

AN IMPULSIVE PREDATOR-PREY SYSTEM WITH BEDDINGTON-DEANGELIS FUNCTIONAL RESPONSE AND TIME DELAY

HONG ZHANG

Department of Mathematics, Jiangsu University ZhenJiang, JiangSu 212013, P. R. China cnczzhanghong@163.com hongzhang@ujs.edu.cn

PAUL GEORGESCU

Department of Mathematics "Gh. Asachi" Technical University of Iaşi Bd. Copou 11, 700506 Iaşi, Romania

an.d

Department of Mathematics and Its Applications Central European University, Nador u. 9 H-1051 Budapest, Hungary vpgeo@go.com

LANSUN CHEN

Department of Applied Mathematics Dalian University of Technology DaLian, LiaoNing, 116024, P. R. China lschen@amss.ac.cn

Received 18 September 2007

This paper deals with an impulsive predator-prey model with Beddington–DeAngelis functional response and time delay, in which the evolution of the predators takes them through two stages, juvenile and mature. It is assumed that only mature predators are able to hunt for prey and reproduce and the time delay is understood as being the time spent by the juvenile predators from birth to maturity. It is first seen that the dynamics of the model can be completely determined through the use of a reduced system consisting of the equations for prey and mature predators, respectively. Using the discrete dynamical system determined by the stroboscopic map, one first determines the mature predator-free periodic solution of the reduced system. By means of comparison techniques, one then deduces sufficient criteria for the global stability of the mature predator-free periodic solution and for the permanence of the reduced system, which yield similar properties for the initial system. As a result, it is observed that time delay and pulses have a crucial effect upon the dynamics of our model.

Keywords: Predator-prey system; stage structure; maturation delay; impulsive perturbation; Beddington-DeAngelis functional response.

Mathematics Subject Classifications 2000: 34K45, 92D25

1. Introduction

Generally, predator-prey models take the following very general form, indicated by Yodzis in [1]

$$\begin{cases} N' = f(N) - PF(N, P), \\ P' = PG(N, P), \end{cases}$$

where N=N(t) and P=P(t) represent the sizes of the prey population and of the predator population, respectively, at time t. The function f=f(N) characterizes the growth rate of the prey population in the absence of predation, the function F=F(N,P) describes the predator's functional (behavioral) response, that is, the dependence of its per capita consumption rate upon the sizes of the prey and predators classes, respectively, and the function G=G(N,P) describes the predator's numerical response, that is, the per capita growth rate of the predator population, again as a function which depends on the sizes of both population classes.

To elaborate upon the functional and numerical response of the predator, it is important to characterize the way in which the predators interact with one another. In some situations, especially at low predator densities, it can safely be assumed that predators do not interfere and consequently their functional and numerical responses depend upon the size of the prey population only, that is, F = F(N), G = G(N). Following the terminology given in Arditi and Ginzburg in [2] or in Huisman and DeBoer [3], this sort of model is called prey-dependent.

However, as seen above, prey-dependent functional responses fail to model the interference among predators or, although less likely, the cooperation which is sometimes achieved, and have been facing challenges from biologists and physiologists [2–6]. In the general case F = F(N,P), G = G(N,P), this sort of model is called, following again [2,3], predator-dependent, or, in the particular case in which F and G are functions of the prey-to-predator abundance, that is, F = F(N/P), G = G(N/P), ratio-dependent.

There is much significant evidence to suggest that predator dependence in the functional response occurs quite frequently in laboratory and natural systems (see, for instance, Jost and Ellner [7] or Skalski and Gilliam [8]) and due to large numbers of experiments and observations, the models with predator-dependent functional response stand as reasonable alternatives to the models with prey-dependent functional response. Arditi and Ginzburg [2] first proposed and investigated the following ratio-dependent predator-prey model:

$$\left\{ \begin{aligned} N' &= N(a-bN) - \frac{cNP}{mP+N}, \\ P' &= -dP + \frac{fNP}{mP+N}. \end{aligned} \right.$$

Note that the above model is a result of replacing the Holling type II prey-dependent functional response N/(m+N) with a ratio-dependent one (N/P)/(m+N/P).

The Beddington–DeAngelis functional response $F = \frac{\alpha N}{a+bN+cP}$ was originally introduced by Beddington [9] and DeAngelis [10], independently, and actually for different reasons. This functional response has some qualitative features of the ratiodependent functional responses but keeps away from the "low densities problem" which has been a source of controversy. Specifically, for $P \to 0$, the attack rate of ratio-dependent predators tends to ∞ , that is, such predators become unreasonably efficient.

As noted by Skalski and Gilliam in [8], predator-dependent functional responses can provide better descriptions of predator feeding than prey-dependent functional responses over a range of predator-prey abundances, and in some cases the Beddington–DeAngelis functional response performed best. An experimental awkward fact is that although the predator-dependent models that they considered fit those data reasonably well, no single functional response best describes all the data sets.

The original predator-prey model with Beddington-DeAngelis functional response has the form:

$$\begin{cases} x' = x \left(r - \frac{x}{k} \right) - \frac{\alpha xy}{a + bx + cy}, \\ y' = -dy + \frac{\beta xy}{a + bx + cy}. \end{cases}$$
 (1.1)

Motivated by this system, many scholars proposed and studied models consisting of ordinary or functional differential equations incorporating Beddington-DeAngelis type functional responses. For instance, in his papers [11,12], Hwang showed that the interior equilibrium of the above system is globally stable provided that it is locally asymptotically stable. Further, he obtained sufficient conditions for the uniqueness of limit cycles of the system. Motivated by the work of Beretta and Kuang [14], Liu and Yuan [13] considered the situation in which the numerical response term appearing in the predator equation of (1.1) contains a delay term τ , which can be regarded as a gestation period or reaction time of the predators. Further, incorporating a stage structure for the predator population, Liu and Beretta [15] proposed and studied the case in which a time delay τ appears in the response term of the immature predator equation as well as in the mature predator equation. Here, τ , dissimilar to the above delay, represents the time taken from birth to maturity. The stability of the interior equilibrium, the permanence of the system and conditions for the delay-induced stability switch were also considered in [16, 17]. Since biological and environmental parameters are naturally subject to fluctuation in time. In order to describe the model more accurately, Fan and Kuang [18] studied the dynamics of a nonautonomous, periodic (almost periodic) predator-prey system with Beddington-DeAngelis functional response by using the coincidence degree theory, as proposed by Gaines and Mawhin [21].

From the above-mentioned brief literature survey, it may be noted that the effect caused by the periodic impulsive perturbation of the prey population on the dynamics of the stage-structured predator-prey model with Beddington–DeAngelis functional response and time delay has not been modeled and analyzed. The aim of this paper is to model and explain this phenomenon from a mathematical viewpoint. More precisely, hunting and harvesting usually occur seasonally or yearly, with fixed periodicity, and as a result the prey population decreases significantly over a short period of time. That is, hunting and harvesting can be modeled, up to some extent, as occurring in periodic pulses. As a result, the dynamics of the system is considerably affected in a way which is worthy of further study.

The paper is organized in the following manner. In Sec. 2, we propose the model to be studied and give certain preliminary boundedness and comparison results. In Sec. 3, we discuss the global attractivity of the predator-free positive periodic solution. Sufficient conditions for the permanence of the model are obtained in Sec. 4. In the final section, we present some numerical experiments to illustrate our results. A brief discussion of the biological significance of our findings is also provided.

2. Preliminaries

In this paper, we denote by x(t) the size of the prey population. Also, the predator population is divided into juvenile and mature classes, with the size of each class given by $y_j(t)$ and y(t), respectively. The model we shall study has the form:

$$\begin{cases} x'(t) = x(t)g(x(t)) - \frac{bx(t)y(t)}{1+k_1x(t)+k_2y(t)}, \\ y'(t) = \frac{\beta be^{-d_j\tau}x(t-\tau)y(t-\tau)}{1+k_1x(t-\tau)+k_2y(t-\tau)} - dy(t), \\ y'_j(t) = \frac{\beta bx(t)y(t)}{1+k_1x(t)+k_2y(t)} - \frac{\beta be^{-d_j\tau}x(t-\tau)y(t-\tau)}{1+k_1x(t-\tau)+k_2y(t-\tau)} - d_jy_j(t), \\ \Delta x(t) = -\mu x(t), \end{cases}$$

$$(2.1)$$

with initial conditions

$$\begin{cases}
\left(x(t), y(t), y_j(t)\right) = \left(\varphi_1(t), \varphi_2(t), \varphi_3(t)\right) \in \mathbf{C}_3^+ \\
\text{for } t \in [-\tau, 0], \varphi_i(0) > 0, \quad i = 1, 2, 3, \\
\varphi_3(0) = \int_{-\tau}^0 e^{d_j \theta} \frac{\beta b \varphi_1(\theta) \varphi_2(\theta)}{1 + k_1 \varphi_1(\theta) + k_2 \varphi_2(\theta)} d\theta,
\end{cases}$$
(2.2)

in which,

$$\mathbf{C}_3^+ \doteq C([-\tau, 0], \mathbf{R}_+^3),$$

where $\mathbf{R}_{+}^{3} \doteq \{(z_1, z_2, z_3): z_i \geq 0, i = 1, 2, 3\}$ and $\tau, T > 0$. Here, $\Delta x(t) = x(t^+) - x(t)$. The following assumptions are made for deriving the mathematical

model:

- (A_1) In the absence of predation, the dynamics of the prey population follows the logistic law of growth with intrinsic growth rate r and carrying capacity $\frac{r}{c}$, i.e. xg(x) = x(r - cx).
- (A₂) Juvenile predators are raised by their parents because of their weakness. Moreover, they cannot breed.
- (A_3) The parameter τ represents a constant maturation time which, from a mathematical point of view, introduces a delay in our model. The product term $\frac{\beta b e^{-d_j \tau} x(t-\tau) y(t-\tau)}{1+k_1 x(t-\tau)+k_2 y(t-\tau)}$ denotes the movement of the young predator population to the mature class.
- (A₄) The prey population is subject to a perturbation which causes its proportional reduction, with reduction parameter μ ($0 \le \mu < 1$). This proportional reduction can be interpreted as hunting (or harvesting) with a constant hunting (or harvesting) effort.
- (A_5) The positive constants b and k_1 represent the effects of capture rate and handling time, respectively, on the feeding rate; $\beta > 0$ is the birth rate of the predator and $k_2 \geq 0$ is a constant describing the magnitude of the interference among predators. The positive constants d and d_i denote the death rates of the mature predator population and immature predator population, respectively.

Next, we shall introduce some notations and definitions and state some preliminary results. Let $\mathbf{J} \subset \mathbf{R}$. We introduce the following spaces of functions:

- $PC(\mathbf{J}, \mathbf{R}) \doteq \{u : \mathbf{J} \to \mathbf{R} : u \text{ is continuous at } t \in \mathbf{J}, t \neq \tau_k, \text{ continuous from the } \mathbf{J}\}$ left at $t \in \mathbf{J}$, and has discontinuities of the first kind at the points $\tau_k \in \mathbf{J}, k \in \mathbf{N} \}$, and
- $PC^{1}(\mathbf{J}, \mathbf{R}) \doteq \{u \in PC(\mathbf{J}, \mathbf{R}) : u \text{ is continuously differentiable at } t \in \mathbf{J}, t \neq \tau_{k};$ $u'(\tau_k^+)$ and $u'(\tau_k^-)$ exist, $k \in \mathbb{N}$ }.

Definition 2.1. A map $X: [-\tau, \infty) \to \mathbf{R}^n$ is said to be a solution of the Cauchy problem

$$\begin{cases} X'(t) = f(t, X(t), X(t - \tau)), & t \neq kT, k \in \mathbf{N}, \\ \Delta X(kT) = I_k(X(kT)), & X(0) = X_0, \end{cases}$$
 (2.3)

if it satisfies the following conditions:

- (H1) X(t) is continuous on [0,T] and on each interval $(kT,(k+1)T], k \in \mathbf{N}$. The points $\{kT\}, k \in \mathbb{N}$, are discontinuities of the first kind for f, f being continuous at the left of each point.
- (H2) X(t) satisfies the former n equations of the system (2.3) on $[0,\infty)\setminus \{kT,k\in$ **N**} and satisfies the latter equations for every t = kT, $k \in \mathbf{N}$.

Denote $\mathfrak{f} = (\mathfrak{f}_1, \mathfrak{f}_2, \dots, \mathfrak{f}_n)$ the map defined by the right-hand side of the first n equations in the system (2.3). Let $V : \mathbf{R}_+ \times \mathbf{R}^n \to \mathbf{R}_+$. Then $V \in V_0$ if

(i) V is continuous on $(t_k, t_{k+1}] \times \mathbf{R}^n$ and for each $X \in \mathbf{R}^n_+, k \in \mathbf{N}$,

$$\lim_{(t,z)\to (t_k^+,X)}V(t,z)=V(t_k^+,X)$$

exists.

(ii) V is locally Lipschitzian in the second variable.

Definition 2.2. If $V \in V_0$, then for $(t, X) \in (t_k, t_{k+1}] \times \mathbf{R}^n$, the upper right time derivative of V(t, X) with respect to the system (2.3) is defined as

$$D^{+}V(t,X) = \lim_{h \to 0^{+}} \sup \frac{1}{h} [V(t+h,X+h\mathfrak{f}(t,X)) - V(t,X)].$$

The proofs of the following comparison and estimation lemmas are obvious.

Lemma 2.3. Suppose that X(t) is a solution of the system (2.1) with initial conditions (2.2). Then $X(t) \geq 0$.

Lemma 2.4 [19]. Let $V : \mathbf{R}_+ \times \mathbf{R}^n \to \mathbf{R}_+^n$ and $V \in V_0$. Assume that

$$\begin{cases} D^{+}V(t,X(t)) \leq (\geq)\mathfrak{g}(t,V(t,X(t))), & t \neq t_{k}, \\ V(t,X(t^{+})) \leq (\geq)\Psi_{k}(V(t,X(t))), & t = t_{k}, \ k \in \mathbf{N}, \\ X(0^{+}) = X_{0}, \end{cases}$$

where $\mathfrak{g}: \mathbf{R}_+ \times \mathbf{R}_+^n \to \mathbf{R}^n$ is continuous on $(t_k, t_{k+1}] \times \mathbf{R}_+^n$ and for each $v \in \mathbf{R}_+^n$, $k \in \mathbf{N}$

$$\lim_{(t,z)\to(kT^+,v)}\mathfrak{g}(t,z)=\mathfrak{g}(kT^+,v)$$

exists and is finite, $\mathfrak{g}(t,U)$ is quasimonotone nondecreasing in U and $\Psi_k: \mathbf{R}^n_+ \to \mathbf{R}^n_+$ are nondecreasing. Let $R(t) = R(t,0,U_0)$ be the maximal solution of the scalar impulsive differential equation

$$\begin{cases} U'(t) = \mathfrak{g}(t, U), & t \neq kT, \\ U(t^{+}) = \Psi_{k}(U(t)), & t = kT, \\ U(0^{+}) = U_{0} \geq 0, \end{cases}$$
 (2.4)

existing on $[0,\infty)$. Then $V(0^+,X_0) \leq (\geq)U_0$ implies that

$$V(t, X(t)) \le (\ge)R(t), \quad t \ge 0,$$

where X(t) is any solution of (2.3) existing on $[0, \infty)$.

Note that if we have sufficient smoothness conditions on \mathfrak{g} to guarantee the existence and uniqueness of solutions for (2.4), then R(t) is the unique solution of (2.4).

Lemma 2.5 [20]. Let the function $u \in PC^1(\mathbf{R}_+, \mathbf{R})$ satisfy the inequalities

$$\begin{cases} u'(t) \le (\ge)\mathfrak{p}(t)u(t) + f(t), & t \ne \tau_k, \ t > 0, \\ u(\tau_k^+) \le (\ge)d_k u(\tau_k) + h_k, & \tau_k > 0, \\ u(\tau_0^+) = u(0^+) \le u_0, \end{cases}$$

where \mathfrak{p} , $f \in PC(\mathbf{R}_+, \mathbf{R})$ and $d_k \geq 0, h_k$ and u_0 are constants. Then, for t > 0,

$$u(t) \leq (\geq) u_0 \prod_{0 < \tau_k < t} d_k \exp\left(\int_0^t \mathfrak{p}(s) ds\right)$$
$$+ \int_0^t \prod_{s \leq \tau_k < t} d_k \exp\left(\int_s^t \mathfrak{p}(\tau) d\tau\right) f(s) ds$$
$$+ \sum_{0 < \tau_k < t} \left(\prod_{\tau_k < \tau_j < t} d_j \exp\left(\int_{\tau_k}^t \mathfrak{p}(\tau) d\tau\right)\right) h_k.$$

Under these circumstances, it can be shown that the positive solutions of (2.1)are bounded, the fact which is accomplished in the following lemma.

Lemma 2.6. There exists a constant M > 0 such that $x(t) \leq M, y_i(t) \leq M$ and $y(t) \leq M$ for each positive solution $(x(t), y(t), y_i(t))$ of the system (2.1) and t large enough.

Proof. Let $N(t) = x(t) + \frac{1}{\beta}(y_j(t) + y(t))$. Since $N \in V_0$, by a simple computation, we have

$$D^+N\big|_{(2.1)} = xg(x) - \frac{1}{\beta} (d_j y_j(t) + dy(t)), \quad t \in (kT, (k+1)T].$$

Obviously, from (A_1) , it is easy to see that there exists a constant $\lambda > 0$ such that

$$D^+N|_{(2.1)} + \overline{\delta}N < \lambda, \ t \in (kT, (k+1)T], \text{ for } k \text{ large enough,}$$

where $\bar{\delta} = \min\{d, d_i\}$. When t = kT, we get

$$N(kT^+) \le N(kT).$$

According to Lemma 2.5, applied for $\tau_k = kT$, we obtain

$$\begin{split} N(t) < N(0)e^{-\overline{\delta}t} + \int_0^t \lambda e^{-\overline{\delta}(t-s)} ds \\ & \to \frac{\lambda}{\overline{\delta}} \ as \ t \to \infty. \end{split}$$

Let $M \doteq \max\left\{\frac{\lambda}{\delta}, \frac{\beta\lambda}{\delta}\right\}$. Therefore, by the definition of N(t), we derive that each positive solution of system (1.1) is uniformly ultimately bounded with ultimate boundedness constant M. This completes the proof. A very important notion, with immediate biological significance, is that of uniform persistence (permanence), defined as follows.

Definition 2.7. The system (2.1) is said to be uniformly persistent (permanent) if there are constants $m_i > 0$ (i = 1, 2, 3) and a finite time \mathbb{T}_0 depending on m_1, m_2, m_3 , but not on the initial data, such that every positive solution $x(t) = (x(t), y(t), y_j(t)) \in \mathbf{R}_+^3$ of this system with initial conditions (2.2), satisfies

$$x(t) \ge m_1, \ y(t) \ge m_2, \ y_j(t) \ge m_3$$
 for all $t \ge \mathbb{T}_0$.

Due to the boundedness lemma proved above, this definition is equivalent to the following.

Definition 2.8. The system (2.1) is said to be uniformly persistent (permanent) if there exists a compact region $D \subset \operatorname{int} \mathbf{R}^3_+$ such that every solution of system (2.1) with initial conditions (2.2) will eventually enter and remain in the region D.

Finally, we indicate an exponential estimation which shall be used in the following for proving asymptotic stability results.

Lemma 2.9 [22]. Let \mathfrak{t}_0 be a real number and τ_0 be a nonnegative number. If $m: [\mathfrak{t}_0 - \tau_0, \infty) \to [0, \infty)$ satisfies

$$\dot{m}(t) \le -\rho m(t) + \varrho \Big[\sup_{t-\tau_0 \le s \le t} m(s) \Big] \quad for \ t \ge \mathfrak{t}_0,$$

and if $\rho > \varrho > 0$, then there exist positive numbers ι and κ such that

$$m(t) \le \iota e^{-\kappa(t-\mathfrak{t}_0)}$$
 for $t \ge \mathfrak{t}_0$.

Before going into any detail, we need to simplify the model (2.1). Since

$$y_j(t) = \int_{t-\tau}^t e^{-d_j(t-\theta)} \frac{\beta bx(\theta)y(\theta)}{1 + k_1x(\theta) + k_2y(\theta)} d\theta,$$

i.e. $y_j(t)$ is completely determined by x(t), y(t), we may restrict ourselves to the following reduced model:

$$\begin{cases}
 x'(t) = x(t)g(x(t)) - \frac{bx(t)y(t)}{1+k_1x(t)+k_2y(t)}, \\
 y'(t) = \frac{\beta be^{-d_j\tau}x(t-\tau)y(t-\tau)}{1+k_1x(t-\tau)+k_2y(t-\tau)} - dy(t), \\
 x(t^+) = (1-\mu)x(t), & t = kT.
\end{cases}$$
(2.5)

3. Mature Predator-Free Periodic Solution

3.1. Existence

Consider the following case in which $y(t) \equiv 0$ in (2.5):

$$\begin{cases} x'(t) = x(t)(r - cx(t)), & t \neq kT, \\ \Delta x(t) = -\mu x(t), & t = kT \end{cases}$$
(3.1)

After a few computations, we then derive the following lemma:

Lemma 3.1. Assume that $\mu < \mu^* = 1 - e^{-rT}$. Then the system (3.1) has a unique positive periodic solution $x^*(t)$ which is globally asymptotically stable, expressed as

$$x^*(t) = \frac{\frac{r}{c}(1 - \mu - e^{-rT})}{1 - \mu - e^{-rT} + \mu e^{-r(t - (n-1)T)}}, \quad t \in ((n-1)T, nT], \ n \in \mathbf{N}^*.$$

The proof of Lemma 3.1 is trivial and may be done by solving the first equation of the system (2.5) between pulses and using the discrete dynamical system determined by the stroboscopic map. We then omit it.

Consequently, the system (2.5) has a mature predator-free periodic solution $(x^*(t), 0).$

3.2. Global attractivity

From (2.5), one notes that

$$\begin{cases} x'(t) \le x(t)(r - cx(t)), & t \ne kT, \\ \Delta x(t) = -\mu x(t), & t = kT. \end{cases}$$

Then, by using Lemma 3.1, we obtain that for each arbitrary small positive constant ε , there exists a positive integer n_1 such that for all $t \geq n_1 T$,

$$x(t) \le x^*(t) + \varepsilon.$$

As a consequence, for all $t \ge n_1 T + \tau$, we have

$$x(t-\tau) \le x^*(t-\tau) + \varepsilon \le \frac{\frac{r}{c} \left(1 - \mu - e^{-rT}\right)}{\left(1 - \mu\right) \left(1 - e^{-rT}\right)} + \varepsilon = \eta + \varepsilon. \tag{3.2}$$

Further, in view of (3.2) and the second equation of (2.5), we have that for all $t \geq n_1 T + \tau$

$$y'(t) \le \frac{\beta b e^{-d_j \tau} (\eta + \varepsilon) y(t - \tau)}{1 + k_1 (\eta + \varepsilon)} - dy(t). \tag{3.3}$$

According to the above analysis, the following result is easily derived.

Theorem 3.2. Assume that $\mu < \mu^* = 1 - e^{-rT}$. If

$$R_1 = \frac{\beta b e^{-d_j \tau} \eta}{1 + k_1 \eta} < d,$$

then the mature predator-free periodic solution $(x^*(t),0)$ is globally attractive.

Proof. Let $\varepsilon > 0$ be such that

$$\frac{\beta b e^{-d_j \tau} (\eta + \varepsilon)}{1 + k_1 (\eta + \varepsilon)} < d.$$

Consider the comparison equation

$$z'(t) = \frac{\beta b e^{-d_j \tau} (\eta + \varepsilon) z(t - \tau)}{1 + k_1 (\eta + \varepsilon)} - dz(t).$$

According to the conditions of Theorem 3.2 and with the help of Lemma 2.9, one obtains that

$$\lim_{t \to \infty} z(t) = 0.$$

Since $y(s) = z(s) = \varphi_2(s) > 0$ for all $s \in [\tau, 0]$, by a comparison argument, we have

$$\limsup_{t \to \infty} y(t) \le \limsup_{t \to \infty} z(t) = 0.$$

Using the positivity of y(t), we then obtain that $\lim_{t\to\infty} y(t) = 0$.

Therefore, for any sufficiently small $\epsilon_1(0 < \epsilon_1 < \frac{r}{b})$, there exists an integer $n_2 > n_1$ such that $y(t) < \epsilon_1$ for all $t > n_2T \ge n_1T + \tau$.

From the first equation of the system (2.5), we obtain

$$x(t)\left(r - \frac{b\epsilon_1}{1 + k_2\epsilon_1} - cx(t)\right) \le x'(t) < x(t)g(x(t)), \quad t \ne kT.$$

From Lemmas 2.4 and 3.1, there exists a $n_3(>n_2)$ such that $x_1(t) \le x(t) \le x_2(t)$ as $t > n_3T$ and $x_1(t) - \tilde{x}(t) \to 0$, $x_2(t) - x^*(t) \to 0$ as $t \to \infty$, where $x_1(t)$ and $x_2(t)$ are, respectively, the solutions of

$$\begin{cases} x_1'(t) = x_1(t) \left(r - \frac{b\epsilon_1}{1 + k_2 \epsilon_1} - cx_1(t) \right), & t \neq kT, \\ \Delta x_1(t) = -\mu x_1(t), & t = kT, \\ x_1(0^+) = x_0 & \end{cases}$$

and

$$\begin{cases} x_2'(t) = x_2(t)g(x_2(t)), & t \neq kT, \\ \Delta x_2(t) = -\mu x_2(t), & t = kT, \\ x_2(0^+) = x_0, & \end{cases}$$

while

$$\widetilde{x}(t) = \frac{\frac{r - \frac{b\epsilon_1}{1 + k_2 \epsilon_1}}{c} (1 - \mu - e^{-(r - \frac{b\epsilon_1}{1 + k_2 \epsilon_1})T})}{1 - \mu - e^{-(r - \frac{b\epsilon_1}{1 + k_2 \epsilon_1})T} + \mu e^{-(r - \frac{b\epsilon_1}{1 + k_2 \epsilon_1})(t - (n - 1)T)}},$$

$$(n - 1)T < t < nT, \quad n > n_2,$$

Therefore, for any $\varepsilon_1 > 0$ we have $\widetilde{x}(t) - \varepsilon_1 < x(t) < x^*(t) + \varepsilon_1$ for t large enough. For $\epsilon_1 \to 0$, we get $\widetilde{x}(t) \to x^*(t)$. Hence $x(t) \to x^*(t)$ as $t \to \infty$. This completes the proof.

From the above, one may easily obtain the following result

Corollary 3.3. The mature predator-free periodic solution $(x^*(t),0)$ of the system (2.5) is globally attractive provided that one of the following conditions holds:

- $$\begin{split} &\text{(I)} \ \ R_0 \leq d, \ where \ R_0 = \frac{\beta b e^{-d_j \tau}}{k_1}; \\ &\text{(II)} \ \ R_0 > d \ \ and \ \frac{r}{c} \leq \Theta(1-e^{-rT}), \ where \ \Theta = \frac{d}{k_1(R_0-d)}. \\ &\text{(III)} \ \ R_0 > d, \frac{r}{c} > \Theta(1-e^{-rT}) \ \ and \ \mu > \mu_*, \ where \ \mu_* = \frac{\left(1-\Theta\frac{c}{r}\right)\left(1-e^{-rT}\right)}{1-\Theta\frac{c}{r}\left(1-e^{-rT}\right)}. \end{split}$$

Remark 3.4. Considering the pulses-free case in the system (2.5), one notes from [15] that if $R = \frac{\beta b e^{-d_j \tau} \frac{r}{c}}{1 + k_1 \frac{r}{c}} < d$ holds, then $\lim_{t \to \infty} (x(t), y(t)) = (\frac{r}{c}, 0)$. After adding the periodic impulsive perturbations of the prey population, we first consider for the new system the dynamics of the boundary periodic solution $(x^*(t), 0)$ which corresponds to the trivial equilibrium $(\frac{r}{c},0)$ of the pulses-free system. It is easy to see that for $\mu \to 0$ one has that $\eta \to \frac{r}{c}$, so $R_1 \to R$ and we obtain the persistence result given in [15] from Theorem 3.2. Obviously, a similarity among R, μ^* and $R_i(i=0,1)$ is that these critical values are independent of the effect of k_2 , which introduces a self-limiting term into the predator equation.

Remark 3.5. The fraction $\frac{\beta b \eta_1}{1+k_1\eta_1}$ approximates the mature predator's numerical response when (x(t),y(t)) is near the mature predator-free periodic solution $(x^*(t),0)$, while $e^{-d_j\tau}$ is a correction term incorporating the "degree of stage structure" $d_i\tau$, named as such by Liu et al. [23], meant to describe the loss of juvenile predators due to through-stage mortality. In this regard, Theorem 3.2 can be interpreted as if few predators introduced into an environment stabilized at the periodic mature predator-free solution cannot reproduce fast enough, compensating through-stage mortality, as described by the degree of stage structure, then the mature predator-free periodic solution is globally asymptotically stable.

Remark 3.6. It is interesting to note that, as far as the effect of the delay τ is concerned, a large delay τ may always stabilize the predator-free equilibrium by bringing R_0 below d, as seen from (I) of Corollary 3.3. Also, from (II) of Corollary 3.3, it is seen that the systems with low resources $(\frac{r}{c} < \Theta(1 - e^{-rT}))$ are more likely to be stabilized to the mature predator-free periodic solution. Having also in view (III) of Corollary 3.3, it is seen that increasing the carrying capacity of the system may destabilize an otherwise stable mature predator-free periodic solution, which is certainly conceivable from a purely biological point of view.

Remark 3.7. Clearly, one notes that the global attractivity of juvenile and mature predator-free periodic solution $(x^*(t), 0, 0)$ of the system (2.1) is equivalent to the global attractivity of mature predator-free periodic solution $(x^*(t), 0)$ of the system (2.5). Its biological implication is that under the determinable carrying capacity of the prey population and suitable periodic harvesting or hunting rate, the predator population vanishes in time.

4. Permanence

Uniform persistence (or permanence) is an important property of systems arising in ecology, epidemics, population dynamics and not only. It is actually a concept which is important in itself, addressing the long-term survival of some or all components of a system. In this section, we focus our attention on the permanence of the system (2.5).

In the following, we first consider the single species model with delay described below:

$$v'(t) = \frac{a_1 v(t - \nu)}{a_2 + a_3 v(t - \nu)} - a_4 v(t), \tag{4.1}$$

where $a_i(i=1,2,3,4)$ and ν are positive constants. Obviously, v(t) is strictly positive if

$$v(t) = \widetilde{\varphi}(t) > 0 \text{ for } t \in [-\nu, 0]. \tag{4.2}$$

The following lemma is an application of [17, Chap. 4, Theorem 9.1].

Lemma 4.1. Equation (4.1) has a unique positive equilibrium $v^* = \frac{a_1 - a_2 a_4}{a_3 a_4}$, which is absolutely globally asymptotically stable provided that $a_1 > a_2 a_4$.

Here, the absolute global asymptotic stability of v^* means that v^* is globally asymptotically stable for all $\nu > 0$. We now start investigating the permanence of the system (2.5). Let $\varepsilon > 0$ be an arbitrary positive constant. Recalling (3.2), together with the second equation of (2.5), one notes that there exists a $n_4 > n_3$ such that for $t > n_4 T$,

$$y'(t) \le \frac{\beta b e^{-d_j \tau} (\eta + \varepsilon) y(t - \tau)}{1 + k_1 (\eta + \varepsilon) + k_2 y(t - \tau)} - dy(t). \tag{4.3}$$

Hence from the above lemma, combined with a comparison argument, one obtains that for an arbitrary small positive constant $\tilde{\varepsilon}$, there exists a $n_5 > n_4$ such that if

$$\frac{\beta b e^{-d_j \tau} (\eta + \varepsilon)}{(1 + k_1 (\eta + \varepsilon)) d} > 1,$$

then

$$y(t) \le \frac{\beta b e^{-d_j \tau} (\eta + \varepsilon) - (1 + k_1 (\eta + \varepsilon)) d}{dk_2} + \widetilde{\varepsilon} = \zeta(\varepsilon, \widetilde{\varepsilon})$$
(4.4)

for $t > n_5 T$. Consequently, we obtain that for $t > n_5 T$ and $t \neq kT$,

$$x'(t) \ge x(t)g(x(t)) - \frac{b\zeta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1(\eta + \varepsilon) + k_2\zeta(\varepsilon, \widetilde{\varepsilon})}x(t). \tag{4.5}$$

Next let $r(\varepsilon, \widetilde{\varepsilon}) = r - \frac{b\zeta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1(\eta + \varepsilon) + k_2\zeta(\varepsilon, \widetilde{\varepsilon})} > 0$. In view of Lemmas 2.4 and 3.1, it follows that there exists a $n_6 > n_5$ such that for $\mu < 1 - e^{-r(\varepsilon, \widetilde{\varepsilon})T}$ and $t \ge n_6 T$,

$$x(t) \ge \frac{\frac{r(\varepsilon, \widetilde{\varepsilon})}{c} (1 - \mu - e^{-r(\varepsilon, \widetilde{\varepsilon})T})}{1 - \mu - e^{-r(\varepsilon, \widetilde{\varepsilon})T} + \mu} = \vartheta(\varepsilon, \widetilde{\varepsilon}). \tag{4.6}$$

In the following, we define

$$W(t) = y(t) + \beta b e^{-d_j \tau} \int_{t-\tau}^t \frac{x(s)y(s)}{1 + k_1 x(s) + k_2 y(s)} ds.$$

Then the derivative of W(t) with respect to the solutions of the system (2.5) is given by

$$\frac{dW}{dt}\Big|_{(2.5)} = \left(\frac{\beta b e^{-d_j \tau} x(t)}{1 + k_1 x(t) + k_2 y(t)} - d\right) y(t)
\geq \left(\frac{\beta b e^{-d_j \tau} \vartheta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1 \vartheta(\varepsilon, \widetilde{\varepsilon}) + k_2 y(t)} - d\right) y(t). \tag{4.7}$$

If

$$\frac{\beta b e^{-d_j \tau} \vartheta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1 \vartheta(\varepsilon, \widetilde{\varepsilon})} - d > 0, \tag{4.8}$$

we can choose sufficiently small y^* such that

$$\frac{\beta b e^{-d_j \tau} \vartheta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1 \vartheta(\varepsilon, \widetilde{\varepsilon}) + k_2 y^*} - d > 0. \tag{4.9}$$

We claim that for any $t_0 > 0$, it is impossible that $y(t) < y^*$ for all $t \ge t_0$. Suppose that the claim is not valid. Then there is a $t_0 > 0$ such that $y(t) < y^*$ for all $t \ge \max\{t_0, n_6T\}$. From (4.7), one notes there exists a $t_1 > \max\{t_0 + \tau, n_6T + \tau\}$ such that for $t \ge t_1$,

$$\frac{dW}{dt}\Big|_{(2.5)} \ge \left(\frac{\beta b e^{-d_j \tau} \vartheta(\varepsilon, \widehat{\varepsilon})}{1 + k_1 \vartheta(\varepsilon, \widehat{\varepsilon}) + k_2 y^*} - d\right) y(t).$$
(4.10)

Set

$$y_l \doteq \min_{t \in [t_1, t_1 + \tau]} y(t).$$

We will show that $y(t) \geq y_l$ for all $t \geq t_1 > t_0$. Otherwise, there exists a $T_0 \geq 0$ such that $y(t) \geq y_l$ for $t_1 \leq t \leq t_1 + \tau + T_0$, and $y(t_1 + \tau + T_0) = y_l$. Hence, from the second equation of (2.5), we derive

$$y'(t_1 + \tau + T_0) \ge \left(\frac{\beta b e^{-d_j \tau} \vartheta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1 \vartheta(\varepsilon, \widetilde{\varepsilon}) + k_2 y^*} - d\right) y_l$$

and so $y'(t_1 + \tau + T_0) > 0$. Consequently, y is locally increasing near $t_1 + \tau + T_0$ and cannot fall below y_l . Thus

$$y(t) \ge y_l \tag{4.11}$$

for all $t \geq t_1$. As a consequence, (4.10) and (4.11) lead to

$$\frac{dW}{dt}\Big|_{(2.5)} > \tilde{\delta}$$
 for some $\tilde{\delta} > 0$ and $t \ge t_1$,

which implies that $W(t) \to \infty$ as $t \to \infty$. This contradicts the boundedness of W(t). The claim that $y(t) \geq y_l$ is then proved.

By the above claim, we need to consider two cases. First, $y(t) \ge y^*$ for all large t, which yields the uniform persistence of the mature predator. Combined with (4.6), this means that our system (2.5) is uniformly persistent. Second, y(t) oscillates about y^* for all large t. Let us define

$$q = \min\left\{\frac{y^*}{2}, \ y^*e^{-d\tau}\right\}.$$

We want to show that $y(t) \ge q$ for all large t, which, as done above, will yield the uniform persistence of the system (2.5). Let $t^* > 0$ and $\widetilde{\nu} > 0$ satisfy

$$y(t^*) = y(t^* + \widetilde{\nu}) = y^*$$

and

$$y(t) < y^*, \quad t \in (t^*, t^* + \widetilde{\nu}).$$

It is seen that y(t) is uniformly equicontinuous since the positive solutions of (2.5) are ultimately bounded and y(t) is not affected by impulses. Thus, there exists a \widetilde{T} (0 < \widetilde{T} < τ , and \widetilde{T} is independent of the choice of t^*) such that

$$y(t) > \frac{y^*}{2}$$

for $t^* < t < t^* + \widetilde{T}$. If $\widetilde{\nu} \le \widetilde{T}$, there is nothing to prove. Let us consider the case $\tau \ge \widetilde{\nu} > \widetilde{T}$. It follows that for $t^* + \widetilde{T} \le t \le t^* + \widetilde{\nu}$,

$$y'(t) \ge -dy(t)$$
.

Hence

$$y(t) \ge y^* e^{-d\tau}$$

for $t^* + \widetilde{T} \leq t \leq t^* + \widetilde{\nu} \leq t^* + \tau$, since $y(t^*) = y^*$. If $\widetilde{\nu} > \tau$, it is obvious that $y(t) \geq q$ for $t \in [t^*, t^* + \tau]$. Then, proceeding exactly as the for the derivation of (4.11), we see that $y(t) \geq q$ for $t \in [t^* + \tau, t^* + \widetilde{\nu}]$. Since this interval $[t^*, t^* + \widetilde{\nu}]$ is chosen in an arbitrary way (we only need t^* to be large), we conclude that $y(t) \geq q$ for all large t. Due to the above-mentioned analysis, we obtain the following result.

Theorem 4.2. The system (2.5) is permanent provided that

$$r(0,0) > 0$$
, $\mu < 1 - e^{-r(0,0)T}$, $R_1 > d$, $\frac{\beta b e^{-d_j \tau} \vartheta(0,0)}{1 + k_1 \vartheta(0,0)} - d > 0$.

Thus, after further computations, it is easy to deduce the following result.

Corollary 4.3. The system (2.5) is permanent provided that one of the following conditions holds:

(I)
$$d < R_1, r \ge \frac{b}{k_2} + c\Theta, \mu < \overline{\mu}_1^*, where$$

$$\overline{\mu}_1^* = (1 - e^{-r(0,0)T}) \left(1 - \frac{c\Theta}{r(0,0)} \right),$$

$$r(0,0) = \left(r - \frac{b}{k_2} \right) + \frac{bd}{R_1 k_2}.$$

(II)
$$d < R_1 < d^*, r < \frac{b}{k_2} + c\Theta, \mu < \overline{\mu}_1^*, where$$

$$d^* = \frac{bd}{b + k_2 c\Theta - rk_2}.$$

Remark 4.4. From [15], we note that if $R = \frac{\beta b e^{-d_j \tau} \frac{r}{c}}{1 + k_1 \frac{r}{c}} \ge d$ holds, then the corresponding pluses-free system is permanent. After adding periodic impulsive perturbations of the prey population, in order to keep the permanence of the new system (2.5) we have to fulfill a related condition, although there is still room for improvement in the estimations given in Corollary 4.3.

5. Numerical Analysis and Discussion

To facilitate the interpretation of our mathematical results and to further establish the importance of the proportional impulsive part and of the delay term, we proceed to investigate further by using numerical simulations. A first example is indicated in Table 1, which illustrates the loss of permanence due to the effects of the impulsive perturbation. Let us also choose a set of parameters given as follows:

•
$$r = 1.8, c = 0.2, \beta = 1, b = 0.1, d_j = 0.01, T = 0.3, \tau = 1, d = 0.15, k_1 = 0.5, k_2 = 0.1, \mu = 0.1.$$

After a few computations, one gets that

•
$$r(0,0) \approx 1.756 > 0$$
, $1 - e^{-r(0,0)T} = 0.409 > \mu$, $R_1 - d = 0.006 > 0$, $\frac{\beta b e^{-d_j \tau} \vartheta(0,0)}{1 + k_1 \vartheta(0,0)} - d \approx 0.002 > 0$.

Hence, by applying Theorem 4.2, it is shown that the system (2.1) with the above coefficients is permanent. However, when $\mu = 0.2$ and the other coefficients remain fixed, it follows that $R_1 = 0.147 < d$ and the corresponding impulsive system is not permanent, the mature predator-free periodic solution being globally asymptotically stable from Theorem 3.2. Similarly, when $\tau = 6$ and the other coefficients remain fixed, it follows that $R_1 = 0.149$ and the corresponding impulsive system loses again its permanence. As a consequence, from Table 1 and the above-mentioned example, it is easy to see that the impulsive perturbation and the time delay play an important role in the dynamics of the system.

Table 1.			
		the corresponding	

Pulses-free system [15]	r, β, k_1 1	c 5/8	<i>b</i> 1.5	$d \\ 0.5$	$k_2 \\ 0.1$	$d_j \\ 0.01$	τ 0.8	Permanence Yes
Impulsive system	r, β, k_1 1	c $5/8$	b 1.5	d 0.5	$k_2 \\ 0.1$	$\begin{array}{c} d_j \\ 0.01 \end{array}$	τ 0.8	$R_1 \approx 0.251 < d$
	Θ ≈ 0.506	T 1	$\mu_* \approx 0.540$	$\mu^* \approx 0.6321$	$\eta \approx 0.203$	$R_0 \approx 1.488$	μ 0.6	Permanence No

Obviously, from Corollary 4.3, we see that when the prey has a large intrinsic growth rate, the proportional reduction μ is small and the predators can breed quickly, then the prey population and predator population can coexist forever. The same happens if the carrying capacity is lower, provided that the breeding rate of the mature predators remains also lower than a certain value.

In this paper, we have studied a delayed predator-prey model with stage-structure, Beddington–DeAngelis functional response and impulsive perturbations of the prey population. The novel aspect of the system is the incorporation of periodic human exploiting behavior due to seasonal periodic hunting or harvesting, on the basis of the model in [15]. As far as the the impulsive control for the prey population is concerned, we have shown that the system tends to a state of "total extinction of the predator" if conditions in Theorem 3.2 were satisfied. However, from the point of view of protecting the predator population and subsistence hunting or harvesting, the aim is to keep two species at an acceptable level. In this regard, sufficient conditions guaranteeing the permanence of the system were found in Theorem 4.2.

Acknowledgment

The work was supported by National Natural Science Foundation of China (10771104).

References

- P. Yodzis, Predator-prey theory and management of multispecies fisheries, Ecol. Appl. 4 (1994) 51–58.
- [2] R. Arditi and L. R. Ginzburg, Coupling in predator-prey dynamics: Ratiodependence, J. Theor. Biol. 139 (1989) 311–326.
- [3] C. Huisman and R. J. DeBoer, A formal derivation of the Beddington functional response, *J. Theor. Biol.* **185** (1997) 389–400.
- [4] A. Abrams and L. R. Ginzburg, The nature of predation: Prey dependent, ratio dependent or neither? *Trends Ecol. Evol.* **15** (2000) 337–341.
- [5] Y. Kuang and E. Beretta, Global qualitative analysis of a ratio-dependent predatorprey system, J. Math. Biol. 36 (1998) 389-406.
- [6] A. P. Gutierrez, The physiological basis of ratio-dependent predator-prey theory: A metabolic pool model of Nicholsons blowflies as an example, *Ecology* 73 (1992) 1552–1563.
- [7] C. Jost and S. Ellner, Testing for predator dependence in predator-prey dynamics: A nonparametric approach, Proc. Royal Soc. London Ser. B 267 (2000) 1611–1620.
- [8] G. T. Skalski and J. F. Gilliam, Functional responses with predator interference: Viable alternatives to the Holling type II model, *Ecology* **82** (2001) 3083–3092.
- [9] J. R. Beddington, Mutual interference between parasites or predators and its effect on searching efficiency, *J. Anim. Ecol.* 44 (1975) 331–340.
- [10] D. L. DeAngelis, R. A. Goldstein and R. V. O'Neill, A model for tropic interaction, Ecology 56 (1975) 881–892.
- [11] Z. W. Hwang, Global analysis of the predator-prey system with Beddington– DeAngelis functional response, J. Math. Anal. Appl. 281 (2003) 395–401.

- [12] Z. W. Hwang, Uniqueness of limit cycles of the predator-prey system with Beddington-DeAngelis functional response, J. Math. Anal. Appl. 290 (2004) 113-122.
- [13] Z. Liu and R. Yuan, Stability and bifurcation in a delayed predator-prey system with Beddington-DeAngelis functional response, J. Math. Anal. Appl. 296 (2004) 521 - 537.
- [14] E. Beretta and Y. Kuang, Global analysis in some delayed ratio-dependent predatorprey systems, Nonlinear Anal. TMA 32 (1998) 381–408.
- [15] S. Liu and E. Beretta, A stage-structured predator-prey model of Beddington-DeAngelis type, SIAM J. Appl. Math. 66 (2006) 1101–1129.
- [16] K. Gopalsamy, Stability and Oscillations in Delay Differential Equations of Population Dynamics (Kluwer Academic Publishers, Boston, 1991).
- [17] Y. Kuang, Delay Differential Equations with Applications in Population Dynamics (Springer, New York, 1993).
- [18] M. Fan and Y. Kuang, Dynamics of a nonautonomous predator-prey system with the Beddington-DeAngelis functional response, J. Math. Anal. Appl. 295 (2004) 15–39.
- [19] V. Lakshmikantham, D. D. Bainov and P. S. Simeonov, Theory of Impulsive Differential Equations (World Scientific, Singapore, 1989).
- [20] D. D. Bainov and P. S. Simeonov, Impulsive Differential Equations: Periodic Solutions and Applications (Longman, London, 1993).
- [21] R. E. Gaines and R. M. Mawhin, Coincidence Degree and Nonlinear Differential Equations (Springer-Verlag, Berlin, 1977).
- [22] A. Halanay, Differential Equations: Stability, Oscillations, Time Lags (Academic Press, New York, 1966).
- [23] S. Liu, L. Chen, G. Luo and Y. Jiang, Asymptotic behavior of competitive Lotka-Volterra system with stage structure, J. Math. Anal. Appl. 271 (2002) 124–138.