Coexistence and stability of predator–prey model with Beddington–DeAngelis functional response and stage structure

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Abstract

We present a predator–prey model of Beddington–DeAngelis type functional response with stage structure on prey. The constant time delay is the time taken from birth to maturity about the prey. By the uniform persistence theories and monotone dynamic theories, sharp threshold conditions which are both necessary and sufficient for the permanence and extinction of the model as well as the sufficient conditions for the global stability of the coexistence equilibria are obtained. Biologically, it is proved that the variation of prey stage structure can affect the permanence of the system and drive the predator into extinction by changing the prey carrying capacity: Our results suggest that the predator coexists with prey permanently if and only if predator’s recruitment rate at the peak of prey abundance is larger than its death rate; and that the predator goes extinct if and only if predator’s possible highest recruitment rate is less than or equal to its death rate; furthermore, our results also show that a sufficiently large mutual interference by predators can stabilize the system.
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1. Introduction

This paper studies a predator–prey model of Beddington–DeAngelis type functional response with stage structure on prey, the main goal of this paper is to study the combined effects of the stage structure on prey and the mutual interferences by predator on the dynamics of the system. As pointed out by Murdoch, Briggs and Nisbet in their famous book on consumer–resource dynamics [28], the consumer–resource interaction is “arguably the fundamental unit of ecological communities,” and “virtually every species is part of a consumer–resource interaction,” hence it is a central goal for ecologists to understand the relationship between predator–prey model, which is an important type of consumer–resource interaction. One significant component of the predator–prey relationship is the predator’s...
functional responses, i.e., the rate of prey consumption by an average predator. There have been several famous functional response types: Holling types I–III [12,13]; Hassell–Varley type [11]; Beddington–DeAngelis type by Beddington [2] and DeAngelis, Goldstein, and Neill [7] independently; the Crowley–Martin type [6]; and recent well-known ratio-dependence type by Arditi and Ginzburg [1] later studied by Kuang and Beretta [17]. But in [24], by comparing the statistical evidence from 19 predator–prey systems with three predator–dependent functional responses, Skalski and Gilliam pointed out that the predator–dependent can provide better descriptions of predator feeding over a range of predator–prey abundances, and in some cases, the Beddington–DeAngelis-type functional response (hereafter the BD model) performed even better. The Beddington–DeAngelis response can be generated by a number of natural mechanisms [2,5,23] and because it admits rich but biologically reasonable dynamics [3], it is worthy for us to further study the BD model.

The per capita feeding rate of BD model takes the form [2]

$$f(x, y) = \frac{bx}{1 + k_1x + k_2y},$$

(1.1)

and thus the BD model takes form

$$\begin{cases}
x'(t) = rx(t) \left(1 - \frac{x(t)}{K}\right) - \frac{bx(t)y(t)}{1 + k_1x(t) + k_2y(t)}, \\
y'(t) = \frac{nbx(t)y(t)}{1 + k_1x(t) + k_2y(t)} - dy(t),
\end{cases}$$

(1.2)

where \(x\) and \(y\) represent prey and predator densities; \(b\) (units: 1/time) and \(k_1\) (units: 1/prey) are positive constants that describe the effects of capture rate and handling time, respectively, on the feeding rate; \(n\) is the birth rate of the predator; and \(k_2 \geq 0\) (units: 1/predator) is a constant describing the magnitude of interference among predators [7]. The BD model is similar to the well-known Holling II type functional response (hereafter the H2 model) but has an extra term \(k_2 y\) in the denominator modeling mutual interference among predators. Hence this kind of type functional response given in (1.1) is affected by both predator and prey, i.e., the so-called predator dependence by Arditi and Ginzburg [1]. Dynamics for the H2 model have been much studied ([14,16], and references therein). Then how the mutual interference term affects the dynamic of the whole system is an interesting problem.

Many recent works have contributed to the BD model (1.2) such as [3,4,8,15,21,22,26]. When considering the diversities during the life history of predators, Liu and Beretta [18] proposed the following BD model with stage structure on predators, based on the modeling methods in [9]:

$$\begin{cases}
x'(t) = rx(t) \left(1 - \frac{x(t)}{K}\right) - \frac{bx(t)y(t)}{1 + k_1x(t) + k_2y(t)} - \lambda x(t), \\
y'(t) = \frac{nbe^{-d_j\tau}x(t-\tau)y(t-\tau)}{1 + k_1x(t-\tau) + k_2y(t-\tau)} - dy(t), \\
y_j'(t) = \frac{nbe^{-d_j\tau}x(t-\tau)y(t-\tau)}{1 + k_1x(t-\tau) + k_2y(t-\tau)} - d_jy_j(t),
\end{cases}$$

(1.3)

where \(x(t)\) represents prey densities at time \(t\), \(y_j(t)\), \(y(t)\) represent the densities of immature and mature predator at time \(t\), respectively. The delay \(\tau\) is the time taken from birth to maturity, \(d_j\) is the death rate of the juvenile predator, thus \(e^{-d_j\tau}\) is the surviving rate of each immature predator before reaching maturity.

In [18], Liu and Beretta showed permanence, extinction, global attractiveness of the interior equilibrium in system (1.3). It is shown [18] that if the system is permanent, then a sufficiently large degree of \(k_2\), the predator interference cannot only stabilize the system but also guarantee the stability of the system against the increase of the carrying capacity \(K\) of prey and the increase of birth rate \(b\) of the adult predator, and it is shown that an proper increase of the maturation delay \(\tau\) may deduce stability switches.

Although much progress has been seen in the above work on BD model, such models are not well studied yet in the sense that all the known results are for models that ignore the enormous diversity during the life histories of the prey. Unfortunately, this is not realistic due to the following reasons:

1. Juvenile preys have a time lag from their birth to maturity.
2. Young preys are raised by their parents or are dependent on the nutrition, and they can avoid the hunting from predators by staying in the eggs, nests and burrow; and they cannot breed.
3. Young prey reach maturity after surviving the immature stage; if the juvenile death rate (through-stage death rate) is nonzero, then not all immature preys can survive the juvenile stage. Therefore, it is realistic and interesting for us to construct the stage-structured predator–prey model and study its local and global behaviors. Enlightened by the modeling methods in [18], we formulate the BD model with stage structure on prey as follows:

\[
\begin{align*}
    x'_i(t) &= bx_m(t) - d_i x_i(t) - be^{-d_i \tau} x_m(t - \tau), \\
    x'_m(t) &= be^{-d_i \tau} x_m(t - \tau) - ax_m^2(t) - \frac{m x_m(t) y(t)}{1 + k_1 x_m(t) + k_2 y(t)}, \\
    y'(t) &= \frac{nx_m(t) y(t)}{1 + k_1 x_m(t) + k_2 y(t)} - dy(t),
\end{align*}
\]

(1.4)

where \(x_m(\theta) > 0\) is continuous on \(-\tau \leq \theta \leq 0\), and \(x_i(0), x_m(0), y(0) > 0, x_m\) and \(y\) represent mature prey and the predator densities, respectively, and \(x_i\) denotes the immature or juvenile prey densities. The constant \(b\) is the birth rate of the mature prey. We assume that immature prey suffer a mortality rate of \(d_i\) and take \(\tau\) units of time to mature; thus \(e^{-d_i \tau}\) is the surviving rate of each immature prey to reach maturity. The predator consumes the mature prey with functional response of Beddington–DeAngelis type \(mx_my/(1 + k_1 x_m + k_2 y)\) and contributes to its growth with rate \(nmx_m y/(1 + k_1 x_m + k_2 y)\). The constant \(d\) is the death rate of predator. Obviously, all the constants are positive for their biological sense.

For the continuity of the solutions to system (1.4), in this paper, we require

\[
x_i(0) = b \int_{-\tau}^{0} e^{d_i \tau} x_m(s) \, ds.
\]

(1.5)

By the first equation of system (1.4), the initial conditions (1.5), and the arguments similar to Lemma 3.1 in [20, p. 672], we have

\[
x_i(t) = b \int_{-\tau}^{0} e^{d_i \tau} x_m(t + s) \, ds,
\]

(1.6)

i.e., \(x_i(t)\) is completely determined by \(x_m(t)\). For the goal of convenience, we denote

\[
x \rightarrow x_m, \quad y \rightarrow y, \quad r = be^{-d_i \tau}, \\
K = \frac{be^{-d_i \tau}}{a}, \quad f = m, \quad g = ne^{d_i \tau},
\]

(1.7)

thus the following system can be separated from system (1.4):

\[
\begin{align*}
    x'(t) &= rx(t - \tau) - r \frac{x^2(t)}{K} - \frac{fx(t)y(t)}{1 + k_1 x(t) + k_2 y(t)}, \\
    y'(t) &= \frac{fg e^{-d_i \tau} x(t) y(t)}{1 + k_1 x(t) + k_2 y(t)} - dy(t),
\end{align*}
\]

(1.7)

where \(x(\theta) > 0\) is continuous on \(-\tau \leq \theta \leq 0\), and \(x(0), y(0) > 0\).

**Remark 1.1.** Because \(x_i(t)\) is completely determined by \(x_m(t)\), by (1.6) we can get all the asymptotical behaviors at the equilibria of system (1.4). Hence we only study the system (1.7) in the following sections.

This paper is organized as follow. In the next section, we present some important lemmas. In Section 3, we get all the equilibria and prove the existence of the positive equilibrium. In Section 4, we prove the local stability of the equilibria for (1.7). This is followed by a section where the global asymptotically stability of the predator extinction equilibrium as well as that of the coexistence equilibrium is gotten. The paper ends with a discussion.
2. Preliminaries

To prove the main results, we need the following lemmas.
Using the similar arguments to Lemma 1 in [19], we directly have

**Lemma 2.1.** System (1.7) with initial conditions \( x(t) > 0 (−τ \leq t \leq 0) \) and \( x(0) > 0, y(0) > 0 \) has strictly positive solutions for all \( t > 0 \).

**Lemma 2.2.** (See [19, Lemma 2].) For equation

\[
x'(t) = bx(t − τ) − a_1 x(t) − a_2 x^2(t),
\]

where \( a_1 \geq 0, a_2, b, τ > 0, x(0) > 0 \) and \( x(t) > 0 \) for all \( −τ \leq t \leq 0 \), we have

(i) If \( b > a_1 \), then \( \lim_{t \to +∞} x(t) = \frac{b − a_1}{a_2} \).

(ii) If \( b < a_1 \), then \( \lim_{t \to +∞} x(t) = 0 \).

Using Theorem 4.9.1 [17, p. 159] with \( τ = 0 \), we directly have

**Lemma 2.3.** For equation

\[
y'(t) = \left( \frac{fge^{−dτ}M}{1 + k_1 M + k_2 y(t)} − d \right) y(t),
\]

where all coefficients are positive constants and \( y(0) > 0 \), we have

(i) if \( (fge^{−dτ} − dk_1)M − d > 0 \), \( \lim_{t \to +∞} y(t) = \frac{(fge^{−dτ} − dk_1)M − d}{k_2 d} = N; \)

(ii) if \( (fge^{−dτ} − dk_1)M − d \leq 0 \), \( \lim_{t \to +∞} y(t) = 0 \).

**Lemma 2.4.** Solutions of system (1.7) are ultimately bounded.

**Proof.** By Lemma 2.1, the solution of system (1.7) \( x(t), y(t) > 0 \) for all \( t \geq 0 \). By the first equation of system (1.7) there is

\[
x'(t) < rx(t − τ) − r \frac{x^2(t)}{K}.
\]

Let \( u(t) \) be the solution of

\[
u'(t) = ru(t − τ) − r \frac{u^2(t)}{K}
\]

with \( u(t) = x(t) \) on \( −τ \leq t \leq 0 \). Then \( u(t) > x(t) > 0 \) \( (t \geq 0) \). By Theorem 2 in [19], \( u(t) \) is ultimately bounded which implies \( x(t) \) is ultimately bounded, too. No less of generality, we suppose that there exists \( T_1 > 0 \) and \( M > K \) such that \( x(t) < M \) for all \( t > T_1 \). Substitute \( x(t) < M \) into the second equation of system (1.4), we get

\[
y'(t) < \left( \frac{fge^{−dτ}M}{1 + k_1 M + k_2 y(t)} − d \right) y(t).
\]

By Lemma 2.3 and the comparison theorem, we denote \( N = \frac{(fge^{−dτ} − dk_1)M − d}{k_2 d} > 0 \), then for the sufficiently small positive constant \( ε \) there exists \( T_2 > T_1 > 0 \) such that \( y(t) < N + ε \) for all \( t > T_2 \). Hence \( y(t) \) is ultimately bounded, proving Lemma 2.4. \( \square \)

3. Equilibria and permanence

Consider the equilibria \( (x, y) \) of system (1.7), which are solutions of the system
\[
\begin{align*}
\left\{ \begin{array}{l}
rx \left( 1 - \frac{x}{K} \right) - \frac{fxy}{1 + k_1x + k_2y} = 0, \\
\frac{fge^{-d_1\tau}xy}{1 + k_1x + k_2y} - dy = 0.
\end{array} \right.
\end{align*}
\]  
(3.1)

It is easy to see that for all parameter values system (1.7) has the equilibria \( E_0 = (0, 0), \ E_1 = (K, 0) \). By (3.1), system (1.7) has the positive equilibrium \( E = (x^*, y^*) \) iff

\[
\frac{fge^{-d_1\tau}K}{1 + k_1K} > d.
\]  
(3.2)

Here

\[
x^* = \frac{1}{2} \left( -B + \sqrt{B^2 + 4C} \right), \quad y^* = \frac{x^*(fge^{-d_1\tau} - dk_1) - d}{dk_2}
\]  
(3.3)

with \( B = \frac{K}{r} (fge^{-d_1\tau} - dk_1) - r \), \( C = -\frac{Kd}{rge^{-d_1\tau}k_2} \).

Hence the positive equilibrium \( E \) exists for all prey’s maturation times \( \tau \) in the interval \( I = [0, \tau^*) \), where

\[
\tau^* = \frac{1}{d_1} \ln \frac{Kfg}{d(1 + k_1K)}.
\]  
(3.4)

Increase of \( \tau \) in \( I \) will lower \( y^* \) until \( E \) will coincide with \( E_1 \) at the finite value \( \tau^* \), and for higher \( \tau \) there is no positive equilibrium. On the other hand, \( k_2 \) does not affect the existence of the positive equilibrium since \( k_2 \) is not involved in (3.2). However, (3.3) indicates that increase of \( k_2 \) will lower \( y^* \) until \( E \) will coincide with \( E_1 \) at the infinite value \( k_2 \).

Here the following results give conditions which are both necessary and sufficient for the permanence, extinction of system (1.7):

**Theorem 3.1.** System (1.7) is permanent iff it satisfies (3.2).

To prove Theorem 3.1, we engage the uniform persistence theory developed by Hale and Waltman [10] for infinite dimensional systems, we also refer to Thieme [25]. Now, we present the persistence theory [10] as follows.

Consider a metric space \( X \) with metric \( d \). A is a continuous semifluid on \( X \), i.e., a continuous mapping \( T : [0, \infty) \times X \to X \) with the following properties: \( T_i \circ T_s = T_{i+s}, \ i, s \geq 0; \ T_0(x) = x, x \in X \). Here \( T_i \) denotes the mapping from \( X \) to \( X \) given by \( T_i(x) = T(t, x) \). The distance \( d(x, y) \) of a point \( x \in X \) from a subset \( Y \) of \( X \) is defined by

\[
d(x, Y) = \inf_{y \in Y} d(x, y).
\]

Recall that the positive orbit \( \gamma^+(x) \) through \( x \) defined as \( \gamma^+(x) = \bigcup_{t \geq 0} T(t)x \), and its \( \omega \)-limit set is \( \omega(x) = \bigcap_{t \geq 0} CL \bigcup_{t \geq \tau} \{ T(t)x \} \), where \( CL \) means closure. Define \( W^s(A) \) the stable set of a compact invariant set \( A \) as \( W^s(A) = \{ x \mid x \in X, \ \omega(x) \neq \emptyset, \ \omega(x) \subset A \} \); define \( \widetilde{A}_0 \) the particular sets of interest as \( \widetilde{A}_0 = \bigcup_{x \in A_0} \omega(x) \).

(H1) Assume \( X \) is the closure of open set \( X^\circ \); \( \partial X^\circ \) is nonempty and is the boundary of \( X^\circ \). Moreover the \( C^0 \)-semigroup \( T(t) \) on \( X \) satisfies

\[
T(t) : X^\circ \to X^\circ, \quad T(t) : \partial X^\circ \to \partial X^\circ.
\]

**Lemma 3.1.** (See [10, Theorem 4.1, p. 392].) Suppose \( T(t) \) satisfies (H1) and

(i) there is \( t_0 \geq 0 \) such that \( T(t) \) is compact for \( t > t_0 \);
(ii) \( T(t) \) is point dissipative in \( X \);
(iii) \( \widetilde{A}_0 \) is isolated and has an acyclic covering \( M \).

Then \( T(t) \) is uniformly persistent iff for each \( M_i \in M, \ W^s(M_i) \cap X^\circ = \emptyset. \)
Proof of Theorem 3.1. First we show that the condition (3.2) leads to the permanence of system (1.7). Now we verify that the boundary planes of $R^2_+ = \{(x, y) \mid x \geq 0, y \geq 0\}$ repel the positive solutions to system (1.7) uniformly.

Let $C^+((-\tau, 0], R^2_+)$ denote the space of continuous function mapping $[-\tau, 0]$ into $R^2_+$. We choose

$$
C_1 = \{(\varphi_0, \varphi_1) \in C^+([-\tau, 0], R^2_+) \mid \varphi_0(\theta) \equiv 0, \varphi_1(\theta) \geq 0, \theta \in [-\tau, 0]\},
$$

$$
C_2 = \{(\varphi_0, \varphi_1) \in C^+([-\tau, 0], R^2_+) \mid \varphi_0(\theta) \equiv 0, \varphi_1(\theta) > 0, \theta \in [-\tau, 0]\}.
$$

Denote $C = C_1 \cup C_2$, $X = C^+([-\tau, 0], R^2_+)$, and $X^o = \text{Int}(C^+([-\tau, 0], R^2_+))$; then $C = \partial X^o$. It is easy to see that system (1.7) possesses two constant solutions in $C = \partial X^o$: $\tilde{E}_0 \in C_1$, $\tilde{E}_1 \in C_2$ with

$$
\tilde{E}_0 = \{(\varphi_0, \varphi_1) \in C^+([-\tau, 0], R^2_+) \mid \varphi_0(\theta) \equiv \varphi_1(\theta) \equiv 0, \theta \in [-\tau, 0]\},
$$

$$
\tilde{E}_1 = \{(\varphi_0, \varphi_1) \in C^+([-\tau, 0], R^2_+) \mid \varphi_0(\theta) \equiv K, \varphi_1(\theta) \equiv 0, \theta \in [-\tau, 0]\}.
$$

We verify below that the conditions of Lemma 3.1 are satisfied. By the definition of $X^o$ and $\partial X^o$ and system (1.7), it is easy to see that conditions (i) and (ii) of Lemma 3.1 are satisfied and that $X^o$ and $\partial X^o$ are invariant. Hence (H1) is also satisfied.

Consider condition (iii) of Lemma 3.1. We have

$$
x'(t)|_{(\varphi_0, \varphi_1) \in C_1} \equiv 0,
$$

thus $x'(t)|_{(\varphi_0, \varphi_1) \in C_1} \equiv 0$, for all $t \geq 0$. Hence we have

$$
y'(t)|_{(\varphi_0, \varphi_1) \in C_1} = -dy(t) \leq 0,
$$

from which follows that all points in $C_1$ approach $\tilde{E}_0$, i.e., $C_1 = W^s(\tilde{E}_0)$. Similar we can prove that all point in $C_2$ approach $\tilde{E}_1$, i.e., $C_2 = W^s(\tilde{E}_1)$. Hence $A_0 = \tilde{E}_0 \cup \tilde{E}_1$ and clearly it is isolated. Noting that $C_1 \cap C_2 = \emptyset$, it follows from these structural features that the flow in $A_0$ is acyclic, satisfying condition (iii) of Lemma 3.1.

Now we show that $W^s(\tilde{E}_i) \cap X^o = \emptyset$, $i = 0, 1$. By Lemma 2.1, we have $x(t), y(t) > 0$ for all $t > 0$. Assume $W^s(\tilde{E}_i) \cap X^o \neq \emptyset$, i.e., there exists a positive solution $(x(t), y(t))$ with $\lim_{t \to \infty} (x(t), y(t)) = (0, 0)$. Hence for sufficiently small $\varepsilon > 0$ and $\varepsilon < r$, there exists $T > 0$ such that

$$
\frac{f_y(t)}{1+k_1x(t)+k_2y(t)} < \varepsilon
$$

for all $t > T$. Then using the first equation of (1.7), we get

$$
x'(t) > rx(t-\tau) - \frac{x^2(t)}{K} - ex(t)
$$

for all $t > T$. By Lemma 2.2 and the comparison theorem, we have for sufficiently small $\varepsilon > 0$ there exists $T_1 > T$ such that $x(t) > K(t-\tau) - \varepsilon > 0$ for all $t > T_1$, contradicting $\lim_{t \to \infty} x(t) = 0$; this proves $W^s(\tilde{E}_0) \cap X^o = \emptyset$.

Now we verify $W^s(\tilde{E}_1) \cap X^o = \emptyset$; assume the contrary, i.e., $W^s(\tilde{E}_1) \cap X^o \neq \emptyset$. Then there exists a positive solution $(x(t), y(t))$ to system (1.7) with $\lim_{t \to \infty} (x(t), y(t)) = (K, 0)$, and for sufficiently small positive constant $\varepsilon$ with

$$
\varepsilon < \frac{(f_{ge^{-d_1\tau}} - dK)K - d}{f_{ge^{-d_1\tau}} - dK_1 + dk_2},
$$

there exists a positive constant $T = T(\varepsilon)$ such that

$$
x(t) > K - \varepsilon > 0, \quad y(t) < \varepsilon \quad \text{for all } t \geq T.
$$

By the second equation of (1.7) we have

$$
y'(t) > \frac{f_y(t)(K-\varepsilon)y(t)}{1+k_1(K-\varepsilon)+k_2y(t)} - dy(t), \quad t \geq T.
$$

Consider the equation

$$
\left\{
\begin{aligned}
v(t) &= \frac{f_y(t)(K-\varepsilon)v(t)}{1+k_1(K-\varepsilon)+k_2v(t)} - dv(t), \quad t \geq T, \\
v(T) &= y(T) > 0.
\end{aligned}
\right.
$$

\[\text{(3.6)}\]
By (3.5) and the comparison theorem, we have \( y(t) \geq v(t) \) for all \( t \geq T \). On the other hand, by Lemma 2.3 we have \( \lim_{t \to \infty} v(t) = v^* \) for all solutions to system (3.6), where \( v^* = \frac{(f_{ge} - d_i + K)(\kappa - \delta)}{k_3^d} > 0 \) is the unique positive equilibrium of system (3.6). Hence we get \( \lim_{t \to \infty} v(t) \geq v^* > 0 \), contradicting \( v(t) < \varepsilon \) as \( t \to T \). Thus we have \( W^s(\tilde{E}_i) \cap X^c = \emptyset \), \( i = 0, 1 \). Now we get that system (1.7) satisfies all conditions of Lemma 3.1, thus \( (x(t), y(t)) \) is uniformly persistent, noting Lemma 2.4 shows that \( (x, y) \) is ultimately bounded, and this proves the permanence of system (1.7).

We verify below that permanence of system (1.7) indicates (3.2). Assume the contrary, i.e., \( \frac{f_{ge} - d_i K}{1 + k_1 K} \leq d \); then by the system (3.2) we cannot get a positive equilibrium, thus cannot get the permanence of (1.7). (Permanence guarantees the existence of a coexistence equilibrium; see [27].) This proves Theorem 3.1. \( \square \)

4. Local behaviors of equilibria

Considering the characteristic equation of (1.7), we write (1.7) as

\[
X'(t) = F(X(t), X(t - \tau))
\]

and denote \( G = (\frac{\partial F}{\partial X}) X^*, H = (\frac{\partial F}{\partial (a - \tau)}) X^* \). Thus characteristic equation of (1.7) at the equilibrium \( X^* \) takes the form as follows:

\[
\det(G + He^{-\lambda \tau} - \lambda I) = 0.
\]

We have

\[
G = \begin{pmatrix}
-\frac{2rx}{K} - q_x & -q_y \\
ge^{-d_i \tau} q_x & ge^{-d_i \tau} q_y - d
\end{pmatrix}
\]

and

\[
H = \begin{pmatrix}
r & 0 \\
0 & 0
\end{pmatrix}
\]

where

\[
q(x, y) = \frac{fxy}{1 + k_1 x + k_2 y}, \quad q_x' = \frac{fy(1 + k_2 y)}{(1 + k_1 x + k_2 y)^2}, \quad q_y' = \frac{fx(1 + k_1 x)}{(1 + k_1 x + k_2 y)^2}.
\]

**Theorem 4.1.** The equilibrium \( E_0 = (0, 0) \) is unstable.

**Proof.** The characteristic equation of (1.7) at \( E_0 \) is given by

\[ F(\lambda) = (\lambda - re^{-\lambda \tau})(\lambda + d) = 0. \]

Since \( F(0) = -rd < 0 \) and \( F(+\infty) = +\infty \), then \( F(\lambda) = 0 \) has at least one positive root and \( E_0 \) is unstable. This proves Theorem 4.1. \( \square \)

**Theorem 4.2.** The equilibrium \( E_1 = (K, 0) \) are

(i) unstable if \( \frac{f_{ge} - d_i K}{1 + k_1 K} > d \);

(ii) asymptotically stable if \( \frac{f_{ge} - d_i K}{1 + k_1 K} < d \).

**Proof.** The characteristic equation at \( E_1 \) is \( G(\lambda) = (\lambda + 2r + re^{-\lambda \tau})(\lambda - (\frac{f_{ge} - d_i K}{1 + k_1 K} - d)) = 0 \).

(i) Assume that \( \frac{f_{ge} - d_i K}{1 + k_1 K} > d \), then \( \lambda = \frac{f_{ge} - d_i K}{1 + k_1 K} - d \) is a positive root of the equation \( G(\lambda) = 0 \). Hence \( E_1 \) is unstable.

(ii) Assume now that \( \frac{f_{ge} - d_i K}{1 + k_1 K} < d \), i.e., \( \lambda = \frac{f_{ge} - d_i K}{1 + k_1 K} - d \) is a negative root of the equation \( G(\lambda) = 0 \). Let \( \lambda + 2r - re^{-\lambda \tau} = 0 \); then if the root is \( \lambda = \alpha + i\omega \), we have \( \alpha + 2r - re^{-\alpha \tau} \cos \omega \tau = 0 \). Assume that \( \alpha \geq 0 \), then \( \alpha + 2r - re^{-\alpha \tau} \cos \omega \tau \geq r > 0 \) is a contradiction, hence \( \alpha < 0 \). This shows that all the roots of \( G(\lambda) = 0 \) must have negative real parts, and therefore \( E_1 \) is asymptotically stable. This proves Theorem 4.2. \( \square \)

To show the stability of \( E \), we need some preparative work as follows.
By (4.5), we get

$$q^* = \frac{f x^* y^*}{1 + k_1 x^* + k_2 y^*}, \quad q'_x = \frac{f y^*(1 + k_2 y^*)}{(1 + k_1 x^* + k_2 y^*)^2}, \quad q'_y = \frac{f x^*(1 + k_1 x^*)}{(1 + k_1 x^* + k_2 y^*)^2}. \quad (4.1)$$

Then we get that the characteristic equation at $E$ is as follows:

$$D(\lambda, \tau) = \left( \lambda + \frac{2 r x^*}{K} + q'_x, -r e^{-\lambda \tau} \right) \left( \lambda - g e^{-d_i \tau} q'_y + d \right) + q'_y g e^{-d_i \tau} q'_x$$

$$= P(\lambda, \tau) + Q(\lambda, \tau) e^{-\lambda \tau} = 0, \quad (4.2)$$

where

$$\begin{align*}
P(\lambda, \tau) &= \lambda^2 + P_1(\tau) \lambda + P_0(\tau), \\
P_1(\tau) &= \frac{2 r x^*}{K} - R + q'_x, \\
P_0(\tau) &= \frac{2 r x^*}{K} R + q'_x d, \\
Q(\lambda, \tau) &= Q_1(\tau) \lambda + Q_0(\tau), \\
Q_1(\tau) &= -r, \\
Q_0(\tau) &= r R,
\end{align*} \quad (4.3)$$

$$= g e^{-d_i \tau} q'_y - d.$$ \quad (4.4)

Of course, the characteristic equation (4.2) must be considered in the interval $I = [0, \tau^*)$ of existence of the positive equilibrium.

Now we verify that $\lambda = 0$ cannot be a root of (4.2) for any $\tau \in I$, i.e.,

$$P(0, \tau) + Q(0, \tau) = P_0(\tau) + Q_0(\tau) \neq 0.$$ \quad (4.5)

For the positive equilibrium $E$, we have

$$\begin{align*}
r &= \frac{r x^*}{K} + \frac{f y^*}{1 + k_1 x^* + k_2 y^*}, \\
d &= \frac{f g e^{-d_i \tau} x^*}{1 + k_1 x^* + k_2 y^*}.
\end{align*} \quad (4.5)$$

By (4.5), we get

$$P_0(\tau) + Q_0(\tau) = \frac{2 r x^*}{K} R + q'_x d + r R$$

$$= \left( r - \frac{2 r x^*}{K} \right) \left( g e^{-d_i \tau} q'_y - d \right) + q'_x d$$

$$= \left( \frac{f y^*}{1 + k_1 x^* + k_2 y^*} - \frac{r x^*}{K} \right) \left( \frac{1 + k_1 x^*}{1 + k_1 x^* + k_2 y^*} - 1 \right) + q'_x \right) d$$

$$= \left( - \frac{f y^* k_2 y^*}{(1 + k_1 x^* + k_2 y^*)^2} + \frac{r k_2 x^* y^*}{(1 + k_1 x^* + k_2 y^*)^2} + \frac{f y^* (1 + k_2 y^*)}{(1 + k_1 x^* + k_2 y^*)^2} \right) d$$

$$= \frac{y^*}{1 + k_1 x^* + k_2 y^*} \left( \frac{f}{K (1 + k_1 x^* + k_2 y^*)} + \frac{r k_2 x^*}{K} \right) d > 0.$$

The characteristic equation (4.2) at $\tau = 0$ becomes $P(\lambda, 0) + Q(\lambda, 0) = 0$, i.e.,

$$\lambda^2 + (P_1(0) + Q_1(0)) \lambda + P_0(0) + Q_0(0) = 0,$$

where $P_0(0) + Q_0(0) > 0$ since $P_0(\tau) + Q_0(\tau) > 0$ for all $\tau \in I$. Then
\[ P_1(0) + Q_1(0) = \frac{2rx^*}{K} - (gq'_y - d) + q'_y - r \]
\[ = \frac{2rx^*}{K} - \frac{fgx(1 + k_1x^*)}{(1 + k_1x^* + k_2y^*)^2} + \frac{fgx^*}{1 + k_1x^* + k_2y^*} + \frac{fy^*(1 + k_2y^*)}{(1 + k_1x^* + k_2y^*)^2} - \left( \frac{rx^*}{K} + \frac{fy^*}{1 + k_1x^* + k_2y^*} \right) \]
\[ = \frac{fgx^*y^*}{(1 + k_1x^* + k_2y^*)^2} \left( k_2 - \frac{k_1}{g} \right) + \frac{rx^*}{K}. \]

Thus we have \[ P_1(0) + Q_1(0) = \frac{rx^*gk_2(K - x^*) + k_1(2x^* - K) + 1 + k_2y^*}{K(1 + k_1x^* + k_2y^*)}. \]

Stability switch for increasing \( \tau \) in \( I = [0, \tau^*] \) may occur only with a pair of roots \( \lambda = i\omega(\tau), \omega(\tau) \) real, that cross the imaginary axis.

Assume \( \lambda = i\omega(\tau), \omega(\tau) \) real, we have
\[
\begin{align*}
P(i\omega, \tau) &= -\omega^2 + i\omega P_1(\tau) + P_0(\tau), \\
Q(i\omega, \tau) &= i\omega Q_1(\tau) + Q_0(\tau).
\end{align*}
\]

By (4.2), we have \( |P(\lambda, \tau)| = |Q(\lambda, \tau)e^{-\lambda\tau}|. \) Let \( \lambda = i\omega(\tau) \), then we get \( F(\omega, \tau) = |P(i\omega, \tau)|^2 - |Q(i\omega, \tau)|^2 \) in \( I = [0, \tau^*] \).

Since
\[
F(\omega, \tau) = (P_0(\tau) - \omega^2)^2 - \omega^2 P_1^2(\tau) - (Q_0^2(\tau) + \omega^2 Q_1^2(\tau))
\]
\[ = \omega^4 + \omega^2(-2P_0(\tau) + P_1^2(\tau) - Q_1^2(\tau)) + P_0^2(\tau) - Q_0^2(\tau), \]

hence we have
\[
\begin{align*}
F(\omega, \tau) &= \omega^4 + b(\tau)\omega^2 + c(\tau) = 0, \\
b(\tau) &= -2P_0(\tau) + P_1^2(\tau) - Q_1^2(\tau), \\
c(\tau) &= P_0^2(\tau) - Q_0^2(\tau).
\end{align*}
\]

Now, we prove that \( E \) is asymptotically stable provided that \( k_2 \) is sufficiently large. We have

**Theorem 4.3.** The positive equilibrium \( E \) of (1.7) is asymptotically stable provided that system (1.7) is permanent, \( r > d \) and
\[
k_2 > \frac{2fK(fg e^{-d_1\tau} - dk_1)}{r((fg e^{-d_1\tau} - dk_1)K - d)}.
\]

**Proof.** To complete the proof, it suffices to prove that \( E \) has no stability switches as \( \tau \) increases and that \( E \) is stable at \( \tau = 0 \). Hence we only need to consider the roots of (4.2) at \( \tau = 0 \), i.e., (4.6).

By Theorem 3.1, permanence of system (1.7) implies (3.2). Thus from (4.9) follows
\[
k_2 > 2 \cdot \frac{fge^{-d_1\tau} - dk_1}{rge^{-d_1\tau}}.
\]

Using (3.3), and noting that \( B \) in (3.3) is negative under (4.10), we have
\[
x^* > \frac{1}{2}(-B + |B|) = -B = K \left( 1 - \frac{fge^{-d_1\tau} - dk_1}{rge^{-d_1\tau}} \right) > \frac{K}{2} > 0.
\]

We can get \( x^* < K \) easily, so we have \( P_0(0) + Q_0(0) > 0 \) and \( P_1(0) + Q_1(0) = \frac{rx^*[gk_2(K - x^*) + k_1(2x^* - K) + 1 + k_2y^*]}{K(1 + k_1x^* + k_2y^*)} > 0 \), thus the roots of (4.6) must have negative real parts, proving \( E \) is asymptotically stable at \( \tau = 0 \).
Now we show $E$ has no stability switches as $\tau$ increases in $I = [0, \tau^*)$. Thus we only need to prove that (4.8) has no real roots in $I$, i.e., the equation

$$\varphi(\theta) = \theta^2 + b(\tau)\theta + c(\tau) = 0$$  \hspace{1cm} (4.12)$$

has no positive real root, where $\theta$ is equivalent to $\omega^2$ in (4.8). Using (4.1) and (4.5), we have

$$R = ge^{-d_1\tau}q_{y^*}^2 - d = d\frac{1 + k_1x^*}{1 + k_1x^* + k_2y^*} - d < 0.$$  \hspace{1cm} (4.13)$$

Thus by (4.11) and (4.13), we get

$$b(\tau) = -2P_0(\tau) + P_1^2(\tau) - Q_1^2(\tau) \leq 0$$

and

$$c(\tau) = P_0^2(\tau) - Q_0^2(\tau) \geq 0.$$  \hspace{1cm} (5.1)$$

Thus (4.12) has no positive real roots, i.e., (4.8) has no real roots. Hence there are no stability switches for $\tau \in I = [0, \tau^*)$. This proves Theorem 4.3. $\square$

5. Global attractiveness

**Theorem 5.1.** $\lim_{t \to +\infty} (x(t), y(t)) = (K, 0)$ iff $\frac{nhb^{-d_1\tau}}{1 + k_1K} \leq d$ holds true.

**Proof.** Given $\lim_{t \to +\infty} (x(t), y(t)) = (K, 0)$, then we have $\frac{nhb^{-d_1\tau}}{1 + k_1K} \leq d$, otherwise, if $\frac{nhb^{-d_1\tau}}{1 + k_1K} > d$, then using Theorem 3.1 we have that system (1.7) is permanent, contradicting the condition $\lim_{t \to +\infty} (x(t), y(t)) = (K, 0)$, this proves $\frac{nhb^{-d_1\tau}}{1 + k_1K} \leq d$.

Now, we prove that either $\frac{nhb^{-d_1\tau}}{1 + k_1K} < d$ or $\frac{nhb^{-d_1\tau}}{1 + k_1K} = d$ deduces to $\lim_{t \to +\infty} (x(t), y(t)) = (K, 0)$.

Given $\frac{nhb^{-d_1\tau}}{1 + k_1K} < d$, then there exists a sufficiently small positive constant $\varepsilon$ such that $\frac{ghb^{-d_1\tau}(K + \varepsilon)}{1 + k_1(K + \varepsilon)} < d$ holds true.

For the first equation of system (1.7), we have

$$x'(t) = r(x(t) - x(t - \tau)) - \frac{f(x(t), y(t))}{1 + k_1x(t) + k_2y(t)} < r(x(t) - x(t - \tau)) - \frac{tx^2(t)}{K}.$$  \hspace{1cm} (5.2)$$

Consider the equation

$$\begin{cases}
  u'(t) = ru(t - \tau) - r\frac{u^2(t)}{K}, \\
  u(t) = x(t) > 0, \quad t \in [-\tau, 0], \quad r, K > 0.
\end{cases}$$

By Lemma 2.2, we have $\lim_{t \to +\infty} u(t) = K$. Then, by the comparison theorem, we have $x(t) \leq u(t)$ for all $t \geq -\tau$. Hence, for above $\varepsilon$ there exists $T_\varepsilon > 0$ such that $x(t) < K + \varepsilon$ for all $t > T_\varepsilon$; substitute it into the second equation of (1.7), we get that for all $t > T_\varepsilon$, there is

$$y'(t) \leq \left(1 + \frac{f(x(t), y(t))}{1 + k_1x(t) + k_2y(t)} - d\right)y(t).$$

By Lemma 2.3 and the comparison theorem, we get easily $\lim_{t \to +\infty} y(t) = 0$. Hence, for all $\delta > 0$ and $\delta < r$ there exists $T_\delta > 0$ such that $\frac{y(t)}{1 + k_1x(t) + k_2y(t)} < \delta$ holds true for all $t > T_\delta$. Then for the first equation of (1.7), we
have $rx(t - \tau) - \delta x(t) - \frac{r^2(t)}{K} < \frac{x'(t) < rx(t - \tau) - \frac{r^2(t)}{K}}$. By Lemma 2.2 and the comparison theorem, we get $\lim_{t \to +\infty} x(t) = K$.

Using the similar arguments to Case 2 of Theorem 3.1 in [17], we can prove that $\frac{r e^{-d_j t}}{1 + k_1 K} = d$ deduces to $\lim_{t \to +\infty} (x(t), y(t)) = (K, 0)$. This proves Theorem 5.1. □

Lemma 5.1. For the equation

$$x'(t) = rx(t - \tau) - \frac{x^2(t)}{K} - \frac{fy_0 x(t)}{1 + k_1 x(t) + k_2 y_0}$$

(5.1)

with $x(\theta) > 0$ on $-\tau \leq \theta \leq 0$, given $r > \frac{f y_0}{1 + k_2 y_0}$, we have $\lim_{t \to +\infty} x(t) = x^*$, where $x^* = \frac{U_0 + \sqrt{U_0^2 + 4V_0}}{2}$ with $U_0 = K - \frac{1 + k_2 y_0}{k_1} \sqrt{r + r k_2 y_0 - f y_0}$.

Proof. By the analogous arguments with Lemma 2.1, we get $x(t) > 0$ for all $t > 0$.

Then for Eq. (5.1), we have $rx(t - \tau) - \frac{x^2(t)}{K} - \frac{fy_0 x(t)}{1 + k_1 x(t) + k_2 y_0} < x'(t) < rx(t - \tau) - \frac{x^2(t)}{K}$. By the comparison theorem and Lemma 2.2, for sufficiently small $\varepsilon > 0$ there is $T_1 > 0$ such that

$${\bar{x}}_1 = \frac{1}{1 + k_1 y_0} - \varepsilon < x(t) < K + \varepsilon \equiv \bar{x}_1, \quad t > T_1.$$  

Then we get $x(t) > 0$ and $\lim_{t \to +\infty} x(t) = x^*$, where $x^* = \frac{U_0 + \sqrt{U_0^2 + 4V_0}}{2}$ with $U_0 = K - \frac{1 + k_2 y_0}{k_1} \sqrt{r + r k_2 y_0 - f y_0}$. By the comparison theorem and Lemma 2.2, for the above select $\varepsilon > 0$, there exists $T_2 > T_1$ such that

$${\bar{x}}_2 = \frac{1}{1 + k_1 y_0} - \varepsilon < x(t) < K + \varepsilon \equiv \bar{x}_2, \quad t > T_2.$$  

Therefore, we have

$$0 < \bar{x}_1 < \bar{x}_2 < x(t) < \bar{x}_2 < \bar{x}_1, \quad t > T_2.$$  

Repeating the above arguments, we can get the sequence $\{x_n\}_{n=1}^\infty$ and $\{\bar{x}_n\}_{n=1}^\infty$ with $0 < \bar{x}_1 < \bar{x}_2 < \cdots < \bar{x}_n < \bar{x}_n < \cdots < \bar{x}_2 < \bar{x}_1, t > T_n$, and here

$$x_n = K\left[1 - \frac{fy_0}{r(1 + k_1 x_{n-1} + k_2 y_0)}\right] - \varepsilon, \quad \bar{x}_n = K\left[1 - \frac{fy_0}{r(1 + k_1 x_{n-1} + k_2 y_0)}\right] + \varepsilon.$$

(5.2)

Hence we know that the limit of sequence $\{x_n\}_{n=1}^\infty$ and $\{\bar{x}_n\}_{n=1}^\infty$ exists. Denote

$$\bar{x} = \lim_{n \to +\infty} \bar{x}_n, \quad \bar{x} = \lim_{n \to +\infty} x_n.$$  

Then we have $\bar{x} - \varepsilon < x(t) < \bar{x} + \varepsilon$, and after some simple computation to (5.2) we can get easily

$$\bar{x} = \bar{x}, \quad x^* = \frac{U_0 + \sqrt{U_0^2 + 4V_0}}{2} \text{ with } U_0 = K - \frac{1 + k_2 y_0}{k_1} \sqrt{r + r k_2 y_0 - f y_0}.$$  

Hence $\lim_{t \to +\infty} x(t) = x^*$, this proves Lemma 5.1. □

Theorem 5.2. The positive equilibrium $E$ in system (1.7) is globally attractive provided that system (1.7) is permanent and

$$k_2 > \frac{2fK(fge^{-d_1 T} - dk_1)}{r((fge^{-d_1 T} - dk_1) - d)}, \quad k_2 > \frac{fK(fge^{-d_1 T} - dk_1)}{rd}$$

(5.3)

holds true.

Proof. By the first condition and Theorem 3.1, we have that (3.2) holds. For the first equation of (1.7), by Lemma 2.2 and the comparison theorem, for sufficiently small $\varepsilon > 0$, there is $T_1 > 0$ such that $x(t) < K + \varepsilon = \bar{x}$ for $t \geq T_1$.

Replacing this inequality into the second equation of (1.7), we have $y'(t) < \frac{fge^{-d_1 T} x_1}{1 + k_1 \bar{x}_1 + k_2 u(t)} - d) y(t), t \geq T_1$.

Consider the system

$$\begin{cases}
  u'(t) = \left(\frac{fge^{-d_1 T} \bar{x}_1}{1 + k_1 \bar{x}_1 + k_2 u(t)} - d\right) u(t), & t \geq T_1, \\
  u(T_1) = u(T_1) > 0.
\end{cases}$$
We have \( \lim_{t \to +\infty} u(t) = \frac{(f \geq d_t - dk_1) x_1 - d}{k_2 d} > 0 \). By the comparison theorem, we have \( y(t) < u(t), t > T_1 \). Then for the sufficiently small \( \varepsilon > 0 \), there exists \( T_2 > T_1 \) such that for all \( t \geq T_2 \), we have

\[
y(t) < \frac{(f \geq d_t - dk_1) x_1 - d}{k_2 d} + \varepsilon = \bar{y}_1.
\] (5.4)

Replacing (5.4) into the first equation of (1.7), we have \( x'(t) > r x(t - \tau) - r \frac{x^2(t)}{K} = \frac{f x(t) \bar{y}_1}{1 + k_1 x(t) + k_2 \bar{y}_1}, t \geq T_2 \). By (5.3), and using Lemma 5.1 and the comparison theorem, for sufficiently small \( \varepsilon > 0 \), there exists \( T_3 > T_2 \) such that

\[
x(t) > z^*_1 - \varepsilon = \bar{x}_1 > 0, \quad t \geq T_3,
\] (5.5)

where \( z^*_1 = \frac{U_1 + \sqrt{U_1^2 + 4 V_1}}{2} > 0 \) with \( U_1 = K - \frac{1 + k_2 \bar{y}_1}{k_1}, V_1 = \frac{K}{k_1 r} (r + r k_2 \bar{y}_1 - f \bar{y}_1) \), and \( z^*_1 \) is the positive root for the equation

\[
x(t) - r \frac{x^2(t)}{K} - \frac{f x(t) \bar{y}_1}{1 + k_1 x(t) + k_2 \bar{y}_1} = 0.
\]

Replacing (5.5) into the second equation of (1.7), we have \( y'(t) > \frac{(f \geq d_t - dk_1) x_1 - d}{1 + k_1 z_1 + k_2 \bar{y}_1} y(t), t \geq T_3 \). By (5.5), we have

\[
(f \geq d_t - dk_1) x_1 - d
\]

\[
= (f \geq d_t - dk_1) \left\{ \frac{1}{2} \left( K - \frac{1 + k_2 \bar{y}_1}{k_1} \right) + \sqrt{\frac{1}{4} \left( K + \frac{1 + k_2 \bar{y}_1}{k_1} \right)^2 - \frac{K f \bar{y}_1}{k_1 r} - \varepsilon} \right\} - d
\]

\[
= (f \geq d_t - dk_1) \left\{ \frac{1}{2} \left( K - \frac{1 + k_2 \bar{y}_1}{k_1} \right) + \frac{1}{2} \left( K + \frac{1 + k_2 \bar{y}_1}{k_1} \right) \sqrt{1 - \frac{4 K f \bar{y}_1 k_1}{r (K k_1 + 1 + k_2 \bar{y}_1)^2} - \varepsilon} \right\} - d
\]

\[
> (f \geq d_t - dk_1) \left\{ \frac{1}{2} \left( K - \frac{1 + k_2 \bar{y}_1}{k_1} \right) + \frac{1}{2} \left( K + \frac{1 + k_2 \bar{y}_1}{k_1} \right) \left( 1 - \frac{4 K f \bar{y}_1 k_1}{r (K k_1 + 1 + k_2 \bar{y}_1)^2} - \varepsilon \right) \right\} - d
\]

\[
= (f \geq d_t - dk_1) \left\{ K - \frac{2 K f \bar{y}_1}{r (K k_1 + 1 + k_2 \bar{y}_1)} - \varepsilon \right\} - d > (f \geq d_t - dk_1) \left\{ K \left( 1 - \frac{2 f}{r k_2} \right) - \varepsilon \right\} - d
\]

\[
= \frac{(f \geq d_t - dk_1) (K - \varepsilon) - d}{k_2} - \frac{2 f K (f \geq d_t - dk_1)}{r ((f \geq d_t - dk_1) (K - \varepsilon) - d)}.
\]

Using (5.3), we can get

\[
(f \geq d_t - dk_1) x_1 - d > 0 \quad \text{for sufficient small } \varepsilon.
\] (5.6)

By the similar argument to \( \bar{y}_1 \), for the above selected \( \varepsilon > 0 \), there exists \( T_4 > T_3 \) such that

\[
y(t) > \frac{(f \geq d_t - dk_1) x_1 - d}{k_2 d} - \varepsilon = \bar{y}_1 > 0, \quad t \geq T_4.
\] (5.7)

Therefore we have that \( x_1 < x(t) < \bar{x}_1, y_1 < y(t) < \bar{y}_1, t \geq T_4 \), hold true for system (1.7).

Replacing (5.7) into the first equation of (1.7), we have \( x'(t) > r x(t - \tau) - r \frac{x^2(t)}{K} = \frac{f x(t) y_1}{1 + k_1 x(t) + k_2 y_1}, t \geq T_4 \). By (5.3), and using Lemma 5.1 and the comparison theorem, for sufficiently small \( \varepsilon > 0 \), there is \( T_5 > T_4 \) such that

\[
x(t) < z^*_2 + \varepsilon = \bar{x}_2 > 0, \quad t \geq T_5,
\] (5.8)

where \( z^*_2 = \frac{U_2 + \sqrt{U_2^2 + 4 V_2}}{2} > 0 \) with \( U_2 = K - \frac{1 + k_2 \bar{y}_1}{k_1}, V_2 = \frac{K}{k_1 r} (r + r k_2 \bar{y}_1 - f \bar{y}_1) \).

By comparison we get

\[
\bar{x}_2 < K < \bar{x}_1.
\]
Replacing (5.8) into the second equation of (1.7), we have
\[ y'(t) < (f g e^{-d t} - d k_1) x_2 - d \] \( y_1 \), \( y_2 \), \( t \geq T_5 \). By comparison we have \( x_2 > x_1 \) and noting (5.6), we get \( (f g e^{-d t} - d k_1) x_2 - d > (f g e^{-d t} - d k_1) x_1 - d > 0 \). Thus using the similar arguments to above, for the sufficiently small \( \varepsilon > 0 \), there is \( T_6 > T_5 \) such that
\[ y(t) < \frac{(f g e^{-d t} - d k_1) x_2 - d}{k_2 d} + \varepsilon = y_2 > 0, \quad t \geq T_6. \] (5.9)
by (5.4), (5.9) we get \( y_2 < y_1 \).

Replacing (5.9) into the first equation of (1.7), we have \( x'(t) > r x(t - \tau) - r x^2(t) - \frac{x(t) y_2}{k_1} \), \( t \geq T_6 \). By (5.3), Lemma 5.1 and using the comparison theorem, we have that for sufficiently small \( \varepsilon > 0 \), there is \( T_7 > T_6 \) such that
\[ x(t) > z_3^* - \varepsilon = x_2 > 0, \quad t \geq T_7, \] (5.10)
where \( z_3^* = \frac{U_3 + \sqrt{U_3^2 + 4 V_3}}{2} > 0 \) with \( U_3 = K - \frac{1 + k_2 \tau}{k_1}, V_3 = \frac{K}{k_1} (r + r k_2 y_2 - f y_2) \). By comparison we have \( x_2 > x_1 \).

Replacing (5.10) into the second equation of (1.7), by arguments similar to those for \( y_2 \), we get that there is \( T_8 > T_7 \) such that \( y(t) > \frac{(f g e^{-d t} - d k_1) x_2 - d}{k_2 d} - \varepsilon = y_2 > 0, \quad t \geq T_8 \). And we have \( y_2 > y_1 \).

Therefore, we have
\[ 0 < x_1 < x_2 < x(t) < x_2 < x_1, \quad 0 < y_1 < y_2 < y(t) < y_2 < y_1, \quad t \geq T_8, \]
Replacing the above arguments, we get the four sequences \( \{x_n\}_{n=1}^{\infty}, \{y_n\}_{n=1}^{\infty}, \{\bar{y}_n\}_{n=1}^{\infty}, \{y_n\}_{n=1}^{\infty} \) with
\[ 0 < x_1 < x_2 < \cdots < x_n < x(t) < x_n < \cdots < x_1, \]
\[ 0 < y_1 < y_2 < \cdots < y_n < y(t) < y_n < \cdots < y_1, \quad t \geq T_m. \] (5.11)
From (5.11) follows that the limit of each sequence in \( \{x_n\}_{n=1}^{\infty}, \{x_n\}_{n=1}^{\infty}, \{\bar{y}_n\}_{n=1}^{\infty}, \{y_n\}_{n=1}^{\infty} \) exist. Denote
\[ \bar{x} = \lim_{n \to +\infty} x_n, \quad \bar{y} = \lim_{n \to +\infty} y_n, \]
\[ \bar{x} = \lim_{n \to +\infty} x_n, \quad \bar{y} = \lim_{n \to +\infty} y_n, \]
thus we get \( \bar{x} \geq x, \bar{y} \geq y \). To complete the proof, it suffices to prove \( \bar{x} = x, \bar{y} = y \).

By the definition of \( \bar{y}_n, y_n \), we have \( \bar{y}_n = f g e^{-d t} - d k_1 \bar{x}_n - d \) by \( y_n = f g e^{-d t} - d k_1 y_n - d \) then we get
\[ \bar{y}_n - y_n = \frac{f g e^{-d t} - d k_1}{k_2 d} (\bar{x}_n - x_n) + 2 \varepsilon. \] (5.12)
By the definition of \( \bar{x}_n, y_n \) and using (5.12), we have
\[ \bar{x}_n - x_n = \frac{1}{2} \left[ K - \frac{1 + k_2 \bar{y}_{n-1}}{k_1} \right] + \frac{1}{2} \sqrt{\left( K + \frac{1 + k_2 \bar{y}_{n-1}}{k_1} \right)^2 - 4 K f y_{n-1}} - \frac{K f y_{n-1}}{k_1 r} + \frac{1}{2} \sqrt{\left( K + \frac{1 + k_2 \bar{y}_{n-1}}{k_1} \right)^2 - 4 K f y_{n-1}} + 2 \varepsilon \]
\[ = \frac{1}{2} \left( \frac{k_2}{k_1} (\bar{y}_n - y_{n-1}) + \sqrt{\left( K + \frac{1 + k_2 \bar{y}_{n-1}}{k_1} \right)^2 - 4 K f y_{n-1}} - \frac{K f y_{n-1}}{k_1 r} \right) + 2 \varepsilon, \]
then we get
\[ \bar{x}_n - \bar{y}_n = \frac{1}{2} \left( \frac{k_2}{k_1} (\bar{y}_n - \bar{y}_{n-1}) - \frac{[ \frac{2k_2}{k_1} + \frac{2k_2}{k_1} \frac{k_1}{k_1} (\bar{y}_n + \bar{y}_{n-1}) - \frac{4k_f}{k_1} (\bar{y}_n - \bar{y}_{n-1})]}{[(K + \frac{1+k_2}{k_1})^2 - \frac{4k_f}{k_1}]^2 + [(K + \frac{1+k_2}{k_1})^2 - \frac{4k_f}{k_1}]^2} \right) + 2\varepsilon \]

\[ \leq \frac{k_2}{2k_1} (\bar{y}_n - \bar{y}_{n-1}) \left[ 1 - \frac{2K + \frac{2}{k_1} + \frac{k_2}{k_1} (\bar{y}_n + \bar{y}_{n-1}) - \frac{4k_f}{k_2}}{2K + \frac{2}{k_1} + \frac{k_2}{k_1} (\bar{y}_n + \bar{y}_{n-1})} \right] + 2\varepsilon \]

\[ = \left( \bar{y}_n - \bar{y}_{n-1} - \frac{2k_f}{r} (\bar{y}_n + \bar{y}_{n-1}) \right) + 2\varepsilon \]

\[ < \frac{fK}{k_2d_f} (fg e^{-d_1} - dk_1) (\bar{x}_n - \bar{x}_{n-1}) + 2\varepsilon \left( 1 + \frac{fK}{r} \right). \]

Let \( n \to +\infty \), then we have \( \bar{x} - \bar{x} \leq \frac{fK}{k_2d_f} (fg e^{-d_1} - dk_1) (\bar{x} - \bar{y}) + 2\varepsilon \left( 1 + \frac{fK}{r} \right) \), hence \( [1 - \frac{fK}{k_2d_f} (fg e^{-d_1} - dk_1)](\bar{x} - \bar{y}) \leq 2\varepsilon \left( 1 + \frac{fK}{r} \right) \). From (5.3), we have

\[ 1 - \frac{fK}{k_2d_f} (fg e^{-d_1} - dk_1) > 0. \]

Noting that \( \varepsilon > 0 \) can be arbitrarily small, we have \( \bar{x} = \bar{y} \). By (5.12) and let \( n, m \to +\infty \), we get \( \bar{y} = \bar{y} \). This proves Theorem 5.2. \( \square \)

By Sections 4 and 5, we get our primary results:

**Corollary 5.1.** The equilibrium \( E_1 = (K, 0) \) is global asymptotically stable if \( \frac{fg e^{-d_1} K}{1+k_1 K} < d \).

**6. Discussion**

In this paper, we study the predator–prey model (1.4) of Beddington–DeAngelis type functional response with stage structure on prey, which is an extension of both the ODE models studied by Cantrell and Cosner [3], Hwang [15,16].

We give the sharp threshold conditions which are both necessary and sufficient for the permanence and extinction of system (1.7) (see Theorems 3.1, 5.1), and we give the sufficient conditions for the global stability of the coexistence equilibrium, see Theorem 5.2.

By Theorems 3.1, 5.1 and (1.7)', we have that system (1.7) is permanent if and only if the following condition holds true:

\[ \frac{nmb}{ae^{d_1} + k_1b} > d, \]

and that \( \lim_{t \to +\infty} (x(t), y(t)) = (K, 0) \) if and only if the following condition holds true:

\[ \frac{nmb}{ae^{d_1} + k_1b} \leq d. \]

Our results suggest that the predator coexists with prey permanently if and only if predator’s recruitment rate at the peak of prey abundance is larger than its death rate; and that the predator goes extinct if and only if predator’s possible highest recruitment rate is less than or equal to its death rate; moreover, these results suggest that the mutual interference by predators \( k_2 \) does not affect the permanence and the extinction of system (1.7), while the mature delay of prey \( \tau \) and the death rate of the immature prey \( d_1 \) do.

Given the system (1.7) permanent, then a sufficient increase of \( \tau \) or \( d_1 \) can destroy the permanent condition and thus drive the predator into extinction. This implies that predator may be driven into extinction by the decrease of prey carrying capacity \( K = \frac{be^{d_1} \tau}{a} \) due to either a large prey maturation \( \tau \) or a high juvenile prey morality rate \( d_1 \).

On the other hand, taking a further study of the effects of predators interference \( k_2 \) on the permanence of the system, then we can find that, as pointed out in Section 3, given system (1.7) permanent, an increase of \( k_2 \) can lower
y∗ until y∗ → 0 at the infinite value k2. Therefore an extremely large k2 may also drive the predator into the risk of stochastic extinction in reality.

Interesting results from this BD model are the effects by the degree of predator interference k2. By (1.7)′ and Theorem 5.2, the coexistence equilibrium in system (1.7) is globally asymptotically stable provided that

\[ k_2 > \max \left\{ \frac{2m(mn - dk_1)}{((mn - dk_1)he^{-d\tau} - ad)} \frac{m(mn - dk_1)}{ad} \right\} \]

holds true. That means, when \( E \) is unstable, a sufficient increase of k2 can drive the system into a globally stable one. This indicates that the interior equilibrium for BD model is usually more stable than that for the corresponding H2 model.

References