Modeling insect growth regulators for pest management

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Abstract

Insect growth regulators (IGRs) have been developed as effective control measures against harmful insect pests to disrupt their normal development. This study is to propose a mathematical model to evaluate the cost-effectiveness of IGRs for pest management. The key features of the model include the temperature-dependent growth of insects and realistic impulsive IGRs releasing strategies. The impulsive releases are carefully modeled by counting the number of implements during an insect's temperature-dependent development duration, which introduces a surviving probability determined by a product of terms corresponding to each release. Dynamical behavior of the model is illustrated through dynamical system analysis and a threshold-type result is established in terms of the net reproduction number. Further numerical simulations are performed to quantitatively evaluate the effectiveness of IGRs to control populations of harmful insect pests. It is interesting to observe that the time-changing environment plays an important role in determining an optimal pest control scheme with appropriate release frequencies and time instants.

Keywords: Insect growth regulators; delay differential equation; net reproduction number; pest control

1 Introduction

Control measures in the integrated pest management (IPM) program against a specific pest insect should be efficient against pests, but also have a low toxicity to biological control organisms [7]. In this context, insect growth regulators (IGRs), a type of insecticides, have been developed to inhibit metamorphosis and consequently insect proliferation. They have some advantages over conventional ones, such as their relatively low toxicity to beneficial insects, and greater specificity for some target insect species. For example, pyriproxyfen, an insect growth regulator, has been recommended for vector control by The World Health Organization due to its safety in humans and effectiveness at extremely low concentrations [28]. They may be applied in drinking-water sources and containers [28], as well as bednets [26]. IGRs have shown promising results on controlling pests such as mosquitoes [26], two stored-product pests in wheat and maize [17], predators [7] and other insect pests [7].

It becomes interesting and important to evaluate IGRs' effectiveness as potential integrated pest management (IPM) components through mechanistic models. There have been extensive studies on the population growth models with integrated pest management, see, e.g., [6, 12, 16, 24] and references therein. An age-structured model was formulated to assess the effectiveness of culling as a tool to eradicate vector-borne diseases, which was further reduced to a system of autonomous delay differential equations with impulses (in the case where the adult vector is subject to culling) or a system of nonautonomous delay differential equations where the time-varying coefficients are determined by the culling times and rates (in the case where only the immature vector is subject to culling) [13]. By careful formulation on the age-structured density evolution and individual movement between patches, a spatial model was derived and analyzed to evaluate the effects of impulsive culling of the immatures and adults in a patchy environment [31]. A two patch model with adult impulsive culling was analyzed in [25] and a pest control population model with threshold policy was proposed and studied in [23].

This manuscript will formulate a model by considering the impulsive releases of IGRs in a population growth model. The growth of insect species is assumed to be affected by environmental conditions, such as temperature and humidity level. As a reasonable approximation to the situation that the dominating environmental conditions vary in a periodic pattern, such as seasonal or day-night cycles, the population growth model includes periodic parameters. Due to the mode of IGRs actions, the development of an insect in the juvenile stage should be carefully argued when impulsive releases of IGRs are considered, which will be presented in Section 2. It turns out the model takes a novel framework of impulsive differential equations with periodic delay. To our knowledge, this is the first mathematical model to assess the effectiveness of IGRs on pest control, in particular, when the pest population is regulated by time-varying environmental conditions. Theoretical analysis and numerical simulations will be presented in Sections 3 and 4, respectively.

2 Model formulation with impulsive IGR releases

Considering that the insect growth regulators target directly at the larval stage, the population is stratified into two different age stages: larval $L(t)$ and adult $A(t)$ stages. In order to distinguish the effect of IGR on population growth, individuals in each stage are further divided into three classes: (i) Unregulated class with subscript U; (ii) Individuals surviving in the IGR-treated environment but can still develop to adults and reproduce (IGR-treated class with subscript T), possibly with a reduced capability in reproduction; and (iii) Individuals subject to strong growth regulation and can not reproduce (the removed class). Since IGR-removed immatures can not reproduce, there is no need to consider this removed class in modeling the reproduction cycle. Considering the fact that the efficacy of IGR is not 100% in regulating the development of larvae in the treated environment, it is essential to consider the individuals in class T. On the other hand, it is biologically observed that individuals in different classes T and U share different demographic characteristics in fecundity (birth rates), mortality (death rates) and development (maturation duration) [7, 17]. The model variables are represented in the flow diagram 1.

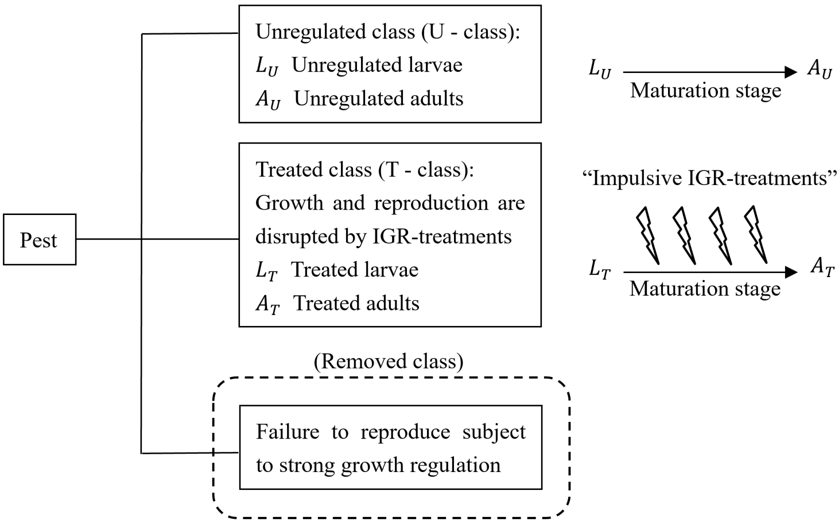


Fig. 1 Flow diagram.

To quantify the population sizes in the IGR-treated class T and IGR-unregulated class U, we introduce variables $\rho_i(t, a)$ (with $i \in \{T, U\}$) to denote the population density of individuals at age a and time t. Then the population sizes in the larval stage $L(t)$ and adult stage $A(t)$ can be represented as cumulative individuals with ages less than, and greater than, some threshold age τ (the development time for the cohort that matures at time t), respectively. Considering that the development time needed for immature individuals is sensitive to the time-varying ambient environment conditions, we assume the threshold age is dependent on time t and denote it as $\tau(t)$. To incorporate possible effect of IGRs on extending the developmental durations, the threshold ages $\tau_T(t)$ and $\tau_U(t)$ for different classes are introduced. In other words, the development stages are stratified by the time-dependent threshold ages $\tau_i(t)$, which measure the maturation time for a larval individual that matures at time t for different classes ($i \in \{T, U\}$). Hence, we have the following identities for larval (L_U and L_T) and adult population sizes (A_U and A_T) of different classes:

$$L_i(t) = \int_0^{\tau_i(t)} \rho_i(t,a)\mathrm{d}a \quad \text{and} \quad A_i(t) = \int_{\tau_i(t)}^{\infty} \rho_i(t,a)\mathrm{d}a. \tag{1}$$

We will formulate the mechanistic model for $L_i(t)$ and $A_i(t)$ through those for population densities of $\rho_i(t,a)$.

The density distribution at the boundary $a = 0$ for treated class can be described by

$$\rho_T(t,0) = qB(t, \gamma A_T(t) + A_U(t)),$$

where $B(t,\cdot)$ is the birth function which depends both on time t and weighted adult population size of adults. In this boundary condition, two tuning parameters, q and γ, are incoporated. The parameter $\gamma \in (0,1]$ depicts the potential reduction in fecundity when an individual is exposed to the pesticide. Conversely, the parameter $q \in (0,1)$ signifies the proportion of newly-laid eggs that are likely to be affected by the pesticide. Analogous arguments induce the density distribution at the boundary $a = 0$ for unregulated class

$$\rho_U(t,0) = (1-q)B(t, \gamma A_T(t) + A_U(t)).$$

Before presenting the explicit equations that depict the population growth for each class, we state the following assumptions for our model formulation: (i) We are examining a closed system where insects neither enter nor exit the habitat; (ii) At the beginning, mature insects that belong to the treated and untreated classes exist; (iii) The drug is not vertically transmitted. Instead, it effectively impacts all larvae born in the environment with a proportion of q.

2.1 Number of IGR releases in the maturation window of treated individuals

We first describe the dynamics for the density of IGR treated individuals $\rho_T(t,a)$. We argue that it is important to quantify the number of IGR releases for larval individuals over the time window of length $\tau_T(t)$ during larval development (the time interval $[t - \tau_T(t), t]$). We assume IGR is employed at certain discrete time instants t_j, then the age density of larvae $\rho_T(t,a)$ subject to IGR-treated environment satisfies

$$\frac{\partial \rho_T(t,a)}{\partial t} + \frac{\partial \rho_T(t,a)}{\partial a} = -d_T(t)\rho_T(t,a) - \sum_{j=1}^{\infty} p_j \rho_T(t_j^-, a)\delta(t - t_j), \quad 0 < a < \tau_T(t). \tag{2}$$

In equation (2), $d_T(t)$ is the natural death rate for larvae, δ is the Dirac delta function and $\delta(t - t_j)$ represents the removal of individuals due to IGR-induced disrupted development at time instants t_j, $\rho_T(t_j^-, a)$ is the left-hand limit of $\rho_T(t,a)$ as t goes towards t_j from below, $p_j \in [0,1]$ is the fraction of individuals that are removed at the treatment timing t_j, that is, the survival probability of surviving through IGR release at the time instant t_j is $1-p_j$. Integrating (2) from t_j^- to t_j, we can observe that

$$\rho_T(t_j,a)=(1-p_j)\rho_T(t_j^-,a). \tag{3}$$

We assume the adult individuals are not affected by the use of IGR, and their natural per-capita death rate is a time-dependent function $\mu_T(t)$. Thus, we have

$$\frac{\partial\rho_T}{\partial t}+\frac{\partial\rho_T}{\partial a}=-\mu_T(t)\rho_T, \qquad a>\tau_T(t).$$

Differentiating $A_T(t)$ in (1) and use the above equation, we have

$$\begin{aligned}\frac{\mathrm{d}A_T(t)}{\mathrm{d}t}&=(1-\tau_T'(t))\rho_T(t,\tau_T(t))-\mu_T(t)A_T(t)-\rho_T(t,\infty)\\&=(1-\tau_T'(t))\rho_T(t,\tau_T(t))-\mu_T(t)A_T(t).\end{aligned} \tag{4}$$

Here, $\rho_T(t,\infty)=0$ is assumed as no individual can live forever. It becomes essential to find the expression for $\rho_T(t,\tau_T(t))$ in (4). To do that, we introduce a new variable $V^s(t)=\rho_T(t,t-s)$ with parameter s. By direct calculations, we have

$$\frac{\mathrm{d}V^s(t)}{\mathrm{d}t}=-d_L(t)V^s(t)-\sum_{j=1}^{\infty}p_j\rho_T(t_{j-},t-s)\delta(t-t_j), \quad 0<t-s<\tau_T(t).$$

Solving the above system at the period between culls at times t_{i-1} and t_i, we obtain

$$\rho_T(t_i^-,t_i^--s)=V^s(t_i^-)=\exp\left(-\int_{t_{i-1}}^{t_i^-}d_T(\xi)\mathrm{d}\xi\right)\rho_T(t_{i-1},t_{i-1}-s).$$

Setting $s=t_i-a$ and dropping the superscript $-$ on t_i where unnecessary, together with (3), we have

$$\begin{aligned}\rho_T(t_i^-,a)&=\exp\left(-\int_{t_{i-1}}^{t_i}d_T(\xi)\mathrm{d}\xi\right)\rho_T(t_{i-1},a-(t_i-t_{i-1}))\\&=\exp\left(-\int_{t_{i-1}}^{t_i}d_T(\xi)\mathrm{d}\xi\right)(1-p_i)\rho_T(t_{i-1}^-,a-(t_i-t_{i-1})).\end{aligned} \tag{5}$$

Replacing i by $i-1$ and a by $a-(t_i-t_{i-1})$ in (5), we get

$$\rho_T(t_i^-,a)=\exp\left(-\int_{t_{i-2}}^{t_i}d_T(\xi)\mathrm{d}\xi\right)(1-p_i)(1-p_{i-1})\rho_T(t_{i-2}^-,a-(t_i-t_{i-2})).$$

To accurately account the probability of surviving through all treatments (there may possible be more than one IGR releases during an individual's maturation time interval $[t-\tau_T(t), t]$), we introduce two time-dependent indices to measure the number of treatments during the development interval $[t-\tau_T(t), t]$ as follows:

$$\underline{k}(t) = \min\{j : t_j > t - \tau_T(t)\} \text{ and } \overline{k}(t) = \max\{j : t_j \leq t\}.$$

Please note that these two indices are motivated by the study [13]. Larvae develop during the interval $[t-\tau_T(t), t]$ should survive through j-th treatment, with $j \in [\underline{k}(t), \overline{k}(t)]$. The probability of these treated larvae remaining in T class through IGR treatment is a joint probability:

$$\prod_{j=\underline{k}(t)}^{\overline{k}(t)} (1-p_j).$$

Then for a given t, we have the expression for $\rho_T(t, \tau_T(t))$ on time interval from $t-\tau_T(t)$ to t:

$$\begin{aligned}
&\rho_T(t, \tau_T(t)) \\
&= \exp\left(-\textstyle\int_{t-\tau_T(t)}^{t} d_T(\xi)\mathrm{d}\xi\right) \prod_{j=\underline{k}(t)}^{\overline{k}(t)} (1-p_j)\rho_T(t-\tau_T(t), 0), \\
&= \underbrace{\exp\left(-\int_{t-\tau_T(t)}^{t} d_T(\xi)\mathrm{d}\xi\right)}_{\text{survival through natural death}} \underbrace{\prod_{j=\underline{k}(t)}^{\overline{k}(t)} (1-p_j)}_{\text{remaining in } T \text{ class through IGR}} \underbrace{qf(t-\tau_T(t))}_{\text{birth rate at time } t-\tau_T(t)},
\end{aligned}$$

where $f(t) = B(t, \gamma A_T(t) + A_U(t))$. The above term accounts the density of individuals at time t and age $\tau_T(t)$ by considering the birth of individuals at a previous time instant $t-\tau_T(t)$ and survival probabilities. It immediately follows from (4) that

$$\begin{aligned}
\frac{\mathrm{d}A_T(t)}{\mathrm{d}t} = &\, q(1-\tau_T'(t))f(t-\tau_T(t)) \exp\left(-\textstyle\int_{t-\tau_T(t)}^{t} d_T(\xi)\mathrm{d}\xi\right) \prod_{j=\underline{k}(t)}^{\overline{k}(t)} (1-p_j) \\
&-\mu_T(t)A_T(t).
\end{aligned}$$

2.2 IGR-unregulated individuals

For unregulated individuals, their age density $\rho_U(t,a)$ satisfies the following equation

$$\begin{aligned}
&\frac{\partial \rho_U(t,a)}{\partial t} + \frac{\partial \rho_U(t,a)}{\partial a} = -m(t,a)\rho_U(t,a), \\
&\rho_U(t,0) = (1-q)f(t),
\end{aligned} \tag{6}$$

with the age-dependent death rates

$$m(t,a) = d_U(t) \text{ if } a < \tau_U(t) \quad \text{and} \quad m(t,a) = \mu_U(t) \text{ if } a > \tau_U(t).$$

Taking derivatives of $A_U(t)$, and using (6), we get

$$\frac{\mathrm{d}A_U(t)}{\mathrm{d}t} = (1-\tau_U'(t))\rho_U(t,\tau_U(t)) - \mu_U(t)A_U(t) - \rho_U(t,\infty),$$

where $\rho_U(t,\infty)=0$ as no individual can survive forever. By the technique of integration along characteristics as argued for $\rho_T(t,\tau_T(t))$, we can obtain the expression of $\rho_U(t,\tau_U(t))$ as follows:

$$\rho_U(t,\tau_U(t)) = (1-q)f(t-\tau_U(t))e^{-\int_{t-\tau_U(t)}^{t} d_U(\xi)\,d\xi}.$$

2.3 Model and baseline assumptions

Hence, we arrive at the system:

$$\begin{aligned}\frac{\mathrm{d}A_T(t)}{\mathrm{d}t} &= R_T(t) - \mu_T(t)A_T(t),\\ \frac{\mathrm{d}A_U(t)}{\mathrm{d}t} &= R_U(t) - \mu_U(t)A_U(t),\end{aligned} \tag{7}$$

with following recruitment rates

$$\begin{aligned}&R_T(t) = (1-\tau_T'(t))qf(t-\tau_T(t))e^{-\int_{t-\tau_T(t)}^{t} d_T(\xi)\,d\xi}\prod_{k=\underline{k}(t)}^{\overline{k}(t)}(1-p_k) \quad \text{and}\\ &R_U(t) = (1-\tau_U'(t))(1-q)f(t-\tau_U(t))e^{-\int_{t-\tau_U(t)}^{t} d_U(\xi)\,d\xi}.\end{aligned} \tag{8}$$

Here $f(t)=B(t,\gamma A_T(t)+A_U(t))$, and the terms $1-\tau_i'(t)$, $i\in\{T,U\}$, are involved in the recruitment rates to correct the time-varying development velocity [4, 19]. It can be ecologically argued that $1-\tau_i'(t)>0$ [19].

For the population growth model (7)-(8), we propose the following assumptions:

(H1) The parameters $d_i(t)$, $\mu_i(t)$ and $\tau_i(t)$, $i\in\{T,U\}$, are ω-periodic in time t to reflect the effect of seasonality. Moreover, they are positive and continuous functions.

(H2) $B(\cdot,\cdot)\in C^1(\mathbb{R}\times\mathbb{R}_+,\mathbb{R}_+)$ and $B(t,A)$ is ω-periodic in time t with the following properties:

  (i) $B(t,0)=0$, $\dfrac{\partial B}{\partial A}>0$, $\forall t\in\mathbb{R}$, and $\sup_{A\geq 0,t\in[0,\omega]} B(t,A)=\hat{B}<\infty$.

  (ii) For each $t>0$, $B(t,\cdot)$ is strictly subhomogeneous on $\mathbb{R}_+$, that is, $B(t,\alpha A)>\alpha B(t,A)$, $\forall A>0$ and $\alpha\in(0,1)$.

(H3) For the treatment timing sequence $\{t_j\}_{j=1}^{\infty}$, we assume that the initial IGR treatment is implemented within the first ω-period, denoted as $t_1\in[0,\omega)$. Moreover, suppose there are fixed N releases of IGR within each period ω, and the removal rate p_j and the timing of deployment t_j are both periodic, that is, $p_{j+N}=p_j$ and $t_{j+N}=t_j+\omega$.

Assumptions (H1) and (H3) are natural, which reflect the impact of periodic environmental changes on population dynamics. Moreover, the IGR is released periodically in terms of concentration and timing. Condition (H2) implies the self-regulation in the birth rate. If one considers a bounded and increasing birth rate function $B(t, A) = Ag(t, A)$, then (H2) is satisfied when the density-dependent per-capita birth rate $g(t, A)$ is a strictly decreasing function of A.

Remark 2.1. *Before proceeding to the next section on model analysis, we argue that the term of overall survival probability for larvae subject to IGR treatments, i.e.,* $\prod_{j=\underline{k}(t)}^{\overline{k}(t)}(1-p_j)$, *is a periodic step function with period* ω. *In fact, denote*

$$g(t) = \prod_{j=\underline{k}(t)}^{\overline{k}(t)}(1-p_j), \tag{9}$$

with $\underline{k}(t) = \min\{j : t_j > t - \tau_T(t)\}$ *and* $\overline{k}(t) = \max\{j : t_j \leq t\}$. *It follows from assumption (H3) that*

$$\begin{aligned}\underline{k}(t+\omega) &= \min\{j : t_j > t + \omega - \tau_T(t+\omega)\}\\ &= \min\{j : t_{j+N} > t - \tau_T(t+\omega)\}\\ &= \min\{j : t_{j+N} > t - \tau_T(t)\}\\ &= \min\{j : t_j > t - \tau_T(t)\} + N = \underline{k}(t) + N,\end{aligned}$$

as t_j *is increasing. Similarly, we have*

$$\overline{k}(t+\omega) = \max\{j : t_j \leq t+\omega\} = \max\{j : t_{j+N} \leq t\} = \max\{j : t_j \leq t\} + N = \overline{k}(t) + N.$$

Therefore,

$$\begin{aligned}&g(t+\omega)\\ =&\prod_{j=\underline{k}(t+\omega)}^{\overline{k}(t+\omega)}(1-p_j) = \prod_{j=\underline{k}(t)+N}^{\overline{k}(t)+N}(1-p_j) = \prod_{j=\underline{k}(t)}^{\overline{k}(t)}(1-p_{j+N}) = \prod_{j=\underline{k}(t)}^{\overline{k}(t)}(1-p_j)\\ =&g(t).\end{aligned}$$

This argument, together with other assumptions on periodic parameters in (H1-H3), imply that the model is a periodic system. This observation will be used in Lemma 3.3 later. Meanwhile, we point out that if the parameter q*, which measures the fraction of larvae treated with IGRs, is* ω*-periodic in time* t*, that is,* $q = q(t)$*, all consequent analytical results still hold.*

3 The net reproduction number and population dynamics

In this section, we first show the population growth model (7)-(8) is well-posed mathematically. Let $\hat{\tau} = \max_{t\in[0,\omega]}\{\tau_T(t), \tau_U(t)\}$. Denote $X = C([-\hat{\tau},0],\mathbb{R}^2)$, and $X_+ := C([-\hat{\tau},0],\mathbb{R}^2_+)$. Then (X,X_+) is an ordered Banach space equipped with the maximum norm. For any given continuous function $u : [-\hat{\tau},\varsigma) \to \mathbb{R}^2$ with $\varsigma > 0$, define $u_t \in X$ by

$$u_t(\theta) = u(t+\theta),\ \forall\theta \in [-\hat{\tau},0]$$

for any $t \in [0,\varsigma)$. We rewrite system (7)-(8) into the following integral form:

$$\begin{aligned} u_1(t,\phi) &= e^{-\int_0^t \mu_T(s)ds}\phi_1(0) \\ &\quad + \int_0^t e^{-\int_s^t \mu_T(a)\mathrm{d}a} H_T(s)B(s-\tau_T(s), ru_1(s-\tau_T(s)) + u_2(s-\tau_T(s)))\mathrm{d}s, \\ u_2(t,\phi) &= e^{-\int_0^t \mu_U(s)ds}\phi_2(0) \\ &\quad + \int_0^t e^{-\int_s^t \mu_U(a)\mathrm{d}a} H_U(s)B(s-\tau_U(s), ru_1(s-\tau_U(s)) + u_2(s-\tau_U(s)))\mathrm{d}s, \end{aligned}$$

whose solutions are called mild solutions to system (7)-(8), where

$$\begin{aligned} H_T(t) &= (1-\tau_T'(t))qe^{-\int_{t-\tau_T(t)}^t d_T(\xi)\,d\xi} \prod_{j=\underline{k}(t)}^{\overline{k}(t)} (1-p_j) \quad \text{and} \\ H_U(t) &= (1-\tau_U'(t))(1-q)e^{-\int_{t-\tau_U(t)}^t d_U(\xi)\,d\xi}. \end{aligned} \tag{10}$$

Then we introduce the following definition.

Definition 3.1. *An upper (a lower) solution of system (7)-(8) is a continuous and bounded function $v : [-\hat{\tau},a) \to \mathbb{R}^2_+$ with $a > 0$ satisfying*

$$\begin{aligned} v_1(t) &\geq (\leq)\ e^{-\int_0^t \mu_T(s)ds}v_1(0) \\ &\quad + \int_0^t e^{-\int_s^t \mu_T(a)\mathrm{d}a} H_T(s)B(s-\tau_T(s), rv_1(s-\tau_T(s)) + v_2(s-\tau_T(s)))\mathrm{d}s, \\ v_2(t) &\geq (\leq)\ e^{-\int_0^t \mu_U(s)ds}v_2(0) \\ &\quad + \int_0^t e^{-\int_s^t \mu_U(a)\mathrm{d}a} H_U(s)B(s-\tau_U(s), rv_1(s-\tau_U(s)) + v_2(s-\tau_U(s)))\mathrm{d}s \end{aligned}$$

for any $t \in [0,a)$.

Since $H_T(t)$ and $H_U(t)$, which are given in (10), are piecewise continuous, we only focus on the mild solutions. For the completeness, we present the proof of the comparison principle for solutions of the integral form in the following theorem, which also shows the non-negative solutions of system (7)-(8) exist globally and are bounded.

It is worth to point out that the comparison principle for the cooperative systems of delay differential equations could be found in [22, Chapter 5] for the case where system coefficients are continuous in time t.

Theorem 3.1. *For any $\phi \in X_+$, system (7)-(8) has a unique mild solution $u(t,\phi) = (A_T(t,\phi), A_U(t,\phi))$ with $u_0 = \phi$ on $[0,\infty)$ and $u_t \in X_+$ for all $t \geq 0$. Moreover, Let $\tilde{w}(t)$ and $w(t)$ be a pair of lower and super solutions of system (7)-(8) on $[-\hat{\tau}, +\infty)$, respectively, with $\tilde{w}(\theta) \leq w(\theta), \theta \in [-\hat{\tau}, 0]$. Then $\tilde{w}(t) \leq w(t)$ for all $t \geq 0$.*

Proof. Note that $B(t,\phi)$ is Lipschitz continuous in ϕ on each compact subset of $\mathbb{R} \times X$. It follows from the discussion in [15, Chapter 2, Section 2.6] that for any $\phi \in X_+$, system (7)-(8) has a unique mild solution, denoted by $u(t,\phi)$ on its maximal interval of existence $[0, \varsigma_\phi)$ with $u_0 = \phi$, where $\varsigma_\phi \leq \infty$. Indeed, $u(t,\phi)$ is absolutely continuous in t, satisfying (7)-(8) almost everywhere on $[0, \varsigma_\phi)$.

Let $m(t) = \tilde{w}(t) - w(t)$, then by Definition 3.1, we have

$$\begin{aligned}
m_1(t) \leq \int_0^t & e^{-\int_s^t \mu_T(\tau)\mathrm{d}\tau} H_T(s) \Big[B(s-\tau_T(s), r\tilde{w}_1(s-\tau_T(s)) + \tilde{w}_2(s-\tau_T(s))) \\
& - B(s-\tau_T(s), rw_1(s-\tau_T(s)) + w_2(s-\tau_T(s))) \Big] \mathrm{d}s, \quad t > 0, \\
m_2(t) \leq \int_0^t & e^{-\int_s^t \mu_U(\tau)\mathrm{d}\tau} H_U(s) \Big[B(s-\tau_U(s), r\tilde{w}_1(s-\tau_U(s)) + \tilde{w}_2(s-\tau_U(s))) \\
& - B(s-\tau_U(s), rw_1(s-\tau_U(s)) + w_2(s-\tau_U(s))) \Big] \mathrm{d}s, \quad t > 0.
\end{aligned} \tag{11}$$

By (H2), there exists an $L > 0$ such that

$$|B(t,u) - B(t,v)| \leq L|u - v|, \quad t \in \mathbb{R}, \ u \geq 0, \ v \geq 0.$$

It follows from (11) that

$$\begin{aligned}
m_1(t) &\leq \int_0^t e^{-\int_s^t \mu_T(\tau)\mathrm{d}\tau} L H_T(s) \Big(r[m_1(s-\tau_T(s))]_+ + [m_2(s-\tau_T(s))]_+ \Big) \mathrm{d}s, \ t > 0, \\
m_2(t) &\leq \int_0^t e^{-\int_s^t \mu_U(\tau)\mathrm{d}\tau} L H_U(s) \Big(r[m_1(s-\tau_U(s))]_+ + [m_2(s-\tau_U(s))]_+ \Big) \mathrm{d}s, \ t > 0,
\end{aligned} \tag{12}$$

where $[a]_+ = \max\{a, 0\}$ for $a \in \mathbb{R}$.

Let $\tilde{\tau} = \min\{\tilde{\tau}_T, \tilde{\tau}_U\}$, where we denote $\tilde{\tau}_T = \min_{t\in[0,\omega]} \tau_T(t)$ and $\tilde{\tau}_U = \min_{t\in[0,\omega]} \tau_U(t)$. Since $t - \tau_i(t)$, $i \in \{T, U\}$, is strictly increasing in t, it follows that for any $t \in [0, \tilde{\tau}]$,

$$\begin{aligned}
-\hat{\tau} &\leq \max\{0 - \tau_T(0), 0 - \tau_U(0)\} \\
&< \max\{t - \tau_T(t), t - \tau_U(t)\} \\
&\leq \max\{\tilde{\tau} - \tau_T(\tilde{\tau}), \tilde{\tau} - \tau_U(\tilde{\tau})\} \leq 0.
\end{aligned}$$

This implies that, for any $t \in [0, \tilde{\tau}]$, we have

$$m_1(t - \tau_i(t)) \leq 0, m_2(t - \tau_i(t)) \leq 0, \ \forall\, t \in [0, \tilde{\tau}], i \in \{T, U\}$$

due to the fact that $\tilde{w}(\theta) \leq w(\theta)$, $\theta \in [-\hat{\tau}, 0]$. Thus, it follows from (12) that $m_i(t) \leq 0$ for all $t \in [-\hat{\tau}, \tilde{\tau}]$.

Note that for any $t \in [0, 2\tilde{\tau}]$, we have

$$\begin{aligned} -\hat{\tau} \leq \max\{0 - \tau_T(0), 0 - \tau_U(0)\} &\leq \max\{t - \tau_T(t), t - \tau_U(t)\} \\ &\leq \max\{2\tilde{\tau} - \tau_T(2\tilde{\tau}), 2\tilde{\tau} - \tau_U(2\tilde{\tau})\} \\ &\leq \max\{2\tilde{\tau} - \tilde{\tau}, 2\tilde{\tau} - \tilde{\tau}\} = \tilde{\tau}. \end{aligned}$$

This implies that, for any $t \in [0, 2\tilde{\tau}]$, we have

$$m_1(t - \tau_i(t)) \leq 0 \text{ and } m_2(t - \tau_i(t)) \leq 0, \ i \in \{T, U\}$$

due to the fact that $m_i(t) \leq 0, t \in [-\hat{\tau}, \tilde{\tau}], i = 1, 2$. Hence we can conclude from (12) that $m_i(t) \leq 0$ for all $t \in [-\hat{\tau}, 2\tilde{\tau}]$. Repeating the same procedure for $t \in [n\tilde{\tau}, (n+1)\tilde{\tau}]$, $\forall n \in \mathbb{N}$, we conclude that $m_i(t) \leq 0$ for any $t \geq 0$, $i = 1, 2$. The proves the comparison principle.

Let $\bar{A} = (\bar{A}_T, \bar{A}_U) := \left(\frac{(1-\tilde{\tau}_\partial)q\hat{B}}{\tilde{\mu}_T}, \frac{(1-\tilde{\tau}_\partial)(1-q)\hat{B}}{\tilde{\mu}_U}\right)$, where $\hat{B}$ is defined in assumption (H2), $\tilde{\mu}_i = \min_{t\in[0,\omega]} \mu_i(t)$, $i \in \{T, U\}$, and $\tilde{\tau}_\partial = \min_{t\in[0,\omega]}\{\tau_U'(t), \tau_T'(t)\}$. For any $\kappa \geq 1$, we introduce the order interval

$$[0, \kappa\bar{A}]_X := \{\psi \in X : 0 \leq \psi(\theta) \leq \kappa\bar{A}, \forall\theta \in [-\hat{\tau}, 0]\}.$$

Next we claim that $[0, \kappa\bar{A}]_X$ is positive invariant for system (7)-(8). Indeed, it is easy to check that $(0, 0)$ is a solution of system (7)-(8). It suffices to check that $\kappa\bar{A}$ is an upper solution of system (7)-(8). Note that

$$\begin{aligned} &e^{-\int_0^t \mu_T(s)ds}\kappa\bar{A}_T + \int_0^t e^{-\int_s^t \mu_T(a)\mathrm{d}a} H_T(s)B(s - \tau_T(s), \kappa(r\bar{A}_T + \bar{A}_U))\mathrm{d}s, \\ \leq\ & e^{-\tilde{\mu}_T t}\kappa\bar{A}_T + \kappa\int_0^t \hat{B}(1-q)(1-\tilde{\tau}_\partial)e^{-\tilde{\mu}_T(t-s)}\mathrm{d}s, \\ =\ & e^{-\tilde{\mu}_T t}\kappa\bar{A}_T + \kappa\frac{\hat{B}(1-q)(1-\tilde{\tau}_\partial)(1-e^{-\tilde{\mu}_T t})}{\tilde{\mu}_T} = \kappa\bar{A}_T, \end{aligned} \tag{13}$$

where the second inequality is due to the fact that $B(\cdot, u)$ is subhomogeneous in u and bounded above by $\hat{B}$. Similarly, we can show that

$$e^{-\int_0^t \mu_U(s)ds}\kappa\bar{A}_U + \int_0^t e^{-\int_s^t \mu_U(a)\mathrm{d}a} H_U(s)B(s - \tau_U(s), \kappa(r\bar{A}_T + \bar{A}_U))\mathrm{d}s \leq \kappa\bar{A}_U. \tag{14}$$

For any given initial value ϕ, we can choose $\kappa > 1$ to be sufficiently large such that $\phi \in [0, \kappa \bar{A}]_X$. Then the comparison principle yields that $0 \leq u(t, \phi) \leq \kappa \bar{A}$ for all $t \in [0, \varsigma_\phi)$, which implies the boundedness of solutions $u(t, \phi)$, and $\varsigma_\phi = \infty$. $\square$

Next, we introduce the net reproduction number $\mathcal{R}_0$, and then investigate the threshold dynamics in terms of $\mathcal{R}_0$. The net reproduction number $\mathcal{R}_0$ is an ecologically meaningful index, which measures the average number of offspring that a female individual can produce during her lifetime when density-dependent regulations are not considered. The pest free state of system (7)-(8) is $(0,0)$ and the corresponding linearized system is

$$\begin{aligned} \frac{\mathrm{d}A_T(t)}{\mathrm{d}t} &= L_T(t)\left(\gamma A_T(t-\tau_T(t)) + A_U(t-\tau_T(t))\right) - \mu_T(t)A_T(t), \\ \frac{\mathrm{d}A_U(t)}{\mathrm{d}t} &= L_U(t)\left(\gamma A_T(t-\tau_U(t)) + A_U(t-\tau_U(t))\right) - \mu_U(t)A_U(t), \end{aligned} \tag{15}$$

with

$$\begin{aligned} L_T(t) &= (1-\tau_T'(t))qe^{-\int_{t-\tau_T(t)}^t d_T(\xi)\,d\xi} \prod_{j=\underline{k}(t)}^{\overline{k}(t)} (1-p_j)\gamma B_\partial(t-\tau_T(t),0) \\ L_U(t) &= (1-\tau_U'(t))(1-q)e^{-\int_{t-\tau_U(t)}^t d_U(\xi)\,d\xi} B_\partial(t-\tau_U(t),0), \end{aligned} \tag{16}$$

where $B_\partial(t,0) = \frac{\partial B(t,A)}{\partial A}|_{A=0}$. Define the operators $F(t)$ and $V(t)$ as follows:

$$F(t)\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix} = \begin{pmatrix} L_T(t)\left(\gamma\phi_1(-\tau_T(t)) + \phi_2(-\tau_T(t))\right) \\ L_U(t)\left(\gamma\phi_1(-\tau_U(t)) + \phi_2(-\tau_U(t))\right)\end{pmatrix}, \tag{17}$$

and

$$V(t) = \begin{pmatrix} \mu_T(t) & 0 \\ 0 & \mu_U(t)\end{pmatrix}.$$

Then we can rewrite the linear system (15)-(16) into

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = F(t)u_t - V(t)u(t),\ \forall\ t \geq 0.$$

We observe that $F(t) : X \to \mathbb{R}^2$ is positive in the sense that $F(t)X_+ \subset \mathbb{R}^2_+$, and hence, the condition (H1) in [33] holds. It is easy to see that $-V(t)$ is cooperative. Let $Z(t,s),\ t \geq s$, denote the evolution family on $\mathbb{R}^2$ associated with the following system

$$\frac{\mathrm{d}u(t)}{dt} = -V(t)u(t),$$

that is, for each $s \in \mathbb{R}$, $Z(t,s)$ satisfies

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

where I is the 2×2 identity matrix. Clearly, $Z(t,s)$ can be expressed as

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

Let $\Omega(Z)$ represent the exponential growth bound of the evolution family $\{Z(t,s),\ t \geq s\}$, which is defined by

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

Then we have $\Omega(Z) \leq -\min\{\tilde{\mu}_T, \tilde{\mu}_U\} < 0$, where $\tilde{\mu}_i = \min_{t\in[0,\omega]} \mu_i(t)$, $i \in \{T, U\}$, and hence, condition (H2) in [33] holds.

Now we can employ theories developed in [32, 33] to define the net reproduction number $\mathcal{R}_0$ for system (7)-(8). Let $C_\omega(\mathbb{R}, \mathbb{R}^2)$ be the Banach space consisting of all ω-periodic and continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$, where $\|\varphi\|_{C_\omega(\mathbb{R},\mathbb{R}^2)} = \max_{\theta\in[0,\omega]} |\varphi(\theta)|_{\mathbb{R}}$, $\forall\varphi \in C_\omega(\mathbb{R}, \mathbb{R}^2)$. We assume that $v \in C_\omega(\mathbb{R}, \mathbb{R}^2)$ and $v(t)$ is the initial distribution of adult pests at time $t \in \mathbb{R}$. For any $s \geq 0$, $F(t-s)v_{t-s}$ represents the density distribution of new born pests at time $t-s$ with $t \geq s$. Then $Z(t, t-s)F(t-s)v_{t-s}$ represents the distribution of those pests who were newly reproduced at time $t-s$ and still survive in the environment at time t for $t \geq s$. Thus, the integral

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

quantifies the distribution of accumulative pest individuals at time t produced by all those pests introduced at all previous time to t. Motivated by the concept of next generation operators (see, e.g., [2, 3, 8, 11, 27]), we introduce the next generation operator G by

$$[Gv](t) := \int_0^\infty Z(t,t-s)F(t-s)v(t-s+\cdot)\mathrm{d}s,\ \forall\, t \in \mathbb{R},\ v \in C_\omega(\mathbb{R}, \mathbb{R}^2).$$

Note that although $F(t)$ is a piecewise continuous function of t, where $F(t)$ is defined in (17), we can still verify that $G : C_\omega(\mathbb{R}, \mathbb{R}^2) \to C_\omega(\mathbb{R}, \mathbb{R}^2)$ through standard arguments. Further, we define the spectral radius of G as the net reproduction number for system (7)-(8), that is, $\mathcal{R}_0 = r(G)$.

Let P_t be the solution map of system (15)-(16), that is, $P_t\phi = v_t(\phi)$, $t \geq 0$, where $v(t,\phi)$ is the unique solution of system (15)-(16) with $v_0 = \phi \in X$. By [33, Theorem 2.1], we have the following observation.

Lemma 3.2. *$\mathcal{R}_0 - 1$ has the same sign as $r(P_\omega) - 1$, where $r(P_\omega)$ is the spectral radius of P_ω.*

To investigate the dynamics of the model system, we introduce a new functional space. Let

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

where $\hat{\tau}(0) = \max\{\tau_T(0), \tau_U(0)\}$. Then $(\mathcal{X}, \mathcal{X}_+)$ is an ordered Banach space. Please note that the functional space $\mathcal{X}$ is introduced to establish stronger properties of the solution maps, as presented later in Lemmas 3.4 and 3.5. Given a function $w : [-\hat{\tau}(0), \infty) \to \mathbb{R}^2$, we define $w_t \in \mathcal{X}$, $\forall t \geq 0$, by

$$w_t(\theta) = (w_1(t + \theta), w_2(t + \theta)), \ \forall \ \theta \in [-\hat{\tau}(0), 0].$$

Lemma 3.3. *For any $\varphi = (\varphi_1, \varphi_2) \in \mathcal{X}_+$, system (7)-(8) admits a unique nonnegative solution $w(t, \varphi)$ on $[0, \infty)$ with $w_0 = \varphi$. Moreover, system (7)-(8) generates an ω-periodic semiflow Q_t with $Q_t\varphi = w_t(\cdot, \varphi)$, $\forall t \geq 0$ in the sense that (i) $Q_0 = I$, (ii) $Q_{t+\omega} = Q_t \circ Q_\omega$, for all $t \geq 0$, and (iii) $Q_t\varphi$ is continuous in $(t, \varphi) \in [0, \infty) \times \mathcal{X}_+$. Furthermore, $Q_{n\omega}$ is compact on $\mathcal{X}_+$ for each $n > \hat{\tau}/\omega$.*

Proof. Let $\tilde{\tau} = \min\{\tilde{\tau}_T, \tilde{\tau}_U\}$, where we denote $\tilde{\tau}_T = \min_{t \in [0,\omega]} \tau_T(t)$ and $\tilde{\tau}_U = \min_{t \in [0,\omega]} \tau_U(t)$. Since $t - \tau_i(t)$, $i \in \{T, U\}$, is strictly increasing in t, it follows that for any $t \in [0, \tilde{\tau}]$,

$$\begin{aligned} -\hat{\tau}(0) = 0 - \max\{\tau_T(0), \tau_U(0)\} &= \max\{0 - \tau_T(0), 0 - \tau_U(0)\} \\ &< \max\{t - \tau_T(t), t - \tau_U(t)\} \\ &\leq \max\{\tilde{\tau} - \tau_T(\tilde{\tau}), \tilde{\tau} - \tau_U(\tilde{\tau})\} \leq 0. \end{aligned}$$

This implies that, for any $t \in [0, \tilde{\tau}]$, we have $w_1(t - \tau_i(t), \varphi) = \varphi_1(t - \tau_i(t))$ and $w_2(t - \tau_i(t), \varphi) = \varphi_2(t - \tau_i(t))$, $\forall \ t \in [0, \tilde{\tau}]$, $i \in \{T, U\}$. Then system (7)-(8) becomes the following ordinary differential equations for $t \in [0, \tilde{\tau}]$:

$$\begin{aligned} \frac{\mathrm{d}A_T(t)}{\mathrm{d}t} &= H_T(t) B\left(t - \tau_T(t), \gamma\varphi_1(t - \tau_T(t)) + \varphi_2(t - \tau_T(t))\right) - \mu_T(t) A_T(t), \\ \frac{\mathrm{d}A_U(t)}{\mathrm{d}t} &= H_U(t) B\left(t - \tau_U(t), \gamma\varphi_1(t - \tau_U(t)) + \varphi_2(t - \tau_U(t))\right) - \mu_U(t) A_U(t), \end{aligned}$$

where $H_T(t)$ and $H_U(t)$ are given in (10). Hence, for any given $\varphi = (\varphi_1, \varphi_2) \in \mathcal{X}_+$, the solution $(w_1(t, \varphi), w_2(t, \varphi))$ of the above linear system exists uniquely for $t \in [0, \tilde{\tau}]$. In other words, we have obtained values of $z_1(\theta) = w_1(\theta, \varphi)$ and $z_2(\theta) = w_2(\theta, \varphi)$ for $\theta \in [-\hat{\tau}(0), \tilde{\tau}]$.

Note that for any $t \in [\tilde{\tau}, 2\tilde{\tau}]$, we have

$$\begin{aligned} -\hat{\tau}(0) = \max\{0 - \tau_T(0), 0 - \tau_U(0)\} &\leq \max\{\tilde{\tau} - \tau_T(\tilde{\tau}), \tilde{\tau} - \tau_U(\tilde{\tau})\} \\ &\leq \max\{t - \tau_T(t), t - \tau_U(t)\} \\ &\leq \max\{2\tilde{\tau} - \tau_T(2\tilde{\tau}), 2\tilde{\tau} - \tau_U(2\tilde{\tau})\} \end{aligned}$$

$$\leq \max\{2\tilde{\tau}-\tilde{\tau}, 2\tilde{\tau}-\tilde{\tau}\} = \tilde{\tau}.$$

Thus, $w_1(t-\tau_i(t),\varphi) = z_1(t-\tau_i(t))$ and $w_2(t-\tau_i(t),\varphi) = z_2(t-\tau_i(t))$, $i \in \{T,U\}$ are known. Solving the following ordinary differential equation system for $t \in [\tilde{\tau}, 2\tilde{\tau}]$ with $w_1(\tilde{\tau}) = z_1(\tilde{\tau})$ and $w_2(\tilde{\tau}) = z_2(\tilde{\tau})$:

$$\begin{aligned}
\frac{\mathrm{d}A_T(t)}{\mathrm{d}t} &= H_T(t)B\left(t-\tau_T(t), \gamma z_1(t-\tau_T(t)) + z_2(t-\tau_T(t))\right) - \mu_T(t)A_T(t),\\
\frac{\mathrm{d}A_U(t)}{\mathrm{d}t} &= H_U(t)B\left(t-\tau_T(t), \gamma z_1(t-\tau_U(t)) + z_2(t-\tau_U(t))\right) - \mu_U(t)A_U(t),
\end{aligned}$$

where $H_T(t)$ and $H_U(t)$ are defined in (10), we get the solution $(w_1(t,\varphi), w_2(t,\varphi))$ on the interval $[\tilde{\tau}, 2\tilde{\tau}]$. By repeating this procedure for $t \in [n\tilde{\tau}, (n+1)\tilde{\tau}]$, $\forall\ n \in \mathbb{N}$, it then follows that for any initial values $\varphi = (\varphi_1,\varphi_2) \in \mathcal{X}_+$, the solution $w(t,\varphi)$ exists uniquely for all $t \geq 0$. By Remark 2.1 and standard arguments as in [19, Lemma 3.5], we can prove that the solution map Q_t is an ω-periodic semiflow.

It remains to show the compactness of $Q_{n\omega}$ on $\mathcal{X}_+$ for each $n > \frac{\hat{\tau}}{\omega}$. Let $w(t,\varphi)$ be the unique solution of system (7)-(8) with $w_0 = \varphi \in \mathcal{X}_+$. Since $n\omega > \hat{\tau}$, it then follows that $[Q_{nw}\phi](\theta) = w(n\omega+\theta,\varphi)$, $\theta \in [-\hat{\tau}(0), 0]$ satisfies

$$\begin{aligned}
w_1(n\omega+\theta,\varphi) &= \varphi_1(0) + \int_0^{n\omega+\theta} -\mu_T(s)w_1(s)ds\\
&\quad + \int_0^{n\omega+\theta} H_T(s)B\left(s-\tau_T(s), \gamma w_1(s-\tau_T(s)) + w_2(s-\tau_T(s))\right)\mathrm{d}s,\\
w_2(n\omega+\theta,\varphi) &= \varphi_2(0) + \int_0^{n\omega+\theta} -\mu_U(s)w_2(s)\mathrm{d}s\\
&\quad + \int_0^{n\omega+\theta} H_U(s)B\left(s-\tau_U(s), \gamma w_1(s-\tau_U(s)) + w_2(s-\tau_U(s))\right)\mathrm{d}s.
\end{aligned} \tag{18}$$

Let S be a bounded set of $\mathcal{X}_+$. For any $\varphi \in \mathcal{X}_+$, it is easily seen from the proof of Theorem 3.1 that $w(s,\varphi)$ is bounded for $0 \leq s \leq n\omega$, and hence, $Q_{n\omega}(S)$ is bounded.

Next, we prove that the set $Q_{n\omega}(S)$ is equicontinuous whenever $n\omega > \hat{\tau}$. Since $B(t,u) \leq \hat{B}$ for any $(t,u) \in \mathbb{R}\times\mathbb{R}_+$, where $\hat{B}$ is defined in (H2), and $w(s,\phi)$ is bounded for $0 \leq s \leq n\omega$, then there exists $M_1 > 0$, dependent only on S, such that

$$\max\{\mu_T(t)w_1(t,\varphi), \mu_U(t)w_2(t,\varphi)\} + \max\{H_T(t), H_U(t)\}\hat{B} \leq M_1$$

for any $0 \leq t \leq n\omega$. It then follows that for any $\theta_1, \theta_2 \in [-\hat{\tau}(0), 0]$ with $\theta_1 < \theta_2$

$$|w_1(n\omega+\theta_1,\varphi) - w_1(n\omega+\theta_2,\varphi)| \leq \int_{n\omega+\theta_1}^{n\omega+\theta_2} \mu_T(s)w_1(s) + \hat{B}H_T(s)ds \leq M_1|\theta_1-\theta_2|,$$

which also holds true for w_2. Now for any $\epsilon > 0$ and $\varphi \in S$, there exists $\delta \in (0, \epsilon/M_1)$, such that

$$|w_i(n\omega + \theta_1, \varphi) - w_i(n\omega + \theta_2, \varphi)| \leq M|\theta_1 - \theta_2| < \epsilon, \ i = 1, 2.$$

provided $|\theta_1 - \theta_2| < \delta$ with $\theta_1, \theta_2 \in [-\hat{\tau}(0), 0]$. As a consequence, we see that $Q_{n\omega}$ is compact on $\mathcal{X}_+$ for $n\omega > \hat{\tau}$. □

Remark 3.1. *By the uniqueness of solutions in Theorem 3.1 and Lemma 3.3, we know that for any* $\psi \in X_+$ *and* $\varphi \in \mathcal{X}_+$, *if* $\psi_1(\theta) = \varphi_1(\theta)$ *and* $\psi_2(\theta) = \varphi_2(\theta)$, $\forall \theta \in [-\hat{\tau}(0), 0]$, *then* $w(t, \varphi) = u(t, \psi)$, $\forall t \geq 0$, *where* $w(t, \varphi)$ *and* $u(t, \psi)$ *are solutions of system (7)–(8) with initial data satisfying* $w_0 = \varphi$ *and* $u_0 = \psi$, *respectively.*

Next, we will show that the periodic semiflow Q_t is eventually strongly monotone on $\mathcal{X}_+$.

Lemma 3.4. *For any* $\varphi = (\varphi_1, \varphi_2)$, $\tilde{\varphi} = (\tilde{\varphi}_1, \tilde{\varphi}_2) \in \mathcal{X}_+$ *with* $\varphi > \tilde{\varphi}$ *in the sense that* $\varphi(\theta) \geq \tilde{\varphi}(\theta)$ *for all* $\theta \in [-\hat{\tau}(0), 0]$ *with* $\hat{\tau}(0) = \max\{\tau_T(0), \tau_U(0)\}$ *but* $\varphi \not\equiv \tilde{\varphi}$, *the solutions* $w(t) = w(t, \varphi)$ *and* $\tilde{w}(t) = w(t, \tilde{\varphi})$ *of system (7)-(8) with initial values* $w_0 = \varphi$ *and* $\tilde{w}_0 = \tilde{\varphi}$ *satisfy* $w_1(t) - \tilde{w}_1(t) > 0$ *and* $w_2(t) - \tilde{w}_2(t) > 0$ *for all* $t > 2\hat{\tau}$. *Thus,* $Q_t\varphi \gg Q_t\tilde{\varphi}$, $\forall t > 3\hat{\tau}$.

Proof. Without loss of generality, we assume $\tau_T(0) \geq \tau_U(0)$, and hence, $\hat{\tau}(0) = \max\{\tau_T(0),\ \tau_U(0)\} = \tau_T(0)$. By adopting arguments similar to those in Theorem 3.1 and Lemma 3.3, it follows that the comparison principle holds true on $\mathcal{X}_+$, that is, $w_i(t) - \tilde{w}_i(t) \geq 0$ for all $t \geq 0$, $i = 1, 2$.

Next, for any given $\varphi := (\varphi_1, \varphi_2) \in \mathcal{X}_+$, the solution $(w_1(t, \varphi),\ w_2(t, \varphi))$ satisfies the following system of integral equations

$$\begin{aligned}
w_1(t, \varphi) &= e^{-\int_0^t \mu_T(s)\mathrm{d}s}\varphi_1(0) \\
&\quad + \int_0^t e^{-\int_s^t \mu_T(a)\mathrm{d}a} H_T(s) B\left(s - \tau_T(s), \gamma w_1(s - \tau_T(s)) + w_2(s - \tau_T(s))\right) \mathrm{d}s, \\
w_2(t, \varphi) &= e^{-\int_0^t \mu_U(s)\mathrm{d}s}\varphi_2(0) \\
&\quad + \int_0^t e^{-\int_s^t \mu_u(a)\mathrm{d}a} H_U(s) B\left(s - \tau_U(s), \gamma w_1(s - \tau_U(s)) + w_2(s - \tau_U(s))\right) \mathrm{d}s,
\end{aligned} \tag{19}$$

for all $t \geq 0$, where $H_T(t)$ and $H_U(t)$ are defined in (10). Note that $m_T(t) = t - \tau_T(t)$ and $m_U(t) = t - \tau_U(t)$ are increasing in $t \in \mathbb{R}$. It follows that $[-\tau_T(0), 0] \subset m_T([0, \hat{\tau}])$ and $[-\tau_U(0), 0] \subset m_U([0, \hat{\tau}])$. Without loss of generality, we assume that, $\varphi_2 - \tilde{\varphi}_2 > 0$. Then there exists an $\eta \in [-\tau_T(0), 0]$ such that $\varphi_2(\eta) - \tilde{\varphi}_2(\eta) > 0$. It follows from the first equation of system (19) that $w_1(t, \varphi) - w_1(t, \tilde{\varphi}) > 0$ for $t > \hat{\tau}$. Furthermore, if $s > 2\hat{\tau}$, then $s - \hat{\tau}_U(s) > 2\hat{\tau} - \hat{\tau} = \hat{\tau}$. By the second equation of system (19), we have $w_2(t, \varphi) - w_2(t, \tilde{\varphi}) > 0$ for $t > 2\hat{\tau}$. It implies that $w_i(t, \varphi) - w_i(t, \tilde{\varphi}) > 0$, $i = 1, 2$. Therefore, Q_t is strongly monotone on $\mathcal{X}_+$, for all $t > 3\hat{\tau}$. □

By the arguments similar to those in [19, Lemma 3.7], together with assumption (H2), we can infer that Q_t is strongly subhomogeneous.

Lemma 3.5. *For any* $\varphi \gg 0$ *in* $\mathcal{X}$ *and* $\kappa \in (0,1)$, *we have* $w_i(t,\kappa\varphi) > \kappa w_i(t,\varphi)$ *for all* $t > 0$, $i = 1, 2$, *and hence, the Poincaré map* Q_ω *satisfies* $Q^n_\omega(\kappa\varphi) > \kappa Q^n_\omega(\varphi)$, *where* $Q^n_\omega = Q_{n\omega}$, *in* $\mathcal{X}$ *for all integers* n *with* $n\omega > \hat{\tau}$.

Proof. Let $u(t) = w(t,\kappa\varphi)$ and $v(t) = \kappa w(t,\varphi)$, where $w(t,\varphi)$ is the unique solution of system (7)-(8) with $w_0 = \varphi \gg 0$ in $\mathcal{X}$. From the proof of Lemma 3.3, we see that $u(t) > 0$ and $v(t) > 0$ for all $t \geq 0$. Moreover, we have the following observations for $v(t)$:

$$\begin{aligned} v_1(t) &= e^{-\int_0^t \mu_T(s)ds} v_1(0) \\ &\quad + \int_0^t e^{-\int_s^t \mu_T(a)\mathrm{d}a} \kappa H_T(s) B(s-\tau_T(s), rw_1(s-\tau_T(s)) + w_2(s-\tau_T(s)))\mathrm{d}s, \\ v_2(t) &= e^{-\int_0^t \mu_U(s)ds} v_2(0) \\ &\quad + \int_0^t e^{-\int_s^t \mu_U(a)\mathrm{d}a} \kappa H_U(s) B(s-\tau_U(s), rw_1(s-\tau_U(s)) + w_2(s-\tau_U(s)))\mathrm{d}s. \end{aligned}$$

By (H2), we further have

$$\begin{aligned} v_1(t) &< e^{-\int_0^t \mu_T(s)ds} v_1(0) \\ &\quad + \int_0^t e^{-\int_s^t \mu_T(a)\mathrm{d}a} H_T(s) B(s-\tau_T(s), rv_1(s-\tau_T(s)) + v_2(s-\tau_T(s)))\mathrm{d}s, \\ v_2(t) &< e^{-\int_0^t \mu_U(s)ds} v_2(0) \\ &\quad + \int_0^t e^{-\int_s^t \mu_U(a)\mathrm{d}a} H_U(s) B(s-\tau_U(s), rv_1(s-\tau_U(s)) + v_2(s-\tau_U(s)))\mathrm{d}s. \end{aligned}$$

That is, $(v_1(t), v_2(t))$ is a lower solution of system (7)-(8) in the integral sense (see Definition 3.1 with $-\hat{\tau}$ replaced by $-\hat{\tau}(0)$ where $\hat{\tau}(0) = \max\{\tau_T(0), \tau_U(0)\}$). It is clear that for all $\theta \in [-\hat{\tau}(0), 0]$,

$$u_1(\theta) = \kappa\phi_1(\theta) = v_1(\theta) \text{ and } u_2(\theta) = \kappa\phi_2(\theta) = v_2(\theta).$$

By the comparison principle, we have

$$0 < v_i(t) \leq u_i(t), \quad \forall t \in [-\hat{\tau}(0), +\infty),\ i \in \{1, 2\}. \tag{20}$$

Furthermore, a direct computation leads to

$$\begin{aligned} u_1(t) - v_1(t) > \int_0^t e^{-\int_s^t \mu_T(\tau)\mathrm{d}\tau} H_T(s) \Big[& B(s-\tau_T(s), ru_1(s-\tau_T(s)) + u_2(s-\tau_T(s))) \\ & - B(s-\tau_T(s), rv_1(s-\tau_T(s)) + v_2(s-\tau_T(s)))\Big]\mathrm{d}s \geq 0, \quad t > 0, \end{aligned}$$

where the second inequality follows from (H2) and $u_i(t) \geq v_i(t)$ for $t \in [-\hat{\tau}(0), +\infty), i \in \{1, 2\}$.

Similarly, we have $u_2(t) > v_2(t)$ for $t > 0$. This completes our claim, that is, $w_i(t, \kappa\varphi) > \kappa w_i(t, \varphi)$ for all $t > 0$ and $\varphi \gg 0$, $i \in \{1, 2\}$.

Thus, $Q_\omega^n(\kappa\varphi) = Q_{n\omega}(\kappa\varphi) > \kappa Q_{n\omega}(\varphi) = \kappa Q_\omega^n(\varphi)$ in $\mathcal{X}$ for all integers n with $n\omega > \hat{\tau}$. □

For any given $t \geq 0$, let $\mathcal{P}_t$ be the solution map of linear system (15)-(16) on $\mathcal{X}$, that is, $\mathcal{P}_t\varphi = w_t(\varphi)$, $\forall\ \varphi \in \mathcal{X}_+$. Fix a sufficiently large n_0 such that $n_0\omega > 3\hat{\tau}$, then a similar argument as that in Lemma 3.4 shows that $\mathcal{P}_\omega^{n_0} = \mathcal{P}_{n_0\omega}$ is strongly positive. Hence, [19, Lemma 3.8] establishes the following claim:

Lemma 3.6. *Two Poincaré maps $P_\omega : X \to X$ and $\mathcal{P}_\omega : \mathcal{X} \to \mathcal{X}$ have the same spectral radius, that is, $r(P_\omega) = r(\mathcal{P}_\omega)$.*

Now we are ready to present the main result of this section.

Theorem 3.7. *The following statements are valid:*

(i) If $\mathcal{R}_0 \leq 1$, then $(0, 0)$ is globally asymptotically stable for system (7)-(8) in $\mathcal{X}_+$.

(ii) If $\mathcal{R}_0 > 1$, then system (7)-(8) a unique positive ω-periodic solution $(A_T^*(t), A_U^*(t))$, and it is globally asymptotically stable in $\mathcal{X}_+ \setminus \{(0, 0)\}$.

Proof. We choose a sufficiently large integer n_0 such that $n_0\omega > 3\hat{\tau}$. From Lemmas 3.3-3.5, we know that Q_t is an $n_0\omega$-periodic semiflow, with $Q_{n_0\omega}$ being strongly monotone and strongly subhomogeneous. Meanwhile, Lemma 3.3 imply that $Q_{n_0\omega}$ is compact, and further, is β-contraction by definition (see, e.g., [32, Definition 1.1.2]). Hence, ensured by [14, Lemma 2.3.4], $Q_{n_0\omega}$ is asymptotically smooth. It follows that the Frechét derivative of $Q_{n_0\omega}$ at 0, denoted by $DQ_{n_0\omega}(0)$, is compact (see, e.g., [9, Proposition 8.2]). Note that $DQ_{n_0w}(0)\varphi = \mathcal{P}_{n_0\omega}\phi$, $\phi \in \mathcal{X}$. It yields that $DQ_{n_0\omega}(0)$ is strongly positive by employing similar arguments to those in the proof of Lemma 3.4. Applying [32, Theorem 2.3.4] to $Q_{n_0\omega}$, we obtain

(i) If $r(DQ_{n_0\omega}(0)) \leq 1$, then $(0, 0)$ is globally asymptotically stable for system (7)-(8) in $\mathcal{X}_+$.

(ii) If $r(DQ_{n_0\omega}(0)) > 1$, then system (7)-(8) admits a unique positive $n_0\omega$-periodic solution $(A_T^*(t), A_U^*(t))$ which is globally asymptotically stable in $\mathcal{X}_+ \setminus \{(0, 0)\}$.

Further, it follows from Lemmas 3.2 and 3.6, together with the fact that $r(DQ_{n_0\omega}(0)) = r(\mathcal{P}_{n_0\omega}) = [r(\mathcal{P}_\omega)]^{n_0}$, that $\text{sign}(\mathcal{R}_0 - 1) = \text{sign}(r(DQ_{n_0\omega}(0)) - 1)$.

It remains to show that the $n_0\omega$-periodic solution $(A_T^*(t), A_U^*(t))$ is also ω-periodic. Indeed, we let $\varphi^* = w_0^* \in \mathcal{X}$ with $w^*(t) = (A_T^*(t), A_U^*(t))$. Then $Q_{n_0\omega}\varphi^* = \varphi^*$. Note that

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

By the uniqueness of the positive fixed point of $Q_\omega^{n_0} = Q_{n_0\omega}$, it follows that $Q_\omega\varphi^* = \varphi^*$, which implies that $(A_T^*(t), A_U^*(t)) = u(t, \varphi^*)$ is an ω-periodic solution of system (7)-(8). □

4 Simulation

In this section, we apply the model (7)-(8) to the species *T. granarium* to investigate the impact of IGRs on pest control numerically. The khapra beetle, *T. granarium* is one of the most serious insect pest of various stored food worldwide. It not only affects the quality and quantity of stored products, but also posts threats to public health [1]. Research shows that its growth, including development, birth patterns, maturation and mortality, is sensitive to temperatures [21]. In the simulations, we assume the adult and larval death rates, and the maturation duration of unregulated individuals are temperature-dependent responses, that is, $\mu_U(T)$, $d_U(T)$ and $\tau_U(T)$ are subject to temperature variations. Motivated by [20], we further assume the temperature is a function of time t (in day) in the following form

$$T(t) = c_K + d_K \times \sin\left(\frac{2\pi}{365} \times (t - t_0)\right), \tag{21}$$

where $T(t)$ is the temperature in °K on day t, c_K is mean annual temperature, d_K is half the annual temperature range, and t_0 is day-of-the-year when temperature increases to its annual mean. We show all temperatures in °C for clarity, but we need to transform the temperatures into °K to get the temperature-dependent coefficients [20]. Here we set $c_K = 25°\mathrm{C}$, $d_K = 10°\mathrm{C}$ and $t_0 = 121$ day. Based on the data from [21], those aforementioned parameters for untreated *T. granarium* individuals can be estimated through the following formulas:

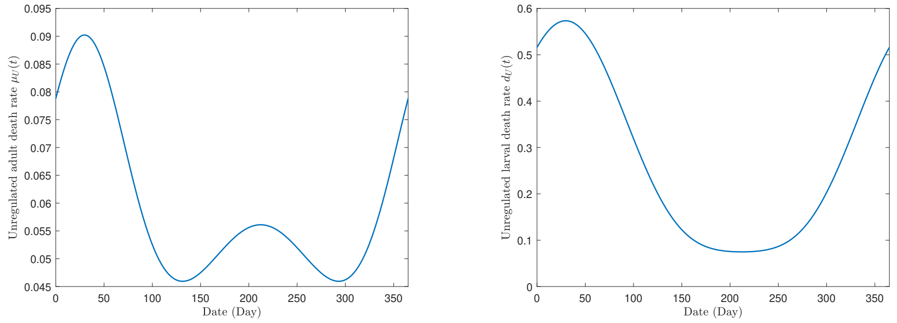
$$\begin{aligned}
&\mu_U(T) = 3.106 \times 10^6 \exp\left(-\left(\frac{T + 219.3}{55.9}\right)^2\right) + 2.724 \exp\left(-\left(\frac{T - 185.8}{75.96}\right)^2\right) \ \mathrm{day}^{-1},\\
&d_U(T) = 0.001066T^2 - 0.07823T + 1.507 \ \mathrm{day}^{-1},\\
&\tau_U(T) = 0.1228T^2 - 8.458T + 168.7 \ \mathrm{day}^{-1},
\end{aligned}$$

respectively. With expression (21), we can therefore obtain the corresponding seasonal parameters $\mu_U(t)$, $d_U(t)$ and $\tau_U(t)$, with a period $\omega = 365$ days. These periodic parameters are shown as curves in Figure 2. Furthermore, Figure 2(d) numerically indicates that $1 - \tau_U'(t) > 0$ is valid. We assume the birth function of *T. granarium* as

$$B(t, A) = \frac{a(t)A}{b(t) + A}, \tag{22}$$

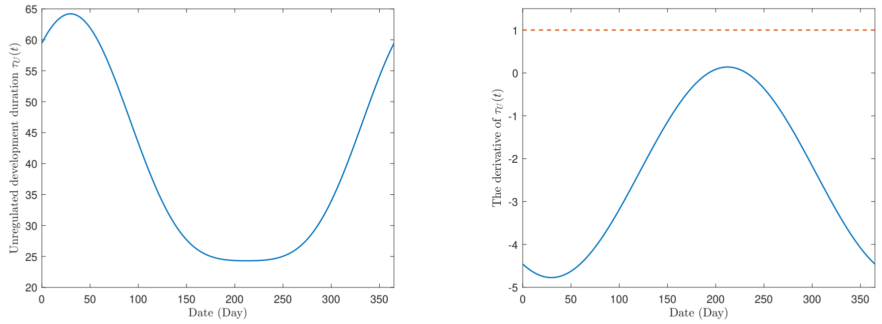
where A denotes the population size of effective *T. granarium* adults. For illustration, we take $a(t) = 100\left(a_0 + a_1 \sin\left(\frac{2\pi t}{365} + a_2\right)\right)$, where $a_0 = 0.71421$, $a_1 = 0.2856$, $a_2 = 4.2$, and $b(t) = 2$. Clearly, $B(t, A)$ of form (22) satisfies assumption (H2).

In order to control and eradicate infestations of *T. granarium*, apart from insecticides [5], IGRs can also be applied as grain protectants by increasing adult and larval mortality, and prolonging the immature developmental stage [1]. For simplicity, we assume $\mu_T(t) = \eta_1\mu_U(t)$, $d_T(t) = \eta_2 d_U(t)$, and $\tau_T(t) = \eta_3\tau_U(t)$, with $\eta_i \in (1, 1.5)$,



(a) Adult death rate $\mu_U(t)$

(b) Larval death rate $d_U(t)$



(c) Maturation time $\tau_U(t)$

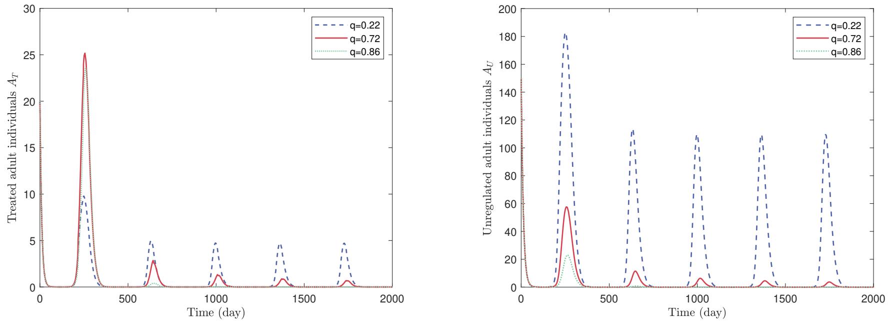
(d) Derivative $\tau'_U(t)$

Fig. 2 Seasonal parameters for unregulated class (U). The curves in (a), (b) and (c) show the adult death rate μ_U, larval death rate d_U, development duration τ_U in unregulated class in response to time t, respectively. The curve in (d) shows that the condition $1 - \tau'_U(t) > 0$ is satisfied.

$i \in \{1, 2, 3\}$, to reflect the direct efficacy of IGRs on *T. granarium*. As a baseline setting, we assume $\eta_i = \eta$, $i \in \{1, 2, 3\}$, and the IGR-treatments are considered to occur at equally spaced times with the same treatment removal rates, that is, the length of time interval between any two consecutive treatments is denoted by Δt, where $\Delta t = \omega/N$ and N stands for the total number in one period ω, and the removal rate $p_j = p$. Therefore, assumption (H3) becomes valid. The releasing times for each treatment t_j can be determined by $t_j = t_1 + (j-1)\omega/N$, $j = 1, 2, 3, ...$ and $0 \leq t_1 < \omega$.

To observe the long-term behaviour of system (7)-(8), we choose $\eta = 1.2$, $p = 0.5$, $\gamma = 0.8$, $t_1 = 4$, $N = 12$, and initial data as $A_T(t) = 20$, $A_U(t) = 150$, for $t \in [-\hat{\tau}, 0]$. Figure 3 shows solution simulations of $A_T(t)$ and $A_U(t)$ in different values of q, where q denotes the fraction of larvae subject to the treatment of IGRs. When $q = 0.22$, the net reproduction number can be numerically computed as $\mathcal{R}_0 = 2.523 > 1$. In this case, both treated and untreated individuals persist in the stored products and exhibit periodic fluctuations eventually (blue dash curve). When we increase q to the value of 0.72 by widely employing IGRs, $\mathcal{R}_0$ decreases to $\mathcal{R}_0 = 1.04$, and there exists a sharp decline in both A_T and A_U after their first peaks at around time $t_T \approx 254$

day and $t_U \approx 261$ day, respectively (red solid curve). When most larvae are treated with IGRs, for instance, at the level $q = 0.86$, the solution $(A_T(t), A_U(t))$ goes to zero with $\mathcal{R}_0 = 0.62 < 1$, which indicates the pest population can be controlled and further eradicated gradually (green dotted curve).



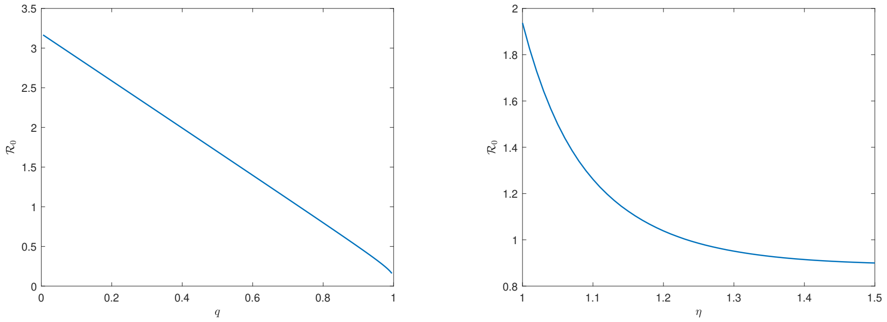
(a) A_T

(b) A_U

Fig. 3 Solution simulations in different treated fractions q. The number of treated and unregulated individuals are plotted against time, respectively. The blue dash, red solid, and green dotted curves in both (a) and (b) represent the cases $q = 0.22, 0.72, 0.86$, respectively.

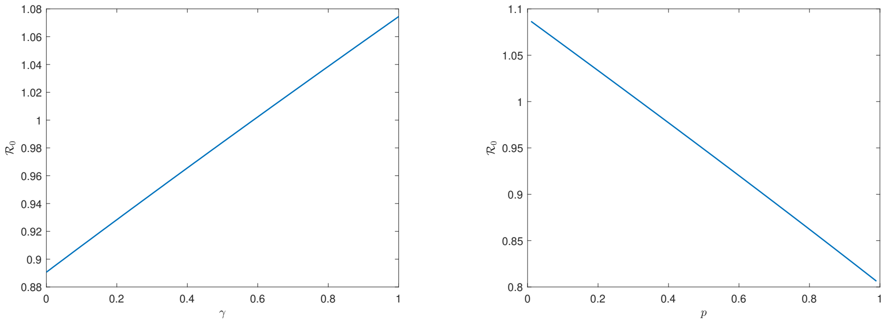
Next, we explore the relationship between $\mathcal{R}_0$ and system parameters to evaluate the cost-effectiveness of IGRs. Figure 4(a) shows that $\mathcal{R}_0$ is a decreasing function of q on the interval $(0, 1)$. It further indicates that increasing the fraction of larvae treated with IGRs is effective for pest control, which is consistent with the numerical observation presented in Figure 3. Recall that parameter η denotes the direct consequence of the use of IGR-treatment on *T. granarium*. We see from Figure 4(b) that it could first decrease $\mathcal{R}_0$ very quickly when it varies in the interval $(1, 1.1)$. However, the relative contribution of increasing η on reducing $\mathcal{R}_0$ becomes smaller when η becomes larger. To measure the efficacy of IGRs on suppressing the fecundity of treated adults (γ), Figure 4(c) shows that $\mathcal{R}_0$ is an increasing function of γ, which indicates that fecundity reduction of adult individuals developing in the IGR-treated environment may help to control the outbreak risk of *T. granarium* on stored products. Figure 4(d) plots the change of $\mathcal{R}_0$ in response to the removal rate. Here, we assume each IGR-treatment share the same removal rate $p_j = p$ for simplicity. Clearly, $\mathcal{R}_0$ gets smaller and drops blow the critical value 1 by increasing the removal rate.

In reality, it is important to propose optimal releasing strategies for pest control. For a given scenario, for instance, suppose that the resource allocation for the control is fixed in one period ω with the same removal rates $p_j = p$, the challenge lies in how to propose an optimal releasing frequency N and set the initial date of the first treatment t_1 in the pest control scheme. For that purpose, Figure 5 is produced. Figures 5(a) and (b) show the number of treated individuals $A_T(t)$ and unregulated ones $A_U(t)$ under three different frequencies: (i) the low frequency case where the treatments are released approximately 91 days (that is, $N = 4$ and $\Delta t \approx 91$ days), we have $\mathcal{R}_0 = 1.25$ (blue dash curve); (ii) the medium frequency case where the treatments are released



(a) $\mathcal{R}_0$ *vs* q on the range $(0, 1)$

(b) $\mathcal{R}_0$ *vs* η on the range $(1, 1.5)$



(c) $\mathcal{R}_0$ *vs* γ on the range $(0, 1)$

(d) $\mathcal{R}_0$ *vs* p on the range $(0, 1)$

Fig. 4 $\mathcal{R}_0$ *versus* system parameters. Other parameters are: (a) $\eta = 1.2$, $p = 0.5$, $\gamma = 0.8$, $N = 12$, $t_1 = 4$; (b) $q = 0.72$, $p = 0.5$, $\gamma = 0.8$, $N = 12$, $t_1 = 4$; (c) $q = 0.72$, $\eta = 1.2$, $p = 0.5$, $N = 12$, $t_1 = 4$; (d) $q = 0.75$, $\eta = 1.2$, $\gamma = 0.8$, $N = 12$, $t_1 = 4$.

monthly ($N = 12$ and $\Delta t \approx 30$ days), we compute $\mathcal{R}_0 = 1.16$ (red solid curve); (iii) the high frequency case where the treatments are released bi-weekly with $N = 26$ and $\Delta t \approx 14$ days, we obtain $\mathcal{R}_0 = 1.08$ (green dotted curve). Clearly, we see that increasing the release frequency directly results in smaller net reproduction number and reduced pest population sizes. For example, by comparing the first peak value under three different frequencies ($A_T^{N4} = 48.97 > A_T^{N12} = 24.59 > A_T^{N26} = 10.91$), there is a notable decline in treated class when the releasing number N gets larger (Figure 5(a)). Nevertheless, we also notice that the increase in the number of IGR-treatments does not have a significant impact on the population control of unregulated class (Figure 5(b)). Figure 5(c) plots the relationship between the number of IGR releases in one period (N) and the pest outbreak risk ($\mathcal{R}_0$). It illustrates that, in general, increasing the IGR-implement frequency reduces pest outbreak risk (measured in $\mathcal{R}_0$). Even though the general tendency of $\mathcal{R}_0$ with respect to N goes downward if the IGR-implement frequency N keeps increasing, the change of $\mathcal{R}_0$ is non-monotone. On the other hand, we also carry out a simulation to explore the impact of the first releasing time instant t_1 on $\mathcal{R}_0$, and plot the numerical result in Figure 5(d). $\mathcal{R}_0$

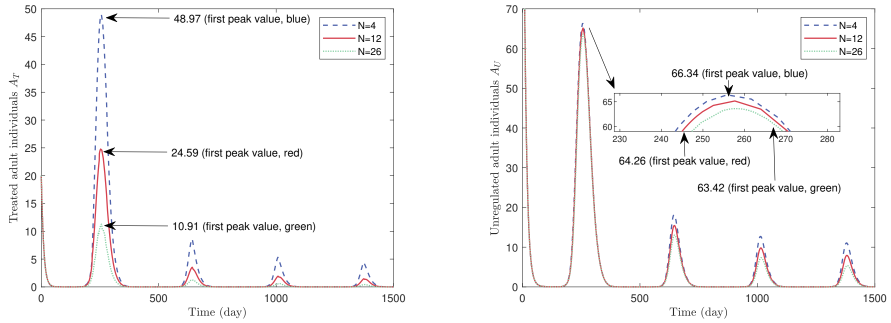
always stays above the critical value 1, which makes sense that the eradication of *T. granarium* is impossible by just changing the first implement time, but meanwhile $\mathcal{R}_0$ fluctuates in a wave-like pattern as we choose different time instants for the first IGR treatment. Figure 5(e) numerically evaluates the joint impacts of releasing frequency N and the first implement time t_1 on $\mathcal{R}_0$. We observe that when the implement frequency is low, the choice of t_1 might be very crucial on determining the outbreak risk $\mathcal{R}_0$. However, as N gets larger, the relative contribution of t_1 becomes smaller. The observation indicates that when N is small, it becomes an important issue to carefully select the initial implement date t_1.

5 Discussion

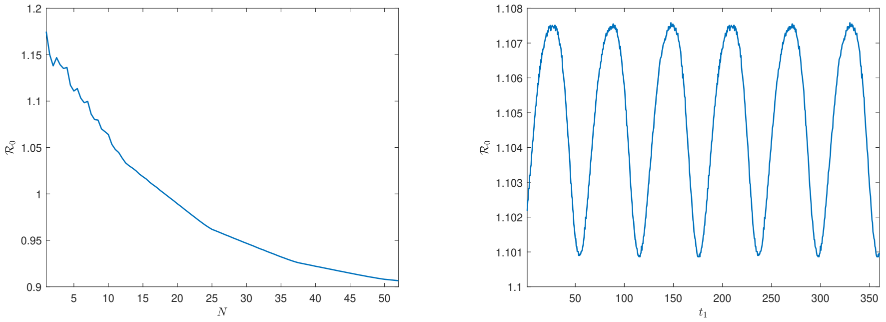
In this paper, we formulate a stage-structure pest-control model (7)-(8) where impulsive IGR-treatments occur within time-varying developmental durations of pest species. More precisely, we consider the IGR-treated larval pests into two classes: individuals that can and can not successfully develop into the adult stage. The age-structured modeling framework is employed with impulsive culling. However, careful arguments are needed to derive the overall survival probability of larvae subject to IGR-treatments (expression (9)). Another modeling challenge is posed by the time-varying parameters, in particular, the time-dependent maturation durations. The model becomes a periodic system when the ambient environment is assumed to change periodically. Under mild assumptions on pest growth and IGR efficacy, we define the net reproduction number $\mathcal{R}_0$ for the model system, and further establish the threshold dynamics in terms of $\mathcal{R}_0$: when $\mathcal{R}_0 > 1$, both treated and unregulated pest individuals persist and fluctuate periodically, when $\mathcal{R}_0 \leq 1$, the pest population can be eradicated in the environment.

Numerical simulations are designed to assess the impact of IGRs on *T. granarium* population growth. Model parameters are first estimated through given temperatures, the long-term behaviors of model solutions are presented under different scenarios, and the relationship between $\mathcal{R}_0$ and selected parameters is quantitatively investigated. Further simulations are focusing on the impact of various factors in the IGR control strategy, including the fraction of larvae that has been treated q, efficacy of IGRs on regulating pest growth η, the first releasing time instant t_1, and the number of releases N within one period. All these factors can have great impact on the net reproduction number $\mathcal{R}_0$, as well as the population size. One interesting insight observed from simulations is that for the low implement frequency of IGR, an appropriate initial date of applying the first IGR-treatment should be carefully designed, which is very sensitive to the periodic model parameters. However, when the implement occurs frequently enough, the effect of seasonality on determining the initial IGR releasing date could be ignored.

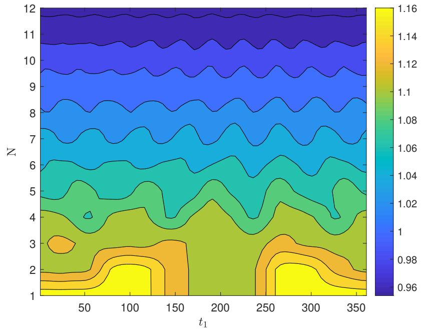
The mechanistic model in this paper can serve as a starting point to design optimal control IGR programs. It may also be extended when other control measures, for example, other insecticides are employed in an integrated pest management program [18, 29, 30]. Further refinements on the model system may include other factors of IGR efficacy on regulating pest growth, for example, the individuals produced by



(a) A_T with different N (b) A_U with different N



(c) $\mathcal{R}_0$ *vs* N on the range $(0, 52)$ (d) $\mathcal{R}_0$ *vs* t_1 on the range $(1, 365)$



(e) $\mathcal{R}_0$ *vs* (t_1, N)

Fig. 5 Effects of frequency and timing of IGR-treatments on pest control. The number of treated and unregulated individuals are plotted against time, respectively. The blue dash, red solid, and green dotted curves in both (a) and (b) represent the cases $N = 4, 12, 26$, respectively. Other parameters are: (a) and (b) $q = 0.68$, $\eta = 1.2$, $\gamma = 0.8$, $p = 0.5$, $t_1 = 4$; (c) $q = 0.72$, $\eta = 1.2$, $\gamma = 0.8$, $p = 0.5$, $t_1 = 4$; (d) $q = 0.72$, $\eta = 1.2$, $\gamma = 0.8$, $p = 0.5$, $N = 6$; (e) $q = 0.72$, $\eta = 1.2$, $\gamma = 0.8$, $p = 0.5$.

IGR treated insects may have different life cycles from those produced by unregulated ones. Other seasonal effects on population growth could also be incorporated [10], including the diapause period when the environmental conditions become unfavorable and individual development is suspended. In that case, designing an effective control releasing scheme, in particular, determining appropriate IGR releasing time instants would be very sensitive to the duration of diapause period.

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