Global dynamics of a predator-prey system with Holling type II functional response*

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Abstract. In this paper, a predator-prey system with Holling type II functional response and stage structure is investigated. By analyzing the corresponding characteristic equations, the local stability of each of feasible equilibria of the system is studied. The existence of the orbitally asymptotically stable periodic solution is established. By using suitable Lyapunov functions and the LaSalle invariance principle, it is proven that the predator-extinction equilibrium is globally asymptotically stable when the coexistence equilibrium is not feasible, and sufficient conditions are derived for the global stability of the coexistence equilibrium.

Keywords: Holling type II functional response, stage structure, periodic solution, LaSalle invariance principle, global stability.

1 Introduction

Mathematical modeling and computer simulation provide an effective tool in the study of contemporary population ecology [1, 2]. In population dynamics, the functional response of predator to prey density refers to the change in the density of prey attacked per unit time per predator as the prey density changes [3]. In [4], based on experiment, Holling suggested three kinds of functional response for different species to model the phenomena of predation, it seems more reasonable than the standard Lotka–Voltera type predator-prey system. In [5], Bazykin proposed the following predator-prey system:

$$\begin{aligned} \dot{u}(t) &= u(t)\left(a - \varepsilon u(t) - \frac{bv(t)}{1+\alpha u(t)}\right), \\ \dot{v}(t) &= v(t)\left(-c + \frac{du(t)}{1+\alpha u(t)} - \eta v(t)\right), \end{aligned} \tag{1}$$

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where $u(t), v(t)$ represent the densities of prey and predator population, respectively. System (1) is called Holling type II predator-prey model in the literature. This system is an extension of the familiar Lotka–Volterra system, in which the divisor $1 + \alpha u$ is missing, i.e., $\alpha = 0$. α is interpreted as a constant handling time for each prey captured. For low prey biomass ($\alpha u \ll 1$) this response approximates the classical Lotka–Volterra one. In [5], the stability of equilibrium, Hopf bifurcation, global existence of limit cycles, global attractivity of equilibria, and codimension two bifurcations are investigated. The global behavior of system (1) has been discussed by many authors (see, e.g., [5–7]).

In system (1), it is assumed that each individual predator has the same ability to feed on prey. However, in the natural world, many species go through two or more life stages as they proceed from birth to death, and in different stages, they have different reactions to the environment. For example, the immature predators are raised by their parents, and the rate they attack the prey and the reproductive rate can not be ignored. Stage-structured population models have received great attention in recent years (see, e.g., [8–13]). In [12], Yu et al. studied the following strengthen type predator-prey model with stage structure

$$\begin{aligned} \dot{x}(t) &= x(t)\big(r - ax(t) - a_1 y_2(t)\big),\\ \dot{y}_1(t) &= e y_2(t) - (r_1 + D) y_1(t),\\ \dot{y}_2(t) &= D y_1(t) - r_2 y_2(t) + a_2 x(t) y_2(t), \end{aligned} \tag{2}$$

where $x(t)$ represents the density of the prey at time t, $y_1(t)$ and $y_2(t)$ represent the densities of the immature and the mature predator at time t, respectively; the parameters a, e, r, a_1, a_2, r_1, r_2 and D are positive constants in which a is the intra-specific competition rate of the prey, a_2/a_1 is the rate of conversing prey into new mature predator, e is the birth rate of new predators, r is the intrinsic growth rate of the prey, r_1 is the death rate of the immature predator and r_2 is the death rate of the mature predator, and D denotes the rate of immature predator becoming mature predator. In system (2), it was assumed that feeding on prey can only make contribution to the increasing of the physique of the predator and does not make contribution to the reproductive ability. In [12], the global asymptotic stability of the coexistence equilibrium was established by constructing suitable Lyapunov functions.

Motivated by the works of Bazykin [5] and Yu et al. [12], in this paper, we are concerned with the effect of functional response and stage structure on the dynamics of a predator-prey system. To this end, we study the following differential equations

$$\begin{aligned} \dot{x}(t) &= x(t)\left(r - ax(t) - \frac{a_1 y_2(t)}{1 + mx(t)}\right),\\ \dot{y}_1(t) &= e y_2(t) - (r_1 + D) y_1(t),\\ \dot{y}_2(t) &= D y_1(t) - r_2 y_2(t) + \frac{a_2 x(t) y_2(t)}{1 + mx(t)}, \end{aligned} \tag{3}$$

where $a_1 x/(1 + mx)$ describes the Holling type II functional response, here a_1 and m represent the effects of capturing rate and handling time, respectively, and $r_2 m > a_2$ is reasonable for biological meaning, and implies that hunting has a reward in the sense of diminishing their mortality rate.

It is easy to show that all solutions of system (3) are defined on $[0, +\infty)$ and remain positive for all $t \geq 0$.

The organization of this paper is as follows. In the next section, by analyzing the corresponding characteristic equations, the local stability of each of nonnegative equilibria of system (3) is discussed. In Section 3, we present conditions for the permanence of system (3). Further, based on discussions above, by using the theory of monotone flows for three-dimensional competitive system, the existence of orbitally asymptotically stable periodic solution is obtained. In Section 4, by using suitable Lyapunov functions and LaSalle invariance principle, sufficient conditions are derived for the global stability of the predator- extinction equilibrium and the coexistence equilibrium of system (3). A brief remark is given in Section 5 to conclude this work.

2 Local stability

In this section, we discuss the local stability of each equilibria of system (3) by analyzing the corresponding characteristic equations. It is easy to show that system (3) always has a trivial equilibrium $E_0(0,0,0)$ and a predator-extinction equilibria $E_1(r/a,0,0)$. Furthermore, if the following holds:

(H1) $a_2 r > (a + rm)[r_2 - \frac{eD}{D+r_1}] > 0$,

then system (3) has a unique coexistence equilibrium $E^*(x^*, y_1^*, y_2^*)$, where

$$x^* = \frac{r_2(D+r_1) - eD}{(a_2 - r_2 m)(D+r_1) + emD},$$
$$y_1^* = \frac{e}{D+r_1} y_2^*, \quad y_2^* = \frac{a_2(D+r_1)(r - ax^*)x^*}{a_1[r_2(D+r_1) - eD]}.$$

We now study the local stability of each of nonnegative equilibria of system (3).

By analyzing the characteristic equation of system (3) at the equilibrium $E_0(0,0,0)$, it is easy to show that E_0 is always unstable.

The characteristic equation of system (3) at the equilibrium $E_1(r/a,0,0)$ takes the form

$$(\lambda + r)\big(\lambda^2 + g_1\lambda + g_0\big) = 0, \tag{4}$$

where

$$g_0 = r_2(D+r_1) - eD - (D+r_1)\frac{a_2 r}{a+rm},$$
$$g_1 = D + r_1 + \frac{r_2(a+rm) - a_2 r}{a+rm}.$$

Eq. (4) always has a negative real root $\lambda = -r$. If $a_2(D+r_1) < (a+rm)[r_2(D+r_1) - eD]$, then $g_0 > 0, g_1 > 0$. It is easy to show that roots of $\lambda^2 + g_1\lambda + g_0 = 0$

have only negative real parts. Accordingly, the equilibrium E_1 of system (3) is locally asymptotically stable. If (H1) holds, Eq. (4) has at least one positive real root. Therefore, E_1 is unstable.

The characteristic equation of system (3) at the coexistence equilibrium $E^*(x^*, y_1^*, y_2^*)$ is of the form

$$\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 = 0, \tag{5}$$

where

$$\begin{aligned} p_0 &= \big[(a_2 - r_2 m)(D + r_1) + emD\big]\frac{a_1 x^* y_2^*}{(1 + mx^*)^2}, \\ p_1 &= (D + r_1 + r_2)\frac{a_1 y_2^*}{(1 + mx^*)^2} + (r - 2ax^*)\left(\frac{a_2 x^*}{1 + mx^*} - (D + r_1 + r_2)\right), \\ p_2 &= D + r_1 + 2ax^* - r + \frac{eD}{D + r_1} + \frac{a_1 y_2^*}{(1 + mx^*)^2}. \end{aligned}$$

It is readily seen that if $p_2 > 0, p_1 p_2 - p_0 > 0$, by the Routh–Hurwitz theorem, the coexistence equilibrium E^* of system (3) is locally asymptotically stable; and E^* is unstable if $p_1 p_2 - p_0 < 0$.

Based on the discussions above, we have the following result.

Theorem 1. *For system* (3)*, we have*:

(i) *The equilibrium $E_0(0, 0, 0)$ is always unstable.*

(ii) *If $a_2 r(D + r_1) < (a + r_2 m)[r_2(D + r_1) - eD]$, then the equilibrium $E_1(r/a, 0, 0)$ is locally asymptotically stable*; *if* (H1) *holds, E_1 is unstable.*

(iii) *Let* (H1) *hold. If $p_2 > 0$, $p_1 p_2 - p_0 > 0$, then the coexistence equilibrium $E^*(x^*, y_1^*, y_2^*)$ of system* (3) *is locally stable*; *if $p_1 p_2 - p_0 < 0$, E^* is unstable.*

3 Permanence and stable periodic solution

In this section, we establish the permanence of system (3) and the existence of orbitally asymptotically stable periodic solution.

Before giving our main results, we need the following lemmas.

Lemma 1. *Let $r_2(D + r_1) > eD$. Then positive solutions of system* (3) *are ultimately bounded.*

Proof. Let $(x(t), y_1(t), y_2(t))$ be any positive solution of system (3).

Define

$$N(t) = a_2 x(t) + k y_1(t) + a_1 y_2(t),$$

where $k = a_1[r_2(D + r_1) + eD]/(2e(D + r_1))$.

Calculating the derivative of $N(t)$ along positive solutions of (3), it follows that

$$\begin{aligned} \dot{N}(t) &= a_2 x(r - ax) - (k(D + r_1) - a_1 D)y_1 - (a_1 r_2 - ke)y_2 \\ &\le a_2 x(r - ax) - \delta(k y_1 + a_1 y_2), \end{aligned} \tag{6}$$

where $\delta = \min\{D + r_1 - a_1 D/k, r_2 - ke/a_1\}$. Noting that $r_2(D + r_1) > eD$, it follows from (6) that

$$\dot{N}(t) = a_2 x(r + \delta - ax) - \delta N(t) \le \frac{a_2(r+\delta)^2}{4a} - \delta N(t). \tag{7}$$

We derive from (7) that

$$\limsup_{t\to+\infty} N(t) \le \frac{a_2(r+\delta)^2}{4a\delta} := M.$$

Hence, for $\varepsilon > 0$ sufficiently small, there exists a $T > 0$ such that, if $t > T$,

$$x(t) < M + \varepsilon, \quad y_1(t) < M + \varepsilon, \quad y_2(t) < M + \varepsilon.$$

This completes the proof. □

Let X be a complete metric space. Suppose that $X^0 \subset X, X_0 \subset X, X^0 \cap X_0 = \phi$. Assume that $T(t)$ is a C_0 semigroup on X satisfying

$$T(t) : X^0 \to X^0, \quad T(t) : X_0 \to X_0. \tag{8}$$

Let $T_b(t) = T(t)|_{X_0}$ and let A_b be the global attractor for $T_b(t)$. The following lemma was introduced by Wang and Chen [10].

Lemma 2. [10] *Suppose that $T(t)$ satisfies* (8) *and the following*:

(i) *there is a $t_0 \ge 0$ such that $T(t)$ is compact for $t > t_0$*;

(ii) *$T(t)$ is point dissipative in X*;

(iii) *$\tilde{A}_b = \bigcup_{x\in A_b} \omega(x)$ is isolated and has an acyclic covering $\tilde{M}$, where*

$$\tilde{M} = \{M_1, M_2, \dots, M_n\};$$

(iv) *$W^s(M_i) \cap X^0 = \phi$ for $i = 1, \dots, n$.*

Then X_0 is uniform repeller with respect to X^0, i.e., there is an $\varepsilon > 0$ such that for any $x \in X^0, \liminf_{t\to+\infty} d(T(t)x, X_0) \ge \varepsilon$, where d is the distance of $T(t)x$ from X_0.

We now investigate the permanence of system (3).

Theorem 2. *If* (H1) *holds, then system* (3) *is permanent.*

Proof. Define

$$U_1 = \{(x, y_1, y_2) \in R^3_+ \colon x \equiv 0\},$$
$$U_2 = \{(x, y_1, y_2) \in R^3_+ \colon y_1 \equiv 0,\ y_2 \equiv 0\}.$$

If $X_0 = U_1 \cup U_2$ and $X^0 = \mathrm{int}\mathrm{R}^3_+$, it is easy to show that X_0 and X^0 are coexistently invariant. Moreover, by Lemma 1, conditions (i) and (ii) of Lemma 2 are clearly satisfied.

Hence, we only need to verify the conditions (iii) and (iv). There are two constant solutions $E_0(0,0,0)$ and $E_1(r/a,0,0)$ in X_0, corresponding, respectively, to $x(t) = y_1(t) = y_2(t) = 0$ and $x(t) = r/a, y_1(t) = y_2(t) = 0$. If $(x(t), y_1(t), y_2(t))$ is a solution of system (3) initiating from U_1, then

$$\begin{aligned}\dot{y}_1(t) &= ey_2(t) - (D + r_1)y_1(t),\\ \dot{y}_2(t) &= Dy_1(t) - r_2y_2(t).\end{aligned}$$

Obviously, if (H1) holds, $y_1(t) \to 0$ and $y_2(t) \to 0$ as $t \to +\infty$. If $(x(t), y_1(t), y_2(t))$ is a solution of system (3) initiating from U_2 with $x(0) > 0$, it is easy to see that $x(t) \to r/a$ as $t \to +\infty$. This shows that if invariant set E_0 and invariant set E_1 are isolated, $\{E_0, E_1\}$ is isolated and is an acyclic covering. It is obvious that E_0 is isolated invariant. The isolated invariance of E_1 will be a consequence of the following proof.

We now prove that $W^s(E_0) \cap X^0 = \phi$ and $W^s(E_1) \cap X^0 = \phi$. We restrict our attention to the second equation, since the proof for the first is simple. Assume the contrary. Then there exists a positive solution $(\tilde{x}(t), \tilde{y}_1(t), \tilde{y}_2(t))$ of system (3) such that

$$\big(\tilde{x}(t), \tilde{y}_1(t), \tilde{y}_2(t)\big) \to \left(\frac{r}{a}, 0, 0\right), \quad \text{as } t \to +\infty.$$

Choose $\xi > 0$ sufficiently small satisfying

$$r_2(D + r_1) - eD < \frac{a_2(D + r_1)(r/a - \xi)}{m(r/a - \xi)}. \tag{9}$$

Let $T > 0$ be sufficiently large such that

$$\frac{r}{a} - \xi < \tilde{x}(t) < \frac{r}{a} + \xi \quad \text{for } t \geq T.$$

Then we have, for $t \geq T$,

$$\begin{aligned}\tilde{y}_1'(t) &= e\tilde{y}_2(t) - (D + r_1)\tilde{y}_1(t),\\ \tilde{y}_2'(t) &\geq D\tilde{y}_1(t) - r_2\tilde{y}_2(t) + \frac{a_2(r/a - \xi)}{1 + m(r/a - \xi)}\tilde{y}_2(t).\end{aligned} \tag{10}$$

We consider the matrix A_ξ defined by

$$A_\xi = \begin{bmatrix} -D - r_1 & e \\ D & \frac{a_2(r/a-\xi)}{1+m(r/a-\xi)} - r_2 \end{bmatrix}.$$

Since A_ξ admits positive off-diagonal elements, the Perron–Frobenius theorem implies that there is a positive eigenvector υ for the maximum eigenvalue α of A_ξ. Moreover, by computing, we see that the maximum eigenvalue α is positive since we have (9).

We now consider the following system:

$$\begin{aligned}y_1'(t) &= -(D + r_1)y_1(t) + ey_2(t),\\ y_2'(t) &= Dy_1(t) - \left(r_2 - \frac{a_2(r/a - \xi)}{1 + m(r/a - \xi)}\right)y_2(t).\end{aligned} \tag{11}$$

Let $\upsilon = (\upsilon_1, \upsilon_2)$ and let $l > 0$ be small enough such that

$$\tilde{y}_1(t_0) > l\upsilon_1, \quad \tilde{y}_2(t_0) > l\upsilon_2.$$

If $(y_1(t), y_2(t))$ is a solution of system (11) satisfying $y_1(t_0) = l\upsilon_1, y_2(t_0) = l\upsilon_2$, since the semiflow of system (11) is monotone and $A_\xi \upsilon > 0$, it follows from [14] that $y_i(t)$ is strictly increasing and $y_i(t) \to +\infty$ as $t \to +\infty$. Note that $\tilde{y}_i(t) \geq y_i(t)$ for $t > t_0$. We have $\tilde{y}_i(t) \to +\infty$ as $t \to +\infty$. This contradicts Lemma 3.1. The above assertion is thus proved. At this time, we are able to conclude from Lemma 3.2 that X_0 repels the positive solutions of (3) uniformly. As a consequence, there exists a $\varepsilon > 0$ such that each positive solution $(x(t), y_1(t), y_2(t))$ of (3) satisfies $\liminf_{t\to+\infty} x(t) \geq \varepsilon$ and lies eventually outside the set Q_1 defined by

$$Q_1 = \{(x, y_1, y_2)\colon\ x > 0,\ 0 < y_1 \leq \varepsilon,\ 0 < y_2 \leq \varepsilon\}.$$

Let

$$0 < \rho < \min\left\{\varepsilon, \frac{D\varepsilon(1 + m\varepsilon)}{2(r_2 + (r_2 m - a_2)\varepsilon)}\right\}$$

be fixed, where $r_2 > a_2\varepsilon/(1 + m\varepsilon)$. Then $y_2'(t) > D\varepsilon/2$ on region Q_2 defined by

$$Q_2 = \{(x, y_1, y_2)\colon\ x > 0,\ y_1 \geq \varepsilon,\ 0 < y_2 \leq \rho\}.$$

It follows that each positive solution $(x(t), y_1(t), y_2(t))$ of system (3) leaves Q_2 eventually and lies eventually outside Q_2. Hence, $y_2(t) \geq \rho$ for t sufficiently large. In view of $\liminf_{t\to+\infty} x(t) \geq \varepsilon$, we see that for t sufficiently large,

$$\dot{y}_1(t) \geq e\rho - (D + r_1)y_1(t).$$

It follows that

$$\liminf_{t\to+\infty} y_1(t) \geq \frac{e\rho}{D + r_1}.$$

Consequently, system (3) is permanent. This completes the proof. □

In the following, we show that there exists an orbitally asymptotically stable periodic orbit in system (3).

Theorem 3. *Let* (H1) *hold. If* $p_2p_1 - p_0 < 0$*, then system* (3) *has an orbitally asymptotically stable periodic solution.*

Proof. Letting $z_1 = -x$, $z_2 = y_1$, $z_3 = -y_2$, system (3) becomes

$$\begin{aligned} z_1' &= z_1\left(r + az_1 + \frac{a_1 z_3}{1 - mz_1}\right),\\ z_2' &= -ez_3 - (D + r_1)z_2,\\ z_3' &= -Dz_2 - r_2 z_3 + \frac{a_2 z_1 z_3}{1 - mz_1}. \end{aligned} \tag{12}$$

If we write (12) as $z' = f(z)$, the Jacobian matrix of f at z is as follows:

$$J(z) = \begin{bmatrix} r + 2az_1 + \frac{a_1 z_3}{(1-mz_1)^2} & 0 & \frac{a_1 z_1}{1-mz_1} \\ 0 & -r_1 - D & -e \\ \frac{a_2 z_3}{(1-mz_1)^2} & -D & -r_2 + \frac{a_2 z_1}{1-mz_1} \end{bmatrix}.$$

Denote $E = \{(z_1, z_2, z_3)\colon z_1 < 0,\ z_2 > 0,\ z_3 < 0\}$. $J(z)$ has nonpositive off-diagonal elements at each point of E. Thus, system (12) is competitive in E. Let $z_1^* = -x^*$, $z_2^* = y_1^*$ and $z_3^* = y_2^*$. It is obvious that (z_1^*, z_2^*, z_3^*) is the unique equilibrium of system (12). Since $p_2p_1 - p_0 < 0$ holds, the analysis above shows that (z_1^*, z_2^*, z_3^*) is unstable and det $J(z^*) < 0$. Moveover, since system (3) is permanent, there exists a compact subset B of E such that for each $z_0 \in E$, there exists a $T(z_0) > 0$ such that $z(t, z_0) \in B$ for all $t \geq T(z_0)$. Hence, by Theorem 1.2 of [15], system (12) has an orbitally asymptotically stable periodic solution. This completes the proof. □

In the following, we give one example to illustrate the main results above.

Example 1. In system (3), we let $a = 1$, $a_1 = 1$, $a_2 = 4$, $e = 2$, $m = 1$, $r = 5$, $r_1 = 1$, $r_2 = 2$, $D = 1$. System (3) with above coefficients has a unique coexistence equilibrium $E^*(1/3, 56/9, 28/9)$. Direct calculation shows that (H1) holds and $p_1p_2 - p_0 \approx -4.8333 < 0$. By Theorem 3, we see that system (3) has an orbitally asymptotically stable periodic solution. Numerical simulation illustrates the above result (see Fig. 1).

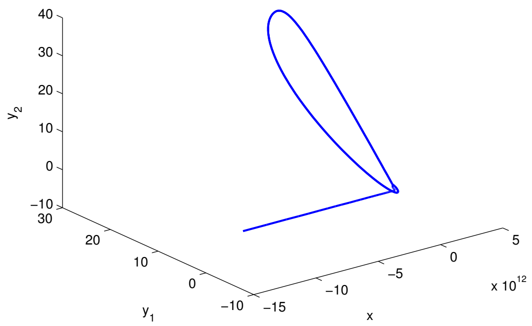

Fig. 1. The numerical solution of system (3) with $a = 1$, $a_1 = 1$, $a_2 = 4$, $e = 2$, $m = 1$, $r = 5$, $r_1 = 1$, $r_2 = 2$, $D = 1$, and $(\phi_1, \phi_2, \phi_3) = (1, 1, 1)$.

4 Global stability

In this section, we discuss the global stability of the coexistence equilibrium E^* and the predator-extinction equilibrium E_1 of system (3), respectively. The strategy of proofs is to construct suitable Lyapunov functions and use LaSalle invariance principle.

Theorem 4. *If* $a_2(D+r_1) < (a+rm)[r_2(D+r_1)-eD]$*, then the equilibrium* $E_1(r/a, 0, 0)$ *of system* (3) *is globally asymptotically stable.*

Proof. Let $(x(t), y_1(t), y_2(t))$ be any positive solution of system (3). Denote $x_0 = r/a$.

Define

$$V_1(t) = \frac{a_2}{1+mx_0}\left(x - x_0 - x_0 \ln \frac{x}{x_0}\right) + ky_1 + a_1 y_2, \tag{13}$$

where $k = a_1 D/(D + r_1)$.

Calculating the derivative of $V_1(t)$ along positive solutions of system (3), we obtain that

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}V_1(t) =& \frac{a_2}{1+mx_0}(1 - \frac{x_0}{x})\left[x(r - ax) - \frac{a_1 x y_2}{1+mx}\right]\\ &+ k\big[ey_2 - (D + r_1)y_1\big] + a_1\left[Dy_1 - r_2 y_2 + \frac{a_2 x y_2}{1+mx}\right].\end{aligned} \tag{14}$$

On substituting $r = ax_0$ into (14), it follows that

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}V_1(t) =& -\frac{aa_2}{1+mx_0}(x - x_0)^2 + \frac{a_1 a_2 x y_2}{1+mx} - \frac{a_1 a_2 x y_2}{(1+mx)(1+mx_0)}\\ &+ \frac{a_1 a_2 x_0 y_2}{(1+mx)(1+mx_0)} + \left(\frac{a_1 e D}{D + r_1} - a_1 r_2\right) y_2\\ =& -\frac{aa_2}{1+mx_0}(x - x_0)^2 + \frac{a_1 a_2 y_2}{1+mx}\left(x - \frac{x}{1+mx_0} + \frac{x_0}{1+mx_0}\right)\\ &+ \frac{a_1}{D + r_1}\big[eD - r_2(D + r_1)\big]y_2.\end{aligned} \tag{15}$$

We derive from (15) that

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}V_1(t) =& -\frac{a^2 a_2}{a+rm}(x - x_0)^2 + \frac{a_1}{(a + rm)(D + r_1)}\\ &\times \big\{a_2(D + r_1) - (a + rm)\big[r_2(D + r_1) - eD\big]\big\}y_2.\end{aligned} \tag{16}$$

Hence, if $a_2(D+r_1) < (a+rm)[r_2(D+r_1) - eD]$, then $V_1'(t) \le 0$. By Theorem 5.3.1 in [16], solutions limit $\mathcal{M}$, the largest invariant subset of $\{V_1'(t) = 0\}$. Clearly, we see from (16) that $V_1'(t) = 0$ if and only if $x = x_0, y_2 = 0$. Noting that $\mathcal{M}$ is invariant, for each element in $\mathcal{M}$, we have $x(t) = x_0$, $y_2(t) = 0$. It therefore follows from the third equation of system (3) that

$$0 = \dot{y}_2(t) = Dy_1(t),$$

which yields $y_1(t) = 0$. Hence, $V_1'(t) = 0$ if and only if $(x, y_1, y_2) = (x_0, 0, 0)$. Accordingly, the global asymptotic stability of E_1 follows from LaSalle invariance principle. This completes the proof. □

Theorem 5. *Let* (H1) *hold. Then the coexistence equilibrium* $E^*(x^*, y_1^*, y_2^*)$ *of system* (3) *is globally stable provided that*

(H2) $\underline{x} > \frac{r}{2a}$.

Here, $\underline{x} > 0$ *is the persistency constant for* x *satisfying* $\liminf_{t\to+\infty} x(t) \ge \underline{x}$.

Proof. Let $(x(t), y_1(t), y_2(t))$ be any positive solution of system (3). Since $\underline{x} > r/(2a)$, it is seen that there is a $T > 0$ such that $x(t) > r/(2a)$ for all $t \geq T$ and also that $x^* > r/(2a)$. Clearly, $p_2 > 0$. By calculations, we derive that

$$\begin{aligned}
&p_1p_2 - p_0 \\
&= \frac{a_1y_2^*}{(1+mx^*)^2}\left[r_2\big(D + r_1 + \frac{eD}{D+r_1}\big) + (D + r_1 + r_2)\big(D + r_1 + \frac{a_1y_2^*}{(1+mx^*)^2}\big)\right] \\
&\quad + (2ax^* - r)\left[eD + (D+r_1)^2 + (D + r_1 + r_2)\frac{a_1y_2^*}{(1+mx^*)^2}\right] \\
&\quad + (2ax^* - r)\left(D + r_1 + \frac{eD}{D+r_1}\right)\left[2ax^* - r + \frac{eD}{D+r_1} + \frac{a_1y_2^*}{(1+mx^*)^2}\right] > 0.
\end{aligned}$$

Accordingly, by Theorem 1, E^* is locally asymptotically stable.

Define

$$\begin{aligned}
V_2(t) &= \frac{a_2}{1+mx^*}\left(x - x^* - x^*\ln\frac{x}{x^*}\right) + k\left(y_1 - y_1^* - y_1^*\ln\frac{y_1}{y_1^*}\right) \\
&\quad + a_1\left(y_2 - y_2^* - y_2^*\ln\frac{y_2}{y_2^*}\right),
\end{aligned} \tag{17}$$

where $k = a_1D/(D + r_1)$.

Calculating the derivative of $V_2(t)$ along positive solutions of system (3), it follows that

$$\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t}V_2(t) &= \frac{a_2}{1+mx^*}\left(1 - \frac{x^*}{x}\right)\left[x(r - ax) - \frac{a_1xy_2}{1+mx}\right] \\
&\quad + k\left(1 - \frac{y_1^*}{y_1}\right)\big[ey_2 - (D + r_1)y_1\big] \\
&\quad + a_1\left(1 - \frac{y_2^*}{y_2}\right)\left[Dy_1 - r_2y_2 + \frac{a_2xy_2}{1+mx}\right].
\end{aligned} \tag{18}$$

On substituting $r = ax^* + a_1y_2^*/(1 + mx^*)$ into (18), we derive that

$$\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t}V_2(t) &= \frac{a_2}{1+mx^*}\left(1 - \frac{x^*}{x}\right)\left[x(r - ax) - x^*(r - ax^*) + \frac{a_1x^*y_2^*}{1+mx^*}\right] \\
&\quad - \frac{a_2}{1+mx^*}\left(1 - \frac{x^*}{x}\right)\frac{a_1xy_2}{1+mx} + \frac{a_1eD}{D+r_1}y_2 - \frac{a_1eD}{D+r_1}y_1^*\frac{y_2}{y_1} \\
&\quad + a_1Dy_1^* - a_1Dy_2^*\frac{y_1}{y_2} - a_1r_2y_2 + a_1r_2y_2^* + \frac{a_1a_2xy_2}{1+mx} - \frac{a_1a_2xy_2^*}{1+mx} \\
&= \frac{a_2}{1+mx^*}\frac{(x-x^*)^2}{x}\big[r - a(x + x^*)\big] + \frac{a_1a_2x^*y_2^*}{(1+mx^*)^2}\left(1 - \frac{x^*}{x}\right) \\
&\quad + \frac{a_1a_2x^*}{1+mx^*}y_2 + \frac{a_1eD}{D+r_1}y_2 - a_1r_2y_2 - \frac{a_1eD}{D+r_1}y_1^*\frac{y_2}{y_1} - a_1Dy_2^*\frac{y_1}{y_2} \\
&\quad + a_1Dy_1^* + a_1r_2y_2^* - \frac{a_1a_2xy_2^*}{1+mx}.
\end{aligned} \tag{19}$$

Noting that $ey_2^* = (D + r_1)y_1^*$, $\frac{eD}{D+r_1} - r_2 + \frac{a_2 x^*}{1+mx^*} = 0$, (19) can be rewritten as

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}V_2(t) &= \frac{a_2}{1+mx^*}\frac{(x-x^*)^2}{x}\big[r - a(x+x^*)\big] + \frac{a_1 eDy_2^*}{D+r_1}\left(2 - \frac{y_1^* y_2}{y_2^* y_1} - \frac{y_2^* y_1}{y_1^* y_2}\right) \\ &\quad + \frac{a_1 a_2 x^* y_2^*}{(1+mx^*)^2}\left(1 - \frac{x^*}{x}\right) + \frac{a_1 a_2 x^* y_2^*}{1+mx^*} - \frac{a_1 a_2 x y_2^*}{1+mx}. \\ &= \frac{a_2}{1+mx^*}\frac{(x-x^*)^2}{x}\big[r - a(x+x^*)\big] + \frac{a_1 eDy_2^*}{D+r_1}\left(2 - \frac{y_1^* y_2}{y_2^* y_1} - \frac{y_2^* y_1}{y_1^* y_2}\right) \\ &\quad + \frac{a_1 a_2 x^* y_2^*}{1+mx^*}\left(2 - \frac{x^*(1+mx)}{(1+mx^*)x} - \frac{(1+mx^*)x}{x^*(1+mx)}\right). \end{aligned} \tag{20}$$

Since the arithmetic mean is greater than or equal to the geometric mean, it is clear that

$$2 - \frac{y_1^* y_2}{y_2^* y_1} - \frac{y_2^* y_1}{y_1^* y_2} \le 0, \quad 2 - \frac{x^*(1+mx)}{(1+mx^*)x} - \frac{(1+mx^*)x}{x^*(1+mx)} \le 0,$$

and the equality hold only for $x = x^*, y_1 = y_1^*, y_2 = y_2^*$. If $x(t) > r/(2a)$ for $t \ge T$, we derive that

$$\frac{a_2}{1+mx^*}\frac{(x-x^*)^2}{x}\big[r - a(x+x^*)\big] \le 0,$$

with equality if and only if $x = x^*$. This implies that if $x(t) > r/(2a)$ for $t \ge T$, $V_2'(t) \le 0$, with equality if and only if $x = x^*$, $y_1 = y_1^*$, $y_2 = y_2^*$. The largest compact invariant subset in $\mathcal{M} = \{(x, y_1, y_2) \mid \dot{V}_2(x, y_1, y_2) = 0\}$ is the singleton $\{E^*\}$. Therefore, by LaSalle invariance principle, the coexistence equilibrium E^* is globally asymptotically stable. This completes the proof. □

Remark. From Theorem 5, we see that if (H1) holds and $\liminf_{t\to+\infty} x(t) \ge r/(2a)$, then the coexistence equilibrium E^* is globally stable. We now give a sufficient condition for this inequality. Denote $\delta = \min\{D + r_1 - a_1 D/k, r_2 - ke/a_1\}$. By Lemma 1, one can show that solutions of system (3) have an ultimately upper bound $M = a_2(r+\delta)^2/(4a\delta)$. Hence, we derive from the first equation of system (3) that $\dot{x}(t) \ge x(t)(r - a_1 M - ax(t))$, which yields $\liminf_{t\to\infty} x(t) \ge \underline{x} = (r - a_1 M)/a = [4ar\delta - a_1 a_2 (r+\delta)^2]/(4a^2\delta)$. Obviously, we need only to choose parameters satisfying $2ar\delta > a_1 a_2 (r+\delta)^2$.

5 Conclusion

In this paper, we have studied the global dynamics of a predator-prey model with Holling type II functional response and stage structure. The global stability of the predator-extinction equilibrium E_1 and the coexistence equilibrium E^* of system (3) has been established by using the Lyapunov–LaSalle type theorem. By Theorem 5, we see that if (H1) and (H2) hold, the coexistence equilibrium E^* is globally asymptotically stable. Biologically, these indicate that when the intrinsic growth rate of the prey, the birth rate of new predators and the rate of immature predator becoming mature predator are large enough, and the death rate of the immature predator and mature predator are small enough, then the prey and the predator population coexist, and the ecological system is therefore permanent.

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