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DYNAMIC BEHAVIOR OF A PREDATOR-PREY MODEL WITH STAGE STRUCTURE AND DISTRIBUTED DELAY

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ABSTRACT. In this paper, a predator-prey model with stage structure and distributed delay is investigated. Mathematical analyses of the model equation with regard to boundedness of solutions, nature of equilibria, permanence, extinction and stability are performed. By the comparison theorem, a set of easily verifiable sufficient conditions are obtained for the global asymptotic stability of nonnegative equilibria of the model. Taking the product of the per-capita rate of predation and the rate of conversing prey into predator as the bifurcating parameter, we prove that there exists a threshold value beyond which the positive equilibrium bifurcates towards a periodic solution.

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1. Introduction

The construction and study of models for the population dynamics of predator-prey systems have been an important topic in theoretical ecology since the famous Lotka-Volterra equations [1-3]. It is assumed in the classical predator-prey model that each individual predator admits the same ability to attack prey.

Stage-structured models have received much attention in recent years (see, for example, [4-8]). This is not only because they are much simpler than the models governed by partial differential equations but also because they can exhibit phenomena similar to those of partial differential equations and many important physiological parameters can be incorporated [9]. The pioneering work of Aiello and Freedman [10] on a single species growth model with stage structure represents a mathematically more careful and biologically meaningful formulation approach. In [11], Chen et. al. proposed a stage-structured single-species

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population model without time delay. Let $N_i(t)$ and $N_m(t)$ denote the immature and mature population densities at time t, respectively. Then the following stage-structured single-species population model was discussed in [11]:

$$\begin{cases} \dfrac{dN_i(t)}{dt} = B(t) - D_i(t) - W(t), \\ \dfrac{dN_m(t)}{dt} = \alpha W(t) - D_m(t). \end{cases} \tag{1.1}$$

In (1.1), $B(t)$ is the birth rate of the immature population at time t; $D_i(t)$ and $D_m(t)$ are the death rates of the immature and mature at time t, respectively; $W(t)$ represents the transformation rate of the immature into the mature; α is the probability of the successful transformation of the immature into the mature. If it is assumed in model (1.1) that the birth rate obeys the Malthus rule, i.e., $B(t) = aN_m(t)$ the death rates of the mature populations is logistic, and the transformation rate of the immature into mature is proportional the immature population, i.e.,

$$D_i(t) = r_i N_i(t), \ D_m(t) = r_m N_m(t) + b_m N_m^2(t),$$

and $W(t) = bN_i(t)$, then we recover the model discussed by Chen et al. for a single species with stage structure

$$\begin{cases} \dfrac{dN_i(t)}{dt} = aN_m(t) - r_i N_i(t) - bN_i(t), \\ \dfrac{dN_m(t)}{dt} = bN_i(t) - r_m N_m(t) - b_m N_m^2(t). \end{cases} \tag{1.2}$$

where $b = \frac{1}{\tau}$ is the transformation rate of the immature into the mature in unit time and s is the maturity. Based on the idea above, many authors studied different kinds of stage-structured population models and a significant body of work has been carried out (see, for example, [12]).

Based on the Michaelis-Menten or Holling type-II function, Arditi and Ginzburg [13] proposed a ratio-dependent function of the form

$$P(\frac{x}{y}) = \frac{c(\frac{x}{y})}{m + (\frac{x}{y})} = \frac{cx}{my + x},$$

and the following ratio-dependent predator-prey model:

$$\begin{cases} \dfrac{dx}{dt} = x(a - bx) - \dfrac{cx}{my + x}, \\ \dfrac{dy}{dt} = y(-d + \dfrac{fx}{my + x}). \end{cases} \tag{1.3}$$

Here $x(t)$ and $y(t)$ represent the densities of the prey and the predator at time t, respectively. $\frac{a}{b}$ is the carrying capacity, $d > 0$ is the death rate of the predator, and a, c, m and $\frac{f}{c}$ are positive constants that stand for the intrinsic growth rate of the prey, capturing rate, half saturation constant and conversion rate of the predator, respectively. The ratio-dependent predator-prey models with or without time delays have been studied by many researchers recently and very rich dynamics have been observed (see, for example, [14-16] and references cited therein).

In [17], Tang et.al. have presented a ratio-dependent predator-prey model with distributed delay

$$\begin{cases} \dfrac{dx}{dt} = rx(1-\dfrac{x}{K}) - \dfrac{cx}{my+x}, \\ \dfrac{dy}{dt} = -dy + h\displaystyle\int_{-\infty}^{t} \dfrac{\delta y(\tau)z(\tau)}{mz(\tau)+y(\tau)} \exp(-\delta(t-\tau))d\tau. \end{cases} \tag{1.4}$$

Motivated by the recent work of Tang et.al. [17], the purpose of the present paper is to perform a dynamic behavior of a ratio-dependent predator-prey model by incorporating stage structure for prey and distributed delay into the model. To do so, we study the following delayed differential system:

$$\begin{cases} \dfrac{dx}{dt} = ay(t) - r_1x(t) - bx(t), \\ \dfrac{dy}{dt} = bx(t) - r_2y(t) - b_1y^2(t) - \dfrac{a_1y(t)z(t)}{mz(t)+y(t)}, \\ \dfrac{dz}{dt} = -dz(t) + h\displaystyle\int_{-\infty}^{t} \dfrac{\delta y(\tau)z(\tau)}{mz(\tau)+y(\tau)} \exp(-\delta(t-\tau))d\tau, \end{cases} \tag{1.5}$$

where the exponential weight function satisfies

$$\int_{-\infty}^{t} \delta\exp(-\delta(t-\tau))d\tau = \int_{0}^{\infty} \delta\exp(-\delta s)ds = 1.$$

In model (1.5), we assume that a is the birth rate of the immature prey, and the constant b is the rate of conversing into mature prey. a_1 is the capturing rate of the predator, m is the half saturation rate of the predator, d is the death rate of the predator, r_1 (r_2) is the death rate of the immature (mature) prey, b_1 denotes the coefficient of the mature prey's inner competition, h denotes the product of the per-capita rate of predation and the rate of conversing prey into predator. We are assuming in a more realistic fashion that the present level of the predator affects instantaneously the growth of the prey, but that the growth of the predator is influenced by the amount of prey in the past. More precisely, the number of predators grows depending on the weight-averaged time of the Michaelis-Menten function of y over the past by means of the function $Q(t)$ given by the integral

$$Q(t) = \int_{-\infty}^{t} \frac{\delta y(\tau)z(\tau)}{mz(\tau)+y(\tau)} \exp(-\delta(t-\tau))d\tau. \tag{1.6}$$

Clearly, this assumption implies that the influence of the past fades away exponentially and the number $\dfrac{1}{\delta}$ might be interpreted as the measure of the influence of the past. So, the smaller the $\delta > 0$, the longer the interval in the past in which the values of y are taken into account.

The integro-differential system (1.5) can be transformed [18, 19] into the system of differential equations on the interval

$$\begin{cases} \dfrac{dx}{dt} = ay(t) - r_1x(t) - bx(t), \\ \dfrac{dy}{dt} = bx(t) - r_2y(t) - b_1y^2(t) - \dfrac{a_1y(t)z(t)}{mz(t)+y(t)}, \\ \dfrac{dz}{dt} = -dz(t) + hQ(t), \\ \dfrac{dQ}{dt} = \dfrac{\delta y(t)z(t)}{mz(t)+y(t)} - \delta Q(t). \end{cases} \tag{1.7}$$

We understand the relationship between the two systems as follows: If (x, y, z) : $[0, +\infty) \to R^3$ is the solution of (1.5) corresponding to continuous and bounded initial function $(\bar{x}_0, \bar{y}_0, \bar{z}_0) : [0, +\infty) \to R^3$, then $(x, y, z, Q) : [0, +\infty) \to R^4$ is a solution of (1.7) with $\bar{x}_0 = x_0$, $\bar{y}_0 = y_0$, $\bar{z}_0 = z_0$, and

$$Q(0) = \int_{-\infty}^{0} \frac{\delta y(\tau)z(\tau)}{mz(\tau)+y(\tau)} \exp(\delta\tau)d\tau.$$

Conversely, if (x, y, z, Q) is any solution of (1.7) defined on the entire real line and bounded on $(-\infty, 0]$, then Q is given by (1.6), and so (x, y, z) satisfies (1.5).

System (1.7) will be analyzed with the following initial conditions

$$x(0) = x_0 > 0, \;\; y(0) = y_0 > 0, \;\; z(0) = z_0 > 0, \;\; Q(0) = Q_0 > 0. \tag{1.8}$$

2. Permanence and extinction of system (1.7)

It is important to show positivity and boundedness for the system (1.7) as they represent populations. Positivity implies that the populations survive and boundedness may be interpreted as a natural restriction to growth as a consequence of limited resources.

Theorem 2.1. *Every solution of system (1.7) with initial conditions (1.8) exists in the interval* $[0, +\infty)$ *and remains positive for all* $t > 0$.

Proof. The model system can be put into the matrix form $\dot{X} = G(X)$, where $X = (x, y, z, Q)^T \in R^4$, $X(0) = (x(0), y(0), z(0), Q(0))$ and $G(X)$ is given by

$$G(X) = \begin{pmatrix} G_1(X) \\ G_2(X) \\ G_3(X) \\ G_4(X) \end{pmatrix} = \begin{pmatrix} ay(t) - r_1x(t) - bx(t) \\ bx(t) - r_2y(t) - b_1y^2(t) - \dfrac{a_1y(t)z(t)}{mz(t)+y(t)} \\ -dz(t) + hQ(t) \\ \dfrac{\delta y(t)z(t)}{mz(t)+y(t)} - \delta Q(t) \end{pmatrix}.$$

Let $R^4_+ = [0, +\infty)^4$ be the nonnegative octant in R^4, the $G : R^{4+1}_+ \to R^4$ is locally Lipschitz and satisfy the condition

$$G_i(X)|_{X_i(t)=0}, X \in R^4_+ \geq 0,$$

where $X_1 = x$, $X_2 = y$, $X_3 = z$, $X_4 = Q$.

Due to the well-known theorem by Nagumo [20], any solution of (1.7) with positive initial point $X(0) \in R^4_+$, say $X(t) = X(t; X(0))$, is such that $X(t) \in R^4_+$ for all $t > 0$.

Theorem 2.2. *Positive solutions of system (1.7) with initial conditions (1.8) are ultimately bounded.*

Proof. Let $(x(t), y(t), z(t), Q(t))$ be any solution of system (1.7) with initial conditions (1.8). Set

$$L(t) = x(t) + y(t) + \frac{a_1}{\delta}Q(t). \tag{2.1}$$

Calculating the derivative of $L(t)$ along solutions of system (1.7), we obtain

$$\begin{aligned}\frac{dL(t)}{dt}|_{(1.7)} &= -r_1x(t) - r_2y(t) - a_1Q(t) + ay(t) - b_1y^2(t)\\ &\leq -AL(t) + ay(t) - b_1y^2(t)\\ &\leq -AL(t) + \frac{a^2}{4b_1},\end{aligned}$$

where $A = \min\{r_1, r_2, a_1\}$. It follows that $\limsup\limits_{t\to+\infty} L(t) = \frac{a^2}{4b_1} := M^*$. Therefore, there exist positive constants $M_1 > M^*$ and $T_1 > 0$ such that if $t \geq T_1$, $L(t) \geq M_1$. Then $x(t)$, $y(t)$ and $Q(t)$ have ultimately above bound. It follows from the third equation of (1.7) that $z(t)$ has an ultimately above bound, say, their maximum is an M. This proof is complete.

Theorem 2.3. *Suppose that the following conditions*

$$ab > (r_2 + \frac{a_1}{m})(r_1 + b), \;\; h > d \tag{2.2}$$

hold. Then system (1.7) is permanent.

Proof. Let $(x(t), y(t), z(t), Q(t))$ be any solution of system (1.7) with initial conditions (1.8). It follows from the first and second equations of system (1.7) that

$$\begin{cases}\dfrac{dx}{dt} = ay(t) - r_1x(t) - bx(t),\\[2mm] \dfrac{dy}{dt} \geq bx(t) - r_2y(t) - b_1y^2(t) - \dfrac{a_1}{m}y(t).\end{cases} \tag{2.3}$$

Consider the following auxiliary system

$$\begin{cases} \dfrac{du_1}{dt} = au_2(t) - r_1u_1(t) - bu_1(t), \\ \dfrac{du_2}{dt} = bu_1(t) - r_2u_2(t) - b_1u_2^2(t) - \dfrac{a_1}{m}u_2(t). \end{cases} \tag{2.4}$$

It is easy to calculate that if $ab > (r_2 + \dfrac{a_1}{m})(r_1 + b)$ holds, system (2.4) has two equilibria: $B_1(0,0)$, $B_2(u_1^*, u_2^*)$, where

$$u_1^* = \frac{r_1 + b}{a}u_2^*, \quad u_2^* = \frac{ab - (r_2 + \frac{a_1}{m})(r_1 + b)}{b(r_1 + b)}.$$

It is easy to verify that if $ab > (r_2 + \dfrac{a_1}{m})(r_1 + b)$ holds, $B_1(0,0)$ is always a saddle point, $B_2(u_1^*, u_2^*)$ is always locally asymptotically stable.

In the following, we shall show $B_2(u_1^*, u_2^*)$ is always globally asymptotically stable for $ab > (r_2 + \frac{a_1}{m})(r_1 + b)$. Consider the following Lyapunov function

$$V(t) = \lambda_1(u_1 - u_1^* - u_1^* \ln \frac{u_1}{u_1^*}) + \lambda_2(u_2 - u_2^* - u_2^* \ln \frac{u_2}{u_2^*}),$$

where λ_1 and λ_2 are suitable constants to be determined in the subsequence steps. Obviously, $V(t)$ is a positive definite function in the region R_2^+ except for at $B_2(u_1^*, u_2^*)$ where it vanishes. Further,

$$\lim_{u_i(t)\to 0} V(u_1, u_2) = \lim_{u_i(t)\to +\infty} V(u_1, u_2) = +\infty, \quad (i = 1, 2).$$

Calculating the derivative of $V(t)$ along solutions of (2.4), we derive

$$\begin{aligned} \dot{V} &= \lambda_1(u_1 - u_1^*)\frac{\dot{u}_1}{u_1} + \lambda_2(u_2 - u_2^*)\frac{\dot{u}_2}{u_2} \\ &= \lambda_1(u_1 - u_1^*)(\frac{au_2}{u_1} - r_1 - b) + \lambda_2(u_2 - u_2^*)(\frac{bu_1}{u_2} - r_2 - \frac{a_1}{m} - bu_2) \\ &= -\frac{\lambda_1 a u_2}{u_1 u_1^*}(u_1 - u_1^*)^2 + (\frac{\lambda_1 a}{u_1^*} + \frac{\lambda_2 b}{u_2^*})(u_1 - u_1^*)(u_2 - u_2^*) - \frac{\lambda_2 b u_1}{u_2 u_2^*}(u_2 - u_2^*)^2 \\ &\quad - \lambda_2 b(u_2 - u_2^*)^2. \end{aligned}$$

Let $\lambda_1 = \frac{u_1^*}{a}$, $\lambda_2 = \frac{u_2^*}{b}$. Thus

$$\dot{V} = -[\sqrt{\frac{u_2}{u_1}}(u_1 - u_1^*) - \sqrt{\frac{u_1}{u_2}}(u_2 - u_2^*)]^2 - u_2^*(u_2 - u_2^*)^2 \le 0.$$

Set

$$D = \{u \in IntR_+^2 | \frac{dV}{dt} = 0\} = \{u \in IntR_+^2 | u_i = u_i^*, \ i = 1, 2.\}$$

According to Lasalle Theorem, $B_2(u_1^*, u_2^*)$ is globally asymptotically stable for $ab > (r_2 + \dfrac{a_1}{m})(r_1 + b)$. Therefore, we have

$$\lim_{t\to +\infty} u_1(t) = u_1^*, \quad \lim_{t\to +\infty} u_2(t) = u_2^*,$$

which imply that there exist a sufficiently small $\varepsilon > 0$ and $T_1 > T$, such that

$$u_1(t) > u_1^* - \frac{\varepsilon}{2}, \quad u_2(t) > u_2^* - \frac{\varepsilon}{2} \quad \text{for all } t \geq T_1.$$

From (2.3), by standard comparison argument shows that

$$\liminf_{t\to+\infty} x(t) \geq u_1^* - \frac{\varepsilon}{2}, \ \liminf_{t\to+\infty} y(t) \geq u_2^* - \frac{\varepsilon}{2}.$$

Thus, there exist a sufficiently small $\varepsilon > 0$ and $T_2 > T$ ($T_2 > T_1$), such that $x(t) \geq \frac{u_1^*}{2}$, $y(t) \geq \frac{u_2^*}{2}$.

From the third and fourth equations of system (1.7), we obtain

$$\begin{cases} \dfrac{dz}{dt} = -dz(t) + hQ(t), \\ \dfrac{dQ}{dt} \geq \dfrac{\frac{\delta u_2^*}{2} z(t)}{mz(t) + \frac{u_2^*}{2}} - \delta Q(t). \end{cases} \tag{2.6}$$

Now, we consider the comparison equations

$$\begin{cases} \dfrac{du_3}{dt} = -du_3(t) + hu_4(t), \\ \dfrac{du_4}{dt} \geq \dfrac{\frac{\delta u_2^*}{2} u_3(t)}{mu_3(t) + \frac{u_2^*}{2}} - \delta u_4(t). \end{cases} \tag{2.7}$$

Obviously, if $h > d$, then the unique positive equilibrium (u_3^*, u_4^*) of (2.7), where

$$u_3^* = \frac{1}{2m}(\frac{h}{d} - 1)u_2^*, \quad u_4^* = \frac{h}{d}u_3^*,$$

exists and is locally asymptotically stale. Let $0 < u_3(t_0) < z(t_0)$, $0 < u_4(t_0) < Q(t_0)$, $t_0 > T_2$. If $(u_3(t), u_4(t))$ is a solution of (2.7) with initial conditions $(u_3(t_0), u_4(t_0))$ for $T_0 > T_2$, then $z(t) \geq u_3(t)$, $Q(t) \geq u_4(t)$ for $t > t_0$. If for (2.7), there exist a solution which is unbounded, say, $(\overline{u}_3(t), \overline{u}_4(t)) \to (+\infty, +\infty)$, as $t \to +\infty$, then it follows that for (1.7) there exists at least one solution, say $(x(t), y(t), z(t), Q(t))$, which is also unbounded provided there is a satisfying initial condition $0 < \overline{u}_3(t_0) < z(t_0)$, $0 < \overline{u}_4(t_0) < Q(t_0)$. This contradicts the boundedness of solutions of (1.7). Hence, we must have that all the solutions of (2.7) are bounded, it follows that the unique positive equilibrium (u_3^*, u_4^*) is globally asymptotically stable. Hence we have

$$\liminf_{t\to+\infty} z(t) \geq u_3^*, \quad \liminf_{t\to+\infty} Q(t) \geq u_4^*.$$

The proof is complete.

Theorem 2.4. *If $r_1 > \delta$, $r_2 - a > \delta$, then system (1.7) is not permanent.*

Proof. If $r_1 > d$, $r_2 - a > d$, then there exists a $\beta > 0$ such that $a = r_2 + \frac{a_1}{m+\beta}$. If we let $\delta_1 = \frac{x(0)+y(0)}{z(0)} < \beta$, we can claim that $\frac{x(t)+y(t)}{z(t)} < \beta$ for all $t \geq 0$, and $\lim_{t\to+\infty}(x(t)+y(t)) = 0$. Otherwise, there is a first time t_1 such that

$$\frac{x(t_1)+y(t_1)}{z(t_1)} = \beta, \quad \frac{x(t)+y(t)}{z(t)} < \beta \quad \text{for } t \in [0, t_1).$$

Thus, for all $t \in [0, t_1]$, from (1.7), we derive that

$$\begin{aligned}\frac{d(x(t)+y(t))}{dt} &= ay(t) - r_1x(t) - r_2y(t) - b_1y^2(t) - \frac{a_1y(t)z(t)}{mz(t)+y(t)} \\ &\leq -r_1x(t) - (r-2-a+\frac{a_1}{m+\beta})y(t) \\ &\leq -d(x(t)+y(t)),\end{aligned}$$

which yields

$$x(t)+y(t) \leq (x(0)+y(0))e^{-dt}. \tag{2.8}$$

On the other hand, from (1.7), it is easy to obtain that $\frac{dz}{dt} \geq -dz(t)$, for all $T \geq 0$, which yields

$$z(t) \geq z(0)e^{-dt}. \tag{2.9}$$

It follows from (2.8) and (2.9) that

$$\frac{x(t)+y(t)}{z(t)} \leq \frac{x(0)+y(0)}{z(0)} = \delta_1 < \beta$$

for all $t \in [0, t_1]$, which leads to a contradiction. Thus, we have $x(t)+y(t) \leq (x(0)+y(0))e^{-dt}$ for all $t > 0$. It follows that

$$\lim_{t\to+\infty}(x(t)+y(t)) = 0,$$

which yields $\lim_{t\to+\infty} x(t) = 0$, $\lim_{t\to+\infty} y(t) = 0$. The proof is complete.

Theorem 2.5. *If $r_1 > d$, $r_2 - a > d$, then there exist positive solutions $(x(t)$, $y(t)$, $z(t)$, $Q(t))$ of system (1.7) such that*

$$\lim_{t\to+\infty}(x(t), y(t), z(t), Q(t)) = (0, 0, 0, 0).$$

Proof. The argument leading to Theorem 2.4 shows that

$$\lim_{t\to+\infty} x(t) = 0, \quad \lim_{t\to+\infty} y(t) = 0,$$

and for $t \geq 0$, $\frac{x(t)+y(t)}{z(t)} < \beta$, provided that $\delta_1 = \frac{x(0)+y(0)}{z(0)} < \beta$.

Let $(x(t), y(t), z(t), Q(t))$ be the solution of (1.7) with $\frac{x(0)+y(0)}{z(0)} < \beta$. Since the solution $(x(t), y(t), z(t), Q(t))$ of (1.7) is bounded, we have

$$0 \leq l_1 := \limsup_{t\to+\infty} z(t) < +\infty, \quad 0 \leq l_2 := \limsup_{t\to+\infty} Q(t) < +\infty.$$

Since $\lim_{t\to+\infty} y(t) = 0$, then there is a t_1, such that for $t > t_1$, $y(t) \le \frac{ml_1}{2}$. If $l_1 > 0$, then there is a t_2 $(> t_1)$, such that $Q(t_2) > \frac{l_1}{2}$ and $\frac{dQ}{dt} > 0$. Moreover $\frac{dQ}{dt} \le \frac{\delta}{m}y(t) - \delta Q(t)$. Hence $0 < \frac{dQ}{dt}|_{t=t_2} \le \frac{\delta}{m}y(t_2) - \delta Q(t_2)$. Then $y(t_2) > \frac{ml_1}{2}$. This is a contradiction to $y(t) \le \frac{ml_1}{m}$ for $t > t_1$. Hence we must have $l_1 = 0$. Incorporating into the positivity of solutions, we have $\lim_{t\to+\infty} Q(t) = 0$. It follows that $\lim_{t\to+\infty} z(t) = 0$. This completes the proof.

3. Equilibria and stability

System (1.7) always has equilibrium $E_0(0,0,0,0)$. Except for equilibrium $E_0(0,0,0)$, system (1.7) also has equilibria: $E_1(x_1, y_1, 0, 0)$, $E^*(x^*, y^*, z^*, Q^*)$, where

$$x_1 = \frac{a(ab - r_1r_2 - br_2)}{b_1(r_1^2 + 2br_1 + b^2)}, \quad y_1 = \frac{ab - r_1r_2 - br_2}{b_1(r_1 + b)},$$

$$x^* = \frac{a(bamh - r_2mr_1h - r_2mbh - a_1r_1h + a_1r_1d - a_1bh + a_1bd)}{b_1mh(r_1 + b)^2},$$

$$y^* = \frac{bamh - r_2mr_1h - r_2mbh - a_1r_1h + a_1r_1d - a_1bh + a_1bd}{b_1mh(r_1 + b)},$$

$$z^* = \frac{bamh - r_2mr_1h - r_2mbh - a_1r_1h + a_1r_1d - a_1bh + a_1bd}{b_1m^2h(r_1 + b)(h - d)d},$$

$$Q^* = \frac{bamh - r_2mr_1h - r_2mbh - a_1r_1h + a_1r_1d - a_1bh + a_1bd}{b_1m^2h^2(r_1 + b)(h - d)}.$$

Obviously, E_1 is nonnegative equilibrium if $ab > r_1r_2 + br_2$ and E^* is positive equilibrium if $bamh + a_1r_1d + a_1bd > r_2mr_1h + r_2mbh + a_1r_1h + a_1bh$ and $h > d$.

Now we shall consider the local geometric properties of the nonnegative equilibria of system (1.7). We shall point out here that, although $E_0(0,0,0,0)$ is defined for system (1.7), it cannot be linearized. Hence, the local stability of $E_0(0,0,0,0)$ cannot be studied. Indeed, this singularity at the origin, while causing much difficulty in our analysis of the system, contributes significantly to the richness of dynamics of the model [21-23].

The Jacobian matrix $J_{E_1} = J(x_1, y_1, 0, 0)$ of system (1.7) at E_1 takes the form of

$$J_{E_1} = \begin{pmatrix} -r_1 - b & a & 0 & 0 \\ b & -r_2 - 2b_2y_1 & -a_1 & 0 \\ 0 & 0 & -d & h \\ 0 & 0 & \delta & -\delta \end{pmatrix},$$

which gives the following characteristic equation in λ as:

$$[\lambda^2+(d+\delta)\lambda+d\delta-h\delta][\lambda^2+(2b_1y_1+r_2+r_1+b)\lambda+(r_1+b)(2b_1y_1+r_2)-ab]=0.$$

If $d<h$ and $(r_1+b)(2hy_1+r_2)<ab$, then four eigenvalues are always real and negative. Hence, E_1 is locally asymptotically stable if $d<h$ and $(r_1+b)(2hy_1+r_2)<ab$. And E_1 is unstable if one of $d>h$ and $(r_1+b)(2hy_1+r_2)>ab$ hold at least.

Theorem 3.1. *Assume that $h\le d$, $(r_1+b)r_2\ge ab$. Then the nonnegative equilibrium $E_1(x_1,y_1,0,0)$ is globally asymptotically stable.*

Proof. From the last two equations of (1.7), we have

$$\begin{cases} \dfrac{dz}{dt}=-dz(t)+hQ(t), \\ \dfrac{dQ}{dt}\le \delta z(t)-\delta Q(t). \end{cases} \tag{3.1}$$

We consider the comparison equations

$$\begin{cases} \dfrac{dw_1}{dt}=-dw_1(t)+hw_2(t), \\ \dfrac{dw_2}{dt}=\delta w_1(t)-\delta w_2(t). \end{cases} \tag{3.2}$$

it is easy to show that if $h\le d$ for any solution of (1.7) with nonnegative initial values we have

$$\lim_{t\to+\infty} w_1(t)=0, \quad \lim_{t\to+\infty} w_2(t)=0.$$

If $(z(t),Q(t))$ is a solution of (1.7) with initial value $(w_1(0),w_2(0))$, then by then comparison theorem we have $z(t)\le w_1(t)$, $Q(t)\le w_2(t)$ for all $t>0$. Hence $\lim_{t\to+\infty} z(t)=0$ and $\lim_{t\to+\infty} Q(t)=0$.

By Theorem 2.3, there exists a $T_2>0$ such that $y(t)>\dfrac{u_2^*}{2}$ for $t>T_2$. Thus, for any given $\varepsilon>0$, there is a $T_3>T_2$ such that $\dfrac{a_1z}{mz+y}<\varepsilon$ for $t>T_3$. From the first equation and the second equation of (1.7), we have

$$\begin{cases} \dfrac{dx}{dt}=ay(t)-r_1x(t)-bx(t), \\ \dfrac{dy}{dt}\ge bx(t)-r_2y(t)-b_1y^2(t)-\varepsilon y(t). \end{cases} \tag{3.3}$$

Consider the following auxiliary system

$$\begin{cases} \dfrac{dw_3}{dt}=aw_4(t)-r_1w_3(t)-bw_3(t), \\ \dfrac{dw_4}{dt}=bw_3(t)-r_2w_4(t)-b_1w_4^2(t)-\varepsilon w_4(t). \end{cases} \tag{3.4}$$

Using the similar arguments in the proof of Theorem 2.3, we obtain

$$\lim_{t\to+\infty} w_3(t) = x_1 - \frac{a\varepsilon}{b(r_1+b)}, \quad \lim_{t\to+\infty} w_4(t) = y_1 - \frac{\varepsilon}{b_1}.$$

by comparison, we have

$$\lim_{t\to+\infty} x(t) \geq x_1 - \frac{a\varepsilon}{b(r_1+b)}, \quad \lim_{t\to+\infty} y(t) \geq y_1 - \frac{\varepsilon}{b_1}. \tag{3.5}$$

Similarly, by considering the equations

$$\begin{cases} \dfrac{dx}{dt} = ay(t) - r_1x(t) - bx(t), \\ \dfrac{dy}{dt} \leq bx(t) - r_2y(t) - b_1y^2(t), \end{cases}$$

we have

$$\lim_{t\to+\infty} x(t) \leq x_1, \ \lim_{t\to+\infty} y(t) \leq y_1. \tag{3.6}$$

Letting $\varepsilon \to 0$, from (3.5) and (3.6), we obtain

$$\lim_{t\to+\infty} x(t) = x_1, \quad \lim_{t\to+\infty} y(t) = y_1.$$

We compute the variational matrix for the equilibrium E^* given by

$$J_{E^*} = \begin{pmatrix} -r_1-b & a & 0 & 0 \\ b & -r_2-2b_1y^* - \frac{a_1z^{*2}}{(mz^*+y^*)^2} & -\frac{a_1y^{*2}}{(mz^*+y^*)^2} & 0 \\ 0 & 0 & -d & h \\ 0 & \frac{\delta z^{*2}}{(mz^*+y^*)^2} & \frac{\delta y^{*2}}{(mz^*+y^*)^2} & -a \end{pmatrix}.$$

The above variational matrix gives the following characteristic equation in λ:

$$\lambda^4 + p_1\lambda^3 + p_2\lambda^2 + p_3\lambda + p_4 = 0, \tag{3.7}$$

where

$$p_1 = d + \delta + r_2 + 2b_1y^* + \frac{a_1z^{*2}}{(mz^*+y^*)^2} + r_1 + b,$$

$$p_2 = d\delta - \frac{h\delta y^{*2}}{(mz^*+y^*)^2} + (d+\delta)(r_2 + 2b_1y^* + \frac{a_1z^{*2}}{(mz^*+y^*)^2})$$
$$+ (r_1+b)(d+\delta+r_2+2b_1y^* + \frac{a_1z^{*2}}{(mz^*+y^*)^2}) - ab,$$

$$p_3 = (r_2 + 2b_1y^* + \frac{a_1z^{*2}}{(mz^*+y^*)^2})(d\delta - \frac{h\delta y^{*2}}{(mz^*+y^*)^2})$$
$$+ (r_1+b)[d\delta - \frac{h\delta y^{*2}}{(mz^*+y^*)^2} + (d+\delta)(r_2+2b_1y^* + \frac{a_1z^{*2}}{(mz^*+y^*)^2})$$
$$+ \frac{a_1z^{*2}}{(mz^*+y^*)^2}\frac{h\delta y^{*2}}{(mz^*+y^*)^2} - ab(d+\delta)],$$

$$p_4 = (r_1 + b)(r_2 + 2b_1 y^* + \frac{a_1 z^{*2}}{(mz^* + y^*)^2})(d\delta - \frac{h\delta y^{*2}}{(mz^* + y^*)^2})$$
$$+ (r_1 + b)\frac{a_1 z^{*2}}{(mz^* + y^*)^2}\frac{h\delta y^{*2}}{(mz^* + y^*)^2} - ab(d\delta - \frac{h\delta y^{*2}}{(mz^* + y^*)^2}).$$

By the Routh-Hurwitz criterion, it follows that all eigenvalues of (3.7) have negative real parts if and only if $p_1 > 0$, $p_3 > 0$ $p_4 > 0$ and $p_1 p_2 p_3 > p_3^2 + p_1^2 p_4$. Hence, E^* is locally stable if $p_1 > 0$, $p_3 > 0$ and $p_1 p_2 p_3 > p_3^2 + p_1^2 p_4$.

Now, we shall find out the conditions for which the equilibrium E^* enters into Hopf bifurcation as h varies over R.

Routh-Hurwitz Criterion and Hopf bifurcation: Let $\psi : (0, \infty) \to R$ be the following continuously differentiable function of h:

$$\psi(h) := p_1(h)p_2(h)p_3(h) - p_3^2(h) - p_4(h)p_1^2(h). \tag{3.8}$$

The assumptions for Hopf bifurcations to occur are the usual ones and these require that the spectrum $\varrho(h) = \{\lambda | D(\lambda) = 0\}$ of the characteristic equation is such that

(A) there exists $h^* \in (0, \infty)$, at which a pair of complex eigenvalues $\lambda(h^*)$, $\bar{\lambda}(h^*) \in \varrho(h)$ are such that

$$Re\lambda(h^*) = 0,\ Im\lambda(h^*) := \omega_0 > 0, \tag{3.9}$$

and the transversality condition

$$\frac{dRe\lambda(h)}{dh}|_{h^*} \neq 0;$$

(B) all other elements of $\lambda(h)$ have negative real parts.

The equivalent criteria for the above assumptions for Hopf bifurcation is as follows:

Hopf bifurcation of the equilibrium E^* occurs at $h = h^*$ if and only if

$$\psi(h^*) = 0,\ \frac{dRe\lambda(h)}{dh}|_{h^*} \neq 0;$$

and all other eigenvalues are of negative real parts, where $\lambda(h)$ is purely imaginary at $h = h^*$.

The existence of $h^* \in (0, \infty)$ is ensured by solving the equation $\psi(h^*) = 0$. At $h = h^*$, the characteristic equation (3.7) becomes

$$(\lambda^2 + \frac{p_3}{p_1})(\lambda^2 + p_1\lambda + \frac{p_1 p_4}{p_3}) = 0.$$

If it has four roots, say λ_i, $(i = 1, 2, 3, 4)$ with the pair of purely imaginary roots at $h = h^*$ as $\lambda_1 = \bar{\lambda}_2$, then we have

$$\lambda_3 + \lambda_4 = -p_1, \tag{3.10}$$
$$\omega_0^2 + \lambda_3\lambda_4 = p_2, \tag{3.11}$$
$$\omega_0^2(\lambda_3 + \lambda_4) = -p_3, \tag{3.12}$$

$$\omega_0^2\lambda_3\lambda_4 = p_4, \tag{3.13}$$

where $\omega_0 = Im\lambda_1(h^*)$. By above

$$\omega_0^2 = \frac{p_3}{p_1}. \tag{3.14}$$

Now, if λ_3 and λ_4 are complex conjugate, then from (3.6), it follows that $2Re\lambda_3 = -p_1 < 0$; if they are real roots, then by (3.10) and (3.14), $\lambda_3 < 0$ and $\lambda_4 < 0$. To complete the discussion, it remains to verify the transversality condition in (3.9).

As $\psi(h)$ is a continuous function of all its roots, so there exists an open interval $h \in (h^* - \epsilon, h^* + \epsilon)$ where λ_1 and λ_2 are complex conjugate for h. Suppose, their general forms in this neighborhood are

$$\lambda_1(h) = \beta_1(h) + i\beta_2(h), \tag{3.15}$$

$$\lambda_2(h) = \beta_1(h) - i\beta_2(h). \tag{3.16}$$

It is to check the following:

$$Re[\frac{d\lambda_j}{dh}]_{h^*} \neq 0, \quad j = 1, 2. \tag{3.17}$$

Substituting $\lambda_1(h) = \beta_1(h) + i\beta_2(h)$ into (3.7) and calculating the derivative, we have

$$K(h)\beta_1' - L(h)\beta_2' + M(h) = 0, \quad L(h)\beta_1' + K(h)\beta_2' + N(h) = 0,$$

where

$$K(h) = 4\beta_1^3 - 12\beta_1\beta_2^2 + 3\lambda_1(\beta_1^2 - \beta_2^2) + 2\lambda_2\beta_1 + \lambda_3,$$
$$L(h) = 12\beta_1^2\beta_2 + 6\lambda_1\beta_1\beta_2 - 4\beta_2^3 + 2\lambda_2\beta_2,$$
$$M(h) = \lambda_1\beta_1^3 - 3\lambda_1'\beta_1\beta_2^2 + \lambda_2'(\beta_1^2 - \beta_2^2) + \lambda_3'\beta_1,$$
$$N(h) = 3\lambda_3'\beta_1^2\beta_2 - \lambda_1'\beta_2^3 + 2\lambda_2'\beta_1\beta_2 + \lambda_3'\beta_2.$$

Since $L(h)N(h) + K(h)M(h) \neq 0$ at $h = h^*$, we have

$$Re[\frac{d\lambda_j}{dh}]_{h^*} = \frac{L(h)N(h) + K(h)M(h)}{K^2(h) + L^2(h)} \neq 0.$$

Thus the conditions for Hopf bifurcation is verified. We may summarize the above discussion in the form of following proposition:

Theorem 3.2. *If the positive equilibrium E^* of the system (1.7) exists, then the system around E^* enters into the Hopf-bifurcation when h passes through h^*.*

Remark 3.1. *Theorem 3.2 shows the importance of h, the conversion rate in controlling the system dynamics.*

Remark 3.2. *The biological implication of Hopf bifurcation for E^* is that the predator coexists with the immature prey and the mature prey, exhibiting oscillatory balance behavior.*

Remark 3.3. *The period τ of the bifurcating periodic orbits for close to $h = h^*$ is given by*

$$\tau(h^*) = \frac{2\pi}{\omega_0},\ \omega_0 = \sqrt{\frac{\lambda_3(h^*)}{\lambda_1(h^*)}}. \tag{3.18}$$

4. Conclusion

In this paper, we have studied a stage-structured (stage structure for prey) predator-prey system with distributed time delay and obtained the sufficient conditions for the permanence and extinction of the system (1.7) and the non-permanence of predators. Taking the product of the per-capita rate of predation and the rate of conversing prey into predator, i.e. the parameter h, as the bifurcating parameter, we prove that there exists a threshold value beyond which the positive equilibrium bifurcates towards a periodic solution. By Theorem 2.3, we see that system (1.7) will be persistent if the birth rate into the immature prey population, the rate of immature prey becoming mature prey, and the conversion rate, the half saturation rate of the predator and the product of the per-capita rate of predation and the rate of conversing prey into predator are high and the capturing rate of the predator and the death rates of both the prey and the predator are low enough satisfying (2.2). By Theorem 2.4 we see that if the conversion rate of the predator is less than its death rate, then the predator will go to extinction, system (1.7) will not be persistent.

The stability as well as the direction of bifurcation near the positive interior equilibrium E^* can be obtained by applying the algorithm due to Poore [24]. The calculations are trivial, we omit.

At the end of this paper, we would like to point out that it is more interesting to investigate the existence of the periodic solutions and their stability (local and global stability) if $a,\ b,\ r_1,\ r_2,\ b_1,\ a_1,\ m,\ d,\ h,$ are continuously positive and periodic functions with period ω, especially by theoretical analysis.

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