

# A series of population models for *Hyphantria cunea* with delay and seasonality<sup>☆</sup>



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## ABSTRACT

In this paper, we establish and study a basic stage-structured model for the population of *Hyphantria cunea*, a delay differential equation model and a model incorporating the resource and seasonality. By introducing the population reproduction number  $\mathbb{R}_0$ , we show that  $\mathbb{R}_0$  acts as a threshold parameter for the existence and stability of equilibria. The trivial equilibria of the above models are all globally asymptotically stable when  $\mathbb{R}_0 < 1$ ; the basic model and the delay-differential model have a unique positive equilibrium respectively, and they are both locally asymptotically stable when  $\mathbb{R}_0 > 1$ ; the model with periodic season is uniformly persistent and admits a positive periodic solution if  $\mathbb{R}_0 > 1$ . Numerical simulations are carried out to illustrate the theoretical results. In addition, we consider the effect of temperature and season on the population of *Hyphantria cunea*.

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## 1. Introduction

*Hyphantria cunea* Drury (*H.cunea*), commonly called fall web-worm, is a kind of defoliator native to North America. This species invaded central Europe and eastern Asia during the 1940s [5,8,26]. It damages ornamental, forest and fruit trees as well as agriculture crops by voracious larval feeding activity. Larvae feed inside the webs which they weave in their hosts until the late instars. Young larvae feed only on the upper surfaces of leaves, but they can consume whole leaves in the webs with their growth. The recorded number of host plants exceeds 600 species in the United States, Japan, Korea and China. With a wide range of host plants and the rapid spread *H.cunea* has caused great economic losses and this species has been listed as one of the worldwide quarantine pests.

In China this pest was first found in 1979 at Dandong City bordering North Korea, Liaoning province. Consequently it spread into Shandong, Shaanxi, Hebei, Jiangsu and Anhui provinces, as well as Tianjing, Beijing and Shanghai Municipalities. Now *H.cunea* has be-

come an established pest in China feeding on over 100 species of trees and caused significant damage to many trees and other plants [35]. In Suqian, a northern area of Jiangsu province, *H.cunea* has become a serious concern of local agriculture and economics [23]. Due to the characteristics of omnivorousness, rapid reproduction and development, higher adaptability and multiple-path of spreading, *H.cunea* has become a “smoke-free blaze” to over 300 kinds of plants, including forest trees, fruit trees, flowers, crops and vegetables in Suqian [24]. Not only Suqian but also many other areas in China have experienced the similar situation [1,2,11,31–33].

*H.cunea* has a bivoltine or trivoltine life cycle. In China, trivoltine populations have prevailed in recent years. Temperature dependence is greater in a trivoltine population than in a bivoltine population. The complete metamorphosis of *H.cunea* entails going through four separate and distinct stages of development, namely egg, larva, pupa and adult *H.cunea*. The life cycle of *H.cunea* begins as an egg. Usually an egg hatches into a larva within either 12–15 days or 7–9 days, depending on the period when the egg is laid and the surrounding climate factors. Larva molts six to seven times as it grows. After the sixth or seventh molt, the larva turns into a pupa. The pupa of the first and second generation is aestivating. It becomes an adult *H.cunea* after 10–30 days. The pupa of the third generation will get into dormancy for overwintering, then it becomes an adult *H.cunea* after about 210 days in normal weather conditions.

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Owing to the significant burden inflicted by *H.cunea* on agriculture and forestry, it has drawn much attention. We have been working with local municipal administration of Suqian, Housing and Urban rural development of Suqian on surveillance program to monitor the density distribution of *H.cunea* for the purpose of better control and prevention. It is essential to understand the biological features of *H.cunea*. Many researches have focused on the biological characteristics, adaptability, the choice of hosts, natural enemies and techniques for bio-control of this invasive insect species [4,9,10,18,25,28,30,34]. However, to our knowledge, due to the complexity of the reproduction and development of *H.cunea*, no studies so far have been done to develop the population dynamical model for *H.cunea* considering the impact of climate factors and environmental conditions.

The purpose of this preliminary study is to develop and analyze stage-structured population dynamical models for *H.cunea* by taking food source and climate factors into account. Firstly, we will ignore the bivoltine or trivoltine life cycle of *H.cunea* and formulate a basic stage-structured model which incorporates the necessary food source for both the reproduction of *H.cunea* and survival of larva. Secondly, since the weather conditions, in particularly the daily temperature of the season has an effect on the development of *H.cunea*, we construct a time-delayed model to study the impact of average seasonal temperature on the population of *H.cunea*. At last, based on the time-delayed model, we formulate a model to study the impact of periodic seasonal changes on the population dynamics of *H.cunea* to study the basic mechanism for the periodicity of the population. We will study the three models to understand the population dynamics and mechanisms responsible for the outbreaks of the population which will be essential to help developing and designing surveillance program for the purpose of effective control.

This paper is organized as follows. In Section 2, we develop a basic stage-structured model for *H.cunea* with a more general reproduction function. We calculate the population reproduction ratio  $\mathbb{R}_0$  and the probability of a major outbreak of *H.cunea*, and then establish the global dynamics for the autonomous model in terms of  $\mathbb{R}_0$ . In Section 3, a time-delayed model with limited food source is established to analyze the impact of temperature on the population of *H.cunea* with a specific Ricker function. In Section 4, we consider the seasonal perturbed delay-differential model to study the impact of season. Numerical simulations are carried out to illustrate the impact of temperature and season on the population dynamics of *H.cunea* in Section 5. We give brief discussions on our findings and future work in Section 6.

## 2. Basic stage-structured model

Suqian is in the north of Jiangsu province, like other areas in northern Jiangsu province and southern Shangdong province, where the weather has four clear alternating seasons. In early spring, when weather warms up and temperature reaches about 15°C in April, the third generation adult *H.cuneas* from previous year begin to feather and lay eggs. An adult female usually lays 500–700 eggs in a batch. Female dies following oviposition. We take the time when the first generation eggs emerge as the beginning time for the modeling, and then consider the four stages of the development of *H.cunea*, namely egg, larva, pupa and adult *H.cunea*.

Let  $T_e$  and  $K_e$  denote the baseline temperature and total accumulative temperature required for the hatching of an egg, respectively. Since the whole course of this transition lasts only several days, we will use the mean temperature  $\bar{T}_e$  of these few days as the daily average temperature. Thus the hatching rate of per egg is  $\beta_e = \max\{\frac{\bar{T}_e - T_e}{K_e}, 0\}$ .

**Table 1**

Description of variables and parameters of model (2.2).

Variables	Description
$E(t)$	Total number of eggs at time $t$
$L(t)$	Total number of larvae at time $t$
$P(t)$	Total number of pupae at time $t$
$H(t)$	Total number of adult <i>H.cuneas</i> at time $t$
$r(H)$	Function of eggs oviposition at time $t$
Parameters	
$d_e$	Natural mortality rate of eggs
$d_l$	Natural mortality rate of larvae
$d_p$	Natural mortality rate of pupae
$d_h$	Natural mortality rate of adult <i>H.cuneas</i>
$\beta_e$	Hatching rate of eggs
$\beta_l$	Development rate of larvae into pupae
$\beta_p$	Development rate of pupae into adult <i>H.cuneas</i>
$\kappa$	Intra-specific competition rate of Larvae

The larva stage is further partitioned into six or seven instars. The larvae hatched from an egg batch stay together in a web they spins in host trees in instars I–IV. They compete for common food resource. Let  $\kappa$  be the intra-specific competition rate. As in egg stage, we can calculate the number of pupae daily developed by a larva,  $\beta_l = \max\{\frac{\bar{T}_l - T_l}{K_l}, 0\}$ , where  $T_l$ ,  $K_l$  represent the baseline temperature and total accumulative temperature required for development from larva to pupa respectively and  $\bar{T}_l$  denotes the mean temperature of this transition course.

It takes longer time for the overwintering pupa to develop into adult *H.cunea* than the aestivating pupa because of the lower temperature in winter. Similarly, we take  $\beta_p = \max\{\frac{\bar{T}_p - T_p}{K_p}, 0\}$  as the transition rate of a pupa, where  $T_p$ ,  $K_p$  and  $\bar{T}_p$  denote the baseline temperature, the total accumulative temperature and the average temperature of the pupa stage, respectively.

We split the total *H.cunea* population at time  $t$  into four mutually-exclusive stages (compartments) of eggs ( $E(t)$ ), larvae ( $L(t)$ ), pupae ( $P(t)$ ) and adult *H.cuneas* ( $H(t)$ ). A stage-structured model is a natural choice since *H.cunea* has different mortality and development rates at different stages.

If we let the development rates of eggs ( $e$ ), larvae ( $l$ ) and pupae ( $p$ ) be as follows

$$\beta_i = \begin{cases} \frac{\bar{T}_i - T_i}{K_i}, & \bar{T}_i > T_i, \\ 0, & \bar{T}_i \leq T_i, \end{cases} \quad i = e, l, p, \quad (2.1)$$

then we develop the following stage-structured model

$$\begin{cases} \frac{dE}{dt} = r(H) - (d_e + \beta_e)E, \\ \frac{dL}{dt} = \beta_e E - (d_l + \beta_l + \kappa L)L, \\ \frac{dP}{dt} = \beta_l L - (d_p + \beta_p)P, \\ \frac{dH}{dt} = \beta_p P - d_h H, \end{cases} \quad (2.2)$$

where  $d_e$ ,  $d_l$ ,  $d_p$  and  $d_h$  denote the natural mortality rate of eggs, larvae, pupae and adult *H.cuneas*, respectively. The density dependent mortality rate  $\kappa L$  of larvae is non-negative. The details about variables and parameters are shown in Table 1.

There have been different functions used to model the reproduction rate of single species population [3]. In model (2.2), we use a general reproduction function  $r(H)$  which represents the daily average number of eggs from the oviposition. The reproduction rate is zero when there is no adult *H.cuneas*, hence  $r(0) = 0$ . The reproduction rate increases with respect to the number of adult *H.cuneas* when the size of the adult population size is small, then we can assume that  $r'(0) > 0$ . Naturally, we will use  $r'(0)$  to represent the intrinsic per-capita reproduction rate of the adult *H.cuneas*. When the adult population size becomes larger, it is reasonable to assume that the average per-capita reproduction rate

$\frac{r(H)}{H}$  will be smaller than the intrinsic reproduction rate  $r'(0)$ . For population of a single species like *H.cunea*, usually there is an intra-species competition due to the crowded effect among the egg-laying adults. Since we will develop a series of models to consider the impact of average temperature and seasons, we simply take the case to assume that the average per-capita egg-laying rate  $r'(H)$  is decreasing when the number of adults increases.

To summarize, we assume that for  $H \geq 0$ , the reproduction function  $r(H)$  satisfies the following conditions:

- (i)  $r(H)$  is smooth on  $R_+$ , also  $r(0) = 0$  and  $r'(0) > 0$ ;
- (ii)  $0 \leq \frac{r(H)}{H} \leq r'(0)$ ;
- (iii)  $r''(H) \leq 0$ .

The details about variable and parameter definitions are shown in Table 1. For convenience, we denote  $d_1 = d_e + \beta_e$ ,  $d_2 = d_l + \beta_l$ ,  $d_3 = d_p + \beta_p$ ,  $d_4 = d_h$  and let  $b = r'(0) > 0$ . To find the equilibria of model (2.2), we let the right-hand side of (2.2) equal 0. One can see that if an equilibrium  $P = (E, L, P, H)$  exists, then its  $H$ -coordinate will satisfy

$$r(H) = \frac{d_1 d_3 d_4}{\beta_e \beta_l \beta_p} \left( d_2 H + \kappa \frac{d_3 d_4}{\beta_l \beta_p} H^2 \right).$$

Let  $g(H) = \frac{d_1 d_3 d_4}{\beta_e \beta_l \beta_p} (d_2 H + \kappa \frac{d_3 d_4}{\beta_l \beta_p} H^2)$ . It follows from the conditions of  $r(H)$  and the graph of  $g(H)$  that:

- If  $r'(0) \leq g'(0)$ , that is,  $b\beta_e\beta_l\beta_p \leq d_1 d_2 d_3 d_4$ , then the equation  $r(H) = g(H)$  has only one root  $H = 0$ ;
- If  $r'(0) > g'(0)$ , that is,  $b\beta_e\beta_l\beta_p > d_1 d_2 d_3 d_4$ , then the equation  $r(H) = g(H)$  has one zero root and a positive root  $H = H^*$ .

Naturally, we define

$$\mathbb{R}_0 = \frac{b\beta_e\beta_l\beta_p}{d_1 d_2 d_3 d_4}$$

as a threshold quantity to measure the population reproduction ratio. One can verify that model (2.2) has a unique trivial equilibrium  $P_0 = (0, 0, 0, 0)$  when  $\mathbb{R}_0 \leq 1$ , and one positive equilibrium  $P_1 = (E^*, L^*, P^*, H^*)$  if and only if  $\mathbb{R}_0 > 1$ , where

$$E^* = \frac{d_3 d_4}{\beta_e \beta_l \beta_p} \left( d_2 H^* + \kappa \frac{d_3 d_4}{\beta_l \beta_p} H^{*2} \right), \quad L^* = \frac{d_3 d_4}{\beta_l \beta_p} H^*, \quad P^* = \frac{d_4}{\beta_p} H^*, \quad (2.3)$$

and  $H^*$  is the unique positive root of equation  $r(H) = g(H)$ .

The threshold quantity,  $\mathbb{R}_0$ , is the population reproduction ratio. It measures the average expected number of new adult *H.cunea* offsprings produced by a single *H.cunea* in its life time. It can be ecologically interpreted as the product of the fraction of eggs that survived and hatched into larvae  $\frac{b\beta_e}{d_1}$ , the fraction of larvae that survived and progressed into pupae  $\frac{\beta_l}{d_2}$ , the fraction of pupae that survived and became adult *H.cunea*  $\frac{\beta_p}{d_3}$ , and the average life span of adult *H.cunea*  $\frac{1}{d_4}$ .

The model (2.2) is a very basic model, but it will allow us to estimate the risk of a major outbreak of *H.cunea* population. As the probability generating function of the distribution of secondary infections introduced in [15], the probability generating function of the distribution of larvae newly hatched by eggs is

$$G_E(s) = \frac{1}{1 + \frac{b\beta_e}{d_1}(1-s)}.$$

$$\text{Similarly, } G_L(s) = \frac{1}{1 + \frac{\beta_l}{d_2}(1-s)}, \quad G_P(s) = \frac{1}{1 + \frac{\beta_p}{d_3}(1-s)}, \quad G_H(s) = \frac{1}{1 + \frac{1}{d_4}(1-s)}$$

are the probability generating functions of the distribution of pupae, adult *H.cuneas* and eggs newly developed in larva stage, pupa stage and adult *H.cunea* stage, respectively.

The extinction probability,  $s$ , which is in above four functions, is found by calculating the smallest nonnegative root of the equation

$$G_H(G_P(G_L(G_E(s)))) = s. \quad (2.4)$$

It is not difficult to show that the relevant solution is

$$s = 1 - \frac{b\beta_e\beta_l\beta_p - d_1 d_2 d_3 d_4}{b\beta_e\beta_l d_3 d_4 + b\beta_e d_2 d_3 d_4 + b\beta_e\beta_l\beta_p d_4 + b\beta_e\beta_l\beta_p}.$$

Obviously,  $s$  is nonnegative. Furthermore, it is smaller than 1, and hence  $s$  is the relevant solution of (2.4) if and only if  $b\beta_e\beta_l\beta_p > d_1 d_2 d_3 d_4$ . This condition is exactly that  $\mathbb{R}_0$  is greater than 1. Consequently, when  $\mathbb{R}_0$  is less than or equal to 1, the relevant solution of (2.4) is 1. For  $\mathbb{R}_0 > 1$ , the probability of a major outbreak is

$$p_0 = 1 - s = \frac{b\beta_e\beta_l\beta_p - d_1 d_2 d_3 d_4}{b\beta_e\beta_l d_3 d_4 + b\beta_e d_2 d_3 d_4 + b\beta_e\beta_l\beta_p d_4 + b\beta_e\beta_l\beta_p} = \frac{d_1 d_2 d_3 d_4}{b\beta_e\beta_l d_3 d_4 + b\beta_e d_2 d_3 d_4 + b\beta_e\beta_l\beta_p d_4 + b\beta_e\beta_l\beta_p} (\mathbb{R}_0 - 1).$$

So for the probability of a major outbreak of the population, we conclude:

- (i) If  $\mathbb{R}_0 < 1$ , a major outbreak of *H.cunea* can never happen.
- (ii) If  $\mathbb{R}_0 > 1$ , the probability of a major outbreak of *H.cunea*,  $p_0$ , increases with  $\mathbb{R}_0$ .

Since all state variables at any time  $t$  and all parameters of model (2.2) are nonnegative, the model can be studied in the following region

$$X = \{(E, L, P, H) \mid (E, L, P, H) \in \mathbb{R}^4, E, L, P, H \geq 0\},$$

where the model is mathematically and ecologically well-posed.

Next we will investigate the local stability of equilibria  $P_0$  and  $P_1$ , and prove global stability of the trivial equilibrium  $P_0$  using Lyapunov functionals (see [17,20–22]).

**Theorem 2.1.** For model (2.2), if  $\mathbb{R}_0 < 1$ , the trivial equilibrium  $P_0$  is locally asymptotically stable. If  $\mathbb{R}_0 > 1$ ,  $P_0$  is unstable.

**Proof.** The Jacobian matrix of system (2.2) at  $P_0$  is

$$J(P_0) = \begin{pmatrix} -d_1 & 0 & 0 & b \\ \beta_e & -d_2 & 0 & 0 \\ 0 & \beta_l & -d_3 & 0 \\ 0 & 0 & \beta_p & -d_4 \end{pmatrix}.$$

The eigenvalues of  $J(P_0)$  satisfy the following characteristic equation

$$\lambda^4 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0, \quad (2.5)$$

where

$$\begin{cases} a_1 = d_1 + d_2 + d_3 + d_4, \\ a_2 = d_1 d_2 + d_1 d_3 + d_1 d_4 + d_2 d_3 + d_2 d_4 + d_3 d_4, \\ a_3 = d_1 d_2 d_3 + d_1 d_2 d_4 + d_1 d_3 d_4 + d_2 d_3 d_4, \\ a_4 = d_1 d_2 d_3 d_4 - b\beta_e\beta_l\beta_p. \end{cases} \quad (2.6)$$

The relevant Routh–Hurwitz determinants of the characteristic Eq. (2.5) are given

$$\begin{cases} \Delta_1 = a_1, \\ \Delta_2 = a_1 a_2 - a_3, \\ \Delta_3 = a_3 \Delta_2 - a_4 a_1^2, \\ \Delta_4 = a_4 \Delta_3. \end{cases} \quad (2.7)$$

Since all parameters of model (2.2) are positive, it is not difficult to see that  $\Delta_1 > 0$  and  $\Delta_2 > 0$ . Let

$$\alpha_0 = (d_1 + d_2)(d_1 + d_3)(d_1 + d_4)(d_2 + d_3)(d_2 + d_4)(d_3 + d_4) > 0.$$

Then we can calculate that

$$\Delta_3 = \alpha_0 + b\beta_e\beta_l\beta_p a_1^2 > 0.$$

We rewrite  $a_4$  as

$$a_4 = d_1 d_2 d_3 d_4 - b \beta_e \beta_l \beta_p = d_1 d_2 d_3 d_4 (1 - \mathbb{R}_0).$$

Now we can draw the following conclusions:

- (i) If  $\mathbb{R}_0 < 1$ , then  $a_4 > 0$  and  $\Delta_4 > 0$ . Hence, all roots of the characteristic Eq. (2.5) are negative. Thus the trivial equilibrium  $P_0$  is locally asymptotically stable.
- (ii) If  $\mathbb{R}_0 > 1$ , then  $a_4 < 0$ . Hence, there exists at least one positive root for the characteristic Eq. (2.5). Thus  $P_0$  is unstable.  $\square$

**Theorem 2.2.** For model (2.2), the trivial equilibrium  $P_0$  is globally asymptotically stable if  $\mathbb{R}_0 < 1$ .

**Proof.** Define the Lyapunov function

$$V_0(t) = \beta_l \beta_p [\beta_e E(t) + d_1 L(t)] + d_1 d_2 [\beta_p P(t) + d_3 H(t)].$$

The derivative of  $V_0(t)$  along system (2.2) is

$$\begin{aligned} \frac{dV_0}{dt} &= \beta_l \beta_p \left[ \beta_e \frac{dE}{dt} + d_1 \frac{dL}{dt} \right] + d_1 d_2 \left[ \beta_p \frac{dP}{dt} + d_3 \frac{dH}{dt} \right] \\ &= \beta_l \beta_p [\beta_e (r(H) - d_1 E(t)) + d_1 (\beta_e E(t) - d_2 L(t) - \kappa L^2(t))] \\ &\quad + d_1 d_2 [\beta_p (\beta_l L(t) - d_3 P(t)) + d_3 (\beta_p P(t) - d_4 H(t))] \\ &= \beta_e \beta_l \beta_p r(H) - d_1 d_2 d_3 d_4 H(t) - \beta_l \beta_p d_1 \kappa L^2(t) \\ &\leq \beta_e \beta_l \beta_p r'(0) H(t) - d_1 d_2 d_3 d_4 H(t) \\ &= H(t) d_1 d_2 d_3 d_4 (\mathbb{R}_0 - 1). \end{aligned}$$

It follows from  $\mathbb{R}_0 < 1$  that  $\frac{dV_0}{dt} \leq 0$  for all  $H(t) \in X$ . The Lyapunov–LaSalle theorem implies that all the solutions approach  $H = 0$ , the largest compact invariant subset of the set  $\frac{dV_0}{dt} = 0$ . Furthermore, all solutions on the plane  $H = 0$  approach the equilibrium  $P_0$  asymptotically. Thus the trivial equilibrium  $P_0$  is globally asymptotically stable whenever  $\mathbb{R}_0 < 1$ .  $\square$

**Theorem 2.3.** For model (2.2), the positive equilibrium  $P_1$  is locally asymptotically stable if  $\mathbb{R}_0 > 1$ .

**Proof.** It has been discussed in Section 2 that the positive equilibrium  $P_1$  exists if and only if  $\mathbb{R}_0 > 1$ . Now we prove  $P_1$  is locally asymptotically stable. The Jacobian matrix of system (2.2) at  $P_1$  is

$$J(P_1) = \begin{pmatrix} -d_1 & 0 & 0 & r'(H^*) \\ \beta_e & -d_2 - 2\kappa L^* & 0 & 0 \\ 0 & \beta_l & -d_3 & 0 \\ 0 & 0 & \beta_p & -d_4 \end{pmatrix}.$$

The eigenvalues of  $J(P_1)$  satisfy the following characteristic equation

$$\lambda^4 + A_1 \lambda^3 + A_2 \lambda^2 + A_3 \lambda + A_4 = 0, \quad (2.8)$$

where

$$\begin{cases} A_1 = d_1 + (d_2 + 2\kappa L^*) + d_3 + d_4, \\ A_2 = d_1(d_2 + 2\kappa L^*) + [d_1 + (d_2 + 2\kappa L^*)](d_3 + d_4) + d_3 d_4, \\ A_3 = d_1(d_2 + 2\kappa L^*)d_3 + d_1(d_2 + 2\kappa L^*)d_4 + d_1 d_3 d_4 \\ \quad + (d_2 + 2\kappa L^*)d_3 d_4, \\ A_4 = d_1(d_2 + 2\kappa L^*)d_3 d_4 - r'(H^*)\beta_e \beta_l \beta_p. \end{cases} \quad (2.9)$$

From (2.3), we have  $d_1 d_3 d_4 \kappa L^* = \frac{\beta_e \beta_l \beta_p r(H^*)}{H^*} - d_1 d_2 d_3 d_4$ . Then

$$\begin{aligned} A_4 &= d_1(d_2 + 2\kappa L^*)d_3 d_4 - r'(H^*)\beta_e \beta_l \beta_p \\ &= d_1 d_2 d_3 d_4 + d_1 d_3 d_4 \kappa L^* - r'(H^*)\beta_e \beta_l \beta_p + d_1 d_3 d_4 \kappa L^* \\ &= \left( \frac{r(H^*)}{H^*} - r'(H^*) \right) \beta_e \beta_l \beta_p + d_1 d_3 d_4 \kappa L^*. \end{aligned}$$

It follows from  $r(H)$  is smooth with  $r(0) = 0$  and Lagrange's Mean Value Theorem that there exists  $\xi \in (0, H^*)$  such that  $r(H^*) = r''(\xi)H^*$ . Since  $r''(H) \leq 0$ , then  $\frac{r(H^*)}{H^*} \geq r'(H^*)$  and hence  $A_4 > 0$ .

Let

$$\begin{aligned} \alpha_1 &= (d_1 + d_2 + 2\kappa L_1)(d_1 + d_3)(d_1 + d_4)(d_2 + 2\kappa L_1 + d_3) \\ &\quad \times (d_2 + 2\kappa L_1 + d_4)(d_3 + d_4). \end{aligned}$$

Since all parameters of model (2.2) are positive, it's easy to see that and  $\alpha_1 > 0$ .

From the proof of Theorem 2.1 and (2.9) we can see that the relevant Routh–Hurwitz determinants of the characteristic Eq. (2.8) satisfy

$$\begin{cases} \Delta_1 = A_1 > 0, \\ \Delta_2 = A_1 A_2 - A_3 > 0, \\ \Delta_3 = A_3 \Delta_2 - A_4 A_1^2 = \alpha_1 + r'(H^*)\beta_e \beta_l \beta_p A_1^2 > 0, \\ \Delta_4 = A_4 \Delta_3 > 0, \end{cases}$$

which means all roots of the characteristic Eq. (2.8) are negative. Thus the positive equilibrium  $P_1$  is locally asymptotically stable.  $\square$

### 3. Time-delayed model considering the impact of temperature

Considering the impact of temperature on the two development stages from egg to larva and from pupa to adult *H.cunea*, we take  $\tau_1$  and  $\tau_2$  as the development durations of these two stages respectively. As in [29], we adopt a Ricker function  $bH(t)e^{-\alpha H(t)}$  ( $b, \alpha > 0$ ) to reflect the available delicious tree leaves resource for the reproduction of eggs. This function is nonlinear and reaches its maximum at  $H(t) = 1/\alpha$ , hence it is reasonable to use  $1/\alpha$  to measure the maximum leaves source of a given region that the maximum eggs reproductivity can be reached. A sufficient small  $\alpha > 0$  means that the region has enough resource for the production of female *H.cuneas*. We develop the following model with two time delays

$$\begin{cases} \frac{dE}{dt} = bHe^{-\alpha H} - (d_e + \beta_e)E, \\ \frac{dL}{dt} = \beta_e e^{-d_e \tau_1} E(t - \tau_1) - (d_l + \beta_l + \kappa L)L, \\ \frac{dP}{dt} = \beta_l L - (d_p + \beta_p)P, \\ \frac{dH}{dt} = \beta_p e^{-d_p \tau_2} P(t - \tau_2) - d_h H. \end{cases} \quad (3.1)$$

Note that model (3.1) reduces to model (2.2) when  $\tau_1 = \tau_2 = 0$  with  $r(H) = bHe^{-\alpha H}$ .

Let

$$X = C([- \tau_1, 0], \mathbf{R}_+^2) \times C([- \tau_2, 0], \mathbf{R}_+^2).$$

$$X_0 = \{ \phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in X : \phi_i > 0, \forall i \in \{1, 2, 3, 4\} \},$$

and

$$\partial X_0 = X \setminus X_0 = \{ \phi \in X : \phi_i(0) = 0, \text{ for some } i \in \{1, 2, 3, 4\} \}.$$

**Lemma 3.1.** For any  $\phi \in X$ , system (3.1) has a unique nonnegative solution through  $\phi$ , and all solutions are ultimately bounded and uniformly bounded.

**Proof.** For any  $\phi \in X$ , define

$$G(t, \phi) = \begin{pmatrix} b\phi_4(0)e^{-\alpha\phi_4(0)} - d_1\phi_1(0) \\ \beta_e e^{-d_e \tau_1} \phi_1(-\tau_1) - (d_2 + \kappa\phi_2(0))\phi_2(0) \\ \beta_l \phi_2(0) - d_3\phi_3(0) \\ \beta_p e^{-d_p \tau_2} \phi_3(-\tau_2) - d_4\phi_4(0) \end{pmatrix}.$$

Then for all  $\phi \in X$ ,  $G(t, \phi)$  is continuous, and  $G(t, \phi)$  is Lipschitzian in  $\phi$  in each compact set in  $\mathbf{R} \times X$ . Hence, there exists a unique solution of system (3.1) through  $(0, \phi)$ . Note that  $G_i(t, \psi) \geq 0$  whenever  $\psi \geq 0$  and  $\psi_i(0) = 0$ . It follows from [19] that  $X$  is positively



invariant. Due to  $\max_{H \in [0, +\infty)} bHe^{-\alpha H} = \frac{be^{-1}}{\alpha}$ , and from the first equation of system (3.1) we have

$$\limsup_{t \rightarrow \infty} E(t) \leq \frac{be^{-1}}{\alpha d_1} \triangleq M_E.$$

Therefore, from the second, third and fourth equations of system (3.1) we have

$$\limsup_{t \rightarrow \infty} L(t) \leq \beta_e e^{-d_e \tau_1} \frac{be^{-1}}{\alpha d_1} \frac{1}{d_2} \triangleq M_L,$$

$$\limsup_{t \rightarrow \infty} P(t) \leq \beta_e e^{-d_e \tau_1} \frac{be^{-1}}{\alpha d_1} \frac{1}{d_2} \frac{\beta_l}{d_3} \triangleq M_P,$$

$$\limsup_{t \rightarrow \infty} H(t) \leq \beta_e e^{-d_e \tau_1} \frac{be^{-1}}{\alpha d_1} \frac{1}{d_2} \frac{\beta_l}{d_3} \frac{\beta_p e^{-d_p \tau_2}}{d_4} \triangleq M_H,$$

which implies that all solutions are ultimately bounded.

Moreover, when  $E(t) > M_E$ ,  $L(t) > M_L$ ,  $P(t) > M_P$  and  $H(t) > M_H$ , we obtain that  $\frac{dE(t)}{dt} < 0$ ,  $\frac{dL(t)}{dt} < 0$ ,  $\frac{dP(t)}{dt} < 0$  and  $\frac{dH(t)}{dt} < 0$ . This implies that all solutions are uniformly bounded.  $\square$

It is not difficult to see that system (3.1) has a trivial equilibrium, denoted by  $P_0 = (0, 0, 0, 0)$ . As discussed in Section 2, we can calculate the population reproduction ratio for system (3.1) as follows

$$\mathbb{R}_0 = \frac{b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)}}{d_1d_2d_3d_4}.$$

In the following we show that system (3.1) has a positive equilibrium  $P_1 = (E^*, L^*, P^*, H^*)$  when  $\mathbb{R}_0 > 1$ , where

$$\begin{cases} E^* = \frac{d_3d_4e^{d_e\tau_1+d_p\tau_2}}{\beta_e\beta_l\beta_p} (d_2 + \kappa \frac{d_3d_4}{\beta_l\beta_p} e^{d_p\tau_2} H^*) H^*, \\ L^* = \frac{d_3d_4}{\beta_l\beta_p} e^{d_p\tau_2} H^*, \\ P^* = \frac{d_4}{\beta_p} e^{d_p\tau_2} H^*, \end{cases} \quad (3.2)$$

with  $H^*$  satisfying

$$be^{-\alpha H^*} = \frac{d_1d_3d_4e^{d_e\tau_1+d_p\tau_2}}{\beta_e\beta_l\beta_p} \left( d_2 + \kappa \frac{d_3d_4}{\beta_l\beta_p} e^{d_p\tau_2} H^* \right). \quad (3.3)$$

One can verify that Eq. (3.3) has a positive solution  $H^*$  if and only if  $\mathbb{R}_0 > 1$ . So the positive equilibrium  $P_1 = (E^*, L^*, P^*, H^*)$  of model (3.1) exists if and only if  $\mathbb{R}_0 > 1$ .

In the following, we consider the local stability and global stability of trivial equilibrium  $P_0$  and positive equilibrium  $P_1$  of model (3.1).

We linearize system (3.1) and the characteristic equation at  $P_0$  is

$$\begin{vmatrix} \lambda + d_1 & 0 & 0 & -b \\ -\beta_e e^{-d_e\tau_1} e^{-\lambda\tau_1} & \lambda + d_2 & 0 & 0 \\ 0 & -\beta_l & \lambda + d_3 & 0 \\ 0 & 0 & -\beta_p e^{-d_p\tau_2} e^{-\lambda\tau_2} & \lambda + d_4 \end{vmatrix} = 0,$$

that is,

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4^* - b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)} e^{-\lambda(\tau_1+\tau_2)} = 0, \quad (3.4)$$

where  $a_1, a_2, a_3$  are defined in (2.6) and  $a_4^* = d_1d_2d_3d_4$ .

Note that

$$\begin{aligned} a_4^* - b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)} &= d_1d_2d_3d_4 - b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)} \\ &= d_1d_2d_3d_4(1 - \mathbb{R}_0). \end{aligned}$$

If  $\mathbb{R}_0 > 1$ , then  $a_4^* < b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)}$ . Hence, there exists at least one positive root of the characteristic Eq. (3.4). Thus  $P_0$  is unstable.

If  $\mathbb{R}_0 < 1$ , then  $a_4^* > b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)}$ , hence any real number  $\lambda \geq 0$  is not the root of (3.4).

If  $i\omega (\omega > 0)$  is a pure imaginary root of (3.4), separating real and imaginary parts leads to

$$\begin{cases} \omega^4 - a_2\omega^2 + a_4^* = b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)} \cos(\omega(\tau_1 + \tau_2)) \\ -a_1\omega^3 + a_3\omega = -b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)} \sin(\omega(\tau_1 + \tau_2)). \end{cases} \quad (3.5)$$

Squaring and adding both sides of (3.5) yields

$$\begin{aligned} \omega^8 + (a_1^2 - 2a_2)\omega^6 + (a_2^2 + 2a_4^* - 2a_1a_3)\omega^4 + (a_3^2 - 2a_2a_4^*)\omega^2 \\ + (a_4^*)^2 - (b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)})^2 = 0. \end{aligned}$$

Letting  $s = \omega^2$ , we have

$$\begin{aligned} g(s) = s^4 + (a_1^2 - 2a_2)s^3 + (a_2^2 + 2a_4^* - 2a_1a_3)s^2 \\ + (a_3^2 - 2a_2a_4^*)s + (a_4^*)^2 - (b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)})^2 = 0. \end{aligned} \quad (3.6)$$

It is easy to see that  $a_1^2 - 2a_2 > 0$  and  $(a_4^*)^2 - (b\beta_e\beta_l\beta_p e^{-(d_e\tau_1+d_p\tau_2)})^2 > 0$  when  $\mathbb{R}_0 < 1$ . We can calculate

$$\begin{aligned} a_2^2 + 2a_4^* - 2a_1a_3 &= d_1^2d_2^2 + d_1^2d_3^2 + d_1^2d_4^2 + d_2^2d_3^2 + d_2^2d_4^2 + d_3^2d_4^2 > 0, \\ a_3^2 - 2a_2a_4^* &= d_1^2d_2^2d_3^2 + d_1^2d_3^2d_4^2 + d_1^2d_3^2d_4^2 + d_2^2d_3^2d_4^2 > 0, \end{aligned}$$

which means Eq. (3.4) has no purely imaginary roots. And we have the following result.

**Theorem 3.2.** For model (3.1), if  $\mathbb{R}_0 < 1$ , the trivial equilibrium  $P_0$  is locally asymptotically stable. If  $\mathbb{R}_0 > 1$ ,  $P_0$  is unstable.

Now we prove the global stability of the trivial equilibrium  $P_0$ .

**Theorem 3.3.** For model (3.1), the trivial equilibrium  $P_0$  is globally asymptotically stable if  $\mathbb{R}_0 < 1$  in  $X$ .

**Proof.** Define the Lyapunov function as follows

$$\begin{aligned} V(t) &= \beta_l\beta_p e^{-d_p\tau_2} [\beta_e e^{-d_e\tau_1} E(t) + d_1L(t)] \\ &\quad + d_1d_2 [\beta_p e^{-d_p\tau_2} P(t) + d_3H(t)] \\ &\quad + d_1\beta_e\beta_l\beta_p e^{-d_e\tau_1-d_p\tau_2} \int_{-\tau_1}^0 E(t+s)ds \\ &\quad + d_1d_2d_3\beta_p e^{-d_p\tau_2} \int_{-\tau_2}^0 P(t+s)ds. \end{aligned}$$

The Lyapunov derivative along system (3.1) is

$$\begin{aligned} \frac{dV}{dt} &= \beta_l\beta_p e^{-d_p\tau_2} [\beta_e e^{-d_e\tau_1} (bH(t)e^{-\alpha H(t)} - d_1E(t)) \\ &\quad + d_1(\beta_e e^{-d_e\tau_1} E(t - \tau_1) - d_2L(t) - \kappa L^2(t))] \\ &\quad + d_1d_2 [\beta_p e^{-d_p\tau_2} (\beta_l L(t) - d_3P(t)) \\ &\quad + d_3(\beta_p e^{-d_p\tau_2} P(t - \tau_2) - d_4H(t))] \\ &\quad + d_1\beta_e\beta_l\beta_p e^{-d_e\tau_1-d_p\tau_2} [E(t) - E(t - \tau_1)] \\ &\quad + d_1d_2d_3\beta_p e^{-d_p\tau_2} [P(t) - P(t - \tau_2)] \\ &= \beta_e\beta_l\beta_p e^{-d_e\tau_1-d_p\tau_2} bH(t)e^{-\alpha H(t)} - d_1d_2d_3d_4H(t) \\ &\leq \beta_e\beta_l\beta_p e^{-d_e\tau_1-d_p\tau_2} bH(t) - d_1d_2d_3d_4H(t) \\ &= H(t)d_1d_2d_3d_4(\mathbb{R}_0 - 1). \end{aligned}$$

It follows from  $\mathbb{R}_0 < 1$  that  $\frac{dV}{dt} < 0$  for all  $H(t) \in X$ . Thus the trivial equilibrium  $P_0$  is globally asymptotically stable whenever  $\mathbb{R}_0 < 1$ .  $\square$

**Theorem 3.4.** For model (3.1), the positive equilibrium  $P_1$  is locally asymptotically stable when  $\mathbb{R}_0 > 1$ .

**Proof.** From the above discussion, the positive equilibrium  $P_1 = (E^*, L^*, P^*, H^*)$  of model (3.1) exists if and only if  $\mathbb{R}_0 > 1$ .

Let  $x_1 = E - E^*$ ,  $x_2 = L - L^*$ ,  $x_3 = P - P^*$ ,  $x_4 = H - H^*$ . Then system (3.1) becomes

$$\begin{cases} \frac{dx_1}{dt} = be^{-\alpha H^*} x_4 e^{-\alpha x_4} - d_1 x_1, \\ \frac{dx_2}{dt} = \beta_e e^{-d_e \tau_1} x_1(t - \tau_1) - (d_2 + 2\kappa L^*) x_2 - \kappa x_2^2, \\ \frac{dx_3}{dt} = \beta_l x_2 - d_3 x_3, \\ \frac{dx_4}{dt} = \beta_p e^{-d_p \tau_2} x_3(t - \tau_2) - d_4 x_4. \end{cases} \quad (3.7)$$

We linearize system (3.7) and obtain the characteristic equation at  $(0, 0, 0, 0)$  as follows

$$\lambda^4 + A_1 \lambda^3 + A_2 \lambda^2 + A_3 \lambda + A_4^* - be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)} e^{-\lambda(\tau_1 + \tau_2)} = 0, \quad (3.8)$$

where  $A_1, A_2, A_3$  are defined in (2.9), and  $A_4^* = d_1(d_2 + 2\kappa L^*)d_3d_4$ .

It follows from (3.2) and (3.3) that  $d_1d_3d_4\kappa L^* = be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)} - d_1d_2d_3d_4$ . Then

$$\begin{aligned} A_4^* - be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)} \\ = d_1(d_2 + 2\kappa L^*)d_3d_4 - be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)} \\ = d_1d_2d_3d_4 - be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)} + 2d_1d_3d_4\kappa L^* \\ = d_1d_3d_4\kappa L^* > 0 \end{aligned}$$

If  $\mathbb{R}_0 > 1$ , then  $A_4^* > be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)}$ , hence there exists no positive real number  $\lambda$  satisfying (3.8).

We now look for pure imaginary roots of (3.8). Let  $\lambda = i\omega$  ( $\omega > 0$ ) be a pure imaginary root of (3.8). Considering the real and imaginary parts of (3.8), we have

$$\begin{cases} \omega^4 - A_2\omega^2 + A_4^* = be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)} \cos(\omega(\tau_1 + \tau_2)) \\ -A_1\omega^3 + A_3\omega = -be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)} \sin(\omega(\tau_1 + \tau_2)). \end{cases} \quad (3.9)$$

Squaring and adding both sides of (3.9) yields

$$\omega^8 + (A_1^2 - 2A_2)\omega^6 + (A_2^2 + 2A_4^* - 2A_1A_3)\omega^4 + (A_3^2 - 2A_2A_4^*)\omega^2 + (A_4^*)^2 - (be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)})^2 = 0.$$

Letting  $s = \omega^2$ , we have

$$h(s) = s^4 + (A_1^2 - 2A_2)s^3 + (A_2^2 + 2A_4^* - 2A_1A_3)s^2 + (A_3^2 - 2A_2A_4^*)s + (A_4^*)^2 - (be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)})^2 = 0.$$

It is easy to see that  $A_1^2 - 2A_2 > 0$  and  $(A_4^*)^2 - (be^{-\alpha H^*} \beta_e \beta_l \beta_p e^{-(d_e \tau_1 + d_p \tau_2)})^2 > 0$  when  $\mathbb{R}_0 > 1$ . We can calculate

$$\begin{aligned} A_2^2 + 2A_4^* - 2A_1A_3 &= d_1^2(d_2^*)^2 + d_1^2d_3^2 + d_1^2d_4^2 + (d_2^*)^2d_3^2 \\ &\quad + (d_2^*)^2d_4^2 + d_3^2d_4^2 > 0, \\ A_3^2 - 2A_2A_4^* &= d_1^2(d_2^*)^2d_3^2 + d_1^2(d_2^*)^2d_4^2 + d_1^2d_3^2d_4^2 + (d_2^*)^2d_3^2d_4^2 > 0, \end{aligned}$$

where  $d_1, d_3, d_4$  are the same as those defined in Section 2, and  $d_2^* = d_1 + \beta_l + 2\kappa L^*$ . So Eq. (3.8) has no pure imaginary roots.

Based on the above discussion, the positive equilibrium  $P_1$  is locally asymptotically stable if  $\mathbb{R}_0 > 1$ . We complete the proof.  $\square$

**Remark 3.5.** It is not difficult to see that if the impact of food source for female *H.cuneas* in a given region is ignored, then  $\alpha$  is 0 in model (3.1), which implies that the resource in a given region is unlimited. Since the larvae hatched from an egg batch stay together in a web in instars I–IV, there still exists intra-specific

competition in larva stage. Then system (3.1) reduces to

$$\begin{cases} \frac{dE}{dt} = bH - (d_e + \beta_e)E, \\ \frac{dL}{dt} = \beta_e e^{-d_e \tau_1} E(t - \tau_1) - (d_l + \beta_l + \kappa L)L, \\ \frac{dP}{dt} = \beta_l L - (d_p + \beta_p)P, \\ \frac{dH}{dt} = \beta_p e^{-d_p \tau_2} P(t - \tau_2) - d_h H. \end{cases} \quad (3.10)$$

For system (3.10), we have the following results which are similar to those for system (3.1).

#### Theorem 3.6.

- If  $\mathbb{R}_0 < 1$ , then the equilibrium  $P_0$  is globally asymptotically stable for system (3.10) in  $X$ .
- If  $\mathbb{R}_0 > 1$ , then system (3.10) admits a positive equilibrium  $P_1$  which is locally asymptotically stable.

### 4. Model with seasonality at larva stage

#### 4.1. The model

Seasonal variations in temperature, humidity and resource availability have strong effect on *H.cunea* dynamics [6,12,16]. The impact of temperature on the development of *H.cunea* during the two stages from egg to larva and from pupa to adult *H.cunea* has been reflected by two time delays  $\tau_1$  and  $\tau_2$  in model (3.1). As mentioned above, the larvae hatched from an egg batch stay together in webs in instars I–IV competing for common food (leaves of the host). Hence it is reasonable to consider the intra-specific competition on the leaves. The availability and abundance of the tree resource (leaves) is closely related with the seasonal changes. One natural option is to consider the impact of seasonality on the intra-specific competition at the larva stage as a positive, continuous and periodic function.

As discussed in [13], we denote the seasonal periodically perturbed parameter  $\kappa$  as

$$\kappa(t) = \kappa_0(1 + \varepsilon \sin(\omega t)), \quad (4.1)$$

where  $\kappa_0$  is the average value of  $\kappa$  in model (3.1) and  $\varepsilon$  is the degree of seasonality,  $\omega > 0$  is the frequency of the seasonal perturbation. Notice that  $\varepsilon\kappa_0$  is the magnitude of the seasonal perturbation. Then the seasonal forced model of (3.1) becomes

$$\begin{cases} \frac{dE}{dt} = bHe^{-\alpha H} - (d_e + \beta_e)E, \\ \frac{dL}{dt} = \beta_e e^{-d_e \tau_1} E(t - \tau_1) - (d_l + \beta_l + \kappa(t)L)L, \\ \frac{dP}{dt} = \beta_l L - (d_p + \beta_p)P, \\ \frac{dH}{dt} = \beta_p e^{-d_p \tau_2} P(t - \tau_2) - d_h H. \end{cases} \quad (4.2)$$

Using a comparison argument similar to that in the proof of Lemma 3.1, we have

**Lemma 4.1.** For any  $\phi \in X$ , system (4.2) has a unique nonnegative solution through  $\phi$ , and all solutions are ultimately bounded and uniformly bounded.

#### 4.2. Threshold dynamics

For given  $\tau > 0$ , define  $C_+ := C([-\tau, 0], \mathbb{R}_+^n)$ . For  $x, y \in \mathbb{R}^n$ , we write  $x \geq y$  if  $x - y \in \mathbb{R}_+^n$ ,  $x > y$  if  $x - y \in \mathbb{R}_+^n \setminus \{0\}$ , and  $x \gg y$  if  $x - y \in \text{int}\mathbb{R}_+^n$ . Let  $\hat{\cdot}$  denote the inclusion  $\mathbb{R}^n \rightarrow C([-\tau, 0], \mathbb{R}^n)$  by  $x \rightarrow \hat{x}$ ,  $\hat{x}_i(\theta) \equiv x_i$ ,  $\theta \in [-\tau, 0]$ ,  $1 \leq i \leq n$ .

As shown in [14], we consider a nonlinear  $\omega$ -periodic delay differential equation

$$\frac{du}{dt} = f(t, u(t), u(t - \tau)), \quad (4.3)$$

with the initial function  $u(s) = \varphi(s)$ ,  $s \in [-\tau, 0]$ , and  $\varphi \in C_+$ , where  $u = (u_1, \dots, u_n)^T$  and  $f = (f_1, \dots, f_n)^T: \mathbf{R} \times \mathbf{R}^n \times \mathbf{R}^n \rightarrow \mathbf{R}^n$  is continuous,  $f(t, u, v)$  is Lipschitzian in  $(u, v)$ , and  $f(t + \omega, u, v) = f(t, u, v)$  for some  $\omega > 0$ .

We further make the following assumptions on  $f$ :

- (H<sub>1</sub>) For any given  $u \geq 0, v \geq 0, t \geq 0$ ,  $\frac{\partial f}{\partial u}(t, u, v)$  is quasi-positive (i.e., all off-diagonal entries are nonnegative),  $\frac{\partial f}{\partial v}(t, u, v)$  is positive (i.e., all entries are nonnegative),  $\frac{\partial f}{\partial u}(t, u, v) + \frac{\partial f}{\partial v}(t, u, v)$  is irreducible, and for each  $j$  there exists  $i$  such that  $\frac{\partial f_i}{\partial v_j}(t, u, v) > 0$ .
- (H<sub>2</sub>) For any  $\phi \in C_+$  with  $\phi_i(0) = 0$ ,  $f_i(t, \phi(0), \phi(-\tau)) \geq 0$  for all  $t \geq 0$ .
- (H<sub>3</sub>) There exists  $K_0 > 0$  such that  $f_i(t, K, K) \leq 0$  for all  $K > K_0$ ,  $1 \leq i \leq n$ .
- (H<sub>4</sub>)  $f$  is strictly subhomogeneous in the sense that  $f(t, \alpha x, \alpha y) > \alpha f(t, x, y)$  for any  $\alpha \in (0, 1)$ ,  $x \gg 0, y \gg 0$ .

By [36, Section 5.3], assumption (H<sub>1</sub>) implies that system (4.3) is cooperative and irreducible. Note that if  $f(t, 0, 0) = 0$ , then  $\hat{0}$  is a trivial periodic solution of (4.3). In this case, let  $\tilde{P}$  be the Poincaré map associated with system (4.3), and  $\rho(D\tilde{P}(0))$  be the spectral radius of the Fréchet derivative of  $\tilde{P}$  at  $\hat{0}$ .

From [14, Lemma 2.1], we have the following result.

**Lemma 4.2.** *Let (H<sub>1</sub>) – (H<sub>4</sub>) hold. If  $f(t, 0, 0) = 0$  and  $\rho(D\tilde{P}(0)) \leq 1$ , then  $\hat{0}$  is globally asymptotically stable for (4.3) in  $C_+$ .*

It is easy to calculate the population reproduction ratio for system (4.2) as follows

$$\mathbb{R}_0 = \frac{b\beta_e\beta_l\beta_p e^{-(d_e\tau_1 + d_p\tau_2)}}{d_1d_2d_3d_4}.$$

From Lemmas 4.1 and 4.2, we have the following result.

**Theorem 4.3.** *If  $\mathbb{R}_0 \leq 1$ , then the periodic solution  $(0, 0, 0, 0)$  is globally asymptotically stable for system (4.2) in  $X$ .*

To prove the uniform persistence of the system, Liu and Zhao [14] gave an assumption which satisfied the condition (H<sub>3</sub>). However, system (4.2) ensures that the condition (H<sub>3</sub>) holds. In the following we prove the uniform persistence of system (4.2) when  $\mathbb{R}_0 > 1$ .

**Theorem 4.4.** *If  $\mathbb{R}_0 > 1$ , then system (4.2) admits a positive  $\omega$ -periodic solution and there exists a real number  $\eta > 0$  such that any solution  $(E(t, \phi), L(t, \phi), P(t, \phi), H(t, \phi))$  of system (4.2) with  $\phi \in X_0$  satisfies  $\liminf_{t \rightarrow \infty} (E(t), L(t), P(t), H(t)) \geq (\eta, \eta, \eta, \eta)$ .*

**Proof.** Let  $X, X_0$  and  $\partial X_0$  be sets defined in Section 3. Let  $\tilde{P}$  be the solution map of system (4.2) on  $X$ , that is,  $\tilde{P}(t)\psi = u_t(\psi)$ ,  $t \geq 0$ , where  $u(t, \psi)$  is the unique solution of system (4.2) satisfying  $u_0 = \psi \in X$ . Then  $\tilde{P} := \tilde{P}(\omega)$  is the Poincaré map associated with system (4.2).

It is easy to see from system (4.2) that  $\tilde{P}(t)X_0 \subseteq X_0$  for all  $t \geq 0$ . It follows from Lemma 4.1 that all solutions to system (4.2) are ultimately bounded and uniformly bounded, which implies that the discrete-time system  $\{\tilde{P}^n: X \rightarrow X\}_{n \geq 0}$  is point dissipative and  $\tilde{P}^n$  is compact for sufficiently large  $n$ . It then follows from [37, Theorem 2.9] that  $\tilde{P}$  admits a global attractor in  $X$ . Now we prove that  $\tilde{P}$  is uniformly persistent with respect to  $X_0$ .

Let  $M = (0, 0, 0, 0)$ . Choose a small positive integer  $\delta_0$  such that  $E^* > \delta_0$ . Since  $\lim_{\phi \rightarrow M} (\tilde{P}(t)\phi - M) = 0$  uniformly for  $t \in [0, \omega]$ , there exists  $\delta_1 > 0$  such that for any  $\phi \in X_0$  with  $\|\phi - M\| < \delta_1$  we have  $\|\tilde{P}(t)\phi - M\| < \delta_0$ ,  $\forall t \in [0, \omega]$ .

Claim  $\limsup_{n \rightarrow \infty} (\tilde{P}(n\omega)\phi - M) \geq \delta_1$  for all  $\phi \in X_0$ .

Suppose, by contradiction, that  $\limsup_{n \rightarrow \infty} (\tilde{P}(n\omega)\psi - M) < \delta_1$  for some  $\psi \in X_0$ . Then there exists an integer  $N_1 \geq 1$  such

that  $\|\tilde{P}(n\omega)\psi - M\| < \delta_1$  for all  $n \geq N_1$ . For any  $t \geq N_1\omega$ , we have  $t = n\omega + t'$  with  $n \geq N_1$  and  $t' \in [0, \omega]$ , and  $\|\tilde{P}(t)\psi - M\| = \|\tilde{P}(t')\tilde{P}(n\omega)\psi - M\| < \delta_0$ . Then  $E(t, \psi) < \delta_0$ , which is a contradiction with  $\lim_{t \rightarrow \infty} E(t, \psi) = E^* > \delta_0$ .

Define

$$M_\partial = \{\phi \in \partial X_0 : \tilde{P}^n(\phi) \in \partial X_0, \forall n \geq 0\}.$$

For any given  $\psi \in \partial X_0$ , we have  $\psi_1(0) = 0$  or  $\psi_2(0) = 0$  or  $\psi_3(0) = 0$  or  $\psi_4(0) = 0$ . If  $\psi_1(0) = 0$ , then from the equations of (4.2) we have  $L(t, \psi) \rightarrow 0, P(t, \psi) \rightarrow 0, H(t, \psi) \rightarrow 0, E(t, \psi) \rightarrow 0$  as  $t \rightarrow \infty$ . Then  $\tilde{P}^n(\psi) \rightarrow M$  as  $n \rightarrow \infty$ . For the case where  $\psi_2(0) = 0$  or  $\psi_3(0) = 0$  or  $\psi_4(0) = 0$ , we can do similar analysis. Finally, we obtain that for any given  $\psi \in M_\partial$ ,  $\tilde{P}^n(\psi) \rightarrow M$  as  $n \rightarrow \infty$ . Thus  $\bigcup_{\phi \in \partial M} \omega(\phi) \subseteq \{M\}$ . From the claim, we know that  $\{M\}$  is the only isolated compact invariant set for  $\tilde{P}$  in  $X$ , and  $W^s(M) \cap X_0 = \emptyset$ , where  $W^s(M)$  is the stable set of  $M$  for  $\tilde{P}$ . By the acyclicity theorem on uniform persistence for maps (see e.g., [38, Theorem 1.3.1 and Remark 1.3.1]), it follows that  $\tilde{P}: X \rightarrow X$  is uniformly persistent with respect to  $X_0$ . Then [38, Theorem 3.1.1] gives that the periodic semiflow  $\tilde{P}(t): X \rightarrow X$  is also uniformly persistent with respect to  $X_0$ . It follows from [37, Theorem 4.5] that system (4.2) admits an  $\omega$ -periodic solution  $\tilde{P}(t)\phi^*$  with  $\phi^* \in X_0$ . Then  $E(t, \phi^*) > 0, L(t, \phi^*) > 0, P(t, \phi^*) > 0, H(t, \phi^*) > 0$ . Therefore,  $(E(t, \phi^*), L(t, \phi^*), P(t, \phi^*), H(t, \phi^*))$  is a positive  $\omega$ -periodic solution of system (4.2).

By [37, Theorem 4.5] with  $\rho(x) = d(x, \partial X_0)$ , it then follows that  $\tilde{P}: X_0 \rightarrow X_0$  has a compact attractor  $A_0$ . For any  $\phi \in A_0$ , we have  $\phi_i(0) > 0$  for all  $i = 1, 2, 3, 4$ . Let  $B_0 = \bigcup_{t \in [0, \omega]} \tilde{P}(t)A_0$ . Then  $\psi_i(0) > 0, i = 1, 2, 3, 4$  for all  $\psi \in B_0$ . Moreover,  $B_0 \subseteq X_0$  and  $\lim_{t \rightarrow \infty} d(\tilde{P}(t)\phi, B_0) = 0$  for all  $\phi \in X_0$ . Define a continuous function  $p: X \rightarrow \mathbf{R}_+$  by

$$p(\phi) = \min_{i \in \{1, 2, 3, 4\}} \{\phi_i(0)\}, \quad \forall \phi \in X.$$

Since  $B_0$  is a compact subset of  $X_0$ , we have  $\inf_{\phi \in B_0} p(\phi) = \min_{\phi \in B_0} p(\phi) > 0$ . Consequently, there exists  $\eta > 0$  such that

$$\begin{aligned} \liminf_{t \rightarrow \infty} \min(E(t, \phi), L(t, \phi), P(t, \phi), H(t, \phi)) \\ = \liminf_{t \rightarrow \infty} p(\tilde{P}(t)\phi) \geq \eta, \quad \forall \phi \in X_0. \end{aligned}$$

□

**Remark 4.5.** When the food source is unlimited, system (4.2) reduces to

$$\begin{cases} \frac{dE}{dt} = bH - (d_e + \beta_e)E, \\ \frac{dL}{dt} = \beta_e e^{-d_e\tau_1} E(t - \tau_1) - (d_l + \beta_l + \kappa(t)L)L, \\ \frac{dP}{dt} = \beta_l L - (d_p + \beta_p)P, \\ \frac{dH}{dt} = \beta_p e^{-d_p\tau_2} P(t - \tau_2) - d_h H. \end{cases} \quad (4.4)$$

For model (4.4) the same results hold as for model (4.2).

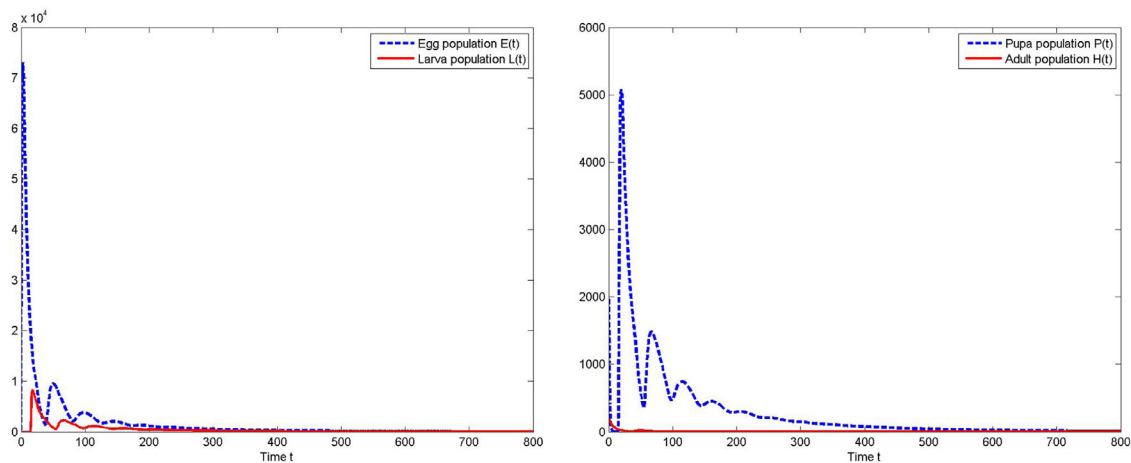
**Theorem 4.6.** *For system (4.4), we have*

- (i) *If  $\mathbb{R}_0 \leq 1$ , then the periodic solution  $(0, 0, 0, 0)$  is globally asymptotically stable in  $X$ .*
- (ii) *If  $\mathbb{R}_0 > 1$  and all solutions are bounded, then system (4.4) admits a positive  $\omega$ -periodic solution and there exists a real number  $\eta_1 > 0$  such that any solution  $(E(t, \phi), L(t, \phi), P(t, \phi), H(t, \phi))$  of system (4.4) with  $\phi \in X_0$  satisfies*

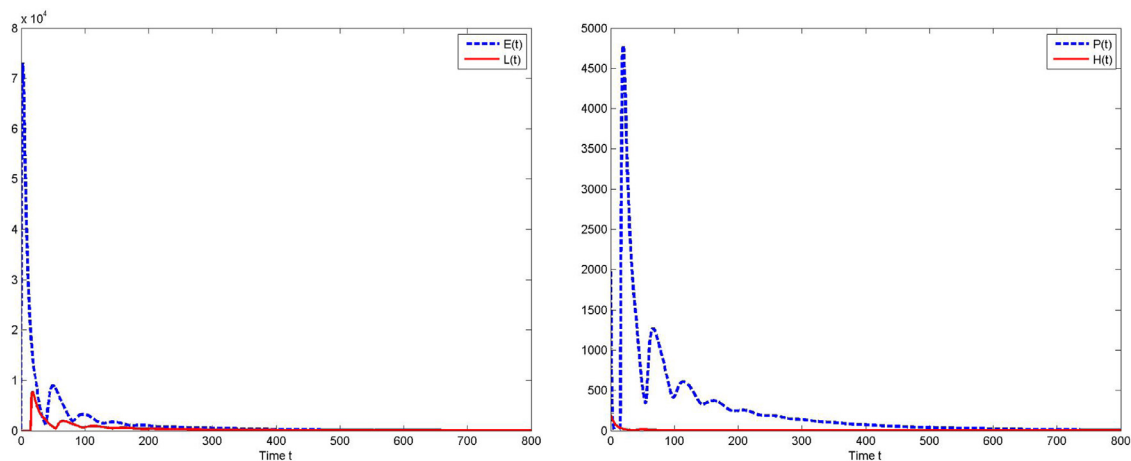
$$\liminf_{t \rightarrow \infty} (E(t), L(t), P(t), H(t)) \geq (\eta_1, \eta_1, \eta_1, \eta_1).$$

## 5. Numerical simulations

In order to explain the impact of temperature and season on the population of *H.cunea* and demonstrate the theoretical results established in this paper, we present some numerical simulations.



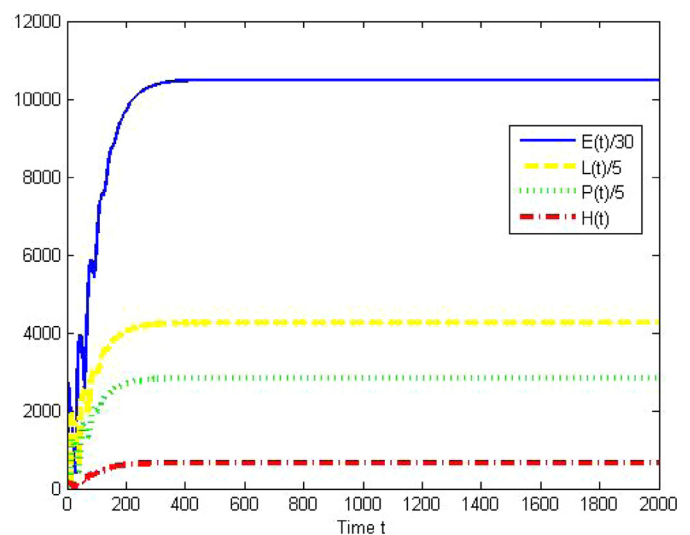
**Fig. 1.** Long term behaviors of the solutions of the time-delayed model (3.1), where  $b = 500$ ,  $\beta_e = 0.9$ ,  $d_e = 1/12$ ,  $d_l = 1/30$ ,  $\beta_l = 0.6$ ,  $\kappa = 0.0001$ ,  $d_p = 3/10$ ,  $\beta_p = 0.6$ ,  $d_h = 1/5$ ,  $\tau_1 = 15$  and  $\tau_2 = 22$ , then  $\mathbb{R}_0 = 0.5632 < 1$ . Left: Time series plot of  $E(t)$  and  $L(t)$  in model (3.1); Right: Time series plot of  $P(t)$  and  $H(t)$  in model (3.1). Note that  $(E(t), L(t), P(t), H(t)) \rightarrow (0, 0, 0, 0)$  with respect to time  $t$  (days).



**Fig. 2.** Long term behaviors of the solutions of the periodic time-delayed model (4.2), where  $\tau_1 = 15$ ,  $\tau_2 = 22$ ,  $\kappa(t) = 0.0001(1 + 0.5 \sin(\frac{2\pi}{365}(t - 30)))$ . Other values of parameters are the same as those listed in Fig. 1, then  $\mathbb{R}_0 = 0.5632 < 1$ . Left: Time series plot of  $E(t)$  and  $L(t)$  in model (4.2); Right: Time series plot of  $P(t)$  and  $H(t)$  in model (4.2). Note that  $(E(t), L(t), P(t), H(t)) \rightarrow (0, 0, 0, 0)$  with respect to time  $t$  (days).

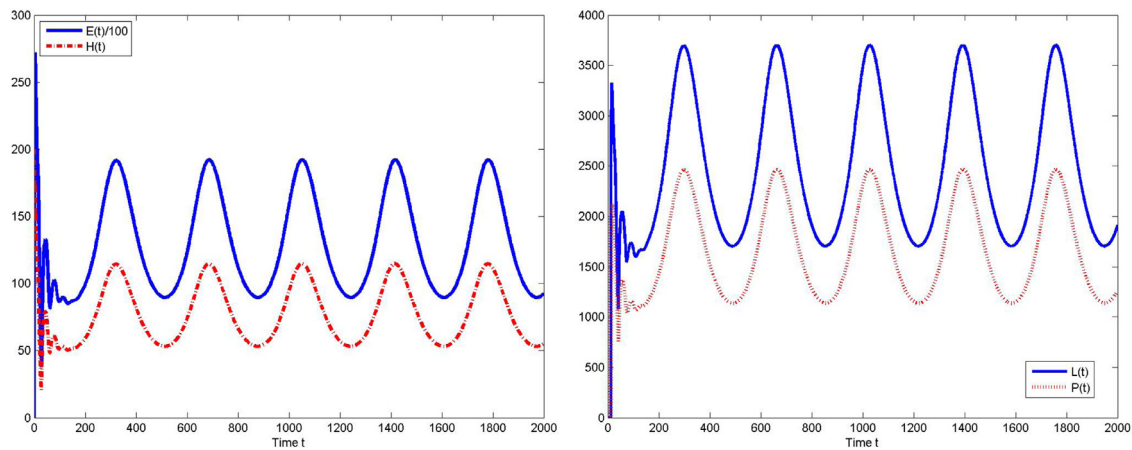
We first illustrate the impact of temperature. From [7,27], we consider a set of parameter values:  $b = 500$ ,  $\beta_e = 0.9$ ,  $d_e = 1/12$ ,  $d_l = 1/30$ ,  $\beta_l = 0.6$ ,  $d_p = 3/10$ ,  $\beta_p = 0.6$ ,  $d_h = 1/5$ ,  $\tau_1 = 15$  and  $\tau_2 = 22$  in system (3.1) and system (4.2), then the population reproduction ratio  $\mathbb{R}_0 = 0.5632 < 1$ . We take  $\kappa = 0.0001$  in system (3.1) and  $\kappa_0 = 0.0001$ ,  $\varepsilon = \frac{1}{2}$ ,  $\omega = \frac{2\pi}{365}$  in system (4.2). It can be seen from Figs. 1 and 2 that  $(E(t), L(t), P(t), H(t)) \rightarrow (0, 0, 0, 0)$ , which means *H.cunea* will die out. If temperature is higher in some year in a given region, then the development duration will be shortened, which means the delays  $\tau_1$  and  $\tau_2$  will decrease. We take  $\tau_1 = 12$  and  $\tau_2 = 15$  in system (3.1), then the population reproduction ratio  $\mathbb{R}_0 = 2.4012 > 1$ . One can see from Fig. 3 that  $(E(t), L(t), P(t), H(t))$  converges to a positive steady state with respect to time  $t$  (days), which means the positive solution  $P_1$  of system (3.1) is stable when  $\mathbb{R}_0 > 1$ .

Now we compare the time-delayed model with the period time-delayed model to demonstrate the effect of seasonality on population dynamics of *H.cunea*. In Fig. 4,  $\kappa(t) = 0.0001(1 + 0.5 \sin(\frac{2\pi}{365}(t - 30)))$ ,  $\tau_1 = 12$ ,  $\tau_2 = 15$  and other parameters are the same as those in Fig. 3, then the population reproduction ratio  $\mathbb{R}_0 = 2.4012 > 1$ . However, Fig. 4 shows that the populations of eggs, larvae pupae and adult *H.cuneas* oscillate seasonally. Unlike the time-delayed model (3.1), the solution of system (4.2) converges to a positive periodic solution. Simulations show that

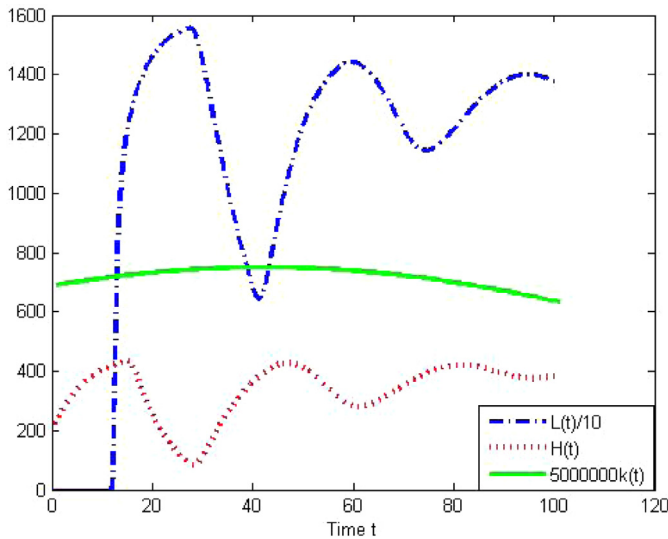


**Fig. 3.** Long term behaviors of the solutions of the time-delayed model (3.1), where  $\tau_1 = 12$ ,  $\tau_2 = 15$  and other values of parameters are the same as those listed in Fig. 1, then  $\mathbb{R}_0 = 2.4012 > 1$ . Note that  $(E(t), L(t), P(t), H(t))$  converges to a stable positive equilibrium with respect to time  $t$  (days).





**Fig. 4.** Long term behaviors of the solutions of the periodic time-delayed model (4.2).  $\kappa(t) = 0.0001(1 + 0.5 \sin(\frac{2\pi}{365}(t - 30)))$ . Other values of parameters are the same as those listed in Fig. 3, then  $\mathbb{R}_0 = 2.4012 > 1$ . Left: Time series plot of  $E(t)/100$  and  $H(t)$  in model (4.2); Right: Time series plot of  $L(t)$  and  $P(t)$  in model (4.2). Note that  $(E(t), L(t), P(t), H(t))$  converges to a positive periodic solution with respect to time  $t$  (days).



**Fig. 5.** The population dynamics of larvae and adult H.cuneas in the first 100 days under the seasonal perturbation.  $\kappa$  function and values of parameters are the same as those listed in Fig. 4.  $\mathbb{R}_0 = 2.4012 > 1$ .

H.cunea will persist and exhibit periodic fluctuation in the next few years if no further intervention is taken.

Fig. 5 further illustrates the impact of seasonality on population dynamics of H.cunea in the first 100 days. When the temperature reaches about 15°C in April, adult H.cunea emerges and begins to feather. Since the lower temperature in the following 30 days, there are few new leaves, so the intra-specific competition rate  $\kappa(t)$  keeps increasing. However, since there exist many overwintering pupae, the population of adult H.cunea  $H(t)$  keeps increasing in the first 15 days, and in the following 15 days  $H(t)$  begins to decrease due to lack of leaf source. About 10–20 days after the eclosion of adult H.cunea the larva population  $L(t)$  increases rapidly because of the high oviposition rate and then it decreases with the decreasing adult number and intra-specific competition at larva stage. In May and June leaves flourish as temperature rises. It can be seen from Fig. 5 that  $\kappa(t)$  begins to keep decreasing, then the population of adult H.cuneas developed from overwintering pupae and larvae begins to increase accordingly. The habit of staying together in a web for larvae hatched by an egg batch makes  $L(t)$  and  $H(t)$  undergo a small decrease and then increase again for the impact of rich leaf source. After another change from decrease to increase in

the following 30 days  $H(t)$  and  $L(t)$  reach the stable positive periodic state eventually (Fig. 4).

## 6. Conclusion and discussion

It is necessary to understand the population dynamics model for H.cunea since its frequent outbreaks and economics losses caused by this species. We study the population dynamics of H.cunea for the purpose of better understanding how temperature and seasonal changes drive the population dynamics of H.cunea. In this paper, we first develop a basic stage-structured model (2.2), then formulate a time-delayed model (3.1) with the impact of average temperature on the base of model (2.2) and further derive a periodic model (4.2) with seasonality.

In Section 2, we first introduce the population reproduction ratio  $\mathbb{R}_0$  and the probability of major outbreak  $p_0$  of the basic stage-structured model (2.2). And we have shown that  $p_0$  is monotone with respect to  $\mathbb{R}_0$ .  $\mathbb{R}_0$  also acts as a threshold parameter for the existence and stability of equilibria. We show in Theorems 2.1–2.3 that if  $\mathbb{R}_0 < 1$ , the trivial equilibrium is globally asymptotically stable and unstable if  $\mathbb{R}_0 > 1$ , and the positive equilibrium is locally asymptotically stable if and only if  $\mathbb{R}_0 > 1$ , that is, H.cunea dies out if  $\mathbb{R}_0 < 1$  and persists if  $\mathbb{R}_0 > 1$ .

In Section 3, considering the effect of the temperature on the egg stage and larva stage, we introduce two time delays  $\tau_1$  and  $\tau_2$ , and then formulate a time-delayed differential equation model (3.1). The responding population reproduction ratio  $\mathbb{R}_0$  is given. For model (3.1), if  $\mathbb{R}_0 < 1$ , the trivial equilibrium is globally asymptotically stable and unstable if  $\mathbb{R}_0 > 1$ , and the positive equilibrium is locally asymptotically stable if  $\mathbb{R}_0 > 1$ , which have been confirmed in Figs. 1 and 3.

On the base of the time-delayed differential equation model we continue to study the population dynamics of H.cunea under the perturbation of the seasonality and derive a periodic time-delayed dynamic model (4.2). We calculate the population reproduction ratio  $\mathbb{R}_0$  for (4.2). And then we show that it acts as a threshold parameter for the uniform persistence and global extinction of H.cunea. But different from model (3.1), if  $\mathbb{R}_0 > 1$ , model (4.2) admits a positive  $\omega$ -periodic solution and there exists a real number  $\eta > 0$  such that any solution  $(E(t, \varphi), L(t, \varphi), P(t, \varphi), H(t, \varphi))$  of system (4.2) with  $\varphi \in X_0$  satisfies  $\liminf_{t \rightarrow \infty} (E(t), L(t), P(t), H(t)) \geq (\eta, \eta, \eta, \eta)$  (Fig. 4).

It follows from both the analytic results and simulations for both models (3.1) and (4.2) that temperature and season have a great impact on the population dynamics of H.cunea. If the tem-

perature is low, or the values of two time delays  $\tau_1$  and  $\tau_2$  are bigger, then it takes longer time for egg to hatch into larva and for pupa to become adult *H.cunea*. In this case the population reproduction ratio  $\mathbb{R}_0$  is smaller. If the average temperature in a given region remains at a lower level such that  $\mathbb{R}_0$  be less than 1, it follows from Theorems 3.3 and 4.3 that  $(E(t), L(t), P(t), H(t)) \rightarrow (0, 0, 0, 0)$ , that is, this species in this region will die out, which can be seen from Figs. 1 and 2.

We can see from the simulations in Fig. 5 for model (4.2) that  $\kappa(t)$  increases in April, which means the shortage of leaf source. Lacking of leaves causes the number of adult *H.cunea* to change from increase to decrease. And the same change happen to larva population. As there exist many overwintering pupae, the adult *H.cunea* population then increase again. But after a short term the increasing intra-specific competition rate  $\kappa(t)$  leads to a small diminution of adult *H.cuneas* and larvae. However, with the increasing number of leaves of host plants in May and June,  $\kappa(t)$  keeps decreasing and *H.cunea* population increases accordingly. The high oviposition rate and the habit of staying together in a web for larvae hatched by an egg batch reduce the number larvae and adult *H.cuneas*. Then the plenty of leaves makes *H.cunea* population increase and reach the stable positive periodic solution.

In this paper, we took the mean temperature at each development stage as the daily temperature and calculated mortality rates  $d_i (i = e, l, p, h)$  and development rates  $\beta_i (i = e, l, p)$  by the mean temperature and the baseline temperature as well as the total accumulated temperature. And the durations from egg to larva and from pupa to adult *H.cunea* are assumed to be constants  $\tau_1$  and  $\tau_2$ . It should be more reasonable to consider these parameters as time-dependent functions of temperature. Moreover, we did not incorporate the complex of bivoltine or trivoltine life cycle in the models for *H.cunea*, we leave these problems for our future work.

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