Analysis of a negative binomial host–parasitoid model with two maturation delays and impulsive resource input

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ABSTRACT
To study the interaction of parasitoids and their insect hosts in laboratory environment, we propose a mathematical model incorporating impulsive resource inputs, stage-structure, maturation times and negative binomial distribution of parasitoid attacks. According to the adaptability of the insect host to the environment, we obtain conditions under which the system is uniformly permanent in two cases, which guarantee that the host and its parasitoid can coexist. By applying fixed point theory, we show existence of the positive periodic solution where the host and its parasitoid can coexist, and also obtain the conditions that ensure the existence of the parasitoid-extinction periodic solution. Our numerical analysis confirms and extends our theoretical results. The simulations show that when the total amount of resource is fixed, a smaller amount of recourse inputs with a shorter period of impulsive delivery results in smaller oscillation amplitude in the insect host population. However, the development of parasitoid population is not affected by the resource management strategy. It is also demonstrated that larger maturation times, either the host’s or the parasitoid’s, lead to the decline of the parasitoid population. But larger parasitoid’s maturation time does accelerate the host’s population growth. These are helpful for us to acquire a deeper knowledge of the host–parasitoid interaction in laboratory environment.

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1. Introduction
Insect host–parasitoid interactions are typical examples of antagonistic trophic interactions between species. Parasitoids make up about 10 % or more of all metazoan species, and they usually fall into two families: the Hymenoptera (such as wasps, sawflies and bees) and the Diptera (e.g. two-winged flies) [20]. The study of host–parasitoid systems is an important part of insect biology and agriculture management. Ecologists and biologists have been studying host–parasitoid interactions for decades and related results have been increasingly applied in the field of biological pest control [4,13,14,31]. The feature that some hosts and their parasitoids can be easily cultured in experimental environment makes them be biological model systems for the study of the biology of predator–prey/host–parasitoid systems and their population dynamics. In the past half century,
many empirical and theoretical studies about host–parasitoid interactions have been done [8,15,26,30,36,37,43–49,52].

The behavioural and evolutionary ecology of parasitoids was well introduced in [1,16]. Bailey et al. [3] studied the host–parasitoid interactions in the case where some hosts are less likely to be attached than others. Interacting systems with features like prolonged diapauser, patch parasitism and global change were investigated mainly for their persistence in [8,9,21,22,35]. Maron and Harrison [34] and Ottar et al. [5] explored the spatial pattern formation and the influence of trophic interactions on spatial synchrony while Penczykowski et al. [38] reviewed the literature to examine the understanding of host–parasitoid interactions with temporal and spatial structures. Godfray and Hassell [17] discussed population cyclic behaviours of host–parasitoid interactions from the point of view of both endogenous factors in constant environment and exogenous mechanisms in varying environment. Host feeding, as a specific behaviour, has also been widely studied to recognize its dynamical effects on population development [6,11,12]. Furthermore, experimental approaches were proposed and then widely applied to the research of interactions between hosts and their parasitoids under controlled conditions in microcosm [27,40,44].

In experimental settings for insect hosts and parasitoids such as bruchid host and its braconid parasitoid, host resource (usually beans of some genus) is renewed and the numbers/densities of insects are recorded every few days. Based on empirical data, the population dynamics will then be studied to investigate biological mechanisms of population dynamic behaviours [10,43–45]. Food resource supply strategy may affect the dynamical behaviours of host–parasitoid interactions, resulting in extinction of hosts and/or parasitoids, system persistence and even cyclic behaviours. In this paper, we mainly focus on modelling the impacts of exogenous host resource input in lab on host–parasitoid interactions when the population dynamical features such as the persistence, cyclic behaviours and steady states happen.

According to the operation mode in lab, a certain amount of host resource is complemented into an assigned compartment every few days. Normally each resource input is completed in a relatively short time. Mathematically, these types of pulses can be described more precisely by impulsive differential equations. In the past decades, impulsive differential equations have been applied to the area of biological control such as pest management, optimal harvesting policy of renewable resources, prevention of infectious disease and drug management in clinic pharmacokinetics [23–25,32,41,50]. However, few studies have been done to explore the impacts of impulsive inputs of host resource on the population dynamics of insect host–parasitoid systems. Here, we formulated a mathematical model to describe host–parasitoid interactions with pulses of host food resource. The model captures the major characteristics of hosts and parasitoids: stage structures, density dependent growth of hosts and negative binomial distribution of parasitoid attacks. Our analysis shows that the model exhibits periodic oscillations. This result is particularly meaningful to biologists. Population abundances in lab are always censused based on some time intervals. Therefore, biologists have to pay extra attention to the pulses of host food resource so that their impact does not mix with the impacts of focal factors on the population dynamics.

In the following, we formulate our model in Section 2 to describe host–parasitoid systems with pulses of host resource input in laboratory environment. In Section 3, we analysed the permanence of the system and established the existence of the positive periodic solution and the parasitoid-extinction periodic solution. Our analysis tools mainly involve
comparison theorems and fixed point theory. Some numerical simulations are carried out in Section 4 and a brief discussion section comes to the end of the article.

2. Model formulation

For host–parasitoid systems, two types of mathematical models have been developed, discrete models normally for systems with non-overlapping generations [11,17,33,42] and continuous models for generation-round systems [10,17,52]. Continuous models usually assume fixed development times to describe developmental stages of hosts and parasitoids. The assumption leads to stage-structured models consisting of delay differential equations [7,10,17,18,37,39,51,52]. Murdoch et al. [37] proposed two mathematical models with fixed time delays to describe the development times for the immature host and parasitoid stages, and studied the stability factors of the systems. Godfray [17] and Gordon [18] further developed some new models based on the delay models. Following these previous works, we assume that immature insects stay in immature stages for fixed times, \( \tau_1 \) for hosts and \( \tau_2 \) for parasitoids. The adult hosts consume the resource \( K \) and produce the next generation. Because of intraspecific competition for the resource, the growth rate of immature host \( x_i \) is assumed to be density dependent, taking the form of [19]

\[
\frac{rx(t)K(t)}{(1 + \lambda_1 x(t))^b},
\]

where \( K(t) \) and \( x(t) \) represent the densities of the resource and adult hosts, respectively. \( b \) is a parameter measuring the adaptability of the host to the environment. Smaller \( b \) values imply stronger host viabilities. Assuming the same amount \( \sigma \) of the resource \( K \) is provided to hosts every \( \delta \) time units, we can have the impulsive equations for the resource \( K \)

\[
\frac{dK(t)}{dt} = - \frac{rx(t)K(t)}{(1 + \lambda_1 x(t))^b} - d_K K(t), \quad t \neq k\delta,
\]

\[
K(t^+) = K(t) + \sigma, \quad t = k\delta.
\]

The second equation describes the amount \( \sigma \) of the resource adding to the system at the \( k \)th time.

In general, parasitoid attacks are neither randomly distributed nor evenly distributed among hosts. They are aggregated or clumped distributed [33]. Empirical studies imply that the distribution of attacks is close to negative binomial distributions. Therefore, as in [17,39], we assume that parasitoid attacks follow a negative binomial distribution, having the attack rate

\[
\lambda_2 \ln \left( 1 + \frac{a}{\lambda_2 y(t)} \right),
\]

where \( y(t) \) represents the density of adult parasitoids, \( a \) stands for the per capita searching efficiency of parasitoids and \( \lambda_2 \) measures contagion intensity in the distribution of parasitism among hosts.

Most parasitoids attack a particular life stage of the host insect. The juvenile stages (i.e. eggs, larvae, pupae) are most common to attack, but a few species attack only the adult insects, for example conopid wasps attacking adult bees of several genera. Parasitoids may
use either idiobiont or koinobiont strategy. Idiobiont parasitoids prevent further development of the host once it has been infected, whereas hosts of koinobions continue their development after infection. In this work, we mainly study koinobiont parasitoids of Ichneumonoidea family who typically lay their eggs in live adult hosts without killing them. The eggs hatch and the growing larvae feed on the live hosts. The hosts are kept alive for as long as possible, and its biomass is effectively converted into juvenile host biomass [2].

Combining all the above assumptions, we can obtain the balance equations for immature \((x_i)\) and adult \((x)\) hosts and parasitoids \((y)\), and the following model system

\[
\begin{align*}
\frac{dK(t)}{dt} &= -\frac{rx(t)K(t)}{(1 + \lambda_1 x(t))^b} - d_K K(t), \\
\frac{dx_i(t)}{dt} &= \frac{rB_1 x(t)K(t)}{(1 + \lambda_1 x(t))^b} - d_1 x_i(t) - \frac{rB_1 x(t - \tau)K(t - \tau_1)e^{-d_1 \tau_1}}{(1 + \lambda_1 x(t - \tau_1))^b}, \\
\frac{dx(t)}{dt} &= \frac{rB_1 x(t - \tau_1)K(t - \tau_1)e^{-d_1 \tau_1}}{(1 + \lambda_1 x(t - \tau_1))^b} - d_2 x(t) - \lambda_2 \ln(1 + \frac{a}{\lambda_2} y(t))x(t), \\
\frac{dy(t)}{dt} &= \lambda_2 B_2 x(t - \tau_2) \ln(1 + \frac{a}{\lambda_2} y(t - \tau_2))e^{-d_3 \tau_2} - d_4 y(t), \\
K(t^+) &= K(t) + \sigma, \\
x_i(t^+) &= x_i(t), \\
x(t^+) &= x(t), \\
y(t^+) &= y(t),
\end{align*}
\]

(1)

with initial conditions \(K(t) = K_0 > 0, x_i(t) = 0, x(t) = x_0 > 0, y(t) = y_0 > 0, t \in [-\tau, 0]\), where \(\tau = \max\{\tau_1, \tau_2\}\). The constants \(r, b, B_1, B_2, \lambda_1, \lambda_2, a\) are positive. \(B_1\) and \(B_2\) are conversion rates, while \(d_i > 0, i = 1, 2, 3, 4\) are the natural mortality rates of juvenile hosts, mature hosts, immature parasitoids and mature parasitoids, respectively.

3. Permanence and periodic solution

In this section, we will first show the positivity of the solution to the model and then study the system’s permanence through the comparison theorem. Finally we will apply fixed point theory to establish the existence of periodic solutions where either hosts and parasitoids coexist or parasitoids go to extinction.

3.1. Preliminaries

For convenience, let

\[f_1(x) = \frac{rx}{(1 + \lambda_1 x)^b}, \quad f_2(x) = \lambda_2 \ln\left(1 + \frac{a}{\lambda_2} x\right), \quad r_0 = \frac{r(b - 1)^{b-1}}{\lambda_1 b^b},\]

and one can easily get

(1) if \(b > 1\), then \(f_1(x) \leq r_0, x \geq 0;\)
(2) \(f_2(x) \geq (ax/(1 + \frac{a}{\lambda_2} x)), x \geq 0.\)
In the following, we prove the positivity of all solutions of the system (1).

**Proposition 3.1 (Positiveness):** Assume that \( X(t) = (K(t), x_i(t), x(t), y(t)) \) is a solution of the system (1), then \( K(t) > 0, x_i(t) > 0, x(t) > 0 \) and \( y(t) > 0 \) for all \( t > 0 \).

**Proof:** Let \( (K(t), x_i(t), x(t), y(t)) \) be a solution of the system (1) with \( K(t) = K_0 > 0, x_i(t) = 0, x(t) = x_0 \geq 0 \) and \( y(t) = y_0 \geq 0 \) for all \( t \in [-\tau, 0] \). From the first equation, we know that \( K'(t) = 0 \) if \( K(t) = 0 \). Therefore we have \( K(t) > 0, t > 0 \) provided that \( K(t) = K_0 > 0, t \in [-\tau, 0] \).

Suppose that there is a \( t_0 > 0 \) that satisfies \( x(t_0) \leq 0 \). Letting \( \bar{t} = \inf\{t > 0 | x(t) \leq 0 \} \) one can get \( x(\bar{t}) = 0 \) and \( x'(\bar{t}) \leq 0 \). However, from the third equation of system (1), we obtain that
\[
x'(\bar{t}) = \frac{rB_1x(\bar{t} - \tau_1)}{(1 + \lambda x(\bar{t} - \tau_1))^b} K(\bar{t} - \tau_1) e^{-d_1\tau_1} > 0.
\]
A contradiction. Therefore, we have \( x(t) > 0, t > 0 \). Similar discussion yields \( y(t) > 0, t > 0 \).

The second equation of the system (1) yields
\[
x_i(t) = \int_{t - \tau_1}^{t} e^{-d_1(t-s)} \frac{rB_1x(s)}{(1 + \lambda x(s))^b} K(s) \, ds.
\]
According to the above discussion, we can obtain \( x_i(t) > 0, t > 0 \) because \( x(t) > 0, K(t) > 0 \) for \( t > -\tau_1 \). This completes the proof. \( \blacksquare \)

Now we present some results for the following systems that will be applied in later discussion,
\[
\frac{du(t)}{dt} = \frac{KrB_1 u(t - \tau_1) e^{-d_1\tau_1}}{(1 + \lambda u(t - \tau_1))^b} - d_2 u(t),
\]
\[
u(\theta) \geq 0 \text{ is continuous on } -\tau_1 \leq \theta \leq 0, \text{ and } u(0) > 0
\]
and
\[
\frac{dv(t)}{dt} = \lambda B_2 x \ln \left( 1 + \frac{a}{\lambda} v(t - \tau_1) \right) e^{-d_3\tau_2} - d_4 v(t),
\]
\[
v(\theta) \geq 0 \text{ is continuous on } -\tau_2 \leq \theta \leq 0 \text{ and } v(0) > 0.
\]

For systems (2) and (3), by arguments similar to Theorem 4.9.1 and 4.9.3 in [29], we can obtain Lemma 3.1 and Lemma 3.2 in the following.

**Lemma 3.1:** Consider the system (2) and set \( u(t) \) be a solution with \( u(t) = \phi(t) \geq 0 \) for \( t \in [-\tau_1, 0] \) and \( u(0) > 0 \). Assume \( KrB_1 e^{-d_1\tau_1}/d_2 > 1 \) holds. Then \( \lim_{t \to \infty} u(t) = u^* = (1/\lambda_1) (KrB_1 e^{-d_1\tau_1}/d_2)^{1/b} - 1 \) if one of the following two conditions holds.
(i) \( 0 < b \leq 1 \); (ii) \( b > 1 \) and \( KrB_1 e^{-d_1\tau_1}/d_2 < (1 + 2/(b - 1))^{b+1} \).

**Lemma 3.2:** Consider the system (3) and set \( v(t) \) be a solution with \( v(t) = \varphi(t) \geq 0 \) for \( t \in [-\tau_2, 0] \) and \( v(0) > 0 \). If \( aB_2 x e^{-d_3\tau_2} > d_4 \) holds, then \( \lim_{t \to \infty} v(t) = v^*, \) where \( v^* \) is
the unique positive equilibrium of the system (3), satisfying the equation $B_2 x e^{-d_3 t^2} f_2(v^*) = d_4 v^*$.

**Lemma 3.3:** The following system:

$$\dot{\omega}(t) = c - h \omega(t), \ t \neq k\delta,$$

$$\omega(t^+) = \omega(t) + \nu, \ t = k\delta,$$

$$\omega(0^+) = \omega_0 \geq 0$$

(4)

admits a unique positive periodic solution $\tilde{\omega}(t)$ with period $\delta$, given by

$$\tilde{\omega}(t) = \frac{c}{h} + \frac{\nu e^{-h(t-k\delta)}}{1-e^{-h\delta}}, \ t \in (k\delta, (k+1)\delta], \ k \in \mathbb{Z}_+,$$

$$\tilde{\omega}(0^+) = \frac{c}{h} + \frac{\nu}{1-e^{-h\delta}}.$$  

(5)

$\tilde{\omega}(t)$ is globally asymptotically stable. If $c=0$, the solution is simplified as $\tilde{\omega}(t) = \nu e^{-h(t-k\delta)}/(1-e^{-h\delta})$ with initial value $\tilde{\omega}(0^+) = \nu/(1-e^{-h\delta})$.

**3.2. Permanence**

To show the permanence, we consider the system (1) in two cases according to the adaptability of the host to the environment, $b > 1$ and $0 < b \leq 1$. Note that the density $x_i(t)$ of immature hosts is totally determined by $x(t)$ and $K(t)$. We just need to show that the densities $K(t), x(t)$ and $y(t)$ are bounded by some positive constants.

We study the case of $0 < b \leq 1$ first. According to the first and fifth equations of system (1), we get

$$\frac{dK(t)}{dt} \leq -d_K K(t), \ t \neq k\delta,$$

$$K(t^+) = K(t) + \sigma, \ t = k\delta,$$

$$K(0) = K_0 > 0.$$  

(6)

Define an impulsive differential equation

$$\frac{dX(t)}{dt} = -d_K X(t), \ t \neq k\delta,$$

$$X(t^+) = X(t) + \sigma, \ t = k\delta,$$

$$X(0^+) = K_0 > 0.$$  

(7)

By Lemma 3.3, we know that the impulsive system (7) has the positive periodic solution

$$\tilde{X}(t) = \frac{\sigma e^{-d_K(t-k\delta)}}{1-e^{-d_K\delta}}, \ t \in (k\delta, (k+1)\delta], \ k \in \mathbb{Z}_+,$$

$$\tilde{X}(0^+) = \frac{\sigma}{1-e^{-d_K\delta}},$$

(8)

and the solution to the system (7) satisfies $\lim_{t \to \infty} X(t) = \tilde{X}(t)$. 


From Lemma 3.3 and the comparison theorem, it follows that there exists $t_1 > 0$ such that $K(t) \leq X(t) \leq K_2$ for $t \geq t_1$, where

$$K_2 \triangleq \frac{\sigma}{1 - e^{-d_2 k\delta}}.$$  

(9)

From the third equation of the system (1), it follows that when $t \geq t_1$,

$$\frac{dx(t)}{dt} \leq \frac{K_2 rB_1 x(t - \tau_1) e^{-d_1 \tau_1}}{(1 + \lambda_1 x(t - \tau_1))^b} - d_2 x(t).$$

Consider the comparison equation

$$\frac{du(t)}{dt} = \frac{K_2 rB_1 u(t - \tau_1) e^{-d_1 \tau_1}}{(1 + \lambda_1 u(t - \tau_1))^b} - d_2 u(t).$$

According to Lemma 3.1, the solution $u(t)$ to the equation satisfies $\lim_{t \to \infty} u(t) = u^* = (1/\lambda_1)((K_2 rB_1 e^{-d_1 \tau_1} / d_2)^1/b - 1)$ if $K_2 rB_1 e^{-d_1 \tau_1} / d_2 > 1$. From Lemma 3.1 and the comparison theorem, there exists a time point $t_2$ (greater than $t_1$) such that $x(t) \leq x_2, t > t_2 - \tau_2$, where

$$x_2 \triangleq u^* = \frac{1}{\lambda_1} \left( \left( \frac{K_2 rB_1 e^{-d_1 \tau_1}}{d_2} \right)^{1/b} - 1 \right).$$  

(10)

When $t > t_2$, from the first equation of the system (1), we obtain

$$\frac{dK(t)}{dt} \geq -(f_1(x_2) + d_K)K(t), t \neq k\delta,$$

$$K(t^+) = K(t) + \sigma, t = k\delta,$$

$$K(0) = K_0 > 0.$$

Applying Lemma 3.3 and the comparison theorem again, we have that $\exists t_3 > t_2$ that satisfies $K(t) \geq K_1, t > t_3$, where

$$K_1 \triangleq \frac{\sigma}{e^{(f_1(x_2) + d_2 k\delta)} - 1}.$$  

(11)

The fourth equation of the system (1) leads to

$$\frac{dy(t)}{dt} \leq \lambda_2 B_2 x_2 \ln(1 + \frac{a}{\lambda_2} y(t - \tau_2)) e^{-d_3 \tau_2} - d_4 y(t).$$

Similarly define comparison equation as follows:

$$\frac{dv(t)}{dt} = \lambda_2 B_2 x_2 \ln(1 + \frac{a}{\lambda_2} v(t - \tau_2)) e^{-d_3 \tau_2} - d_4 v(t).$$

According to Lemma 3.2, we can obtain that if $aB_2 x_2 e^{-d_3 \tau_2} > d_4$ holds, then $\lim_{t \to \infty} v(t) = v^*$, where $v^*$ is the unique solution of the equation $B_2 x_2 e^{-d_3 \tau_2} f_2(v^*) = d_4 v^*$.  


From the above inequality for \( y(t) \), it follows that \( \exists t_4 > t_3 \) such that \( y(t) \leq y_2 \overset{\Delta}{=} v^* \) for \( t > t_4 \), where \( y_2 \) is the unique positive root of

\[
B_2 x_2 e^{-d_3 \tau_2} f_2(y_2) = d_4 y_2. \tag{12}
\]

When \( t > t_4 \), by the third equation of (1), we obtain

\[
\frac{dx(t)}{dt} \geq \frac{K_1 r B_1 x(t - \tau_1) e^{-d_1 \tau_1}}{(1 + \lambda_1 x(t - \tau_1))^{b}} - (d_2 + f_2(y_2)) x(t).
\]

By Lemma 3.1, we obtain that if \( K_1 r B_1 e^{-d_1 \tau_1} > d_2 + f_2(y_2) \), then there exists \( t_5 > t_4 \) satisfying \( x(t) \geq x_1, t > t_5 \), where

\[
x_1 \overset{\Delta}{=} \frac{1}{\lambda_1} \left[ \left( \frac{K_1 r B_1 e^{-d_1 \tau_1}}{d_2 + f_2(y_2)} \right)^{1/b} - 1 \right]. \tag{13}
\]

Again from the fourth equation of (1), we have

\[
\frac{dy(t)}{dt} \geq \frac{a y(t - \tau_2)}{\frac{a}{\tau_2} e^{-d_3 \tau_2}} - d_4 y(t) = \frac{a B_2 x_1 e^{-d_3 \tau_2} y(t - \tau_2)}{1 + \frac{a}{\tau_2} y(t - \tau_2)} - d_4 y(t).
\]

From the same argument, we can obtain that if \( a B_2 x_1 e^{-d_3 \tau_2} > d_4 \), then \( \exists t_6 > t_5 \) satisfying \( y(t) \geq y_1 \) if \( t > t_6 \), where

\[
y_1 \overset{\Delta}{=} \frac{\lambda_2}{a} \left( \frac{a B_2 x_1 e^{-d_3 \tau_2}}{d_4} - 1 \right). \tag{14}
\]

To sum up, we can get the following theorem.

**Theorem 3.1:** For \( 0 < b \leq 1 \), if \( K_1 r B_1 e^{-d_1 \tau_1} > d_2 + f_2(y_2) \) and \( a B_2 x_1 e^{-d_3 \tau_2} > d_4 \), there exists a \( T > 0 \) such that the solutions to the system (1) satisfy \( K_1 \leq K(t) \leq K_2, x_1 \leq x(t) \leq x_2, y_1 \leq y(t) \leq y_2 \) for \( t > T \), where \( K_1, K_2, x_1, x_2, y_1 \) and \( y_2 \) are given by the formulas (9)–(14). That is, the system (1) is permanent.

Next, we consider the case of \( b > 1 \). Note that in this case, \( f_1(x) \leq r_0 \). The first and fifth equations of (1) yield

\[
-r_0 - d_k K(t) < \frac{dK(t)}{dt} \leq -d_k K(t), \; t \neq k \delta,
\]

\[
K(t^+) = K(t) + \sigma, \; t = k \delta,
\]

\[
K(0) = K_0 > 0.
\]

By the same arguments as in the above discussion for Theorem 3.1, we can select some positive \( t_1 \) such that \( K_1 \leq K(t) \leq K_2 \) if \( t > t_1 \), where

\[
\bar{K}_1 \overset{\Delta}{=} \frac{\sigma}{e^{(r_0 + d_k) \delta} - 1}, \quad \bar{K}_2 \overset{\Delta}{=} \frac{\sigma}{1 - e^{-d_k \delta}}. \tag{16}
\]
From the third equation of the system (1), we can obtain
\[ \frac{dx(t)}{dt} \leq \frac{\bar{K}_2 r B_1 x(t - \tau_1) e^{-d_1 \tau_1}}{(1 + \lambda_1 x(t - \tau_1))^b} - d_2 x(t) \]
for \( t > t_1 + \tau_1 \). By Lemma 3.1 and the comparison theorem, \( \exists t_2 > t_1 + \tau_1 \), such that \( x(t) \leq \bar{x}_2 \) for \( t > t_2 \) if \( \bar{K}_2 r B_1 e^{-d_1 \tau_1} > d_2 > \bar{K}_2 r B_1 e^{-d_1 \tau_1} / (1 + 2/ (b - 1))^{b+1} \). Here
\[ \bar{x}_2 \triangleq \frac{1}{\lambda_1} \left[ \left( \frac{\bar{K}_2 r B_1 e^{-d_1 \tau_1}}{d_2} \right)^{1/b} - 1 \right]. \] (17)

From the fourth equation of system (1), we have
\[ \frac{dy(t)}{dt} \leq \lambda_2 B_2 \bar{x}_2 \ln(1 + \frac{a}{\lambda_2} y(t - \tau_2)) e^{-d_3 \tau_2} - d_4 y(t), \quad t > t_2 + \tau_2. \]
By Lemma 3.2 and the comparison theorem, \( \exists t_3 > t_2 + \tau_2 \) so that \( y(t) \leq \bar{y}_2, \quad t > t_3. \)
\( \bar{y}_2 \) is the unique positive root of
\[ B_2 \bar{x}_2 e^{-d_3 \tau_2} f_2(\bar{y}_2) = d_4 \bar{y}_2. \] (18)

When \( t > t_3 \), according to the third equation of the system (1), we get
\[ \frac{dx(t)}{dt} > \frac{\bar{K}_1 r B_1 x(t - \tau_1) e^{-d_1 \tau_1}}{(1 + \lambda_1 x(t - \tau_1))^b} - (d_2 + f_2(\bar{y}_2)) x(t). \]
By Lemma 3.1 and the comparison theorem, if \( \bar{K}_1 r B_1 e^{-d_1 \tau_1} > d_2 + f_2(\bar{y}_2) > \bar{K}_1 r B_1 e^{-d_1 \tau_1} / (1 + \frac{2}{b-1})^{b+1} \), there exists \( t_4 > t_3 \) having \( x(t) \geq \bar{x}_1, \quad t > t_4 \), where
\[ \bar{x}_1 \triangleq \frac{1}{\lambda_1} \left[ \left( \frac{\bar{K}_1 r B_1 e^{-d_1 \tau_1}}{d_2 + f_2(\bar{y}_2)} \right)^{1/b} - 1 \right]. \] (19)

When \( t > t_4 \), we can have
\[ \frac{dy(t)}{dt} > \lambda_2 B_2 \bar{x}_1 \frac{a}{\lambda_2} y(t - \tau_2) e^{-d_3 \tau_2} - d_4 y(t) = \frac{a B_2 \bar{x}_1 e^{-d_3 \tau_2} y(t - \tau_2)}{1 + \frac{a}{\lambda_2} y(t - \tau_2)} - d_4 y(t). \]
By the same arguments, we can obtain that if \( a B_2 \bar{x}_1 e^{-d_3 \tau_2} > d_4 \), then \( \exists t_5 > t_4 \) such that \( y(t) \geq \bar{y}_1, \quad t > t_5, \) where
\[ \bar{y}_1 \triangleq \frac{\lambda_2}{a} \left( \frac{a B_2 \bar{x}_1 e^{-d_3 \tau_2}}{d_4} - 1 \right). \] (20)

To sum up, we have the following conclusion.

**Theorem 3.2:** For \( b > 1 \), if \( \bar{K}_1 r B_1 e^{-d_1 \tau_1} > d_2 + f_2(\bar{y}_2), \quad a B_2 \bar{x}_1 e^{-d_3 \tau_2} > d_4 \) and \( d_2 > \bar{K}_2 r B_1 e^{-d_1 \tau_1} / (1 + 2/ (b - 1))^{b+1} \), there exists a \( T > 0 \) such that the solutions to the system (1) satisfy \( \bar{K}_1 \leq K(t) \leq \bar{K}_2, \quad \bar{x}_1 \leq x(t) \leq \bar{x}_2, \quad \bar{y}_1 \leq y(t) \leq \bar{y}_2 \) for \( t > T \), where \( \bar{K}_1, \bar{K}_2, \bar{x}_1, \bar{x}_2, \bar{y}_1 \) and \( \bar{y}_2 \) are positive constants and defined in (16)–(20). That is, the system (1) is permanent.
3.3. Existence of positive periodic solution

In this section, we discuss the existence of positive periodic solutions of system (1). We need the fixed point theorem as follows.

**Lemma 3.4:** Let $X$ be a Banach space and $\tilde{D} \subset X$ be a closed bounded and convex set. Suppose

$$T : \tilde{D} \to \tilde{D}$$

is a compact operator, then $T$ has a fixed point in $\tilde{D}$.

**Theorem 3.3:** System (1) admits a positive periodic solution if conditions in Theorem 3.1 or Theorem 3.2 are satisfied.

To apply Lemma 3.4, define a Banach space $X = \{ z(t) = (e_1(t), e_2(t), e_3(t)) \mid e_1(t) \in (PC[I, R] \cap C^1[I, [\delta, 2\delta, \ldots, k\delta, \ldots], R]), e_2(t) \in C[R, R], e_3(t) \in C[R, R], e_1(t+\delta) = e_1(t), e_2(t+\delta) = e_2(t), e_3(t+\delta) = e_3(t) \}$ with

$$\|z(t)\| = \max\left\{ \sup_{t \in [0, \delta]} e_1(t), \sup_{t \in [0, \delta]} e_2(t), \sup_{t \in [0, \delta]} e_3(t) \right\},$$

where

$$I = [0, \infty), I_0 = [0, \delta], I_k = (k\delta, (k+1)\delta), k = 1, 2, \ldots, $$

and $PC[I, R] = \{ e_1 : I \to R \mid e_1$ is continuous at $t \neq k\delta, e_1(k\delta^-)$ and $e_1(k\delta^+)$ exist, $e_1(k\delta) = e_1(k\delta^-), k = 1, 2, \ldots \}.$

We would introduce another lemma before the proof of Theorem 3.3.

**Lemma 3.5:** Suppose $B \subset PC[I, R]$, the necessary-sufficient condition for $B$ being relatively compact is that all functions in $B$ are uniformly bounded and equicontinuous in each $I_k(k = 1, 2, \ldots)$.

We now present the proof of Theorem 3.3.

**Proof:** To apply Lemma 3.4, we define a subset $\tilde{D} \subseteq X$ as

$$\tilde{D} = \{(e_1, e_2, e_3) \in X : K_1 \leq e_1(t) \leq K_2, \quad x_1 \leq e_2(t) \leq x_2, \quad y_1 \leq e_3(t) \leq y_2 \}.$$

One can follow that $\tilde{D}$ is convex, closed and bounded. Define the mapping $T(e_1, e_2, e_3) = (T_1(e_1, e_2, e_3), T_2(e_1, e_2, e_3), T_3(e_1, e_2, e_3)) : \tilde{D} \to \tilde{D}$ as

$$T_1(e_1(t), e_2(t), e_3(t)) = \frac{\sigma e^{\int_{t}^{k\delta} (f_1(e_2(\theta))) + d_2k d\theta}}{e^{\int_{0}^{k\delta} (f_1(e_2(\theta))) + d_2k d\theta} - 1}, \quad t < k\delta \leq t + \delta, k \in Z^+,$$

$$T_2(e_1(t), e_2(t), e_3(t)) = \int_{t}^{t+\delta} \frac{e^{\int_{s}^{(s+\tau_1)} (f_2(e_3(\theta))) + d_3 s d\theta} B_1 f_1(e_2(s-\tau_1)) e_1(s-\tau_1) e^{-d_1 \tau_1}}{e^{\int_{0}^{(s+\tau_1)} (f_2(e_3(\theta))) + d_3 s d\theta} - 1} ds,$$

and

$$T_3(e_1(t), e_2(t), e_3(t)) = \int_{t}^{t+\delta} e^{\int_{s}^{(s-\tau_2)} e_3(s-\tau_2) e_2(s-\tau_2) e^{-d_3 \tau_2}} ds.$$
In the following, we prove Theorem 3.3 in two steps. We are going to consider the case of $0 < b \leq 1$ only. The same arguments can be applied to the case of $b > 1$ (i.e. the conditions in Theorem 3.1). Therefore, we omit the case.

Step 1. We show that $T : \tilde{D} \rightarrow \tilde{D}$ is compact and continuous.

According to the definition of $\tilde{D}$, for $(e_1, e_2, e_3) \in \tilde{D}$ and $t < k\delta \leq t + \delta$, we have

$$T_1(e_1, e_2, e_3)(t + \delta) = T_1(e_1, e_2, e_3)(t),$$

$$T_2(e_1, e_2, e_3)(t + \delta) = T_2(e_1, e_2, e_3)(t),$$

$$T_3(e_1, e_2, e_3)(t + \delta) = T_3(e_1, e_2, e_3)(t).$$

Besides, we can also get

$$K_1 = \frac{\sigma}{e^{(f_1(x_2) + d_\delta)\delta}} - 1 \leq T_1(e_1, e_2, e_3)(t) = \frac{\sigma e^{-f_1^{+\delta}(f_1(e_2) + d_\delta)\delta}}{1 - e^{-f_0^{+\delta}(f_1(e_2) + d_\delta)\delta}},$$

$$T_2(e_1, e_2, e_3)(t) \leq \int_t^{t+\delta} e^{-f_1^{+\delta}(f_1(e_2) + d_\delta)\delta} B_1 f_1(x_2) K_2 e^{-d_1 \tau_1} \, ds,$$

$$K_2 B_1 e^{-d_1 \tau_1} \frac{1}{d_2} f_1(x_2) = \frac{K_2 B_1 e^{-d_1 \tau_1}}{d_2} \frac{x_2}{(1 + \lambda_1 x_2)^b},$$

$$x_2 \left( \text{Remark: } x_2 = \frac{1}{\lambda_1} \left( \left( \frac{K B_1 e^{-d_1 \tau_1}}{d_2} \right)^{1/b} - 1 \right) \right),$$

$$\text{(21) }$$

$$\text{(22) }$$

$$\text{(23) }$$

$$\text{(24) }$$
\[ T_2(e_1, e_2, e_3)(t) \geq \int_t^{t+\delta} \frac{e^{-(d_2+f_2(y_2))(t+\delta-s)}}{1 - e^{-(d_2+f_2(y_2))\delta}} \, dB_1 f_1(x_1) K_1 e^{-d_1 \tau_1} \]
\[ = \frac{K_1 B_1 e^{-d_1 \tau_1} f_1(x_1)}{d_2 + f_2(y_2)} = \frac{K_1 r B_1 e^{-d_1 \tau_1}}{d_2 + f_2(y_2)} \left(1 + \lambda_1 x_1\right)^\bar{b} \]
\[ = x_1 \quad \text{(Remark: } x_1 = \frac{1}{\lambda_1} \left(\frac{K r B_1 e^{-d_1 \tau_1}}{d_2 + f_2(y_2)}\right)^\bar{b} - 1)\), \quad (25) \]

\[ T_3(e_1, e_2, e_3)(t) \leq \int_t^{t+\delta} \frac{e^{d_4(s-t)}}{e^{d_4 \delta} - 1} \, dB_2 f_2(y_2) x_2 e^{-d_3 \tau_2} \]
\[ = \frac{B_2 x_2 e^{-d_3 \tau_2} f_2(y_2)}{d_4} \]
\[ = y_2 \quad \text{(Remark: } B_2 x_2 e^{-d_3 \tau_2} f_2(y_2) = d_4 y_2), \quad (26) \]

\[ T_3(e_1, e_2, e_3)(t) \geq \int_t^{t+\delta} \frac{e^{d_4(s-t)}}{e^{d_4 \delta} - 1} \, ds \frac{\lambda_2 a}{\lambda_2 a + y_1} B_2 x_1 e^{-d_3 \tau_2} \]
\[ = y_1 \frac{a B_2 x_1 e^{-d_3 \tau_2}}{d_4} \frac{1}{1 + \frac{a}{\lambda_2 y_1}} \]
\[ = y_1 \quad \text{(Remark: } \ln(1 + x) \geq \frac{x}{1 + x})\), \quad (27) \]

thus we have \( T(\tilde{D}) \subseteq \tilde{D} \).

Obviously, \( T \) is a continuous map, and in the following we further prove its compactness.

In fact, assume \( B \subseteq \tilde{D} \), according to Lemma 3.5 we only need to prove that functions in \( T(B) \) are uniformly bounded and \( \text{equicontinuous} \) in each \( I_k(k = 1, 2, \ldots) \).

For each \( (e_1(t), e_2(t), e_3(t)) \in B \) and \( t \in I_k(k = 1, 2, \ldots) \), we know

\[ \|T(e_1(t), e_2(t), e_3(t))\| = \max \sup_{t \in [0,\delta]} T_1(e_1(t), e_2(t), e_3(t)), \]
\[ \sup_{t \in [0,\delta]} T_2(e_1(t), e_2(t), e_3(t)), \sup_{t \in [0,\delta]} T_3(e_1(t), e_2(t), e_3(t))\]
\[ \leq \max\{K_2, x_2, y_2\}, \quad (28) \]

so all functions in \( T(B) \) are uniformly bounded.

Besides, according to the definition of \( T \), we know that the derivative functions of \( T_i(e_1, e_2, e_3)(t), i = 1, 2, 3, \) are also uniformly bounded. Hence all functions in \( T(B) \) are \( \text{equicontinuous} \) in \( I_k \).

From the above discussion, it follows that \( T \) is compact by Lemma 3.5, and it has a fixed point in \( \tilde{D} \) by Lemma 3.4.

Step 2. We will show that if \( (e_1, e_2, e_3) \) is a fixed point of \( T \) in \( \tilde{D} \), then \( (e_1, e_2, e_3) \) is a positive periodic solution of system (1).
In fact, if \((e_1, e_2, e_3) \in \tilde{D}\) and \(T_1(e_1, e_2, e_3) = e_1, T_2(e_1, e_2, e_3) = e_2, T_3(e_1, e_2, e_3) = e_3\), then for \(t < k\delta \leq t + \delta, k = 1, 2, \ldots\), we have

\[
e'_1(t) = \frac{d}{dt} \left( \frac{\sigma e^\int_{t}^{k\delta} (f_1(e_2(t)) + d_K) d\theta}{e^\int_{0}^{\delta} (f_1(e_2(t)) + d_K) d\theta - 1} \right) = \sigma e^\int_{t}^{k\delta} (f_1(e_2(t)) + d_K) d\theta \left( \frac{e^\int_{0}^{\delta} (f_1(e_2(t)) + d_K) d\theta - 1}{e^\int_{0}^{\delta} (f_1(e_2(t)) + d_K) d\theta - 1} \right) \left( -f_1(e_2(t)) - d_K \right)
\]

\[
= T_1(e_1, e_2, e_3)(t)(-f_1(e_2(t)) - d_K) = -f_1(e_2(t))e_1(t) - d_K e_1(t).
\]

(29)

Besides, for \(t < k\delta\) and \(t \to k\delta^–\), we have

\[
e_1(k\delta) = \lim_{t \to k\delta^–} e_1(t) = \lim_{t \to k\delta^–} T_1(e_1, e_2, e_3)(t) = \frac{\sigma}{e^\int_{0}^{\delta} (f_1(e_2(t)) + d_K) d\theta - 1},
\]

and for \(k\delta < t < (k + 1)\delta\), we have

\[
e_1(k\delta^+) = \lim_{t \to k\delta^+} e_1(t) = \lim_{t \to k\delta^+} T_1(e_1, e_2, e_3)(t) = \frac{\sigma e^\int_{t}^{(k+1)\delta} (f_1(e_2(\theta)) + d_K) d\theta}{e^\int_{0}^{\delta} (f_1(e_2(\theta)) + d_K) d\theta - 1} = e_1(k\delta) + \sigma.
\]

(30)

Furthermore,

\[
e'_2(t) = \frac{d}{dt} \int_{t}^{t+\delta} \frac{\sigma e^\int_{t}^{(f_2(e_3(\theta)) + d_2) d\theta} B_1f_1(e_2(s - \tau_1))e_1(s - \tau_1)e^{-d_1\tau_1}}{e^\int_{0}^{\delta} (f_2(e_3(\theta)) + d_2) d\theta - 1} ds
\]

\[
= \frac{e^\int_{t}^{(f_2(e_3(\theta)) + d_2) d\theta} B_1f_1(e_2(t + \delta - \tau_1))e_1(t + \delta - \tau_1)e^{-d_1\tau_1}}{e^\int_{0}^{\delta} (f_2(e_3(\theta)) + d_2) d\theta - 1} - \frac{B_1f_1(e_2(t - \tau_1))e_1(t - \tau_1)e^{-d_1\tau_1}}{e^\int_{0}^{\delta} (f_2(e_3(\theta)) + d_2) d\theta - 1}
\]

\[
= (f_2(e_3(t)) + d_2) \int_{t}^{t+\delta} \frac{\sigma e^\int_{t}^{(f_2(e_3(\theta)) + d_2) d\theta} B_1f_1(e_2(s - \tau_1))e_1(s - \tau_1)e^{-d_1\tau_1}}{e^\int_{0}^{\delta} (f_2(e_3(\theta)) + d_2) d\theta - 1} ds
\]

\[
= B_1f_1(e_2(t - \tau_1))e_1(t - \tau_1)e^{-d_1\tau_1} - (f_2(e_3(t)) + d_2) T_2(e_1, e_2, e_3)(t)
\]

\[
= B_1f_1(e_2(t - \tau_1))e_1(t - \tau_1)e^{-d_1\tau_1} - d_2 e_2(t) - f_2(e_3(t))e_2(t)
\]

(31)
and
\[
e'_3(t) = \frac{d}{dt} \int_t^{t+\delta} \frac{e^{d_4(s-t)} B_2 f_2(e_3(s - \tau_2)) e_2(s - \tau_2) e^{-d_3 \tau_2}}{e^{d_4 \delta} - 1} \, ds
\]
\[
= \frac{e^{d_4 \delta} B_2 f_2(e_3(t + \delta - \tau_2)) e_2(t + \delta - \tau_2) e^{-d_3 \tau_2}}{e^{d_4 \delta} - 1} - \frac{B_2 f_2(e_3(t - \tau_2)) e_2(t - \tau_2) e^{-d_3 \tau_2}}{e^{d_4 \delta} - 1}
\]
\[
- d_4 \int_t^{t+\delta} \frac{e^{d_4(s-t)} B_2 f_2(e_3(s - \tau_2)) e_2(s - \tau_2) e^{-d_3 \tau_2}}{e^{d_4 \delta} - 1} \, ds
\]
\[
= B_2 f_2(e_3(t - \tau_2)) e_2(t - \tau_2) e^{-d_3 \tau_2} - d_4 T_3(e_1, e_2, e_3)(t)
\]
\[
= B_2 f_2(e_3(t - \tau_2)) e_2(t - \tau_2) e^{-d_3 \tau_2} - d_4 e_3(t).
\] (32)

Hence, \((e_1, e_2, e_3)\) represents a positive periodic solution of the system (1).

Therefore, the operator \(T\) has a fixed point in \(\bar{D}\) which is also a positive periodic solution of system (1) with period \(\delta\). The proof is completed. ■

### 3.4. Existence of a parasitoid-extinction periodic solution

We now analyse the existence of a parasitoid-extinction periodic solution to the system (1). This is motivated by the fact that \(y^s = 0\) is an equilibrium solution for variable \(y(t)\). In this situation, the system (1) is reduced into

\[
\begin{aligned}
\frac{dK(t)}{dt} &= - \frac{rx(t)K(t)}{(1 + \lambda_1 x(t))^b} - d_k K(t),
\frac{dx_1(t)}{dt} &= \frac{r B_1 x(t) K(t)}{(1 + \lambda_1 x(t))^b} - d_1 x_1(t) - \frac{r B_1 x(t - \tau_1) K(t - \tau_1) e^{-d_1 \tau_1}}{(1 + \lambda_1 x(t - \tau_1))^b}, \\
\frac{dx(t)}{dt} &= \frac{r B_1 x(t - \tau_1) K(t - \tau_1) e^{-d_1 \tau_1}}{(1 + \lambda_1 x(t - \tau_1))^b} - d_2 x(t),
\end{aligned}
\] (33)

with initial condition \(K(t) = K_0 > 0, x_1(t) = 0, x(t) = x_0 \geq 0, t \in [-\tau_1, 0]\). We will show that the parasitoid-extinction system (33) also has a positive periodic solution with period \(\delta\).

Because \(x_1(t)\) is totally determined by \(x(t)\) and \(K(t)\), we only need to show that there exists a solution whose components \(K(t), x(t)\) are periodic with period \(\delta\). We will prove this by another fixed point theorem – Krasnoselskii’s Fixed Point Theorem. We omit notations and definitions about this fixed point theorem, and interested readers can refer to [28,41].

**Theorem 3.4:** If \(b \geq 1\) and \(r_0 B_1 e^{-d_1 \tau_1} \delta / 1 - e^{-d_2 \delta} \leq \sigma / 1 - e^{-d_k \delta}\), then the system (1) must have a parasitoid-extinction periodic solution, i.e. the system (33) must have a positive periodic solution.
**Proof:** Let Banach space $X_1 = \{z(t) = (e_1(t), e_2(t)) | e_1(t) \in (PC[I, R] \cap C^1[I \setminus \{\delta, 2\delta, \ldots, k\delta, \ldots\}, R]), e_2(t) \in C[R, R], e_1(t + \delta) = e_1(t), e_2(t + \delta) = e_2(t)\}$ equipped with the norm

$$
\|z(t)\| = \max\{\sup_{t \in [0, \delta]} |e_1(t)|, \sup_{t \in [0, \delta]} |e_2(t)|\}.
$$

Define the cone $G$ of $X_1$ as

$$
G = \left\{(e_1, e_2) \in X_1 : e_1(t) \geq \frac{C_1}{C_2} \sup_{t \in [0, \delta]} |e_1(t)|, \quad e_2(t) \geq \frac{C_3}{C_4} \sup_{t \in [0, \delta]} |e_2(t)| \right\},
$$

where

$$
C_1 = \frac{1}{e^{(r_0 + dK)\delta} - 1} > 0, \quad C_2 = \frac{1}{1 - e^{-dK\delta}} > 0,
$$

$$
C_3 = \frac{1}{e^{d_2\delta} - 1} > 0, \quad C_4 = \frac{e^{d_2\delta}}{e^{d_2\delta} - 1} > 0.
$$

One can follow that $C_1 < C_2$ and $C_3 < C_4$. Let $r_1 = C_1\tau$ and $r_2 = C_2\tau$, and define two open sets $\Omega_{r_1}$ and $\Omega_{r_2}$ as

$$
\Omega_{r_1} = \{(e_1, e_2) \in X_1 : \|e_1, e_2\| < r_1\}
$$

and

$$
\Omega_{r_2} = \{(e_1, e_2) \in X_1 : \|e_1, e_2\| < r_2\}.
$$

Then

$$
\partial \Omega_{r_i} = \{(e_1, e_2) \in X_1 : \|e_1, e_2\| = r_i, i = 1, 2,
$$

$$
G \cap (\overline{\Omega_2 \setminus \Omega_1}) = \{(e_1, e_2) \in X_1 : r_1 \leq \|e_1, e_2\| \leq r_2\}.
$$

Define the map $T(e_1, e_2) = (T_1(e_1, e_2), T_2(e_1, e_2)) : G \cap (\overline{\Omega_2 \setminus \Omega_1}) \to X_1$ by

$$
T_1(e_1(t), e_2(t)) = \frac{\sigma e^{\int_{t}^{t+\delta} (f_1(e_2(\theta)) + dK) d\theta}}{e^{\int_{t}^{t+\delta} (f_1(e_2(\theta)) + dK) d\theta} - 1}, \quad t < k\delta \leq t + \delta, k \in Z^+,
$$

$$
T_2(e_1(t), e_2(t)) = \int_{t}^{t+\delta} \frac{e^{d_2(s-t)} B_1 f_1(e_2(s - \tau_1)) e_1(s - \tau_1) e^{-d_1 \tau_1}}{e^{d_2\delta} - 1} ds.
$$

In the following, we will prove Theorem 3.4 in three steps.

Step 1. We want to show that $T : G \cap (\overline{\Omega_2 \setminus \Omega_1}) \to X_1$ is compact and continuous.
According to the definition of $G$, for $(e_1, e_2) \in G$ and $t < k\delta \leq t + \delta$, we have

$$T_1(e_1, e_2)(t + \delta) = \frac{\sigma e^{\int_{t+\delta}^{(k+1)\delta} (f_1(e_2(\theta)) + d_k) d\theta}}{e^{\int_{t}^{\delta} (f_1(e_2(\theta)) + d_k) d\theta} - 1} = T_1(e_1, e_2)(t),$$

$$T_2(e_1, e_2)(t + \delta) = \int_{t+\delta}^{t+2\delta} \frac{e^{d_2(s-t-\delta)} B_1 f_1(e_2(s - \tau_1)) e_1(s - \tau_1) e^{-d_1 t_1}}{e^{d_2\delta} - 1} ds$$

$$= \int_{t}^{t+\delta} \frac{e^{d_2(\rho-t)} B_1 f_1(e_2(\rho + \delta - \tau_1)) e_1(\rho + \delta - \tau_1) e^{-d_1 t_1}}{e^{d_2\delta} - 1} d\rho$$

$$= T_2(e_1, e_2)(t). \quad (34)$$

Besides, for each $(e_1, e_2) \in G \cap (\overline{\Omega_2} \setminus \Omega_1)$ and $t < k\delta \leq t + \delta$,

$$T_1(e_1, e_2)(t) \geq C_1 \sigma = \frac{C_1}{C_2} C_2 \sigma \geq \frac{C_1}{C_2} \sup_{t \in [0, \delta]} |T_1(e_1, e_2)(t)|,$$

$$T_2(e_1, e_2)(t) \geq C_3 \int_{t}^{t+\delta} [B_1 f_1(e_2(s - \tau_1)) e_1(s - \tau_1) e^{-d_1 t_1}] ds$$

$$= \frac{C_3}{C_4} C_4 \int_{t}^{t+\delta} B_1 f_1(e_2(s - \tau_1)) e_1(s - \tau_1) e^{-d_1 t_1} ds$$

$$\geq \frac{C_3}{C_4} \sup_{t \in [0, \delta]} |T_2(e_1, e_2)(t)|. \quad (35)$$

Thus $T(G \cap (\overline{\Omega_2} \setminus \Omega_1)) \subset G$.

One can see that $T$ is continuous. It is compact too. Indeed, consider a bounded subset $B$ in $G \cap (\overline{\Omega_2} \setminus \Omega_1)$. We can show that all component functions of $T(B)$ are uniformly bounded and equicontinuous in each $I_k (k = 1, 2, \ldots)$.

For any $(e_1(t), e_2(t)) \in B$ and $t < k\delta \leq t + \delta$, we know

$$\|T(e_1(t), e_2(t))\| = \max \left[ \sup_{t \in [0, \delta]} |T_1(e_1(t), e_2(t))|, \sup_{t \in [0, \delta]} |T_2(e_1(t), e_2(t))| \right].$$

Besides, from

$$T_1(e_1(t), e_2(t)) \leq C_2 \sigma$$

and

$$T_2(e_1(t), e_2(t)) \leq C_4 \int_{t}^{t+\delta} B_1 f_1(e_2(s - \tau_1)) e_1(s - \tau_1) e^{-d_1 t_1} ds$$

$$\leq C_4 r_0 B_1 \delta e^{-d_1 t_1}, \quad (36)$$

we can get

$$\|T(e_1(t), e_2(t))\| \leq \max \{ C_2 \sigma, C_4 r_0 B_1 \delta e^{-d_1 t_1} \},$$

hence all component functions of $T(B)$ are uniformly bounded.
By similar discussion in Theorem 3.3, we can obtain that all functions in $T(B)$ are equicontinuous in each $I_k$ and then the operator $T$ is compact by Lemma 3.5.

Step 2. We show that if $(e_1, e_2)$ is a fixed point of $T$ in $G$, then $(e_1, e_2)$ is a positive periodic solution of systems (33).

In fact, if $(e_1, e_2) ∈ G ∩ (\bar{\Omega}_2 \setminus \Omega_1)$ and $T_1(e_1, e_2) = e_1$, $T_2(e_1, e_2) = e_2$, then for $t < k\delta ≤ t + \delta, k = 1, 2, \ldots$, similar to the discussion in Theorem 3.3, we have

$$e'_1(t) = -f_1(e_2(t))e_1(t) - d_Ke_1(t)$$

and

$$e_1(k\delta) = \lim_{t \to k\delta^-} e_1(t) = e_1(k\delta^+) - \sigma.$$  

Furthermore,

$$e'_2(t) = \frac{d}{dt} \int_t^{t+\delta} e^{d_2(s-t)}B_1 f_1(e_2(s - \tau_1))e_1(s - \tau_1)e^{-d_1\tau_1} e^{d_2\delta} - 1 ds$$

$$= \frac{e^{d_2\delta}B_1 f_1(e_2(t - \tau_1))e_1(t - \tau_1)e^{-d_1\tau_1} e^{d_2\delta} - 1}{e^{d_2\delta} - 1} - \frac{B_1 f_1(e_2(t - \tau_1))e_1(t - \tau_1)e^{-d_1\tau_1}}{e^{d_2\delta} - 1}$$

$$- d_2 \int_t^{t+\delta} e^{d_2(s-t)}B_1 f_1(e_2(s - \tau_1))e_1(s - \tau_1)e^{-d_1\tau_1} e^{d_2\delta} - 1 ds$$

$$= B_1 f_1(e_2(t - \tau_1))e_1(t - \tau_1)e^{-d_1\tau_1} - d_2 e_2(t), \quad (37)$$

then $(e_1, e_2)$ is a positive periodic solution of system (33).

Step 3. We show that system (33) has a periodic solution.

For $(e_1, e_2) ∈ \partial \Omega_1$, we have $\|(e_1, e_2)\| = r_1$, and $T_1(e_1, e_2) ≥ C_1\sigma = r_1$, thus

$$\|T(e_1, e_2)\| ≥ r_1.$$  

For $(e_1, e_2) ∈ \partial \Omega_2$, we have $\|(e_1, e_2)\| = r_2$, $T_1(e_1, e_2) ≤ C_2\sigma = r_2$ and

$$T_2(e_1, e_2) ≤ C_4 \int_t^{t+\delta} B_1 f_1(e_2(s - \tau_1))e_1(s - \tau_1)e^{-d_1\tau_1} ds ≤ C_4 r_0 B_1 \delta e^{-d_1\tau_1}.$$  

From Krasnoselskii’s Fixed Point Theorem, it follows that if $C_4 r_0 B_1 \delta e^{-d_1\tau_1} < r_2$, then $\|T(e_1, e_2)\| ≤ r_2$ and $T$ has a fixed point in $G ∩ (\bar{\Omega}_2 \setminus \Omega_1)$. That is, the system (33) has a positive periodic solution with period $\delta$, which ends the proof.

4. Numerical simulation

In Section 4, we present some numerical results to explore factors that affect host–parasitoid interacting dynamics. Two example simulations are given first to demonstrate our results in Section 3. In these examples, we carefully select parameter values to illustrate our analytic results and to show the dynamical complexity of the models formulated in this paper.

Just as [17,19,39] suggested, $r$ is the per capita net daily growth rate of host, the scaling parameter $\lambda_1$ determines the amplitude of the equilibrium of the adult host and $b$ is
a constant that measures the severity of density dependence. Constant $a$ is the per capita searching efficiency of the parasitoid and constant $\lambda_2$ is a measure of the degree of contagion in the distribution of parasitism among host individuals. $B_1$ and $B_2$ are constants that represent the convert rates. We observe the host and parasitoid populations every day, so we choose the unit of the metabolic rate or the natural mortality rate $d_i, i = K, 1, 2, 3, 4$ as day$^{-1}$. The maturation delay $\tau_1, \tau_2$ and release period $\delta$ are in days, and we release $\sigma$ grams resource every $\delta$ days.

**Example 4.1:** For given parameters

\[
\begin{align*}
    b &= 1, \quad r = 1, \quad \lambda_1 = 2, \quad \lambda_2 = 0.2, \quad B_1 = 0.95, \quad B_2 = 0.95, \\
    d_K &= 0.1, \quad d_1 = 0.6, \quad d_2 = 0.2, \quad d_3 = 0.4, \quad d_4 = 0.01, \quad \tau_1 = 1, \\
    \tau_2 &= 2, \quad a = 0.4, \quad \sigma = 4, \quad \delta = 1,
\end{align*}
\]

(38)

simple calculation shows that

\[
K_1 r B_1 e^{-d_1 \tau_1} = 2.5626, \quad f_2(y_2) = 1.8065, \quad a B_2 x_1 e^{-d_3 \tau_2} = 0.0237.
\]

Therefore, $K_1 r B_1 e^{-d_1 \tau_1} > d_2 + f_2(y_2)$ and $a B_2 x_1 e^{-d_3 \tau_2} > d_4$.

According to Theorem 3.1 and Theorem 3.3, system (1) is permanent and a positive periodic solution exists. See Figure 1 for the periodic solution.

**Example 4.2:** Given parameter values

\[
\begin{align*}
    b &= 2, \quad r = 1, \quad \lambda_1 = 2, \quad \lambda_2 = 0.2, \quad B_1 = 0.95, \quad B_2 = 0.95, \\
    d_K &= 0.1, \quad d_1 = 0.6, \quad d_2 = 0.5, \quad d_3 = 0.4, \quad d_4 = 0.01, \quad \tau_1 = 1, \\
    \tau_2 &= 2, \quad a = 0.4, \quad \sigma = 4, \quad \delta = 1,
\end{align*}
\]

(39)

**Figure 1.** System (1) is permanent and admits a positive periodic solution when $b \leq 1$. Parameter values are in (38).
calculations yield

\[ \tilde{K}_1 r B_1 e^{-d_1 \tau_1} = 4.1330, \quad f_2(\tilde{y}_2) = 1.0158, \]
\[ a B_2 \tilde{x}_1 e^{-d_3 \tau_2} = 0.0679, \quad \tilde{K}_2 r B_1 e^{-d_1 \tau_1} \left( \frac{2}{b-1} \right)^{b+1} = 0.4057. \]

Then \( \tilde{K}_1 r B_1 e^{-d_1 \tau_1} > d_2 + f_2(\tilde{y}_2), \quad a B_2 \tilde{x}_1 e^{-d_3 \tau_2} > d_4 \) and \( d_2 > \tilde{K}_2 r B_1 e^{-d_1 \tau_1} / (1 + 2/(b-1))^{b+1}. \)

By Theorem 3.2 and Theorem 3.3, the system (1) is also permanent and has a positive periodic solution. The positive periodic solution is demonstrated in Figure 2.

From Figures 1 and 2, one can notice that with periodic impulsive resource inputs, the quantity of the resource \( K \) and mature host population \( x \) are stabilized at oscillatory homeostasis almost simultaneously while the parasitoid population takes much longer time to achieve stability. This demonstrates that in the laboratory environment, the oscillatory homeostasis makes the parasitoid population take more time to reach steady state.

We also studied the impacts of maturation times \( \tau_1 \) and \( \tau_2 \) on the population dynamics. Numerical simulations show that shorter host maturation time \( \tau_1 \) leads to shorter generation periods and higher reproductive capacity for the host, which in return promotes the development of the parasitoid for adequate parasitism chance. Figure 3 demonstrates that smaller \( \tau_1 \) yields higher host population density and parasitoid abundance. Shorter maturation time \( \tau_2 \) for the parasitoid accelerates its population growth while having little impact on the host population. The impacts are illustrated in Figure 4. From both Figures 3 and 4, we can see that longer maturation times (either the host or the parasitoid’s maturation time) result in the decline of parasitoid population.

From Figures 1 and 4, we see that under periodic impulsive resource delivery, the host and parasitoid population present very small oscillation amplitudes when they reach steady state, although they have different average levels due to different resource input and maturation delays.

Figure 2. System (1) is permanent and admits a positive periodic solution when \( b > 1 \). See (39) for parameter values.
Figure 3. Profiles produced by Model (1) for various host maturation time \( \tau_1 \). Other parameter values are given in (39).

Figure 4. Profiles produced by model (1) for various parasitoid maturation time \( \tau_2 \). Except \( \tau_2 \), parameters take the same values as in Figure 3.

Figure 5. Profiles produced by model (1) for various resource inputs. Parameters take the same values as in Figure 4 except \( \delta \) and \( \sigma \).
We also numerically investigate the resource administration strategy. We fix a total input of resource and apply three different delivery frequencies and single input amount. In Figure 5, we set delivery frequency $\delta = 2, 3, 4$ and the corresponding input amount $\sigma = 2, 3, 4$. We compare the profiles and find that impulsive inputs with longer periods and larger input amounts make the host population oscillate with larger amplitudes while having little impact on the parasitoid abundance. From our calculations, we also notice that although the host population exhibits different oscillation amplitudes, the average levels are almost the same.

5. Discussion

In this paper, we proposed a mathematical model to study the impacts of periodic impulsive resource inputs on insect host–parasitoid interactions in laboratory environment. As far as we know, there is little work that formulates a population model consisting of impulsive differential equations to study the impacts. This approach allows us to model resource delivery as periodic pulses. For the model, we built a theoretical framework to gain insights into the dynamics of host–parasitoid interactions with external resource input.

The analytical study of the model (1) shows that the insect host and its parasitoid can coexist provided that some conditions are satisfied (see Theorem 3.1 and 3.2). In the case of coexistence, system (1) also admits a positive periodic solution (refer to Theorem 3.3). Besides, we studied the system with hosts only and obtained the existence of a parasitoid-extinction periodic solution (see Theorem 3.4).

Our numerical study on host resource input reveals that smaller amount of inputs with a shorter period of impulsive input leads to smaller oscillation magnitude in host abundance. However, the resource delivery strategy has little impact on the development of parasitoid population. The numerical simulations also show that larger maturation times, either the host’s or the parasitoid’s, result in population decline of the parasitoid while larger parasitoid’s maturation time can accelerate the host’s population growth. According to the model profiles produced in the simulations, we also found that the periodic impulsive resource delivery just caused very small oscillation amplitudes of the two species when they reached steady state. Our best guess is that the density dependent form $rx(t)K(t)/(1 + \lambda x(t))y$ and the negative binomial distribution weaken effects of impulsive resource on host and parasitoid populations.

For system (1), we discussed the permanence and existence of periodic solutions. Numerical simulations implied the stability of the solutions. However, we did not analytically prove the stability and will continue this work in a future study.

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