is provided in Section 5.

2. Model derivation

In this section, we present the formulation of the model with two seasonal development maturation delays. We use $\tau_x(T)$ and $\tau_y(T)$, respectively, to represent the development maturation time of population x and y, where the T represent the temperature and it is assumed to a function of time t, i.e., $T = T(t)$. Hence, we can denote $\tau_x(T(t)) = \tau_x(t)$ and $\tau_y(T(t)) = \tau_y(t)$, respectively. Throughout this paper, the subscripts x, y stand for species x and species y, respectively. $L_x(t)$ and $A_x(t)$ represent the total densities of immature and mature population x, respectively. $L_y(t)$ and $A_y(t)$ represent the total densities of immature and mature population y, respectively. First, we use the following Fig.1 to represent the interaction of species x and species y:

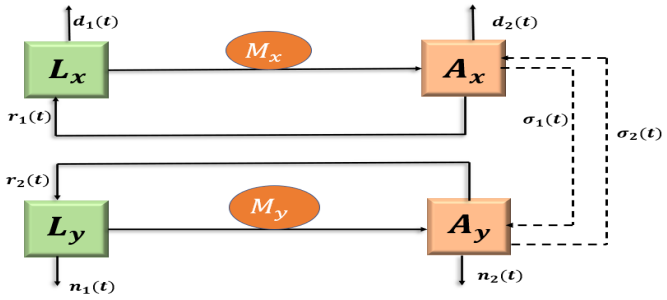


Figure 1. The interaction of species x and species y.

where $d_1(t)$ and $d_2(t)$ represent the natural death rate of the immature population x and adult population x, respectively. $n_1(t)$ and $n_2(t)$ represent the natural death rate of the immature population y and adult population y, respectively. $r_1(t)$ and $r_2(t)$ denote the birth rate of immature population x and immature population y, respectively. $M_i\,(i = x, y)$ represent the transition from the immature population i to adult population i, which is dependent on the maturation delay $\tau_i (i = x, y)$. σ_1 and σ_2 represent the competitive coefficient between adult population x and y. At the same time, d_i, n_i, r_i and σ_i $(i = 1, 2)$ are all positive periodic function in time t.

Fig.1 and the corresponding biological explanation above gives rise to the following nonlinear evolution model:

$$\begin{cases} \dfrac{dL_x(t)}{dt} = r_1(t)A_x(t) - M_x(t) - d_1(t)L_x(t), \\ \dfrac{dA_x(t)}{dt} = M_x(t) - d_2(t)A_x(t) - \sigma_1(t)A_y(t)A_x(t), \\ \dfrac{dL_y(t)}{dt} = r_2(t)A_y(t) - M_y(t) - n_1(t)L_y(t), \\ \dfrac{dA_y(t)}{dt} = M_y(t) - n_2(t)A_y(t) - \sigma_2(t)A_y(t)A_x(t). \end{cases} \tag{2}$$

In order to give the specific expression of M_x and M_y, we start with the investigation on the mechanisms of population development between immature stage and adult stage and it will give us a better understanding of the entire modeling process. Take population x for example, we introduce a new variable q represent the development level of immature population x and it increases with a temperature-dependent rate $k_x(T(t))=k_x(t)$. Moreover, $q = q_L = 0$ at the transition from A_x to L_x, and $q = q_A$ at the transition from L_x to A_x. Denote the density (with respect to the development level q) of immature population x at time t with development level q by $L(t, q)$. Then $M_x(t) = k_x(t)L(t, q_A)$. Let $J(t, q)$ be the flux, in the direction of increasing q, of population x with development level q at time t. Then, we can obtain the following

$$\frac{\partial L(t,q)}{\partial t} = -\frac{\partial J(t,q)}{\partial q} - d_1(t)L(t,q).$$

Since $J(t, q) = k_x(t)L(t, q)$, we have

$$\frac{\partial L(t,q)}{\partial t} = -\frac{\partial [k_x(t)L(t,q)]}{\partial q} - d_1(t)L(t,q), \tag{3}$$

with the boundary conditions

$$L(t,0) = \frac{r_1(t)A_x(t)}{k_x(t)}. \tag{4}$$

Remark 1. *Based on the biological facts $L(t, 0)$ represents the development level $q = 0$, i.e., the immature population completely hatches from the adult. Hence, $L(t, 0)$ equals to the birth rate $r_1(t)$ multiplied by the density of adult population $A_x(t)$ and divided by of the temperature-dependent rate $k_x(t)$.*

To solve the system (3) with boundary condition (4), we introduce a new variable as following:

$$\eta = h(t) := q_L + \int_0^t k_x(s)ds.$$

Let $h^{-1}(\eta)$ be the inverse function of $h(t)$ and denote

$$\hat{L}_p(\eta, q) = L\left(h^{-1}(\eta), q\right), \hat{d}_1(\eta) = d_1\left(h^{-1}(\eta)\right), \hat{k}_x(\eta) = k_x\left(h^{-1}(\eta)\right).$$

In view of system (3), we get

$$\frac{\partial \hat{L}(\eta,q)}{\partial \eta} = -\frac{\partial \hat{L}(\eta,q)}{\partial q} - \frac{\hat{d}_1(\eta)}{\hat{k}_x(\eta)}\hat{L}(\eta,q).$$

Let $V(s, x) = \hat{L}(s, s + q - \eta)$, and then

$$\frac{\partial V(s)}{\partial s} = -\frac{\hat{d}_1(s)}{\hat{k}_x(s)}V(s).$$

Since $\eta - (q - q_L) \le \eta$, we have

$$V(\eta) = V(\eta - q + q_L)e^{-\int_{\eta-(q-q_L)}^{\eta} \frac{\hat{d}_1(s)}{\hat{k}_x(s)}ds}.$$

Then

$$\hat{L}(\eta, q) = \hat{L}(\eta - q + q_L, q_L)e^{-\int_{\eta-(q-q_L)}^{\eta} \frac{\hat{d}_1(s)}{\hat{k}_x(s)}ds}.$$

Let $\tau_x(t, q)$ be the time taken to develop for population x from development level q_L to development level q at time t. Since $\frac{dq}{dt} = k_x(t)$, we obtain

$$q - q_L = \int_{t-\tau_x(t,q)}^{t} k_x(s)ds, \tag{5}$$

and hence,

$$h(t-\tau_x(t,q)) = q_L + \int_0^{t-\tau_x(t,q)} k_x(s)ds = h(t) - (q - q_L).$$

Let $s = h(r)$, we have

$$\int_{\eta-(q-q_L)}^{\eta} \frac{\hat{d}_1(s)}{\hat{k}_x(s)}ds = \int_{t-\tau_x(t,q)}^{t} d_1(r)dr.$$

Then, we can obtain

$$\begin{aligned} L(t,q) &= \hat{L}(h(t),q) \\ &= L(t-\tau_x(t,q),0)e^{-\int_{t-\tau_x(t,q)}^{t} d_1(r)dr} \\ &= \frac{r_1(t-\tau_x(t,q))A_x(t-\tau_x(t,q))}{k_x(t-\tau_x(t,q))}e^{-\int_{t-\tau_x(t,q)}^{t} d_1(r)dr}. \end{aligned} \tag{6}$$

Define $\tau_x(t) = \tau_x(t, q_A)$, which means that $\tau_x(t)$ is the threshold development level for population x, namely, individuals x with development level greater (less) than $\tau_x(t)$ can (not) grow up to adult individuals. Moreover, here $\tau_x(t)$ is assumed to be seasonal, i.e., it is dependent on the temperature. Hence, from system (6), we have

$$k_x(t)L(t,q_A) = r_1(t-\tau_x(t))A_x(t-\tau_x(t))\frac{k_x(t)}{k_x(t-\tau_x(t))}e^{-\int_{t-\tau_x(t)}^{t} d_1(r)dr}.$$

In (5), we take $q = q_A$ and obtain

$$q_A - q_L = \int_{t-\tau_x(t)}^{t} k_x(s)ds. \tag{7}$$

Taking the derivative of equation (7) with respect to t on both sides yields

$$1 - \tau_x'(t) = \frac{k_x(t)}{k_x(t-\tau_x(t))} > 0. \tag{8}$$

Biologically, conditions (8) also make sense. Recall that the definition of the $\tau_x(t)$ means the time taken by immature individual who arrives at the adult stage at time t from the bitrth stage. Then, for small enough $\xi > 0$, the immature individual is still immature at time $t + \xi$, which means $\tau_x(t+\xi) < \tau_x(t) + \xi$, and hence, $\tau_x'(t) = \lim_{\xi\to 0}\frac{\tau_x(t+\xi)-\tau_x(t)}{\xi} \le 1$. Finally, we obtain that

$$\begin{aligned} M_x(t) &= k_x(t)L(t,q_A) \\ &= (1-\tau_x'(t))r_1(t-\tau_x(t))A_x(t-\tau_x(t))\exp[-\int_{t-\tau_x(t)}^{t} d_1(\xi)]d\xi. \end{aligned}$$

In the similar way, we can obtain that

$$M_y(t) = (1-\tau_y'(t))r_2(t-\tau_y(t))A_y(t-\tau_y(t))\exp[-\int_{t-\tau_y(t)}^{t} n_1(\xi)]d\xi.$$

Based on the above derivation, a stage-structured model for two competitive species with time-dependent periodic maturation delays is established as follows:

$$\begin{cases} \dfrac{dL_x(t)}{dt} = r_1(t)A_x(t) - (1-\tau_x'(t))r_1(t-\tau_x(t))A_x(t-\tau_x(t)) \\ \qquad\qquad \times \exp\left[-\displaystyle\int_{t-\tau_x(t)}^{t} d_1(\xi)\right]d\xi - d_1(t)L_x(t), \\ \dfrac{dA_x(t)}{dt} = (1-\tau_x'(t))r_1(t-\tau_x(t))A_x(t-\tau_x(t))\exp\left[-\displaystyle\int_{t-\tau_x(t)}^{t} d_1(\xi)\right]d\xi \\ \qquad\qquad - d_2(t)A_x(t) - \sigma_1(t)A_y(t)A_x(t), \\ \dfrac{dL_y(t)}{dt} = r_2(t)A_y(t) - (1-\tau_y'(t))r_2(t-\tau_y(t))A_y(t-\tau_y(t)) \\ \qquad\qquad \times \exp\left[-\displaystyle\int_{t-\tau_y(t)}^{t} n_1(\xi)\right]d\xi - n_1(t)L_y(t), \\ \dfrac{dA_y(t)}{dt} = (1-\tau_y'(t))r_2(t-\tau_y(t))A_y(t-\tau_y(t))\exp\left[-\displaystyle\int_{t-\tau_y(t)}^{t} n_1(\xi)\right]d\xi \\ \qquad\qquad - n_2(t)A_y(t) - \sigma_2(t)A_y(t)A_x(t). \end{cases} \tag{9}$$

Moreover, based on the biological meanings of $\tau_x(t)$ and $\tau_y(t)$, we can use a more feasible approach to describe the population growth as follows:

$$L_x(0) = \int_{-\tau_x(0)}^{0} r_1(\xi)A_x(\xi)e^{-\int_{\xi}^{0} d_1(s)\,ds}d\xi,\ L_y(0) = \int_{-\tau_y(0)}^{0} r_2(\xi)A_y(\xi)e^{-\int_{\xi}^{0} n_1(s)\,ds}d\xi,$$

where the immature population size L_x at initial time represents the all accumulation of individuals born at moment ξ with birth rate $r_1(\xi)A_x(\xi)$ between $-\tau_x(t)$ to 0 but remains alive with the survival probability $e^{-\int_{\xi}^{0} d_1(s)\,ds}$ and the $L_y(0)$ has the same biological meanings. By the uniqueness of solutions, then we have

$$L_x(t) = \int_{t-\tau_x(t)}^{t} r_1(\xi)A_x(\xi)e^{-\int_{\xi}^{t} d_1(s)\,ds}d\xi,\ L_y(t) = \int_{t-\tau_y(t)}^{t} r_2(\xi)A_y(\xi)e^{-\int_{\xi}^{t} n_1(s)\,ds}d\xi.$$

In terms of the development maturation delay $\tau_x(t)$ of species x, we can use the development proportion $\lambda_x(\xi)$ at time ξ to parameterize it (see [34]), which means the accumulative proportion from $t-\tau_x(t)$ to t reaches unity when the individual grow up to mature stage, i.e.

$$1 = \int_{t-\tau_x(t)}^{t} \lambda_x(\xi)d\xi, \tag{10}$$

where $\lambda_x(\xi)$ is the periodic development proportion at time ξ. From (7), we can easily obtain that

$$\lambda_x(\xi) = \frac{k_x(\xi)}{q}.$$

The periodicity of $\lambda_x(\xi)$ in ξ implies the periodicity of the delay $\tau_x(t)$ in time t. Differentiating (10) with respect to t yields $0 = \lambda_x(t) - (1 - \tau_x'(t))\lambda_x(t - \tau_x(t))$, then we can obtain

$$1 - \tau_x'(t) = \frac{\lambda_x(t)}{\lambda_x(t - \tau_x(t))}. \tag{11}$$

From (11), we can see that $1 - \tau_x'(t) > 0$ for any development delay (see [2,34]).

3. Model analysis

In this section, we first obtain the positivity and boundedness of the solution of system (9). And then, we compute the basic reproduction ratio R_0 for system (9) by using the approach in [43]. Finally, by constructing a periodic semiflow on a special functional space and applying the theory of monotone dynamical systems, we obtain the threshold type results of global dynamics.

3.1. **Positivity and boundedness.** In system (9), equations of the immature species x and y can be decoupled because the other two equations do not exist variables $L_x(t)$ and $L_y(t)$. Moreover, as shown in (6), we can rewrite the other two equations by integral forms:

$$L_x(t) = \int_{t-\tau_x(t)}^{t} r_1(\xi)A_x(\xi)e^{-\int_{\xi}^{t} d_1(\eta)\,d\eta}\,d\xi,\ L_y(t) = \int_{t-\tau_y(t)}^{t} r_2(\xi)A_y(\xi)e^{-\int_{\xi}^{t} n_1(\eta)\,d\eta}\,d\xi.$$

This suggests that the dynamics of $L_x(t)$, $L_y(t)$ can be obtained once the dynamics of $A_x(t)$ and $A_y(t)$ are obtained. Therefore, we mainly investigate the dynamics of following system:

$$\begin{cases} \dfrac{dA_x(t)}{dt} = (1 - \tau_x'(t))r_1(t - \tau_x(t))A_x(t - \tau_x(t)) \exp\left[-\displaystyle\int_{t-\tau_x(t)}^{t} d_1(\xi)\right]d\xi \\ \qquad\qquad - d_2(t)A_x(t) - \sigma_1(t)A_y(t)A_x(t), \\ \dfrac{dA_y(t)}{dt} = (1 - \tau_y'(t))r_2(t - \tau_y(t))A_y(t - \tau_y(t)) \exp\left[-\displaystyle\int_{t-\tau_y(t)}^{t} n_1(\xi)\right]d\xi \\ \qquad\qquad - n_2(t)A_y(t) - \sigma_2(t)A_y(t)A_x(t). \end{cases} \tag{12}$$

To obtain the positivity and boundedness of solutions for the subsystem (12), we give some notations. Let $\hat{\tau} = \max\{\max_{t\in[0,\omega]} \tau_x(t), \max_{t\in[0,\omega]} \tau_y(t)\}$ and $\mathcal{X} := C([-\hat{\tau}, 0], \mathbb{R}^2)$ with the maximum norm. For a function $b(\cdot) \in C([-\hat{\tau}, \infty), \mathbb{R}^2)$, we define $b_t \in \mathcal{X}$ as $b_t(\theta) = b(t + \theta)$ for all $\theta \in [-\hat{\tau}, 0]$. For any $\phi \in \mathcal{X}$, we define $f(t, \phi) = (f_1(t, \phi), f_2(t, \phi))$ with

$$\begin{cases} f_1(t,\phi) = r_1(t - \tau_x(t))(1 - \tau_x'(t))e^{-\int_{t-\tau_x(t)}^{t} d_1(\xi)\,d\xi}\phi_1(-\tau_x(t)) - d_2(t)\phi_1(0) - \sigma_1(t)\phi_1(0)\phi_2(0), \\ f_2(t,\phi) = r_2(t - \tau_y(t))(1 - \tau_y'(t))e^{-\int_{t-\tau_y(t)}^{t} n_1(\xi)\,d\xi}\phi_2(-\tau_y(t)) - n_2(t)\phi_2(0) - \sigma_2(t)\phi_1(0)\phi_2(0). \end{cases}$$

Due to the ω-periodicity of all parameters including $r_1(t), \tau_x(t), d_2(t), \sigma_1(t), r_2(t), \tau_y(t), n_2(t)$ and $\sigma_2(t)$, we get $f(t + \omega, \phi) = f(t, \phi)$. For simplicity, we rewrite system (12) into

$$\begin{cases} \dfrac{dA_x(t)}{dt} = H_x(t)A_x(t - \tau_x(t)) - d_2(t)A_x(t) - \sigma_1(t)A_y(t)A_x(t), \\ \dfrac{dA_y(t)}{dt} = H_y(t)A_y(t - \tau_y(t)) - n_2(t)A_y(t) - \sigma_2(t)A_y(t)A_x(t). \end{cases} \tag{13}$$

where

$$H_x(t) = (1-\tau_x'(t))r_1(t-\tau_x(t))\exp\Big[-\int\limits_{t-\tau_x(t)}^{t} d_1(\xi)\Big]d\xi,$$

$$H_y(t) = (1-\tau_y'(t))r_2(t-\tau_y(t))\exp\Big[-\int\limits_{t-\tau_y(t)}^{t} n_1(\xi)\Big]d\xi.$$

Obviously, all coefficients are positive ω-periodic functions. For a given continuous ω-periodic function $g(t)$, denote

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

On the positivity and boundedness of system (13), we have the following result.

Theorem 1. *For any given initial value $\phi = (\phi_1, \phi_2) \in \mathcal{X}_+ = C([-\hat{\tau}, 0], \mathbb{R}^2_+)$, system (13) exists a unique bounded nonnegative solution $v(t,\phi)$ with $v_0 = \phi$ in $[0,\infty)$.*

Proof. Because $f(t,\phi)$ is continuous and Lipschitzian in ϕ. We can easily obtain that for any $\phi \in \mathcal{X}_+$, system (13) exists a unique solution $u(t,\phi)$ with $u_0 = \phi$ on its maximal existence interval. Denote $z^* = (z_1^*, z_2^*) := (\frac{\hat{H}_y}{\check{\sigma}_2}, \frac{\hat{H}_x}{\check{\sigma}_1})$. For any given $\rho \geq 1$, $[0, \rho z^*]_{\mathcal{X}}$ be the ordered interval as follows

$$[0,\rho z^*]_{\mathcal{X}} := \{\phi \in \mathcal{X} : 0 \leq \phi(\theta) \leq \rho z^* \text{ for all } \quad \theta \in [-\hat{\tau}, 0]\}.$$

We can easily verify that $f_i(t,\psi) \geq 0$ ($f_i(t,\psi) \leq 0$) when $\psi \in [0,\rho z^*]_{\mathcal{X}}$, $t \in \mathbb{R}$ and $\psi_i(0) = 0$ ($\psi_i(0) = \rho z_i^*$) (i=1,2). By the Theorem 5.2.1 and Remark 5.2.1 in [29], it follows that $[0,\rho z^*]_{\mathcal{X}}$ is positively invariant for system (13). Hence, there always exists $\rho \geq 1$ such that $\phi \in [0,\rho z^*]$ for all $\phi \in \mathcal{X}_+$. This proves the positivity and boundedness of system (13) solutions in $\mathcal{X}_+$. □

3.2. **The basic reproduction ratio R_0.** This section we will obtain the basic reproduction ratio for system (13) according to recent theory developed in [43].

The linearized system of system (13) with A_y and A_x free is

$$\begin{cases} \dfrac{dA_x(t)}{dt} = H_x(t)A_x(t-\tau_x(t))\exp[-\displaystyle\int\limits_{t-\tau_x(t)}^{t} d_1(\xi)]d\xi - d_2(t)A_x(t), \\ \dfrac{dA_y(t)}{dt} = H_yA_y(t-\tau_y(t))\exp[-\displaystyle\int\limits_{t-\tau_y(t)}^{t} n_1(\xi)]d\xi - n_2(t)A_y(t). \end{cases} \tag{14}$$

Suppose that

$$F(t)\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix} = \begin{pmatrix} H_x(t)\phi_1(-\tau_x(t))\\ H_y(t)\phi_2(-\tau_y(t))\end{pmatrix} \text{ and } V(t) = \begin{pmatrix} d_2(t) & 0\\ 0 & n_2(t)\end{pmatrix}.$$

Then, system (14) can be rewritten as

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

Here $F(t)$ and $V(t)$ are ω-periodic in t, $F(t)$ denote the growth rate of adult population at time t. We define the following evolution system to represent the decreasing rate of adult population:

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

Let $Z(t,s), t \geq s$, be the evolution matrix of system (14). Then, for each $s \in \mathbb{R}$, the 2×2 matrix $Z(t,s)$ satisfies

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

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

$$Z(t,s) = \begin{pmatrix} e^{-\int_s^t d_2(\xi)d\xi} & 0 \\ 0 & e^{-\int_s^t n_2(\xi)d\xi} \end{pmatrix}.$$

Define $\|Z(t,s)\| = \max_{1\leq i,j\leq 2} |Z_{ij}(t,s)|$. The exponential growth bound of $Z(t,s)$ is defined as

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

Obviously, $\Omega(Z) \leq -\min\{\check{d}_2, \check{n}_2\}$ and $F(t)$ and $V(t)$ satisfy the following assumptions in [43]:

(H_1) $F(t) : \mathcal{X} \to \mathbb{R}^2$ is positive in the sense that $F(t)\mathcal{X}_+ \subseteq \mathbb{R}^2_+$;

(H_2) The periodic matrix $-V(t)$ is cooperative, and $\Omega(Z) < 0$.

Denote C_ω be the Banach space of all ω-periodic functions with the maximum norm and the positive cone $C^+_\omega := \{u \in C_\omega : u(t) \geq 0, \text{ for all } \quad t \in \mathbb{R}\}$. Suppose $v \in C_\omega$ is the initial density of adult populations in this periodic environment, then $F(t-s)v_{t-s}$ is the density of newly born at time $t-s$ with $t \geq s \geq 0$, and $Z(t,t-s)F(t-s)v_{t-s}$ represents the density of those adult population who were newly reproduced at time $t-s$ and still survive 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 density of accumulative adult population burden at time t produced by those adult population reproduced at previous time.

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

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

According to [43], the basic reproduction ratio $R_0 := r(L)$, i.e., spectral radius of L. The details of the computation of R_0 can be founded in [32, 43].

For any given $t \geq 0$, denote $M(t)$ be the map of the linear periodic system (14) on $\mathcal{X}$, i.e., $M(t)\phi = \omega_t(\phi)$, where $\omega(t,\phi)$ is the unique solution of (14) with $\omega_0 = \phi \in \mathcal{X}$. By the Theorem 2.1 in [43], we obtain the result that $R_0 - 1$ is a threshold value for the stability of the zero solution of system (14).

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

Based on this lemma, we obtain the global dynamics of system (13) in the next subsection.

3.3. **Periodic semiflow.** In this subsection, we set up a new phase space on which system (12) generates an eventually strongly monotone periodic semiflow. What's more, based on the the theory of monotone and subhomogeneous semiflows [42], we study the global dynamics of system (13) in terms of R_0. First, we obtain that there exists a unique nonnegative solution on the new phase space by Lemma 2. Denote

$$\mathcal{Y} := C([-\tau_x(0), 0], \mathbb{R}) \times C([-\tau_y(0), 0], \mathbb{R}) \text{ and } \mathcal{Y}_+ := C([-\tau_x(0), 0], \mathbb{R}_+) \times C([-\tau_y(0), 0], \mathbb{R}_+).$$

Then, $(\mathcal{Y}, \mathcal{Y}_+)$ is an ordered Banach space. For a continuous function $u : [-\tau_x(0), +\infty) \times [-\tau_y(0), +\infty) \to \mathbb{R}^2$ and $t \geq 0$, we define $u_t = \big((u_t)_1, (u_t)_2\big) \in \mathcal{Y}$ by

$$(u_t)_1(\theta) = u_1(t+\theta) \text{ for all } \theta \in [-\tau_x(0), 0], \quad (u_t)_2(\eta) = u_2(t+\eta) \text{ for all } \eta \in [-\tau_y(0), 0].$$

Lemma 2. *For any given initial value $\phi \in \mathcal{Y}_+$, system* (13) *exists a unique nonnegative solution $u(t,\phi)$ on $[0,\infty)$ with $u_0 = \phi$.*

Proof. Let $\bar{\tau} = \min\{\check{\tau}_x, \check{\tau}_y\}$. For any $t \in [0,\bar{\tau}]$, $t - \tau_x(t)$ is strictly increasing, then

$$-\tau_x(0) = 0 - \tau_x(0) \le t - \tau_x(t) \le \bar{\tau} - \tau_x(\bar{\tau}) \le \bar{\tau} - \bar{\tau} = 0,$$

$$-\tau_y(0) = 0 - \tau_y(0) \le t - \tau_y(t) \le \bar{\tau} - \tau_y(\bar{\tau}) \le \bar{\tau} - \bar{\tau} = 0.$$

For any $\phi \in \mathcal{Y}_+$, consider the following equations

$$\begin{cases} \dfrac{dA_x}{dt} = H_x(t)\phi_1(t-\tau_x(t)) - d_2(t)A_x(t) - \sigma_1(t)A_y(t)A_x(t), \\ \dfrac{dA_y}{dt} = H_y(t)\phi_2(t-\tau_y(t)) - n_2(t)A_y(t) - \sigma_2(t)A_y(t)A_x(t), \end{cases} \tag{15}$$

with initial values

$$A_x(t-\tau_x(t)) = \phi_1(t-\tau_x(t)),\ A_y(t-\tau_y(t)) = \phi_2(t-\tau_y(t)).$$

Given $\phi \in \mathcal{Y}_+$, from the first equation of (15), we can obtain that

$$\frac{dA_x}{dt} \ge -d_2(t)A_x(t) - \sigma_1(t)A_y(t)A_x(t).$$

Hence, we get the local positivity of the solution $A_x(t) \ge \exp\{-d_2(t) - \sigma_1(t)A_y(t)\}$. Moreover, we can also obtain that

$$\frac{dA_x}{dt} \le H_x(t)\phi_1(t-\tau_x(t)) - d_2(t)A_x(t).$$

In this case, we obtain the local boundness of the solution. Hence, the solution $(A_x(t), A_y(t))$ of system (15) exists for $t \in [0,\bar{\tau}]$. In other words, we obtain the values of $u_1(\theta) = A_x(\theta)$ for $\theta \in [-\tau_x(0),\bar{\tau}]$ and $u_2(\eta) = A_y(\eta)$ for $\eta \in [-\tau_y(0),\bar{\tau}]$. For any $t \in [\bar{\tau}, 2\bar{\tau}]$, we have

$$-\tau_x(0) = 0 - \tau_x(0) \le \bar{\tau} - \tau_x(\bar{\tau}) \le t - \tau_x(t) \le 2\bar{\tau} - \tau_x(2\bar{\tau}) \le 2\bar{\tau} - \bar{\tau} = \bar{\tau}.$$

Then, we get $A_x(t-\tau_x(t)) = u_1(t-\tau_x(t))$. Similarly, $A_y(t-\tau_y(t))$=$u_2(t-\tau_y(t))$ can also be obtained from the previous step. Solving the following DDE for $t \in [\bar{\tau}, 2\bar{\tau}]$ with $A_x(\bar{\tau}) = u_1(\bar{\tau})$ and $A_y(\bar{\tau}) = u_2(\bar{\tau})$ as:

$$\begin{cases} \dfrac{dA_x}{dt} = H_x(t)u_1(t-\tau_x(t)) - d_2(t)A_x(t) - \sigma_1(t)A_y(t)A_x(t), \\ \dfrac{dA_y}{dt} = H_y(t)u_2(t-\tau_y(t)) - n_2(t)A_y(t) - \sigma_2(t)A_y(t)A_x(t), \end{cases}$$

we get the solution $(A_x(t), A_y(t))$ on the interval $[\bar{\tau}, 2\bar{\tau}]$. Extending this procedure to $[n\bar{\tau}, (n+1)\bar{\tau}]$ for all $n \in \mathbb{N}$, we obtain that the solution $(A_x(t), A_y(t))$ exists uniquely for any initial value $\phi \in \mathcal{Y}_+$. □

Remark 2. *Due to the uniqueness of solutions in Theorem 1 and Lemma 2, we can obtain that $u(t,\phi) = v(t,\psi)$ for any $\psi \in \mathcal{X}_+$ and $\phi \in \mathcal{Y}_+$ with $\psi_1(\theta) = \phi_1(\theta)$, for all $\theta \in [-\tau_x(0), 0]$ and $\psi_2(\eta) = \phi_2(\eta)$, for all $\eta \in [-\tau_y(0), 0]$, where $u(t,\phi)$ and $v(t,\psi)$ are solutions of system* (13) *with $u_0 = \phi$ and $v_0 = \psi$, respectively.*

Lemma 3. *Denote $K_t(\phi) = u_t(\phi)$, for all $t \ge 0$. Then, K_t is an ω-periodic semiflow on $\mathcal{Y}_+$, i.e., K_t satisfies the following items:*
(i) $K_0 = I$;
(ii) $K_{t+\omega} = K_t \circ K_\omega$, for all $t \ge 0$;
(iii) $K_t(\phi)$ is continuous in $(t,\phi) \in [0,\infty) \times \mathcal{Y}_+$.

Proof. Item (i) and (iii) obviously hold. We just prove item (ii). Let $v(t) = u(t+\omega, \phi)$, then we verify $v(t) = u(t, u_\omega(\phi))$, for all t ≥ 0.

$$\begin{aligned}\frac{dv_1(t)}{dt} =& \frac{du_1(t+\omega,\phi)}{dt}\\ =& H_x(t+\omega)u_1(t+\omega-\tau_x(t+\omega),\phi) - d_2(t+\omega)u_1(t+\omega,\phi)\\ & - \sigma_1(t+\omega)u_1(t+\omega,\phi)u_2(t+\omega,\phi)\\ =& H_x(t)u_1(t+\omega-\tau_x(t+\omega),\phi) - d_2(t)u_1(t+\omega,\phi) - \sigma_1(t)u_1(t+\omega,\phi)u_2(t+\omega,\phi)\\ =& H_x(t)v_1(t-\tau_x(t)) - d_2(t)v_1(t) - \sigma_1(t)v_1(t)v_2(t).\end{aligned}$$

Similarly, we have

$$\frac{dv_2(t)}{dt} = H_y(t)v_2(t-\tau_y(t)) - n_2(t)v_2(t) - \sigma_2(t)v_1(t)v_2(t).$$

Hence, $v(t)$ is a solution of system (13). Moreover, we have $v_1(\theta) = u_1(\theta+\omega, \phi)$ for $\theta \in [-\tau_x(0), 0]$ and $v_2(\eta) = u_2(\eta+\omega, \phi)$ for $\eta \in [-\tau_y(0), 0]$. Furthermore, denote $w(t) = u(t, u_\omega(\phi))$, then $w(t)$ is also a solution of system (13), and $w_1(\theta) = u_1(\theta, u_\omega(\phi)) = u_\omega(\phi)_1(\theta) = u_1(\theta+\omega, \phi)$ for $\theta \in [-\tau_x(0), 0]$ and $w_2(\eta) = u_2(\eta, u_\omega(\phi)) = u_\omega(\phi)_2(\eta) = u_2(\eta+\omega, \phi)$ for $\eta \in [-\tau_y(0), 0]$. Thus, $v(t)$ and $w(t)$ are solutions of system (13) with the same initial value. From the uniqueness of solution, we get

$$u(t+\omega, \phi) = u(t, u_\omega(\phi)), \quad \text{for all } \ t \geq 0.$$

For any $t \geq 0$ and $\theta \in [-\tau_x(0), 0]$, we have $u_1(t+\theta+\omega, \phi) = u_1(t+\theta, u_\omega(\phi))$ when $t+\theta \geq 0$, i.e., $u_{t+\omega}(\phi)_1(\theta) = u_t \circ u_\omega(\phi)_1(\theta)$. Similarly, $u_1(t+\theta, u_\omega(\phi)) = u_\omega(\phi)_1(t+\theta) = u_1(t+\theta+\omega, \phi)$ when $t+\theta < 0$, 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 $\eta \in [-\tau_y(0), 0]$. Thus, we obtain that $u_t \circ u_\omega(\phi) = u_{t+\omega}(\phi)$, and hence, $K_{t+\omega}(\phi) = K_t \circ K_\omega(\phi)$ for all $\phi \in \mathcal{Y}_+$ and $t \geq 0$. □

Remark 3. *By the Lemma 3, we obtain that the unique nonnegative solution $u_t(\phi)$ on the new phase space is an ω-periodic semiflow. The theory of monotone and subhomogeneous semiflows [42] need the solution $u_t(\phi)$ not only to be an ω-periodic semiflow but also eventually strongly monotone and strictly subhomogeneous. The following two lemmas indicate that the periodic semiflow K_t is eventually strongly monotone and strictly subhomogeneous, respectively.*

Lemma 4. *For any ϕ and ψ in $\mathcal{Y}_+$ with $\phi > \psi$, $u_i(t) > v_i(t)$ for all $t > 2\hat{\tau}$, $i = 1, 2$, where $u(t)$ and $v(t)$ are the solutions of system* (13) *with $u_0 = \phi$ and $v_0 = \psi$, respectively. Hence, $K_t(\phi) \gg K_t(\psi)$ in $\mathcal{Y}$ for all $t > 2\hat{\tau}$.*

Proof. From the proof of Lemma 2, we can obtain that $u_i(t) \geq v_i(t)$ by a simple comparison argument on each interval $[n\bar{\tau}, (n+1)\bar{\tau}]$, $n \in \mathbb{N}$. Moreover, Theorem 1 and Remark 2 imply that the $u(t)$ and $v(t)$ are bounded on $[0, \infty)$. Therefore, there exists a real number $q > 0$ such that u_t and v_t are in the ordered interval $[(0,0), (q,q)]_{\mathcal{Y}}$ for all $t \geq 0$. Thus, we can choose a large number $M > 0$ such that $g_1(t, A_x) := -d_2(t)A_x - \sigma_1(t)A_yA_x + MA_x$ is increasing in $A_x \in [0, q]$, $g_2(t, A_y) := -n_2(t)A_y - \sigma_2(t)A_yA_x + MA_y$ is increasing in $A_y \in [0, q]$ for each $t \in \mathbb{R}$. Then, $u(t)$ and $v(t)$ satisfy the following integral equations:

$$\begin{cases} A_x(t) = e^{-Mt}A_x(0) + \int_0^t e^{-M(t-s)}g_1(s, A_x(s))ds + \int_0^t e^{-M(t-s)}H_x(s)A_x(s-\tau_x(s))ds, \\ A_y(t) = e^{-Mt}A_y(0) + \int_0^t e^{-M(t-s)}g_2(s, A_y(s))ds + \int_0^t e^{-M(t-s)}H_y(s)A_y(s-\tau_y(s))ds, \end{cases} \tag{16}$$

for all $t \geq 0$. Hence, we can easily obtain that $[-\tau_x(0), 0] \subseteq m_x([0, \hat{\tau}])$ and $[-\tau_y(0), 0] \subseteq m_y([0, \hat{\tau}])$ because both $m_x(t) := t - \tau_x(t)$ and $m_y(t) := t - \tau_y(t)$ are increasing in $t \in \mathbb{R}$. Without loss of

generality, we assume that $\phi_2 > \psi_2$. Then, there exists an $\eta \in [-\tau_y(0), 0]$ such that $u_2(\eta) > v_2(\eta)$. From the second equation of (16), we have $u_2(t) > v_2(t)$ for all $t > \hat{\tau}$. Similarly, we can obtain $u_1(t) > v_1(t)$ for all $t > \hat{\tau}$. This shows that $u_i(t) > v_i(t)$ for all $t > \hat{\tau}$, $i = 1, 2$, then solution map K_t is strongly monotone whenever $t > 2\hat{\tau}$. □

Lemma 5. *For any $\phi \gg 0$ in $\mathcal{Y}$ and $\gamma \in (0, 1)$, we have $u_i(t, \gamma\phi) > \gamma u_i(t, \phi)$ for all $t > \hat{\tau}$, $i = 1, 2$. Thus, $K^n_\omega(\gamma\phi) \gg \gamma K^n_\omega(\phi)$ in $\mathcal{Y}$ with $n\omega > 2\hat{\tau}$ for all $n \in \mathbb{R}^+$.*

Proof. Denote $w(t) = u(t, \gamma\phi)$ and $v(t) = \gamma u(t, \phi)$, where $u(t, \phi)$ is the solution of system (13) with $u_0 = \phi \gg 0$ in $\mathcal{Y}$. From the proof of Lemma 2, we obtain that $\omega(t) > 0$ and $v(t) > 0$ for all $t \geq 0$. Moreover, we have

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

for all $\theta \in [-\tau_x(0), 0]$ and $\eta \in [-\tau_y(0), 0]$. We can easily obtain that $v(t)$ satisfies the following system:

$$\begin{cases} \dfrac{dv_1(t)}{dt} = H_x(t)v_1(t - \tau_x(t)) - d_2(t)v_1(t) - \sigma_1(t)\dfrac{v_2(t)}{\gamma}v_1(t), \\ \dfrac{dv_2(t)}{dt} = H_y(t)v_2(t - \tau_y(t)) - n_2(t)v_2(t) - \sigma_2(t)\dfrac{v_1(t)}{\gamma}v_2(t). \end{cases}$$

For any $0 \leq t \leq \bar{\tau}$, we have

$$-\tau_x(0) \leq t - \tau_x(t) \leq \bar{\tau} - \tau_x(\bar{\tau}) \leq 0 \quad \text{and} \quad -\tau_y(0) \leq t - \tau_y(t) \leq \bar{\tau} - \tau_y(\bar{\tau}) \leq 0.$$

Hence, we can get the derivative of $v_1(t)$ and $v_2(t)$ at $t = 0$ as follows:

$$\begin{aligned} \left.\frac{dv_1(t)}{dt}\right|_{t=0} &= H_x(0)v_1(0 - \tau_x(0)) - d_2(0)v_1(0) - \sigma_1(0)\frac{v_2(0)}{\gamma}v_1(0) \\ &< H_x(0)v_1(0 - \tau_x(0)) - d_2(0)v_1(0) - \sigma_1(0)v_2(0)v_1(0) \\ &= H_x(0)w_1(-\tau_x(0)) - d_2(0)w_1(0) - \sigma_1(0)w_1(0)w_2(0) \\ &= \left.\frac{dw_1(t)}{dt}\right|_{t=0} \end{aligned}$$

and

$$\begin{aligned} \left.\frac{dv_2(t)}{dt}\right|_{t=0} &= H_y(0)v_2(0 - \tau_x(0)) - n_2(0)v_2(0) - \sigma_2(0)\frac{v_1(0)}{\gamma}v_2(0) \\ &< H_y(0)v_2(0 - \tau_x(0)) - n_2(0)v_2(0) - \sigma_2(0)v_2(0)v_1(0) \\ &= H_x(0)w_2(-\tau_x(0)) - n_2(0)w_2(0) - \sigma_1(0)w_1(0)w_2(0) \\ &= \left.\frac{dw_2(t)}{dt}\right|_{t=0}. \end{aligned}$$

Since $v_1(0) = w_1(0) > 0$ and $v_2(0) = w_2(0) > 0$, then there exists an $\epsilon \in (0, \bar{\tau})$ such that $0 < v_1(t) < w_1(t)$ and $0 < v_2(t) < w_2(t)$ for all $0 < t < \epsilon$. We assume that $v_1(t) < w_1(t)$ and $v_2(t) < w_2(t)$ for all $0 < t \leq \bar{\tau}$. Otherwise, then there exists $t_0 \in (0, \bar{\tau}]$ such that $v_1(t) < w_1(t)$ and $v_2(t) < w_2(t)$ for all $0 < t < t_0$ while $v_1(t_0) = w_1(t_0)$ and $v_2(t_0) = w_2(t_0)$, which implies $v_1'(t_0) \geq w_1'(t_0)$ and $v_2'(t_0) \geq w_2'(t_0)$. However, we have

$$\begin{aligned} \left.\frac{dv_1(t)}{dt}\right|_{t=t_0} &= H_x(t_0)v_1(t_0 - \tau_x(t_0)) - d_2(t_0)v_1(t_0) - \sigma_1(t_0)\frac{v_2(t_0)}{\gamma}v_1(t_0) \\ &< H_x(t_0)v_1(t_0 - \tau_x(t_0)) - d_2(t_0)v_1(t_0) - \sigma_1(t_0)v_2(t_0)v_1(t_0) \\ &= H_x(t_0)w_1(-\tau_x(t_0)) - d_2(t_0)w_1(t_0) - \sigma_1(t_0)w_1(t_0)w_2(t_0) \\ &= \left.\frac{dw_1(t)}{dt}\right|_{t=t_0} \end{aligned}$$

and

$$\begin{aligned}\left.\frac{dv_2(t)}{dt}\right|_{t=t_0} =& H_y(t_0)v_2(0-\tau_x(0)) - n_2(0)v_2(0) - \sigma_2(0)\frac{v_1(0)}{\gamma}v_2(0)\\ <& H_y(0)v_2(0-\tau_y(0)) - n_2(0)v_2(0) - \sigma_2(0)v_2(0)v_1(0)\\ =& H_y(0)w_2(-\tau_y(0)) - n_2(0)w_2(0) - \sigma_1(0)w_1(0)w_2(0)\\ =& \left.\frac{dw_2(t)}{dt}\right|_{t=0},\end{aligned}$$

which yields a contradiction. This shows that $v_1(t) < w_1(t)$ and $v_2(t) < w_2(t)$ for all $0 < t \le \bar{\tau}$. Extending the arguments to any interval $(n\bar{\tau}, (n+1)\bar{\tau}]$, we can obtain that $v_1(t) \le w_1(t)$ and $v_2(t) < w_2(t)$ for all $t \in (n\bar{\tau}, (n+1)\bar{\tau}]$ with $n \in \mathbb{N}$. Therefore, for any $t > 0$, we have $v_1(t) < w_1(t)$ and $v_2(t) < w_2(t)$, i.e., $u_i(t, \gamma\phi) > \gamma u_i(t, \phi)$ for all $t > \hat{\tau}$, $i = 1, 2$. Thus, $K^n_\omega(\gamma\phi) = K_{n\omega}(\gamma\phi) \gg \gamma K_{n\omega}(\phi) = \gamma K^n_\omega(\phi)$ with $n\omega > \hat{\tau}$ for all $n \in \mathbb{R}^+$.

For any given $t \ge 0$, denote $N(t)$ be the map of the linear periodic system (14) on $\mathcal{Y}$, i.e., $N(t)\phi = z_t(\phi)$, where $z(t, \phi)$ is the unique solution of (14) with $z_0 = \phi \in \mathcal{Y}$. □

In order to study the threshold dynamics of of the whole system, we need to obtain the following Lemma 6.

Lemma 6. *Two Poincaré maps $M(\omega) : \mathcal{X} \to \mathcal{X}$ and $N(\omega) : \mathcal{Y} \to \mathcal{Y}$ have the same spectral radius, i.e., $r(M(\omega)) = r(N(\omega))$.*

Proof. Given an integer n_0 such that $n_0\omega > 2\hat{\tau}$. From the proof of Lemma 4, we obtain $N(\omega)^{n_0} = N(n_0\omega)$ is strongly positive on $\mathcal{Y}$. Further, Theorem 3.6.1 in [13] implies that $N(\omega)^{n_0}$ is compact. Then, according to the Krein-Rutmann Theorem [14] and $r(N(\omega)^{n_0}) = (r(N(\omega)))^{n_0}$, we obtain that $r(N(\omega)) > 0$. For any given $\phi = (\phi_1, \phi_2) \in \mathcal{Y}$, we define $\tilde{\phi} = (\tilde{\phi}_1, \tilde{\phi}_2) \in \mathcal{X}$

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

and

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

Obviously, $\|\phi\|_{\mathcal{Y}} = \|\tilde{\phi}\|_{\mathcal{X}}$. By Remark 2, we have

$$\|N(n\omega)\phi\|_{\mathcal{Y}} \le \|M(n\omega)\tilde{\phi}\|_{\mathcal{X}} \le \|M(n\omega)\|_{\mathcal{X}} \cdot \|\tilde{\phi}\|_{\mathcal{X}} = \|M(n\omega)\|_{\mathcal{X}} \cdot \|\phi\|_{\mathcal{Y}},$$

where $n\omega > \hat{\tau}$ $\phi \in \mathcal{Y}$ and $n \in \mathbb{R}^+$. Hence, $\|N(n\omega)\|_{\mathcal{Y}} \le \|M(n\omega)\|_{\mathcal{X}}$. Since

$$r(N(\omega)) = \lim_{n\to\infty} \|N(\omega)^n\|^{\frac{1}{n}}_{\mathcal{Y}} = \lim_{n\to\infty} \|N(n\omega)\|^{\frac{1}{n}}_{\mathcal{Y}} \text{ and } r(M(\omega)) = \lim_{n\to\infty} \|M(\omega)^n\|^{\frac{1}{n}}_{\mathcal{X}} = \lim_{n\to\infty} \|M(n\omega)\|^{\frac{1}{n}}_{\mathcal{X}},$$

we have $r(M(\omega)) \ge r(N(\omega)) > 0$. Furthermore, we prove that $r(M(\omega)) \le r(N(\omega))$. From Theorem 5.1.1 in [29] and Theorem 3.6.1 in [13], we obtain that the linear operator $M(\omega)^{n_0} = M(n_0\omega)$ is positive and compact on $\mathcal{X}$. By the Krein-Rutmann Theorem [14], $r(M(\omega)^{n_0})$ is an eigenvalue of $M(\omega)^{n_0}$ with eigenvector $\phi^* > 0$ in $\mathcal{X}$. For any $\phi \in \mathcal{X}$, we define $\underline{\phi} \in \mathcal{Y}$

$$\underline{\phi}_1(\theta) = \phi_1(\theta), \text{ for all } \theta \in [-\tau_x(0), 0], \text{ and } \underline{\phi}_2(\eta) = \phi_2(\eta), \text{ for all } \eta \in [-\tau_y(0), 0].$$

By Remark 2, we have $u(t, \phi) = v(t, \underline{\phi})$, for all $t \ge 0$, where $u(t, \phi)$ and $v(t, \underline{\phi})$ are the solutions of system (14) with $u_0 = \phi \in \mathcal{X}$ and $v_0 = \underline{\phi} \in \mathcal{Y}$, respectively. We further assume that $\underline{\phi^*} > 0$ in $\mathcal{Y}$. Otherwise, $\underline{\phi^*} = 0$, then $u(t, \phi^*) = v(t, \underline{\phi^*}) = 0$ for all $t \ge 0$. This implies that

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

then $\phi^* = 0$ in $\mathcal{X}$, which yields a contradiction. Because

$$N(\omega)^{n_0}\underline{\phi^*} = \underline{M(\omega)^{n_0}\phi^*} = \underline{r(M(\omega))^{n_0})\phi^*} = (r(M(\omega)))^{n_0}\underline{\phi^*},$$

$(r(M(\omega)))^{n_0}$ is a positive eigenvalue of $N(\omega)^{n_0}$ with eigenvector $\underline{\phi^*} > 0$ in $\mathcal{Y}$. Then, we obtain that $(r(M(\omega)))^{n_0} \leq r(N(\omega)^{n_0}) = (r(N(\omega)))^{n_0}$ and $r(M(\omega)) \leq r(N(\omega))$. Hence, we get $r(M(\omega)) = r(N(\omega))$. □

Remark 4. *In fact, different solution methodologies exist in the literature to deal with the ordinary differential problems wherein the primary (kinematic) or the secondary (kinetic) field variables are assumed to have a series solution form. In the present study, the governing equation is expressed and numerically solved in terms of primary (kinematic) field variables. Of course, the alternative approach wherein series form is assumed for the secondary (kinetic) field variables is also can be used in the governing equation of our paper. The details can be seen [7–9, 44].*

3.4. **Threshold dynamics.** Based on the previous Lemmas, we prove the main result of this paper.

Theorem 2. *The following statements are valid:*
(i) If $R_0 \leq 1$, then (0, 0) is globally asymptotically stable for system (13) in $\mathcal{Y}_+$.
(ii) If $R_0 > 1$, then system (13) admits a unique positive ω-periodic solution $(A_x^*(t), A_y^*(t))$, which is globally asymptotically stable for system (13) in $\mathcal{Y}_+ \setminus \{(0,0)\}$.

Proof. Given n_0 such that $n_0\omega > 2\hat{\tau}$. From Lemma 3, K_t is $n_0\omega$-periodic semiflow on $\mathcal{Y}_+$. By Lemma 4 and Lemma 5, $K_{n_0\omega}$ is a strongly monotone and strictly subhomogeneous map on $\mathcal{Y}_+$. From the Theorem 2.3.4 in [42], we can obtain the following results:
(a) If $r(DK_{n_0\omega}(0)) \leq 1$, (0, 0) is globally asymptotically stable for system (13) in $\mathcal{Y}_+$.
(b) If $r(DK_{n_0\omega}(0)) > 1$, system (13) exists a unique positive $n_0\omega$-periodic solution $(A_x^*(t), A_y^*(t))$, which is globally asymptotically stable for system (13) in $\mathcal{Y}_+ \setminus \{(0,0)\}$.

By Lemma 1 and Lemma 6, and $r(DK_{n_0\omega}(0)) = r(N(n_0\omega)) = (r(N(\omega)))^{n_0}$, we get $sign(R_0 - 1) = sign(r(DK_{n_0\omega}(0)) - 1)$. Thus, we need to prove $(A_x^*(t), A_y^*(t))$ is also ω-periodic. Let $\psi^* = v_0^* \in \mathcal{Y}$ with $v^*(t) = (A_x^*(t), A_y^*(t))$. Then $K_{n_0\omega}\psi^* = \psi^*$. Note that

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

By the uniqueness of the positive fixed point of $K_\omega^{n_0} = K_{n_0\omega}$, we have $K_\omega\psi^* = \psi^*$, which implies that $(A_x^*(t), A_y^*(t)) = u(t, \psi^*)$ is an ω-periodic solution of system (13).

Next, we study the dynamics of $L_x(t)$ and $L_y(t)$ for system (9). When $R_0 > 1$, we have $\lim_{t\to\infty}[(A_x(t), A_y(t)) - (A_x^*(t), A_y^*(t))] = 0$ for any solution with positive initial data of system (9). From the integral form of the immature species $L_x(t)$ and $L_y(t)$ in (3.1), we obtain

$$\lim_{t\to\infty}\left[L_x(t) - \int_{t-\tau_x(t)}^{t} r_1(\xi)A_x(\xi)e^{-\int_\xi^t d_1(\eta)\,d\eta}\,d\xi\right] = 0,$$

and

$$\lim_{t\to\infty}\left[L_y(t) - \int_{t-\tau_y(t)}^{t} r_2(\xi)A_y(\xi)e^{-\int_\xi^t n_1(\eta)\,d\eta}\,d\xi\right] = 0.$$

Moreover, we can easily obtain that

$$L_x^*(t) := \int_{t-\tau_x(t)}^{t} r_1(\xi)A_x(\xi)e^{-\int_\xi^t d_1(\eta)\,d\eta}\,d\xi,$$

$$L_y^*(t) := \int_{t-\tau_y(t)}^{t} r_2(\xi)A_y(\xi)e^{-\int_\xi^t n_1(\eta)\,d\eta}\,d\xi,$$

are positive ω-periodic functions. When $R_0 \leq 1$, similarly, we have

$$\lim_{t\to\infty}(A_x(t), A_y(t)) = (0,0) \text{ and } \lim_{t\to\infty}(L_x(t), L_y(t)) = (0,0).$$

□

Based on the discussion above, we get the following results on the global dynamics of system (9).

Theorem 3. *The following statements are valid:*

(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 $(L_x^*(t), A_x^*(t), L_y^*(t), A_y^*(t))$, which is globally asymptotically stable for all nontrivial solutions.

4. Numerical simulation

In this section, our goal is to demonstrate our main results on the global dynamics and discuss the effect of temperature variations on the population dynamics by numerical simulations.

4.1. **Determine parameters.** In order to investigate the effect of temperature and maturation delays on population dynamics, we use the method in [11] to consider temperature variations. To this end, we define the temperature (in degrees °C) as a function of time t (in day) in the following form

$$T(t) = c_K + d_K \times \sin\left(\frac{2\pi}{365} \times (t - t_0)\right), \tag{17}$$

where c_K is mean annual temperature, d_K is half the annual temperature range, and t_0 is day-of-the-year when temperature increases to its annual mean.

Moreover, we should use the temperature $T = T(t)$ on each day of the year to parameterize the temperature-dependent coefficients in the system. Several unimodal models exist to describe development duration as a function of temperature [11, 26–28], in which the Sharpe-Schoolfield model is the most popular. This model provides a natural extension about the Van't Hoff-Arrhenius relation by proposing a reversible inactivation of the rate-controlling enzyme for development at high and low temperatures. The development duration $\widetilde{\tau}_{x(y)}(T)$ can be estimated through the Sharpe-Schoolfield formula

$$\begin{aligned}\widetilde{\tau}_{x(y)}(T) =& \tau_0 \times \exp\left(-\frac{E_\tau}{k_B}\left(\frac{1}{T} - \frac{1}{T_0}\right)\right) \\ &\times \left(1 + \exp\left(\frac{E_\tau^L}{k_B}\left(\frac{1}{T} - \frac{1}{T_\tau^L}\right)\right) + \frac{E_\tau^H}{k_B}\left(-\frac{1}{T} + \frac{1}{T_\tau^H}\right)\right).\end{aligned} \tag{18}$$

Like development time, the immature death rate under the temperature $T = T(t)$ also follows the Van't Hoff-Arrhenius relation at intermediate temperatures. We consider a function as similar as (18) to describe the immature death rate:

$$\begin{aligned}d_1(T) =& \mu_0 \times \exp\left(-\frac{E_\mu}{k_B}\left(\frac{1}{T} - \frac{1}{T_0}\right)\right) \\ &\times \left(1 + \exp\left(\frac{E_\mu^L}{k_B}\left(\frac{1}{T} - \frac{1}{T_\mu^L}\right)\right) + \frac{E_\mu^H}{k_B}\left(-\frac{1}{T} + \frac{1}{T_\mu^H}\right)\right).\end{aligned}$$

For simplicity, we assume $d_1(t) = n_1(t)$ and $\tau_x(t) = \tau_y(t)$ in the system. To determine the maturation time $\tau_x(t)$ and $\tau_y(t)$, the development proportion $r(\xi)$ on the interval for $[t-\tau(t), t]$ needs to be obtained, which can be evaluated as the reciprocal of the development time $\widetilde{\tau}_{x(y)}(T(\xi))$ needed under temperature $T(\xi))$, i.e.,

$$\lambda_{x(y)}(\xi) = \frac{1}{\widetilde{\tau}_{x(y)}(T(\xi))}.$$

In summary, the accumulative development proportions in previous $\tau_x(t) = \tau_y(t)$ days should be unity, i.e.,

$$\int_{t-\tau_{x(y)}(t)}^{t} \frac{1}{\widetilde{\tau}_{x(y)}(T(\xi))} d\xi = 1, \tag{19}$$

with $T(\xi)$ being the mean temperature at day ξ. The maturation time $\tau_{x(y)}(t)$ can be estimated from the above relation (19).

For numerical computations, values of the other parameters are taken from the literature. In system (13), the death rates $d_2(t)$ and $n_2(t)$ are assumed to be a period variable, dependent on the stage-structure [18], respectively. All the related parameters with their biological explanation are summarized in Table 1.

Table 1. Values of the parameters.

Symbol	Definition	value	Reference
c_K	Mean annual temperature	10°C	[11]
d_K	The amplitude of temperature variation	15°C	[11]
t_0	Day of the year when temperature increases to its annual mean	121	[11]
T_0	The reference temperature	15°C	[11]
τ_0	The scaling factor for development time at temperature T_0	29.6days	[11]
T_τ^L	Lower temperature threshold for development	2.5°C	[11]
T_τ^H	Upper temperature threshold for development	32.5°C	[11]
T_μ^L	Lower temperature threshold for abruptly mortality increases	-2.5°C	[11]
T_μ^H	Upper temperature threshold for abruptly mortality increases	37.5°C	[11]
E_τ, E_μ	Average activation energy	0.65ev	[11]
E_τ^L	Inactivation energy for lower temperature threshold	$5 \times E_\tau$	[11]
E_τ^H	Inactivation energy for upper temperature threshold	$5 \times E_\tau$	[11]
E_μ^L	An index analogous to the inactivation energy	$5 \times E_\mu$	[11]
E_μ^H	An index analogous to the inactivation energy	$5 \times E_\mu$	[11]
k_B	Boltzmann's constant	8.62×10^{-5}	[11]
$r_1(t)$	The proportionality coefficient of hatching rate of population x	$3+\sin t$	[18]
$r_2(t)$	The proportionality coefficient of hatching rate of population y	$2+\sin t$	[18]
$\sigma_1(t)$	The competitive coefficients of mature population x	0.25	[4]
$\sigma_2(t)$	The competitive coefficients of mature population y	0.20	[4]
$d_2(t)$	The death rate of the mature population x	Variable	-
$n_2(t)$	The death rate of the mature population y	Variable	-

4.2. **Figures of temperature-dependent parameters.** According to the parameters in Table 1, we obtain the annual temperature change in Fig.2(a).

From the metabolic theory in ecology [11], we obtain temperature-dependent developmental time $\widetilde{\tau}_{x(y)}(T)$ (Fig.2(b)). Comparing Fig.2(a) with Fig.2(b), we conclude that the development time $\widetilde{\tau}_{x(y)}(T)$ changes to a great extent of nonlinearity with the temperature (i.e., the relationship is neither simple positive correlation, nor negative correlation).

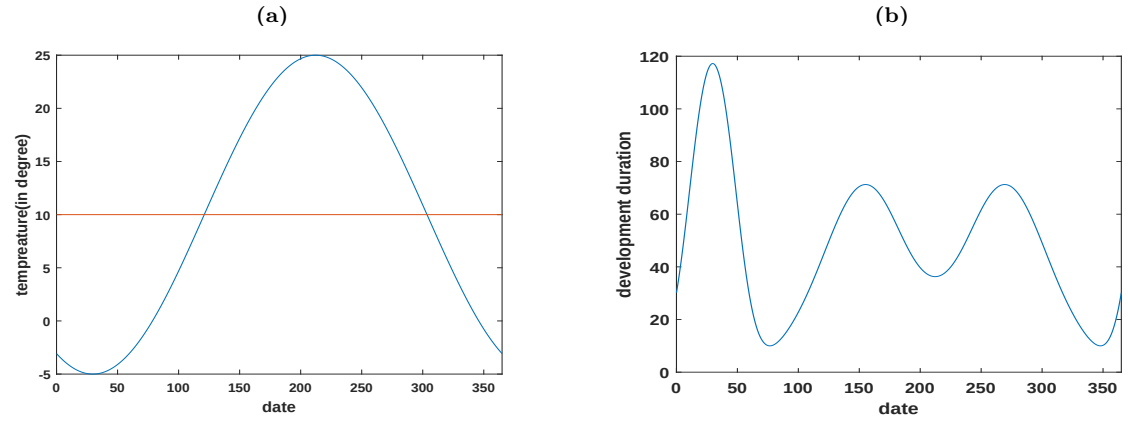


Figure 2. (a): Temperature data of one year. (b): development time $\widetilde{\tau}_{x(y)}(t)$ dependent temperature of one year.

There is one peak temperature in one year (about at the date of 210), while there are three valleys (about at the dates of 75, 220 and 350) for $\widetilde{\tau}_{x(y)}(T)$ with the mild temperature. These results shows that too high, or too low temperatures will prolong the development time, which are consistent with Fig.2 of [11].

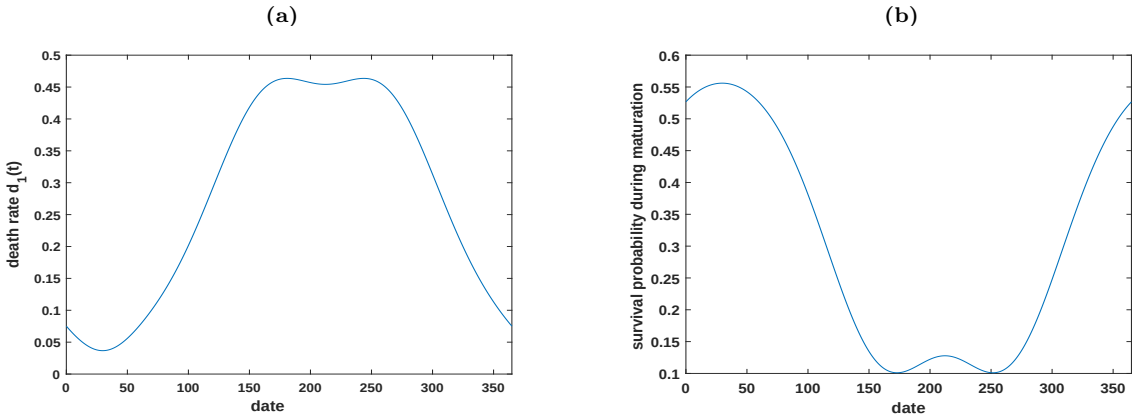


Figure 3. (a): death rate $d_1(t)$ dependent temperature of one year. (b): survival probability $\exp[-\int\limits_{t-\tau_x(t)}^{t} d_1(\xi)]d\xi$ dependent temperature of one year.

The immature death rate $d_1(t)$ (Fig.3(a)) negatively correlates with the immature survival probability $\exp[-\int\limits_{t-\tau_x(t)}^{t} d_1(\xi)]d\xi$ to adult stage (Fig.3(b)). There are two peaks (about at the dates of 150 and 250), while there are two valleys (about at the dates of 150 and 250) for survival probability $\exp[-\int\limits_{t-\tau_x(t)}^{t} d_1(\xi)]d\xi$. These three temperature-dependent parameters exhibit distinct patterns responding to the temperature variation, which call for accurate measurements of the metabolic relationship between biological parameters and temperature conditions.

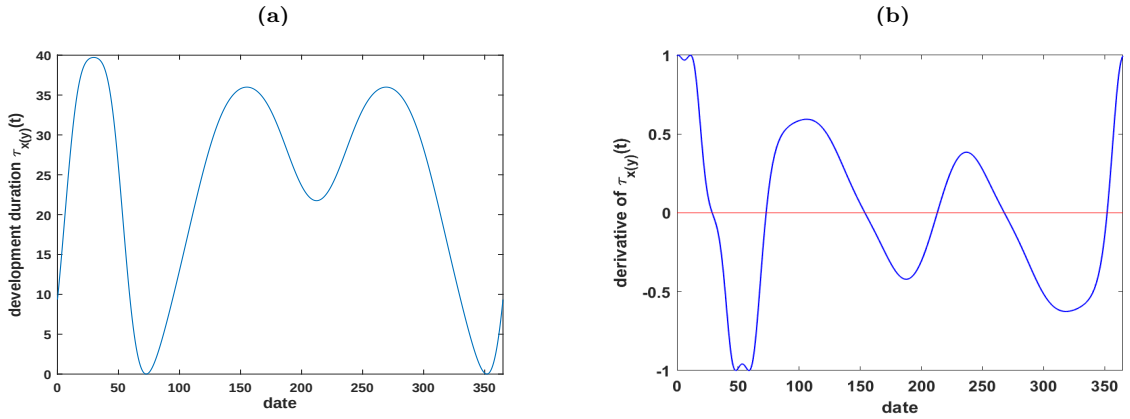
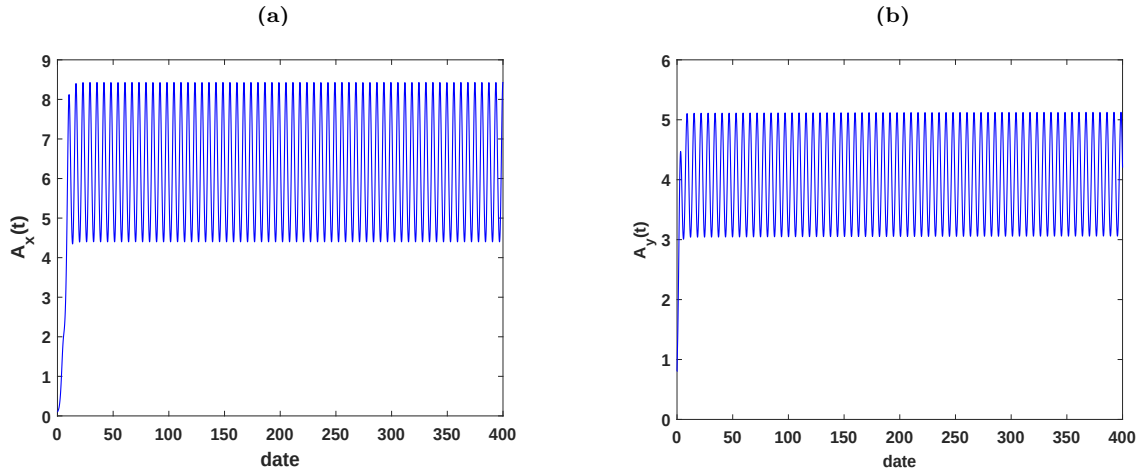


Figure 4. (a): the temperature-dependent development delay $\tau_{x(y)}(t)$. (b): the derivative of the development delay. It is clear from the simulation that the derivative is always smaller than one and therefore $1 - \tau'_{x(y)} > 0$ for all $t \in \mathbb{R}^+$.

In Fig.4(a), there are three valleys and three local peaks. Exactly, there are six points whose derivatives are zero (Fig.4(b)). Moreover, Fig.4(b) shows the derivative of $\tau_{x(y)}$ with respect to time t satisfies the inequality $1 - \tau'_{x(y)}(t) > 0$. We also observe that the immatures not only mature at time t during dates 180 and 270 but also survive through tough time with very small survival probability (Fig.3(b)). Which is the joint effect of a relatively longer developmental duration (shown in Fig.4(a)) and larger death rate during that period (Fig.4(a)). Furthermore, we can obtain that the largest duration $\widetilde{\tau}_{x(y)}(T)$ required is around date 250 because of the extreme (too low) weather condition in the 45-th day (Fig.2(b)). However, in reality, the largest developmental duration $\tau_{x(y)}(t)$ is less than 60 days (Fig.4(a)).

4.3. **Simulation results.** By the parameters presented in Table 1, we obtain the curves of solutions with two different initial values as shown in Fig.5. $d_2(t) = 0.02$, $n_2(t) = 0.05$ (Fig.5 a-b) and $d_2(t) = 2$, $n_2(t) = 1.75$ (Fig.5 c-d). The corresponding basic reproduction ratios are $R_0 = 1.9 > 1$ ($d_2(t) = 0.02$, $n_2(t) = 0.05$) and $R_0 = 0.48 < 1$ ($d_2(t) = 2$, $n_2(t) = 1.75$). The solutions always stabilize at a positive seasonal state when $d_2(t) = 0.02$ and $n_2(t) = 0.05$, while tend to zero when $d_2(t) = 2$, $n_2(t) = 1.75$. These results are consistent with theoretical results in Theorem 3.2, i.e., all solutions starting from various initial values either go to zero when $R_0 < 1$ or stabilize at a periodic state when $R_0 > 1$.



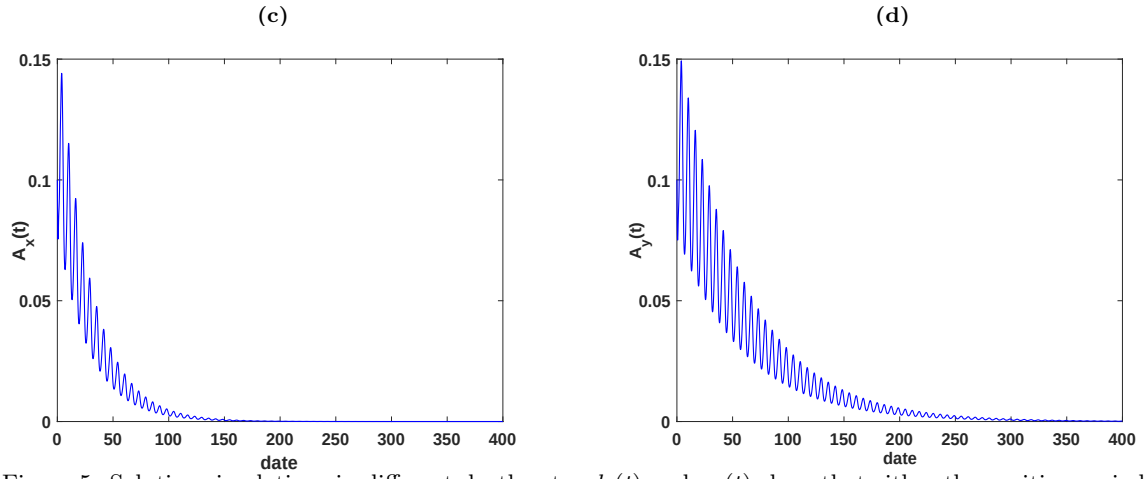
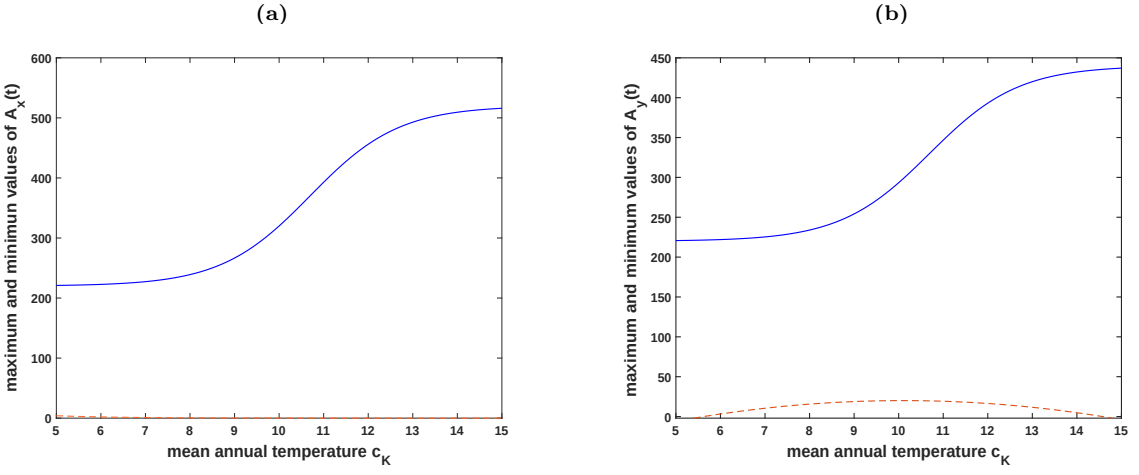


Figure 5. Solution simulations in different death rates $d_2(t)$ and $n_2(t)$ show that either the positive periodic state or the zero solution is globally asymptotically stable. (a)-(b): we take $d_2(t) = 0.02$, $n_2(t) = 0.05$ and the corresponding basic reproduction ratio $R_0 = 1.9 > 1$. (c)-(d): we take $d_2(t) = 2$, $n_2(t) = 1.75$ and the corresponding basic reproduction ratio $R_0 = 0.48 < 1$.

In Fig.6, we predict the impact of temperature on population dynamics with the assume that the annual mean temperature c_K changes (Fig.6 (a)-(b)) or the amplitude d_K of annual temperature varies (Fig.6 (c)-(d)). There exists obvious difference between the minimum and the maximum values of the density when $R_0 > 1$. There is no obvious correlation between the annual temperature and maximum population density for adult population $A_x(t)$ and $A_y(t)$. For example, when the annual temperature is relatively high (for example, at around 11°C), increasing the annual temperature may decrease the maximum density. However, from Fig.6 (c)-(d), we obtain that there exists a negative correlation between minimum densities and temperature amplitude, which implies larger temperature variation can decrease the minimum population densities.



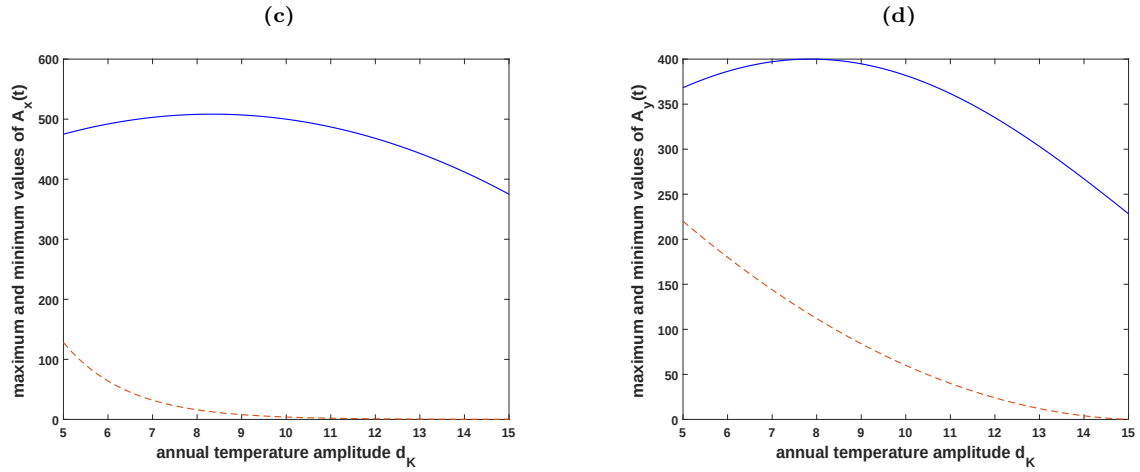


Figure 6. The impact of c_K and d_K in the temperature formula (17) on the maximum and minimum values of the population densities at periodic state.

Lastly, Fig.7 shows the stability change of two adult species x and y as $\tau_x(t)$ and $\tau_y(t)$ simultaneously increase from 0 to 15. It is clear that the two adult species x and y are stable as $(\tau_x(t), \tau_y(t)) \in (0, 9) \times (0, 15]$ approximately, but unstable when $(\tau_x(t), \tau_y(t)) \in (9, 12) \times (0, 15]$.

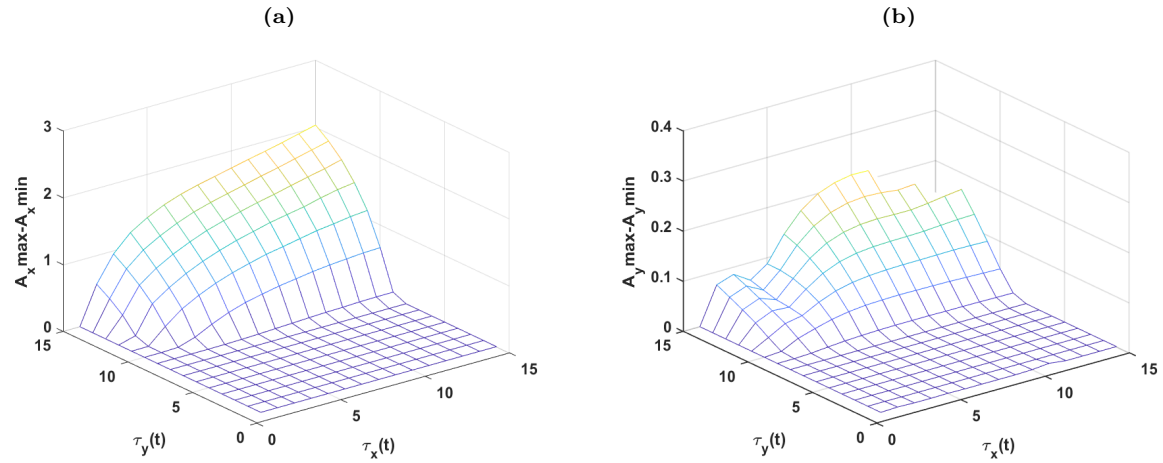


Figure 7. (a): The ultimate oscillation interval of the solution to the system (12) according to increase of $\tau_x(t), \tau_y(t)$, here $t \in [0, 400]$; other parameters are obtained from Table 1.

5. Conclusion

Considering that many populations are affected by seasonal fluctuations in temperature in the process of growth, and there is a general competitive relationship between populations, in this paper, a stage-structured two species competitive model with two periodic maturation delays is proposed to study the effect of temperature and maturation delays on population dynamics. Based on the classical McKendrick von-Foerster stage-structured PDE model [33] and the biological meaning, we give the formulation of the model. Since it is difficult to conduct a direct dynamics analysis on this kind of PDE models, we degenerate the PDE model into ODE model with periodic delay. By introducing the periodic maturation delay, a special term is introduced to reflect the rate of change of periodic maturation delays. At the same time, by describing the population growth of two stages from biological argument, we find that the term is reasonable. Moreover, we show that the derivative of this developmental duration must be smaller than one by mathematic analysis and numerical simulation, which is also required to guarantee the

positivity of solutions. Then, we introduce the basic reproduction ratio R_0 for model (2) by using the approach in [43] and obtain the threshold type result on the global dynamics, which is dependent on the sign of $R_0 - 1$. Moreover, from Fig.5(a)-(d), we can conclude that the periodic parameters, as well as the special term, i.e., the rate of change for the developmental duration, can impose evident impact on the basic reproduction ratio R_0 of the system, i.e., it can change the stability of the system (2). Biologically, the developmental duration dependent on seasonal temperature can change the survival of the population. Meanwhile, in order to investigate the effects of temperature on population dynamics, we estimate the parameters of model as accurate as possible by employing the Sharp-Schoolfield models and Van't Hoff-Arrhenius relation [11, 26–28] to parameterize the periodic coefficients. Other approaches may also be employed to this problem, for example, the parameterization approach used in [34] where the relations between the development components and temperature is obtained via experimental data. Finally, based on the estimated parameters, we conduct some simulations and obtain the Figs.6 and 7. Figs.6 and 7 imply that larger temperature variation can decrease the minimum population densities and the maturation time may change the stability of the system.

6. Acknowledgment

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