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Research Article

An impulsively controlled pest management model with n predator species and a common prey

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ABSTRACT

This paper investigates the dynamics of a competitive single-prey n-predators model of integrated pest management, which is subject to periodic and impulsive controls, from the viewpoint of finding sufficient conditions for the extinction of prey and for prey and predator permanence. The per capita death rates of prey due to predation are given in abstract, unspecified forms, which encompass large classes of death rates arising from usual predator functional responses, both prey-dependent and predator-dependent. The stability and permanence conditions are then expressed as balance conditions between the cumulative death rate of prey in a period, due to predation from all predator species and to the use of control, and to the cumulative birth rate of prey in the same amount of time. These results are then specialized for the case of prey-dependent functional responses, their biological significance being also discussed.

1. Introduction

Recently, impulsively perturbed predator–prey models have been employed by many researchers to discuss the efficiency of integrated pest management strategies (see, for instance, Jiao et al., 2008; Liu et al., 2004; Tang et al., 2005; Mailleret and Grognard, 2009). Usually, a combination of a biological control, consisting in the release of natural predators of the prey (pest), and of a chemical control, consisting in pesticide spraying, is used, possibly together with an epidemiological control, consisting in the release of infective pest individuals, being supposed that these controls occur in periodic pulses. Further developments include considering models with stage structure for the predator (Georgescu and Zhang, 2010), delay due to pest hatching (Zhang et al., 2008), state-dependent impulsive perturbations (Tang and Cheke, 2005), age structure and defence mechanisms for pests (Zhang and Georgescu, 2010), and patch structure (Yang and Tang, 2009). Another direction was considering higher-dimensional food chains (Baek, 2010), multiple prey species (Georgescu, 2011), and multiple predator species (Pei et al., 2005). For a discussion on the optimal control of three-dimensional food chains, see Apreutesei (2011, 2012).

To understand the nature of predator–prey interactions, it is of paramount importance to quantify the effects of predation upon the growth rates of the prey and predator classes, respectively. Ultimately, for predator–prey models quantifying control problems, the predation rate determines the extent to which the prey population can be regulated and the success of the predation-based biocontrol strategy.

In this regard, the canonical form of a predator–prey interaction can be expressed as

$$\begin{cases} \dfrac{dN}{dt}(t) = N(t)f(N(t)) - P(t)F(N(t),P(t)) - d_N(N(t))N(t) \\ \dfrac{dP}{dt}(t) = P(t)G(N(t),P(t)) - d_P(P(t))P(t), \end{cases}$$

where $N = N(t)$ and $P = P(t)$ are the density of prey and predator, respectively, $f = f(N)$ is the per capita growth rate of the prey, $F = F(N, P)$ is the functional response of the predator, that is, the density of prey individuals consumed by a single predator per unit time and $G = G(N, P)$ is the numerical response of the predator, that is, the per capita growth rate of the predator class as a result of predation. Also, $d_N(N)$ and $d_P(P)$ are the natural mortalities of prey and predator, respectively.

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Following the standard Lotka–Volterra reasoning, one often assumes that the growth of the predator population is proportional with the amount of prey ingested, which leads to the numerical response being expressed as $G(N, P) = eF(N, P)$, the constant e being thought as an "efficiency" constant. If $F = F(N)$ (that is, the functional response depends only on prey density), F is termed "prey-dependent", while if $F = F(N, P)$ (that is, the functional response depends on both prey and predator density), F is termed "predator-dependent", as the dependence on prey density is implicit. In the particular case in which $F = F(N/P)$ (that is, F depends on predator density through the ratio between prey and predator density), F is termed "ratio-dependent", the above terminology being introduced in Arditi and Ginzburg (1989). Also, one may denote $F(N, P) = NF_1(N, P)$, F_1 being the per capita death rate of prey due to predation.

A comparative analysis of several functional responses has been carried out in Skalski and Gilliam (2001), a case for predator-dependence being constructed. See also Ginzburg and Colyvan (2004), which point out several fallacies of both prey-dependent functional responses and predator-dependent functional responses (no predator interference, dealing with intrinsically different time scales for consumption and reproduction for prey dependence, perfect resource sharing for ratio dependence), McCallum (2000) for a modelling viewpoint and Jeschke et al. (2002), Křivan and Vrkoč (2004) for other comparative views of functional responses with a particular stress on the role of prey handling.

Recent investigations show that in typical food webs, the prey has to face many types of predators. Investigating a total of 92 food webs, Schoener (1989) found an average of 2.8 predator species preying on each prey species, a close figure (3.2) being obtained by Cohen et al. (1986). Studying a particular desert ecosystem (Coachella Valley), Polis (1991) identified a food web totalling a few thousand species which averages 9.6 predator species per prey species. See also Sih et al. (1998) for a discussion on the emergent effects of multiple predators on a single prey (risk reduction, caused by predator–predator interactions, and risk enhancement, caused by conflicting prey responses to multiple predators). Discussing the suppression of the pea aphid *Acyrtosiphon pisum*, pest of the alfalfa (lucerne) crop *Medicago sativa*, Cardinale et al. (2003) found out that when all its three natural enemies, the coccinnelid beetle *Harmonia axyridis*, the damsel bug *Nabis* sp. and the parasitic wasp *Aphidius ervi* were present, the combined effect was more than predicted from summing the impact of each species alone, which validates the view that biological control can be more effective under a multiple predator structure. In this regard, it has been suggested in Tylianakis and Romo (2010) that a diverse predator structure may be more effective when the prey has a complex life cycle and is patchily distributed in space and time, which narrows the effectiveness of this approach to arthropod control in heterogeneous environments.

The remaining part of this paper is organized as follows. In Section 2, we introduce the mathematical model to be discussed and indicate the biological relevance of the assumptions on which the model is based upon. Several auxiliary notions relating to the Floquet theory of impulsively perturbed differential systems are given in Section 3, where the biological well-posedness of the model is also established. In Section 4, several quantitative properties of the so-called prey-free periodic solution are indicated and the relationship between its stability properties and the success of the pest management strategy is pointed out. Sufficient conditions for the local and global stability of the prey-free periodic solution are established in Section 5. Section 6 is devoted to discussing the permanence of the system, while in Section 7 the previously obtained results are contextualized for the case of prey-dependent functional responses. Finally, a biological interpretation of our results is provided in Section 8, together with a few concluding remarks.

2. The Mathematical Model and its Biological Well-posedness

Following the previously mentioned considerations, we are now ready to formulate the mathematical model which is of concern in this paper in the following form

$$\begin{cases} \dfrac{dx}{dt}(t) = x(t)(r - ax(t)) \\ \quad -\displaystyle\sum_{i=1}^{n} x(t)y_i(t)\varphi_i(x(t), \mathbf{y}(t)) & t \neq (n+l-1)T, \quad t \neq nT; \\ \dfrac{dy_i}{dt}(t) = c_i x(t)y_i(t)\varphi_i(x(t), \mathbf{y}(t)) \\ \quad -d_i y_i(t) & t \neq (n+l-1)T, \quad t \neq nT, \\ & 1 \leq i \leq n; \\ \Delta x(t) = -\delta_x x(t), & t = (n+l-1)T; \\ \Delta y_i(t) = -\delta_i y_i(t), & t = (n+l-1)T, \\ & 1 \leq i \leq n; \\ \Delta x(t) = 0, & t = nT; \\ \Delta y_i(t) = \mu_i, & t = nT, \quad 1 \leq i \leq n. \end{cases} \tag{S}$$

In the above model, $x = x(t)$ represents the density of prey, being understood that all prey individuals belong to the same species, while $y_i = y_i(t)$ represents the density of the predator species i, $1 \leq i \leq n$, and $\mathbf{y} = (y_1, y_2, \ldots, y_n)$ is the vector of all predator densities, where $n \in \mathbb{N}^*$ represents the number of predator species. Generally, bold letters will be used in this paper to denote vector-valued functions or their particular values. The constants r and a denote the intrinsic birth rate of the prey and the effects of intraspecific competition among the prey individuals, respectively, while the constants c_i and d_i, $1 \leq i \leq n$, represent the efficiency of prey conversion into newborn predators of species i and the natural mortality of predator species i, respectively. Also, T is the common periodicity of the impulsive perturbations and $0 < l < 1$ is a parameter used to describe the time lag lT between predator release and pesticide spraying, which do not occur simultaneously. Here, $\Delta\psi(t) = \psi(t+) - \psi(t)$, $\psi \in \{x, y_i, 1 \leq i \leq n\}$, represent the instantaneous jumps of the populations sizes each time the controls are used, $0 \leq \delta_x < 1$ and $0 \leq \delta_i < 1$, $1 \leq i \leq n$, are the fixed proportions of the prey and predator populations, respectively, which are removed from the environment each time the pesticides are sprayed and μ_i is the constant amount of predators from species i, $1 \leq i \leq n$, which are released each time.

The prey death rates due to predation by predator species i, $\varphi_i : [0, \infty)^{n+1} \to [0, \infty)$, $\varphi_i \in C([0, \infty)^{n+1})$, $1 \leq i \leq n$, are assumed to satisfy the following monotonicity assumptions.

(H0) For all $1 \leq i \leq n$, $(x, \mathbf{y}) \to xy_i\varphi_i(x, \mathbf{y})$ is locally Lipschitz.
(H1) For all $1 \leq i \leq n$, $x \to \varphi_i(x, \mathbf{y})$ is nonincreasing for fixed $\mathbf{y} \in [0, \infty)^n$.
(H2a) For all $1 \leq i \leq n$, $y_i \to y_i\varphi_i(x, \mathbf{y})$ is nondecreasing for fixed x and y_k, $k \neq i$.
(H2b) For all $1 \leq i \leq n$, $y_j \to \varphi_i(x, \mathbf{y})$ is nonincreasing for fixed x and y_k, $k \neq j$, for all $1 \leq j \leq n$.

Hypothesis (H1), (H2a), (H2b) are satisfied, for instance, if the functional responses of the predators species are prey-dependent of Holling type I, for which $\varphi(x, \mathbf{y}) = a$, of Holling type II, for which $\varphi(x, \mathbf{y}) = (a/1 + bx)$, or of Holling type IV, for which $\varphi(x,$

$\mathbf{y}) = (a/b + cx + x^2)$, or of Ivlev type, for which $\varphi(x, \mathbf{y}) = (a(1 - e^{-kx})/x)$. They are also satisfied if the functional responses are predator-dependent of Beddington–deAngelis type, for which $\varphi(x, \mathbf{y}) = (b/1 + kx + \sum_{j=1}^{n} k_j y_j)$. Hypothesis (H1) amounts to the fact that if the prey density increases and the amount of predators remains constant, then the death rate of the prey decreases, due to the saturation of predators. Hypothesis (H2a) amounts to the fact that the death rate of prey due to predation from species i increases if the population size of species i increases. Hypothesis (H2b) amounts to the fact that predators from a given species hinder predators from all species (that is, there is intra- and interspecies competition between predators, rather than cooperation).

3. Preliminaries

As our approach relies on the use of Floquet theory and of comparison estimations for impulsively perturbed systems of ordinary differential equations, we shall hereby indicate for future reference several auxiliary results pertaining to the above. We first give a result which provides estimations for the solution of a system of differential inequalities.

Lemma 1. *(Bainov and Simeonov, 1993) Let the function $u \in PC^1(\mathbb{R}_+, \mathbb{R})$ satisfy the inequalities*

$$\begin{cases} \dfrac{du}{dt} \leq (\geq) p(t)u(t) + f(t), & t \neq \tau_k, \ \ t > 0; \\ u(\tau_k+) \leq (\geq) d_k u(\tau_k) + h_k, & k \geq 0; \\ u(0+) \leq (\geq) u_0, \end{cases} \tag{1}$$

where $p, f \in PC(\mathbb{R}_+, \mathbb{R})$ and $d_k \geq 0$, h_k and u_0 are constants and $(\tau_k)_{k\geq 0}$ is an increasing sequence of positive real numbers. Then, for $t > 0$,

$$\begin{aligned} u(t) \ \leq (\geq) u_0 \Big(\prod_{0<\tau_k<t} d_k \Big) e^{\int_0^t p(s)ds} \\ + \int_0^t \Big(\prod_{s\leq\tau_k<t} d_k \Big) e^{\int_s^t p(\tau)d\tau} f(s)ds \\ + \sum_{0<\tau_k<t} \Big(\prod_{\tau_k<\tau_j<t} d_j \Big) e^{\int_{\tau_k}^t p(\tau)d\tau} h_k. \end{aligned}$$

In the above, by $PC(\mathbb{R}_+, \mathbb{R})$ ($PC^1(\mathbb{R}_+, \mathbb{R})$) is meant the class of real piecewise continuous (real piecewise continuously differentiable) functions defined on $\mathbb{R}_+$. For other results on impulsive differential equations, see Bainov and Simeonov (1993) or Benchohra et al. (2006).

It is now possible to prove that the Cauchy problem with strictly positive initial data is well-posed for our system (S), that is, solutions $(x(\cdot), \mathbf{y}(\cdot))$ starting with strictly positive initial data remain strictly positive and bounded on their whole domains, the strict positivity of a vector being understood component-wise.

Lemma 2. *The positive orthant $(\mathbb{R}_+^*)^{n+1}$ is an invariant region for the system (S).*

The proof of Lemma 2 is given in the Appendix. See also Henderson and Luca (2011, 2012) for related results.

We are now ready to show that all solutions of (S) starting in $(\mathbb{R}_+^*)^{n+1}$ remain bounded and are actually defined on the whole $\mathbb{R}_+$.

Lemma 3. *All solutions $(x(\cdot), \mathbf{y}(\cdot))$ of (S) with initial data $(x(0), \mathbf{y}(0)) \in (\mathbb{R}_+^*)^{n+1}$ are bounded and defined on $\mathbb{R}_+$.*

The proof of Lemma 3 is given in the Appendix. Note that, as seen from this proof, y_i, $1 \leq i \leq n$ are ultimately bounded by constants not depending on their initial population sizes.

We now state a local stability (or lack thereof) result for impulsive and periodic systems of ordinary differential equations which will be used in Section 5 to discuss the stability properties of the so-called prey-free periodic solution. To this purpose, let us consider the impulsive linear differential system

$$\begin{cases} \dfrac{dX}{dt}(t) = A(t)X(t), & t \neq \tau_k, \ \ t \in \mathbb{R}; \\ \Delta X = B_k X, & t = \tau_k, \ \ \tau_k < \tau_{k+1}, \ \ k \in \mathbb{Z}. \end{cases} \tag{2}$$

under the following hypotheses.

(A1) $A(\cdot) \in PC(\mathbb{R}, M_n(\mathbb{R}))$ and there is $T > 0$ such that $A(t+T) = A(t)$ for all $t \geq 0$.
(A2) $B_k \in M_n(\mathbb{R})$, $\det(I_n + B_k) \neq 0$ for $k \in \mathbb{Z}$.
(A3) There is $q \in \mathbb{N}^*$ such that $B_{k+q} = B_k$, $\tau_{k+q} = \tau_k + T$ for $k \in \mathbb{Z}$.

Let now $\Phi(t)$ be a fundamental matrix of (2). Then there is a unique nonsingular matrix $\mathcal{M} \in M_n(\mathbb{R})$ such that $\Phi(t+T) = \Phi(t)\mathcal{M}$ for all $t \in \mathbb{R}$, which is called the monodromy matrix of (2) corresponding to Φ. All monodromy matrices of (2) corresponding to different Φ's, being similar, have the same eigenvalues $\lambda_1, \lambda_2, \ldots, \lambda_n$, which are called the Floquet multipliers of (2). These eigenvalues determine the stability of (2), as seen in the following stability result, where by elementary divisors of a square matrix we understand the characteristic polynomials of its Jordan blocks.

Lemma 1. *(Bainov and Simeonov, 1993) Suppose that conditions (A1)-(A3) hold. Then*

(i) *The system (2) is stable if and only if all Floquet multipliers λ_k, $1 \leq k \leq n$ satisfy $|\lambda_k| \leq 1$ and if $|\lambda_k| = 1$, then to λ_k there corresponds a simple elementary divisor.*
(ii) *The system (2) is asymptotically stable if and only if all Floquet multipliers λ_k, $1 \leq k \leq n$ satisfy $|\lambda_k| < 1$.*
(iii) *The system (2) is unstable if there is a Floquet multiplier λ_k such that $|\lambda_k| > 1$.*

See also the paper by Klausmeier (2008) on the use of Floquet theory in ecological and evolutionary modeling, which identifies three potentially important uses: defining fitness of structured populations in periodic environments, calculating invasion criteria for interacting structured populations in periodic environments and testing the stability of a limit cycle.

4. The Prey-free Periodic Solution

A fact with significant consequences for the dynamics of (S) is that the predators are never in short supply, due to the periodic predator release, but the prey may tend to extinction, since there is no periodic prey release. When there are no prey individuals, the equations for the predator species decouple and we are led to consider systems of type

$$\begin{cases} \dfrac{dy}{dt}(t) = -dy(t), & t \neq (n+l-1)T, \ \ t \neq nT \\ \Delta y(t) = -\delta y(t), & t = (n+l-1)T; \\ \Delta y(t) = \mu, & t = nT; \\ & y(0+) = y_0, \end{cases} \tag{3}$$

where $(d, \delta, \mu) \in \{(d_i, \delta_i, \mu_i); 1 \leq i \leq n\}$. It is seen that the system constructed with the first three equations in (3) has a periodic solution which attracts all solutions of (3) starting with strictly positive

y_0, as observed in the following Lemma (Lemma 4.2 of Georgescu and Moroşanu, 2008).

Lemma 2. *(Georgescu and Moroşanu, 2008) The system constructed with the first three equations in (3) has a T-periodic solution $y^*_{d,\delta,\mu}$, given by*

$$y^*_{d,\delta,\mu} = \begin{cases} \dfrac{\mu}{1-e^{-dT}(1-\delta)} e^{-d(t-nT)}, & t \in (nT, (n+l)T] \\ \dfrac{\mu}{1-e^{-dT}(1-\delta)} e^{-d(t-nT)}(1-\delta), & t \in ((n+l)T, (n+1)T]. \end{cases} \tag{4}$$

With this notation, the following properties are satisfied.

(i) $\int_0^T y^*_{d,\delta,\mu}(t)dt = \frac{\mu}{d(1-e^{-dT}(1-\delta))}[(1-e^{-dlT}) + (1-\delta)(e^{-dlT} - e^{-dT})]$.

(ii) $\lim_{t\to\infty} |y(t) - y^*_{d,\delta,\mu}(t)| = 0$ *for all solutions $y(t)$ of (3) starting with strictly positive y_0.*

(iii) $\sup_{t\geq 0} |y^*_{d,\delta,\mu}(t) - y^*_{\tilde{d},\delta,\mu}(t)| \leq f_2(d, \tilde{d}; T, a, \delta, \mu)$, *with* $\lim_{\tilde{d}\to d} f_2(\tilde{d}, d; T, a, \delta, \mu) = 0$.

When the prey species is extinct, the system consisting of the first $n+1$ equations of (S) has a periodic solution $\mathbf{E}^* = (0, \mathbf{y}^*)$, which will be called in what follows the prey-free periodic solution. Here, $\mathbf{y}^*$ is the n-dimensional vector whose ith component is $y^*_{d_i,\delta_i,\mu_i}$, denoted also in what follows by y^*_i. Although in concrete situations the desired outcome of an IPM is not necessarily the complete extinction of all pests, as this may be infeasible from a practical point of view, or may damage the ecosystem, but the stabilization of their total population size under an economically significant threshold called the economic injury level (EIL), it is not a large stretch of imagination to interpret the success of our IPM strategy in terms of the stability properties of $\mathbf{E}^*$. That is, if $\mathbf{E}^*$ is globally asymptotically stable, then the pests can be eradicated irrespective of their initial population sizes, while if $\mathbf{E}^*$ is only locally asymptotically stable, then the pests can be eradicated only in favorable circumstances.

5. Local and Global Stability Results

We shall now search for sufficient conditions for the local and global stability of $\mathbf{E}^*$. In what follows, let us denote $\boldsymbol{\varepsilon} = (\varepsilon, \varepsilon, \ldots, \varepsilon)$ and let $M_1, M_2, \ldots, M_n$ be ultimate boundedness constants for $y_1, y_2, \ldots, y_n$ given by Lemma 3. We shall denote by P and P_M, respectively, cumulative death rates of prey due to predation under certain specific circumstances,

$$\begin{aligned} P(x, \mathbf{y}) &= \sum_{i=1}^n y_i \varphi_i(x, \mathbf{y}), \\ P_M(x, \mathbf{y}) &= \sum_{i=1}^n y_i \varphi_i(x, M_1, \ldots, M_{i-1}, y_i, M_{i+1}, \ldots, M_n) \end{aligned}$$

from which we see that

$$\begin{aligned} P(0, \mathrm{y}^*(t)) &= \sum_{i=1}^n y_i^*(t)\varphi_i(0, \mathrm{y}^*(t)) P_M\left(\frac{r}{a} + \varepsilon, \mathrm{y}^*(t) - \boldsymbol{\varepsilon}\right) \\ &= \sum_{i=1}^n (y_i^*(t) - \varepsilon)\varphi_i \\ &\quad \left(\frac{r}{a} + \varepsilon, M_1, \ldots, M_{i-1}, y_i^*(t) - \varepsilon, M_{i+1}, \ldots, M_n\right). \end{aligned}$$

Note that if φ_i depends only on the size of the prey population and of the size of the ith predator population, then $P_M \equiv P$. Also, P_M is nonincreasing in ε.

Theorem 1. *The prey-free periodic solution $\mathbf{E}^*$ is locally asymptotically stable if*

$$\int_0^T P(0, \mathrm{y}^*(t))dt - \ln(1-\delta_x) > rT. \tag{5}$$

Further, $\mathbf{E}^*$ is globally asymptotically stable if

$$\int_0^T P_M\left(\frac{r}{a}, \mathrm{y}^*(t)\right) dt - \ln(1-\delta_x) > rT. \tag{6}$$

Proof. To discuss the local stability of $\mathbf{E}^*$, we shall use the method of small amplitude perturbations. To this purpose, let us denote

$$x(t) = u(t), \quad y_i(t) = v_i(t) + y_i^*(t), \quad 1 \leq i \leq n,$$

where u and v_i, $1 \leq i \leq n$, are understood to be small amplitude perturbations. The linearization of (S) is then given by

$$\begin{cases} \dfrac{du}{dt}(t) = u(t)(r - P(0, \mathrm{y}^*(t)), & t \neq (n+l-1)T, \quad t \neq nT; \\ \dfrac{dv_i}{dt}(t) = c_i u(t) y_i^*(t)\varphi_i(0, \mathbf{y}^*(t)) - d_i v_i(t) & t \neq (n+l-1)T, \quad t \neq nT, \\ & 1 \leq i \leq n; \\ \Delta u(t) = -\delta_x u(t), & t = (n+l-1)T; \\ \Delta v_i(t) = -\delta_i v_i(t), & t = (n+l-1)T, \\ & 1 \leq i \leq n; \\ \Delta u(t) = \Delta v_i(t) = 0, & t = nT, \quad 1 \leq i \leq n. \end{cases} \tag{7}$$

We need now study the stability of the null solution of (7). Let Φ_L be a fundamental matrix of the differential system constructed with the first $n+1$ equations of (7). Consequently, Φ_L satisfies

$$\frac{d\Phi_L}{dt}(t) = A(t)\Phi_L(t),$$

where

$$A(t) = \begin{pmatrix} r - P(0, \mathrm{y}^*(t)) & 0 & 0 & \ldots & 0 \\ c_1 y_1^*(t)\varphi_1(0, \mathrm{y}^*(t)) & -d_1 & 0 & \ldots & 0 \\ c_2 y_2^*(t)\varphi_2(0, \mathrm{y}^*(t)) & 0 & -d_2 & \ldots & 0 \\ \vdots & \vdots & \vdots & \ldots & \vdots \\ c_n y_n^*(t)\varphi_n(0, \mathrm{y}^*(t)) & 0 & 0 & \ldots & -d_n \end{pmatrix}.$$

A fundamental matrix Φ_L of (7) which satisfies $\Phi_L(0) = I_{n+1}$ is a lower triangular matrix with

$$\begin{aligned} (\Phi_L(t))_{1,1} &= e^{\int_0^t r - P(0, \mathrm{y}^*(s))ds} \\ (\Phi_L(t))_{i,i} &= e^{-d_{i-1}t}, \quad 2 \leq i \leq n+1. \end{aligned}$$

Since

$$u(t+) = (1-\delta_x)u(t), \quad v_i(t+) = (1-\delta_i)v_i(t),$$

for $t = (n+l-1)T$, and

$$u(t+) = u(t), \quad v_i(t+) = v_i(t),$$

for $t = nT$, the monodromy matrix

$$\mathcal{M} = \mathrm{diag}[1-\delta_x, 1-\delta_1, 1-\delta_2, \ldots, 1-\delta_n]\Phi_L(T) \tag{8}$$

is also lower diagonal. Its eigenvalues, found on the main diagonal, are

$$\begin{aligned}\lambda_1 &= (1-\delta_x)e^{\int_0^T r - P(0,\mathbf{y}^*(t))dt} > 0,\\ \lambda_i &= (1-\delta_{i-1})e^{-d_{i-1}T} > 0; \quad 2 \le i \le n+1.\end{aligned}$$

As $\lambda_1 > 0$ and $\lambda_i \in (0, 1)$, $2 \le i \le n+1$, it follows that $\mathbf{E}^*$ is locally asymptotically stable provided that (5) holds.

We shall now prove that $\mathbf{E}^*$ is globally asymptotically stable provided that (6) holds. Due to (6), let us choose $\varepsilon > 0$ such that

$$\xi = (1-\delta_x)e^{\int_0^T r - P_M(\frac{r}{a}+\varepsilon, \mathbf{y}^*(t)-\boldsymbol{\varepsilon})dt} < 1.$$

Since $(dy_i/dt)(t) \ge -d_i y(t)$ for $1 \le i \le n$, it follows from the comparison lemma for systems of impulsively perturbed ordinary differential inequalities (see Bainov and Simeonov, 1993) that $y_i(t) \ge y_{i1}(t)$ for all $t \ge 0$ and $1 \le i \le n$, where y_{i1} satisfies

$$\begin{cases} \dfrac{dy_{i1}}{dt}(t) = -d_i y_{i1}(t), & t \ne nT,\ \ t \ne (n+l-1)T;\\ \Delta y_{i1}(t) = -\delta_i y_{i1}(t), & t = (n+l-1)T;\\ \Delta y_{i1}(t) = \mu_i, & t = nT;\\ y_{i1}(0+) = y_i(0+). \end{cases} \tag{9}$$

It then follows from the properties of y_i^* listed in Lemma 2 that $y_i(t) \ge y_{i1}(t) \ge y_i^*(t) - \varepsilon$ for t large enough; for the sake of simplicity, let us suppose that $y_i(t) \ge y_i^*(t) - \varepsilon$ for all $t \ge 0$. Similarly, since $(dx/dt)(t) \le x(t)(r - ax(t))$, it follows that $x(t) \le x_1(t)$ for all $t \ge 0$, where x_1 satisfies

$$\begin{cases} \dfrac{dx_1}{dt}(t) = x_1(t)(r - ax_1(t)), & t \ne (n+l-1)T;\\ \Delta x_1(t) = -\delta_x x_1(t), & t = (n+l-1)T;\\ x_1(0+) = x(0+). \end{cases} \tag{10}$$

Since $\limsup_{t\to\infty} x_1(t) \le (r/a)$, it then follows that $x(t) \le x_1(t) \le (r/a) + \varepsilon$ for t large enough; for the sake of simplicity, let us suppose that $x(t) \le (r/a) + \varepsilon$ for all $t > 0$. By the monotonicity assumptions on φ_i, it is seen that

$$\begin{aligned}\frac{dx}{dt}(t) &= x(t)(r - ax(t)) - \sum_{i=1}^{n} x(t)y_i(t)\varphi_i(x(t), \mathbf{y}(t)) \le x(t)\\ &\left(r - \sum_{i=1}^{n}(y_i^*(t)-\varepsilon)\varphi_i\left(\frac{r}{a}+\varepsilon, M_1, \ldots, M_{i-1}, y_i^*(t)-\varepsilon, M_{i+1}, \ldots, M_n\right)\right)\\ &\le x(t)\left(r - P_M\left(\frac{r}{a}+\varepsilon, \mathbf{y}^*(t)-\boldsymbol{\varepsilon}\right)\right)\end{aligned}$$

for all $t \ne (n+l-1)T$, $t \ne nT$ and consequently

$$\begin{cases} \dfrac{dx}{dt}(t) \le x(t)\left(r - P_M\left(\frac{r}{a}+\varepsilon, \mathbf{y}^*(t)-\varepsilon\right)\right), & t \ne (n+l-1)T,\ \ t \ne nT;\\ x(t+) = (1-\delta_x)x(t), & t = (n+l-1)T;\\ x(t+) = x(t), & t = nT. \end{cases}$$

By integrating the above inequality on $((n+l-1)T, (n+l)T]$, it is seen that

$$x((n+l)T) \le x((n+l-1)T)(1-\delta_x)e^{\int_0^T r - P_M((r/a)+\varepsilon, \mathbf{y}^*(t)-\boldsymbol{\varepsilon})dt},$$

that is, $x((n+l)T) \le x((n+l-1)T)\xi$. Then $x((n+l)T) \le x(lT)\xi^n$ and consequently

$$x((n+l)T) \to 0 \quad \text{for } n \to \infty. \tag{11}$$

Since

$$0 < x(t) < x((n+l-1)T)e^{rT} \quad \text{for } t \in ((n+l-1)T, (n+l)T],$$

it follows from (11) that $x(t) \to 0$ for $t \to \infty$.

We now prove that $y_i(t) - y_i^*(t) \to 0$ as $t \to \infty$ for all $1 \le i \le n$. To this purpose, let us denote

$$d_{i\varepsilon'} = d_i - c_i\varepsilon'\varphi_i(0, \mathbf{0})$$

and let us choose ε' such that $d_{i\varepsilon'} > 0$ for all $1 \le i \le n$. Since $x(t) \to 0$ for $t \to \infty$, it follows that there is $\tilde{T} > 0$ such that $0 < x(t) < \varepsilon'$ for $t \ge \tilde{T}$; without loss of generality, we may suppose that

$$0 < x(t) < \varepsilon' \quad \text{for } t \ge 0.$$

One then has

$$-d_i y_i(t) \le y_i'(t) \le -d_{i\varepsilon'} y_i(t)$$

for $t \ne (n+l-1)T$, $t \ne nT$. Let us denote

$$\tilde{y}_i^* = y^*_{d_{i\varepsilon'}, \delta_i, \mu_i}.$$

Using a comparison argument, it follows that $y_{i1}(t) \le y_i(t) \le y_{i2}(t)$ and $y_{i1}(t) - y_i^*(t) \to 0$, $y_{i2}(t) - \tilde{y}_i^*(t) \to 0$ as $t \to \infty$, where y_{i1} is as defined in (9) and y_{i2} is defined through a system similar to (9) with d_i replaced by $d_{i\varepsilon'}$.

Let now $\varepsilon_1 > 0$. It follows that

$$y_i^*(t) - \varepsilon_1 \le y(t) \le \tilde{y}_i^*(t) + \varepsilon_1$$

for t large enough. Since $\sup_{t\in[0,T]} |y_i^*(t) - \tilde{y}_i^*(t)| \to 0$ for $\varepsilon' \to 0$, $1 \le i \le n$ and ε_1 is arbitrary, it follows that $y_i(t) - y_i^*(t) \to 0$ as $t \to \infty$, which ends the proof of the global stability result. □

6. The Permanence of the System

We shall now study the permanence of (S). To this purpose, we introduce the following definition.

Definition 1. The system (S) is said to be permanent (uniformly persistent) if there are m, $M > 0$ such that for each solution of (S) with strictly positive initial data $x(0), y_i(0)$, $1 \le i \le n$, it follows that there is $T_0 > 0$ such that $m \le x(t), y_i(t) \le M$ for all $t \ge T_0$ and $1 \le i \le n$. Here, T_0 may depend upon the initial data, but m and M do not.

In biological terms, if (S) is permanent, then for sufficiently large t the pest and its predators will coexist without facing extinction or growing indefinitely, their population sizes varying between bounds not depending on the initial conditions. Obviously, the permanence of (S) excludes any kind of stability of the prey-free periodic solution and it is associated with a failure of our IPM strategy. For further information relating to the mathematical theory of persistence, see the comprehensive monograph of Smith and Thieme (2011). See also Teng et al. (2011), which show that, for a general class of impulsively perturbed models of Kolmogorov type, permanence implies the existence of periodic solutions.

The following result establishes that (5) is a threshold inequality, as far as the stability of (S) is concerned, in the sense that if the inequality with opposite sign is satisfied, then the prey-free

periodic solution $\mathbf{E}^*$ loses its stability and the system (S) becomes persistent.

Theorem 2. *The system (S) is permanent provided that*

$$\int_0^T P(0, y^*(t))dt - \ln(1-\delta_x) < rT. \tag{12}$$

Proof. Suppose that $(x(\cdot), \mathbf{y}(\cdot))$ is a solution of (S) which starts with strictly positive initial data $(x(0), \mathbf{y}(0))$. As previously noted, there is a constant $M>0$ not depending on the initial data such that $x(t)\le M$, $y_i(t)\le M$ for $t\ge 0$ and all $1\le i\le n$. Also, as done above, we note that $y_i(t) > y_i^*(t)-\varepsilon'$ for t large enough, for all $\varepsilon'\in(0,\ (\mu_i e^{-d_i T}(1-\delta)/1-e^{-d_i T}(1-\delta_i)))$. Consequently, $y_i(t)\ge m_{iy}$ for t large enough, where

$$m_{1y} = \frac{\mu_i e^{-d_i T}(1-\delta_i)}{1-e^{-d_i T}(1-\delta_i)} - \varepsilon'$$

and ε' is fixed as indicated above.

We then only need to find $\overline{m}$ such that $x(t)\ge \overline{m}$ for t large enough. Let us choose m and ε small enough, so that

$$0 < m < \min\left\{\frac{d_i}{c_i\varphi_i(0,\mathbf{0})}; 1\le i\le n\right\}, \quad m < \frac{r}{a}, \tag{13}$$

$$\theta = (1-\delta_x)e^{(r-am)T-\int_0^T P^*(m,y^*(t))dt} > 1, \tag{13}$$

where

$$P^*(m,y^*(t)) = \sum_{i=1}^n y^*_{d_i-c_i m\varphi_i(0,\mathbf{0})}(t)\varphi_i(m, y_1^*(t),\dots,$$
$$y^*_{d_i-c_i m\varphi_i(0,\mathbf{0})}(t),\dots,y_n^*(t)),$$

the choice of θ being possible due to (12). We first prove that there is $t_1>0$ such that $x(t_1)>m$. We shall argue by contradiction. Suppose that $x(t)\le m$ for all $t>0$ and let us choose $\eta>0$ such that

$$\theta' = (1-\delta_x)e^{(r-am)T-\int_0^T P^*_\eta(m,y^*(t))dt} > 1,$$

where

$$P^*_\eta(m,y^*(t)) = \sum_{i=1}^n (y^*_{d_i-c_i m\varphi_i(0,\mathbf{0})}(t)+\eta)\cdot\varphi_i(m, y_1^*(t)-\eta,\dots,$$
$$y^*_{d_i-c_i m\varphi_i(0,\mathbf{0})}(t)+\eta,\dots,y_n^*(t)-\eta),$$

the choice of θ' being possible due to the third inequality in (13). Let $1\le i\le n$. One then has

$$-d_i y_i(t) \le y_i'(t) \le -(d_i - c_i m\varphi_i(0,\mathbf{0}))y_i(t)$$

for $t\ne (n+l-1)T$, $t\ne nT$, while

$$y_i(t+) = (1-\delta_i)y_i(t) \quad \text{for } t=(n+l-1)T, \quad y_i(t+) = y_i(t)+\mu_i \quad \text{for } t=nT.$$

Consequently, there is $n\in\mathbb{N}$ such that $y_i^*(t)-\eta\le y_i(t)\le y^*_{d_i-c_i m\varphi_i(0,\mathbf{0})}(t)+\eta$ for $t\ge n_1 T$ and all $1\le i\le n$. One then has

$$\frac{dx}{dt}(t) \ge x(t)((r-am) - P^*_\eta(m,y^*(t)))$$

for $t\ne (n+l)T$, $t\ge n_1 T$, while

$$x(t+) = (1-\delta_x)x(t) \quad \text{for } t=(n+l-1)T.$$

By integrating the above on $((n+l-1)T,(n+l)T]$, $n\ge n_1+1$, one sees that

$$x((n+l)T) \ge x((n+l-1)T)\theta'. \tag{14}$$

Consequently, $x((n+k+l)T)\ge \theta'^k x((n+l)T)\to\infty$ as $k\to\infty$, which is a contradiction, since $x(t)\le m$ for all $t\ge 0$. As a result, there is $t_1>0$ such that $x(t_1)>m$.

If $x(t)\ge m$ for all $t\ge t_1$, there is nothing left to prove. Otherwise, $x(t_m^1)<m$ for some $t_m^1>t_1$. Let us denote $s_1=\inf\{t>t_1; x(t)<m\}$. If $s_1\ne (n+l-1)T$, then $x(s_1)=m$. If $s_1=(n+l-1)T$, then not necessarily $x(s_1)=m$, but $x(s_1)\in[m,(\frac{m}{/}1-\delta_x)]$. Note that it is not possible that $x(s)\le m$ for all $s>s_1$, so necessary $x(t_m^2)>m$ for some $t_m^2>s_1$. Let us denote $s_2=\inf\{t>s_1; x(t)>m\}$ and observe that necessarily $x(s_2)=m$.

By a similar argument, one may construct a sequence $(s_n)_{n\ge 2}$ such that

(1) $x(s_{2k+1})\in\left[m, \frac{m}{1-\delta_x}\right]$, $x(s_{2k})=m$.
(2) $x(s)\le m$ for $s\in(s_{2k+1}, s_{2k+2})$.
(3) $x(s)>m$ for $s\in(s_{2k}, s_{2k+1})$,

showcasing the fact that x oscillates about m.

We now show that $\overline{T} = \sup\{s_{2k}-s_{2k-1}; k\in\mathbb{N}^*\} < \infty$. Suppose that this is not the case. Then there is $(k_j)_{j\ge 1}$ such that $s_{2k_j}-s_{2k_j-1} > jT$. Consequently, in a way similar to the derivation of (14), it follows that

$$x(s_{2k_j}) \ge x(s_{2k_j-1})\theta'^{j+2}e^{-2rT},$$

which is a contradiction, as $\theta'^{j+2}\to\infty$ for $j\to\infty$ and $x(s_{2k})=m$. It then follows that

$$\frac{dx}{dt}(t) \ge x(t)\left(r-am-M\sum_{i=1}^n\varphi_i(0,\mathbf{0})\right)$$

for $t\in(s_{2k+1}, s_{2k+2})$, and consequently

$$x(s)\ge \tilde{m} \quad \text{for } s\in(s_{2k+1}, s_{2k+2}),$$

where

$$\tilde{m} = me^{\left(r-am-M\sum_{i=1}^n\varphi_i(0,\mathbf{0})\right)T}.$$

Putting $\overline{m}=\min(\tilde{m}, m)$, it follows that $x(t)\ge\overline{m}$ for t large enough, so the prey population is permanent, which ends the proof of the permanence result. □

7. Prey-dependent Functional Responses

Although readily interpretable from a biological viewpoint, inequalities (5), (6) and (12) might not be easily expressed in a more explicit form, especially for more complicated dependence of the functional responses upon the predator population sizes. However, in the particular case in which all functional responses are prey-dependent, the integrals involved in the above-mentioned conditions can be computed explicitly. That is, for the case of prey-dependent functional responses $(\varphi_i(x,\mathbf{y})=\varphi_i(x),\ 1\le i\le n)$, it is seen from Lemma 2 that

$$\int_0^T P(\gamma, y^*(t))dt = \sum_{i=1}^n\left(\int_0^T y_i^*(t)dt\right)\varphi_i(\gamma) = \sum_{i=1}^n\varphi_i(\gamma)A_i$$

where by A_i we denote the integral of y_i^* over a period, that is

$$A_i = \frac{\mu_i}{d_i(1-e^{-d_iT}(1-\delta_i))}[(1-e^{-d_iIT})+(1-\delta_i)(e^{-d_iIT}-e^{-d_iT})].$$

From Theorems 1 and 2, one obtains the following result.

Theorem 3. *The prey-free periodic solution* $\mathbf{E}^*$ *is locally asymptotically stable provided that*

$$\sum_{i=1}^{n}\varphi_i(0)A_i - \ln(1-\delta_x) > rT.$$

Further, $\mathbf{E}^*$ *is globally asymptotically stable if*

$$\sum_{i=1}^{n}\varphi_i(\frac{r}{a})A_i - \ln(1-\delta_x) > rT$$

and the system (S) is permanent provided that

$$\sum_{i=1}^{n}\varphi_i(0)A_i - \ln(1-\delta_x) < rT.$$

In particular, for $n=2$ and $\varphi_1(x, \mathbf{y})=(a_1/1+b_1x)$, $\varphi_2(x, \mathbf{y})=(a_2/1+b_2x^2)$, one obtains Theorems 3.1, 3.2 and 3.3 from Pei et al. (2009) as particular cases of Theorem 3. Also, for $\varphi_i(x, \mathbf{y})=a_i(1-e^{-a_ix}/x)$, $1\le i\le n$, one obtains Theorems 3.1 and 3.2 from Wu and Huang (2009), while for $\varphi_i(x, \mathbf{y})=(a_i/1+b_ix)$, $1\le i\le n$, one obtains Theorems 4.1 and 4.3 from Pei et al. (2005).

8. Biological Significance and Concluding Remarks

Since the equation which describes the dynamics of the pest species can be written in the form

$$\frac{dx}{dt}(t) = x(t)\left(r - ax(t) - \sum_{i=1}^{n} y_i(t)\varphi_i(x(t), \mathbf{y}(t))\right)$$

it is seen that the integral $\int_0^T P(0, \mathrm{y}^*(t))dt$, equal to $\sum_{i=1}^{n}\int_0^T y_i^*(t)\varphi_i(0, \mathrm{y}^*(t))dt$, approximates the total per capita loss of pest species in a period T due to predation from all predator species. Also, rT approximates the per capita growth of the pest species near extinction and $-\ln(1-\delta_x)$ represents the per capita loss of pest species due to pesticide spraying.

Consequently, when the pest population is near extinction and the local stability condition (5) holds, its cumulative size loss in a period due to predation and to the use of the chemical control surpasses its growth in the same amount of time and consequently the prey cannot escape extinction. The significance of the global stability condition (6) is similar, with the remark that this time the predation is assumed to be strong even at higher prey densities, when saturation occurs, and in unfavorable circumstances (maximal population sizes for predators in the species other than the current one for each term in the sum).

Similarly, the permanence condition (12) expresses the fact that when the pest is near extinction, its growth surpasses its cumulative size loss due to predation and to the use of control and consequently the pest is able to avoid extinction.

It is interesting to see that neither the stability conditions (local or global) nor the permanence condition depend on the efficiency constants, c_i, $1\le i\le n$, being formulated in terms of the prey death rates φ_i, $1\le i\le n$, only. This can be explained noting that due to the regulatory effect of the periodic forcing represented by the predator release, the dynamics of the population sizes of the predator classes is somewhat predictable once the dynamics of the prey class is known. In this regard, note that the unperturbed system is of Kolmogorov type, the equations for the predator classes being suited to an analysis using comparison estimates as performed above. Of concern is then only the survival of the prey class, which leads to permanence, or its extinction, which leads to a certain stability, in a stronger or weaker sense, of the prey-free periodic solution $\mathbf{E}^*$ via a comparison analysis, the dynamics of the predator species being obtained, in some sense, as a consequence. Note also that our approach is successful even though the functional responses of the predators are predator-dependent rather than prey-dependent only, as it is usually the case in related papers, although certain monotonicity properties with respect to the sizes of the predator classes are still required.

Let us now suppose that φ_i, $1\le i\le n$, are differentiable and denote by L_1 and L_2 the functions defined by moving all terms in the local and global stability conditions, respectively, in the right-hand side of the inequalities, that is,

$$L_1(T) = rT + \ln(1-\delta_x) - \int_0^T P(0, \mathrm{y}^*(t))dt,$$
$$L_2(T) = rT + \ln(1-\delta_x) - \int_0^T P_M(\frac{r}{a}, \mathrm{y}^*(t))dt.$$

It is seen that

$$L_1(0) = L_2(0) = \ln(1-\delta_x) < 0,$$
$$L_1(T) \ge rT + \ln(1-\delta_x) - \sum_{i=1}^{n}\varphi_i(0, \mathbf{0})A_i$$
$$L_2(T) \ge rT + \ln(1-\delta_x) - \sum_{i=1}^{n}\varphi_i(\frac{r}{a}, \mathbf{0})A_i$$

and consequently

$$\lim_{T\to\infty} L_1(T) = \lim_{T\to\infty} L_2(T) = +\infty.$$

Let us also note that

$$\frac{d^2L_1}{dt^2}(T) = \sum_{i=1}^{n} y_i^*(T)\left(d_i\varphi_i(0, \mathrm{y}^*(T)) + \sum_{j=1}^{n}\frac{\partial\varphi_i}{\partial y_j}(0, \mathrm{y}^*(T))d_jy_j^*(T)\right)$$
$$\frac{d^2L_2}{dt^2}(T) = \sum_{i=1}^{n} d_iy_i^*(T)\varphi_i\left(\frac{r}{a}, \mathrm{y}^*(T)\right)\left(\varphi_i\left(\frac{r}{a}, M_1, \ldots, M_{i-1}, y_i^*(T), M_{i+1}, \ldots, M_n\right)\right.$$
$$\left. + y_i^*(T)\frac{\partial\varphi_i}{\partial x_i}(\frac{r}{a}, M_1, \ldots, M_{i-1}, y_i^*(T), M_{i+1}, \ldots, M_n)\right).$$

Consequently, for the case of prey-dependent functional responses, for which $(\partial\varphi_i/\partial y_j)=0$ for all $1\le i, j\le n$, it follows that $(d^2L_1/dt^2)(T)>0$, $(d^2L_2/dt^2)(T)>0$ for all T. As a result, the equations $L_1(T)=0$ and $L_2(T)=0$ have unique strictly positive solutions T_* and T^*, respectively. It then follows that $\mathbf{E}^*$ is globally asymptotically stable for $T\in(0, T^*)$, (at least) locally asymptotically stable for $T\in(T^*, T_*)$ and unstable for $T\in(T_*, +\infty)$. That is, T_* can be regarded as a threshold parameter as far as the stability of the system is concerned.

However, if the functional responses are predator-dependent, then $(\partial\varphi_i/\partial y_j)\le 0$, due to (H2b), and the sign of $(d^2L_1/dt^2)(T)$ is uncertain. As a result, multiple areas of local stability (T_{*1j}, T_{*2j}), $1\le j\le m$, might arise, apart from $(0, T_*)$. A similar analysis, although less precise, since, unlike its local stability counterpart, condition (6) is not of threshold type, can be performed for global stability.

From an immediate analysis of the global stability condition (6), one may deduce that the global success of the pest control strategy can be achieved provided that the pesticides have a strong

impact on the pest species (δ_x close enough to 1) or the controls are employed often enough (T is close enough to 0). Also, since

$$L_2(T) \le rT + \ln(1-\delta_x) - \sum_{i=1}^{n} \varphi_i\left(\frac{r}{a}, \mathbf{M}\right) A_i,$$

where $\mathbf{M} = (M^1, M^2, \ldots, M^n)$, it is seen that predators which are voracious enough when prey is abundant ($\varphi_i((r/a), \mathbf{M})$ large enough for some $1 \le i \le n$) ensure the global success of the pest management strategy.

As far as prey-dependent functional responses are concerned, it is seen that the global success of the pest management strategy can be achieved by releasing many predators, even from a single species (one or more μ_i's large enough). Also, if the pesticides do not have a strong impact on the pest species, their low impact on the predator species does not help (if $\delta_i = 0$, $1 \le i \le n$, then $A_i = \mu_i$, $1 \le i \le n$ and $\sum_{i=1}^{n} \varphi_i(0) A_i - \ln(1-\delta_x)$ may not be large enough).

Finally, let us discuss the influence of intrapredatory interference upon the success of the pest control strategy. In this regard, an impulsive controllability analysis of a very general predator–prey model in which the functional and numerical response (not necessarily proportional) of the predator are given in an abstract form, depending on the sizes of the prey and predator populations through parameter functions which satisfy affine sectorial conditions has been performed by Nundloll et al. (2010). In Nundloll et al. (2010), comparison and direct estimation methods are employed to discuss the stability of the pest-free solution, two types of stability conditions being then obtained.

The first one, an upper bound on the interference between predators, is termed as "biological", the second one, a lower bound on the release rate of predators, being termed as "managerial"; in some sense, the biological condition is obtained as a prerequirement for the managerial condition. A chemical control is not employed in Nundloll et al. (2010). Also, Nundloll et al. (2010) does not rely on monotonicity of the functional responses themselves, but rather on the monotonicity of a certain lower boundedness function which is constructed *ad hoc* and on the possibility to compute explicitly the integrals of the subsequent estimation terms.

Through our analysis, it has been seen that the introduction of a chemical control drastically alters the picture, in the sense that the biological condition is no longer necessary, since the pest control strategy could be always rendered successful through the use of chemical control alone, regardless of the biological characteristics of the predator. To relate our findings with those of Nundloll et al. (2010), let us now suppose that $\delta_x = 0$ (no chemical control) and that $y_i \to y_i \varphi_i(x, \mathbf{y}) \le \alpha_i$ for $1 \le i \le n$. Then, from the local stability condition (5), one sees that

$$rT < \sum_{i=1}^{n} \int_0^T y_i^*(t) \varphi_i(x, y^*(t)) dt \le \sum_{i=1}^{n} \alpha_i T$$

and consequently

$$r < \sum_{i=1}^{n} \alpha_i, \tag{15}$$

which can also be interpreted as an upper bound on the interference between predators. To support this claim, let us suppose that the functional responses are of Beddington–deAngelis type, $\varphi_i(x, \mathbf{y}) = (b_i/1 + k_i x + \sum_{j=1}^{n} k_i^j y_j)$. Then α_i can be taken as (b_i/k_i^i), and condition (15) reads as

$$r < \sum_{i=1}^{n} \frac{b_i}{k_i^i}, \tag{16}$$

being a cumulative upper bound on the intraspecies interference constants k_i^i. In this regard, when (16) is not satisfied, increasing the amount of predators released each time or the release frequency will not contain the pests.

Of course, there is room for improvement in the above results. As pointed out by the referee, there are many assumptions which go into the model itself. Especially, to make the mathematics tenable, it has been assumed that r, a, e, c_i, d_i, $1 \le i \le n$, are constants and that fixed proportions of prey and predators species δ and δ_i, $1 \le i \le n$, are removed from the environment each time the pesticides are used. While these assumptions are conceivable, it would be more realistic to allow a certain degree of time dependence for some or all of these parameters.

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Appendix

Proof of Lemma 2

Proof. Let us consider $(x(\cdot), \mathbf{y}(\cdot)) : [0, T_0) \to \mathbb{R}^{n+1}$ a saturated solution for (S) which starts with strictly positive $(x(0), \mathbf{y}(0))$. It is seen that

$$\begin{cases} \dfrac{dx}{dt}(t) = x(t)\left(r - ax(t) - \displaystyle\sum_{i=1}^{n} y_i(t)\varphi_i(x(t), \mathbf{y}(t))\right), \\ \dfrac{dy_i}{dt}(t) = y_i(t)(c_i x(t)\varphi_i(x(t), \mathbf{y}(t)) - d_i), \end{cases}$$

for $0 \le t < T_0$, $t \ne (n+l-1)T$, $t \ne nT$, $1 \le i \le n$, as long as the solution remains positive component-wise. It then follows from Lemma 1 that

$$\begin{cases} x(t) \ge x(0)(1-\delta_x)^{\left[\frac{t+(1-l)T}{T}\right]} e^{\int_0^t p(s)ds}, & 0 \le t < T_0, 1 \le i \le n; \\ y_i(t) \ge y_i(0)(1-\delta_i)^{\left[\frac{t+(1-l)T}{T}\right]} e^{\int_0^t p_i(s)ds}, \end{cases}$$

where

$$\begin{cases} p(t) = r - ax(t) - \displaystyle\sum_{i=1}^{n} y_i(t)\varphi_i(x(t), \mathbf{y}(t)); \\ p_i(t) = c_i x(t)\varphi_i(x(t), \mathbf{y}(t)) - d_i, \end{cases}$$

that is, x and y_i, $1 \le i \le n$ remain strictly positive on $[0, T_0)$.

Proof. Let us consider a solution $(x(\cdot), \mathbf{y}(\cdot))$ of (S) starting with strictly positive $(x(0), \mathbf{y}(0))$ and define the boundedness function $B : \mathbb{R}_+ \to \mathbb{R}_+$ by

$$B(t) = x(t) + \sum_{i=1}^{n} \frac{1}{c_i} y_i(t), \quad t \ge 0.$$

One then has

$$\frac{dB}{dt}(t) = x(t)(r - ax(t)) - \sum_{i=1}^{n} \frac{d_i}{c_i} y_i(t)$$

and, choosing $0 < d < \min\left\{d_i; 1 \le i \le n\right\}$,

$$\frac{dB}{dt}(t) + dB(t) \le x(t)[(r+d) - ax(t)],$$

for $t > 0$, $t \ne (n+l-1)T$, $t \ne nT$, and consequently

$$\frac{dB}{dt}(t) + dB(t) \le C = (r+d)^2/(4a),$$

for $t > 0$, $t \ne (n+l-1)T$, $t \ne nT$. Also

$$B((n+l-1)T+) \le (1-\delta)B((n+l-1)T),$$

where $\delta = \min\left\{\delta_x, \delta_1, \ldots, \delta_n; 1 \le i \le n\right\}$, and

$$B(nT+) = B(nT) + \sum_{i=1}^{n} \frac{\mu_i}{c_i}.$$

By Lemma 1, it follows that

$$B(t) \le B(0+)e^{-dt} + C\int_0^t e^{-d(t-s)}ds + \sum_{0<nT<t} \mu e^{-d(t-nT)},$$

which yields

$$B(t) \le B(0+)e^{-dt} + \frac{C}{d} + \mu\frac{e^{dT}}{e^{dT}-1}, \quad t > 0, \tag{17}$$

from which the boundedness of B follows. Consequently, $x, y_1, \ldots, y_n$ are bounded and, by an easy argument, defined on the whole $\mathbb{R}_+$. Note also that B is ultimately bounded by $(C/d) + \mu(e^{dT}/e^{dT} - 1 + \alpha)$ for all $\alpha > 0$, that is, by a constant not depending on the initial population sizes.

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