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PREDATOR DISCRIMINATION PROMOTES THE COEXISTENCE OF PREY AND PREDATOR

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Abstract The predator discrimination of prey may affect the density of both prey and predator populations, which, in turn, could influence the coexistence of discriminated prey species. This paper investigates the dynamics of a three-dimensional predator-prey model, which includes unobvious predator discrimination of prey, using a dynamical system approach. We study the existence, local and global stability of equilibria and further discuss the presence and conditions of forward bifurcation in the system. Finally, numerical simulations are performed to illustrate the theoretical results. The findings suggest that prey diversity favors predator discrimination of prey and enhances the coexistence of all species.

Keywords Predator discrimination, multiple predator-prey community, global asymptotic stability, forward bifurcation.

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1. Introduction

To understand the mechanisms of multi-species coexistence is one of the most important topics in ecology. Interspecific interactions will affect the populations of both predators and prey. The impact of a predator species on a prey community depends on the magnitude of predation pressure and its response to changes in prey density. Indeed, the two main aspects of predator species that influence prey coexistence are predator density (numerical response) and predator behavior (functional response) [2]. In predator-prey models, the functional response function describes the predator's reaction to changes in prey abundance. These functions serve as crucial tools for explaining the relationship between predator behavior and prey population dynamics [18, 23]. Common types of functional response functions include linear, saturating, and polynomial responses [25, 35].

Denote N and P as the prey and the predator, respectively. The following functional response functions have been used in various studies.

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- Holling I interaction functional $F(N,P) = aN$ (see [3]),
- Holling II interaction functional $F(N,P) = \frac{aN}{N+b}$ (see [12]),
- Holling III interaction functional $F(N,P) = \frac{aN^2}{N^2+b}$(see [10,17]),
- Holling IV interaction functional $F(N,P) = \frac{aN}{aN^2+bN+c}$(see [26,30]),
- Beddington-DeAngelis interaction functional $F(N,P) = \frac{aN}{a+bN+cP}$ (see [1,9]),
- Ratio-dependent interaction functional $F(N,P) = \frac{aNP}{N+P}$ (see [8,15]).

These functions can be used to predict interactions between different species in ecosystems, such as how changes in prey abundance affect predator numbers and competition between different species. Functional responses have wide applications in ecology [19,24,31,34], environmental science [5], agriculture [22], and other fields [33,36], helping us better understand the interactions and evolutionary processes among different species in ecosystems.

The Lotka-Volterra predator-prey model [21,28] is one of the earliest models in ecology, describing the interaction between a single predator and a single prey. It was first proposed by the American biologist Alfred J. Lotka and the Italian mathematician Vito Volterra in the early 20th century and has since been developed and refined to become one of the fundamental models for studying species interactions in ecosystems. The model has found widespread applications in various fields, including ecology, environmental science, and dynamical systems. Although it comes with some assumptions and limitations, it provides essential insights into understanding the basic principles of predator-prey interactions in ecosystems and offers useful tools for predicting ecosystem responses and adaptations.

In recent years, many scholars have emphasized the complex dynamics of one-prey-two-predator models [6,7,13,20,29]. Simultaneously, some scholars have also studied the equation structure and dynamical behavior of another three-dimensional model involving one predator and two prey species [14,27]. Iwashita et al. [11] proposed a model that considers a community of N_C predator species, with a density C_i (where $i = 1,\ldots,N_C$), and N_R prey species, with a density R_j (where $j = 1,\ldots,N_R$), as follows:

$$\begin{aligned} \frac{\mathrm{d}C_i}{\mathrm{d}t} &= C_i\left(\sum_{k=1}^{N_i} a_{ik}\left(\sum_{j\in K_{ik}} \lambda_{ij} b_j R_j\right) - m_i\right), \\ \frac{\mathrm{d}R_j}{\mathrm{d}t} &= R_j\left(r_j - s_j R_j - \sum_{j}^{N_c} a_{ij}\lambda_{ij} C_i\right). \end{aligned} \tag{1.1}$$

Here, N_i represents the number of predator i's prey groups, K_{ik} is the kth prey group for predator i, m_i is the mortality rate of predator i, r_j is the intrinsic growth rate of prey j, s_j is the intraspecific competition coefficient of prey i, b_j is the assimilation efficiency of prey j, λ_{ij} is the foraging efficiency of predator i on prey j, and a_{ik} is the predation effort of predator i on prey group K_{ik}, which varies adaptively over time according to the following equations:

$$\begin{aligned}
&\frac{\mathrm{d}a_{ik}}{\mathrm{d}t} = Ga_{ik}\left(P_{ik} - \sum_{l=1}^{N_i} a_{il}P_{il}\right), \\
&\sum_{k=1}^{N_i} a_{ik} = 1 \qquad \text{and} \qquad P_{ik} = \sum_{j\in K_{ik}} \lambda_{ij} b_j R_j.
\end{aligned} \tag{1.2}$$

In the above equations, P_{ik} represents the food gain per unit effort from the kth prey group for predator i, and G is the scaling parameter representing the relative speed of adaptive dynamics to population dynamics. The adaptive dynamics are represented by the replicator equation (1.2), which indicates that if the food gain per unit effort for a prey group is above average, the predator species' effort for that group will be increased, whereas if it is lower, the foraging effort will be reduced. Prey species $(j, j^{'})$ that are perceived by predator i to belong to the same group are assumed to be subject to the same predation pressure $(a_{ij} = a_{ij'})$.

In this paper, we only focus on the dynamics of a one-predator (C) and two-prey (R_1, R_2) system. If the predator species distinguishes between the two prey species, the population dynamics model of the three species can be presented as follows:

$$\begin{aligned}
\frac{\mathrm{d}C}{\mathrm{d}t} &= C\left(a_1\lambda_{11}b_1R_1 + a_2\lambda_{12}b_2R_2 - m\right), \\
\frac{\mathrm{d}R_1}{\mathrm{d}t} &= R_1\left(r_1 - s_1R_1 - a_1\lambda_{11}C\right), \\
\frac{\mathrm{d}R_2}{\mathrm{d}t} &= R_2\left(r_2 - s_2R_2 - a_2\lambda_{12}C\right),
\end{aligned} \tag{1.3}$$

and

$$a_1 + a_2 = 1,$$

where a_i is predator C's foraging effort for the prey group R_i (prey R_i), m is the mortality rate of predator, r_i is the intrinsic growth rate of prey R_i, s_i is the intraspecific competition coefficient of prey species R_i, b_i is the assimilation efficiency of prey R_i, and λ_{ij} is the foraging efficiency of predator R_i on prey R_j. Without loss of generality, we still assume that the ratio $(\frac{r_1}{\lambda_{11}})$ of the foraging efficiency of predator C on prey $R_1(\lambda_{11})$ to the intrinsic growth rate of prey $R_1(r_1)$ is greater than that of prey $R_2(\frac{r_1}{\lambda_{11}} \geq \frac{r_2}{\lambda_{12}})$.

It is noted that Iwashita et al. [11] mainly discussed the coexistence of equilibrium points of the system under the boundary of a_i, aiming to explore the identification selection of prey by predators. Different from the above, in this paper, we assume $a_i \in (0, 1)$, which means that if the sum of the foraging efforts of the two prey is unchanged, the predator has the tendency to hunt both prey, but the value of a_i can be equal or not equal. In order to reduce the number of parameters, we introduce the rescale of variable and parameters:

$$x = \frac{Ca_1\lambda_{11}}{m}, \quad y = \frac{R_1s_1}{m}, \quad z = \frac{R_2m}{s_2}, \quad \tau = mt. \tag{1.4}$$

Denote

$$a = \frac{a_1\lambda_{11}b_1}{s_1}, \quad b = \frac{(1-a_1)\lambda_{12}b_2}{s_2}, \quad k_1 = \frac{r_1}{m}, \quad k_2 = \frac{r_2}{m}, \quad c = \frac{(1-a_1)\lambda_{12}}{a_1\lambda_{11}}.$$

System (1.3) is transformed into

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}\tau} &= x(ay + bz - 1), \\ \frac{\mathrm{d}y}{\mathrm{d}\tau} &= y(k_1 - y - x), \\ \frac{\mathrm{d}z}{\mathrm{d}\tau} &= z(k_2 - z - cx). \end{aligned} \tag{1.5}$$

In view of the biological implications, we consider model (1.5) with initial in $\{(x, y, z) \mid x \geq 0,\ y \geq 0,\ z \geq 0\}$. In this paper, the dynamics of predator discrimination in a predator-prey model is investigated using the dynamical system approach. The existence and stability of boundary equilibrium and positive equilibrium are studied in detail. Global stability and forward bifurcation indicate the coexistence of the predator and the prey.

2. Existence of equilibria

In this section, we prove the existence of boundary equilibrium and positive equilibrium and provide a concrete analysis on the stabilities of the equilibria in system (1.5).

2.1. The existence of community equilibria

We analyze the equilibria of system (1.5) and investigate the bifurcations on the basis of the distribution of these equilibria.

(1) The extinction equilibrium $E_1(0, 0, 0)$.

(2) The predator and prey R_1-free equilibrium $E_2(0, 0, k_2)$.

(3) The predator and prey R_2-free equilibrium $E_3(0, k_1, 0)$.

(4) The predator-free equilibrium $E_4(0, k_1, k_2)$.

(5) The prey R_1-free equilibrium $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ if $bk_2 > 1$.

(6) The prey R_2-free equilibrium $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ if $ak_1 > 1$.

(7) The coexistence equilibrium $E^*(x^*, y^*, z^*)$, which is a positive equilibrium of system (1.5)

satisfying

$$\begin{cases} x^*(ay^* + bz^* - 1) = 0, \\ y^*\left(k_1 - y^* - x^*\right) = 0, \\ z^*\left(k_2 - z^* - cx^*\right) = 0. \end{cases}$$

Then we obtain

$$y^* = -x^* + k_1, \quad z^* = -cx^* + k_2,$$

where x^* satisfies the following equation:

$$F(x^*) = -(a + bc)(x^*)^2 + x^*(-1 + ak_1 + bk_2)$$

$$
\begin{aligned}
&= x^*[-(a+bc)x^* + (-1+ak_1+bk_2)] \\
&= 0.
\end{aligned}
$$

Therefore, the positive equilibrium $E^*(x^*, y^*, z^*) = E^*(\frac{ak_1+bk_2-1}{a+bc}, \frac{1+bck_1-bk_2}{a+bc}, \frac{c-ack_1+ak_2}{a+bc})$. To make sure that E^* is a positive equilibrium, x^*, y^*, z^* should satisfy the following two conditions:

(a) Assume $ak_1 + bk_2 > 1$ so that $x^* > 0$;

(b) Assume $1 + bck_1 - bk_2 > 0$ and $c - ack_1 + ak_2 > 0$ so that $y^* > 0$ and $z^* > 0$.

Therefore, the conditions for the existence of positive equilibrium are

$$
\begin{cases}
-1 + ak_1 + bk_2 > 0, \\
1 + bck_1 - bk_2 > 0, \\
c - ack_1 + ak_2 > 0.
\end{cases}
$$

According to the above set of inequalities, we obtain the following results.

Theorem 2.1. *System (1.5) has a positive equilibrium E^* if one of the following conditions holds.*

$$
(i)\ \frac{1-bk_2}{k_1} < a \le \frac{1}{k_1} \ \text{ and } \ c > \frac{bk_2-1}{bk_1}; \quad (ii)\ a > \frac{1}{k_1} \text{ and } \frac{bk_2-1}{bk_1} < c < \frac{ak_2}{ak_1-1}. \tag{2.1}
$$

As a specific case, we have the following results:

Theorem 2.2. *Assume $bk_2 = 1$. The existence condition of the positive equilibrium (1.5) is summarized as follows:*

(i) $0 < a \le \frac{1}{k_1}$ and $c > 0$;

(ii) $a > \frac{1}{k_1}$ and $0 < c < \frac{ak_2}{ak_1-1}$.

The region (brown) of the positive equilibrium is shown in Figure 1(a).

Theorem 2.3. *Assume $bk_2 > 1$. The existence condition of the positive equilibrium (1.5) is summarized as follows:*

(i) $0 < a \le \frac{1}{k_1}$ and $c > \frac{bk_2-1}{bk_1}$;

(ii) $a > \frac{1}{k_1}$ and $\frac{bk_2-1}{bk_1} < c < \frac{ak_2}{ak_1-1}$.

The region (brown) of the positive equilibrium is shown in Figure 1(b).

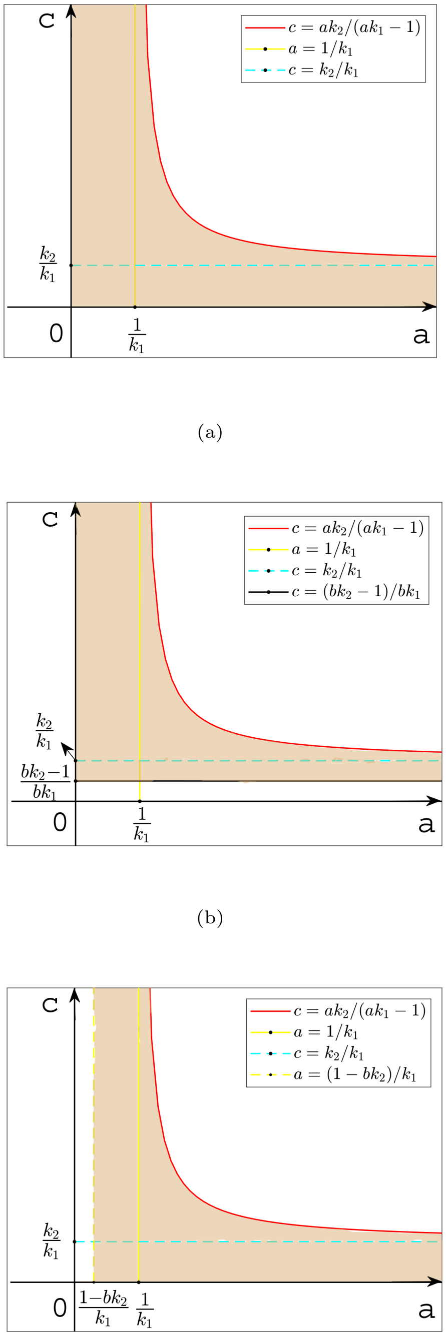
Theorem 2.4. *Assume $-1 < bk_2 - 1 < 0$. The existence condition of the positive equilibrium (1.5) is summarized as follows:*

(i) $\frac{1-bk_2}{k_1} < a \le \frac{1}{k_1}$ and $c > 0$;

(ii) $a > \frac{1}{k_1}$ and $0 < c < \frac{ak_2}{ak_1-1}$.

The region (brown) of the positive equilibrium is shown in Figure 1(c).

We find that the boundary equilibria E_1, E_2, E_3 and E_4 always exist. Table 1 shows the coexistence of E_5, E_6 and E^*.



(a)

(b)

(c)

Figure 1. The positive equilibrium E^* of system (1.5) is located in the brown area: (a) $bk_2 - 1 = 0$; (b) $bk_2 - 1 > 0$; (c) $-1 < bk_2 - 1 < 0$.

Table 1. Coexistence of equilibria of system (1.5)

Range of $bk_2 - 1$	Range of a	Range of c	Existing equilibria
$bk_2 - 1 = 0$	$0 < a \leqslant \frac{1}{k_1}$	$c > 0$	E^*
	$a > \frac{1}{k_1}$	$0 < c < \frac{ak_2}{ak_1 - 1}$	E_6, E^*
		others	E_6
$0 < bk_2 - 1$	$0 < a \leqslant \frac{1}{k_1}$	$c > \frac{bk_2 - 1}{bk_1}$	E_5, E^*
	$a > \frac{1}{k_1}$	$\frac{bk_2 - 1}{bk_1} < c < \frac{ak_2}{ak_1 - 1}$	E_5, E_6, E^*
		others	E_5, E_6
$-1 < bk_2 - 1 < 0$	$\frac{1 - bk_2}{k_1} < a \leqslant \frac{1}{k_1}$	$c > 0$	E^*
	$a > \frac{1}{k_1}$	$0 < c < \frac{ak_2}{ak_1 - 1}$	E_6, E^*
		others	E_6

3. Stability of equilibria

3.1. Stability of boundary equilibria

We study the local stability of boundary equilibria of system (1.5). The Jacobian matrix $J(E_1)$ of system (1.5) at $E_1(0,0,0)$ is

$$J(E_1) = \begin{pmatrix} -1 & 0 & 0 \\ 0 & k_1 & 0 \\ 0 & 0 & k_2 \end{pmatrix}. \tag{3.1}$$

The corresponding eigenvalues of $J(E_1)$ are $\lambda_1 = -1, \lambda_2 = k_1 > 0, \lambda_3 = k_2 > 0$. Thus, $E_1(0,0,0)$ is an unstable saddle point.

The Jacobian matrix $J(E_2)$ of system (1.5) at $E_2(0,0,k_2)$ is

$$J(E_2) = \begin{pmatrix} -1 + bk_2 & 0 & 0 \\ 0 & k_1 & 0 \\ -ck_2 & 0 & -k_2 \end{pmatrix}. \tag{3.2}$$

The corresponding characteristic equation of $J(E_2)$ is

$$(\lambda - (-1 + bk_2))(\lambda - k_1)(\lambda - (-k_2)) = 0. \tag{3.3}$$

There are three eigenvalues: $\lambda_1 = k_1 > 0, \lambda_2 = -k_2 < 0, \lambda_3 = -1 + bk_2$. Thus, $E_2(0,0,k_2)$ is an unstable saddle marginal point if $bk_2 = 1$, otherwise, $E_2(0,0,k_2)$ is an unstable saddle point.

The Jacobian matrix $J(E_3)$ of system (1.5) at $E_3(0,k_1,0)$ is

$$J(E_3) = \begin{pmatrix} -1 + ak_1 & 0 & 0 \\ -k_1 & -k_1 & 0 \\ 0 & 0 & k_2 \end{pmatrix}. \tag{3.4}$$

The characteristic equation of $J(E_3)$ is

$$\begin{aligned}&\lambda^3+\lambda^2\left(-\left((a-1)k_1\right)-k_2+1\right)+\lambda\left(-ak_1^2+k_1\left((a-1)k_2+1\right)-k_2\right)\\&+k_1k_2\left(ak_1-1\right)=0.\end{aligned} \tag{3.5}$$

It's easy to obtain the eigenvalues in (3.5) : $\lambda_1=-k_1<0, \lambda_2=-1+ak_1, \lambda_3=k_2>0$. Thus, $E_3(0,k_1,0)$ is an unstable saddle-node point if $ak_1=1$, and an unstable saddle point if otherwise.

The Jacobian matrix $J(E_4)$ of system (1.5) at $E_4(0,k_1,k_2)$ is

$$J(E_4)=\begin{pmatrix}-1+ak_1+bk_2 & 0 & 0\\ -k_1 & -k_1 & 0\\ -ck_2 & 0 & -k_2\end{pmatrix}. \tag{3.6}$$

The corresponding characteristic equation of $J(E_4)$ is

$$\begin{aligned}&\lambda^3+\lambda^2\left(-\left((a-1)k_1\right)-(b-1)k_2+1\right)\\&+\lambda\left(k_1\left(1-k_2(a+b-1)\right)-ak_1^2-bk_2^2+k_2\right)-k_1k_2\left(ak_1+bk_2-1\right)=0.\end{aligned} \tag{3.7}$$

The roots of (3.7) are: $\lambda_1=-k_1<0, \lambda_2=-k_2<0, \lambda_3=-1+ak_1+bk_2$. Thus, $E_4(0,k_1,k_2)$ is a quasi-stable node marginal point when $ak_1+bk_2=1$. If $ak_1+bk_2<1$, it is a stable node point, and if $ak_1+bk_2>1$, it is a saddle point.

The Jacobian matrix $J(E_5)$ of system (1.5) at $E_5(-\frac{1-bk_2}{bc},0,\frac{1}{b})$ is

$$J(E_5)=\begin{pmatrix}0 & -\frac{a(1-bk_2)}{bc} & -\frac{1-bk_2}{c}\\ 0 & k_1+\frac{1-bk_2}{bc} & 0\\ -\frac{c}{b} & 0 & -\frac{1}{b}\end{pmatrix}. \tag{3.8}$$

The corresponding characteristic equation of $J(E_5)$ is

$$\begin{aligned}&\lambda^3+\frac{\lambda\left((bc+1)\left(bk_2-1\right)-bck_1\right)}{b^2c}-\frac{\left(bk_2-1\right)\left(bck_1-bk_2+1\right)}{b^2c}\\&+\frac{\lambda^2\left(-bck_1+bk_2+c-1\right)}{bc}=0.\end{aligned} \tag{3.9}$$

We have the corresponding eigenvalues of (3.9): $\lambda_1=\frac{bck_1-bk_2+1}{bc}, \lambda_2=\frac{-\sqrt{-4b^2k_2+4b+1}-1}{2b}<0, \lambda_3=\frac{\sqrt{-4b^2k_2+4b+1}-1}{2b}$. Next, we consider the stability of equilibrium E_5 under three different conditions, $\lambda_1>0, \lambda_1=0$ and $\lambda_1<0$. Let $\Delta=-4b^2k_2+4b+1$.

Theorem 3.1. *Assume $k_2-ck_1<\frac{1}{b}$ so that $\lambda_1>0$, the prey R_1-free equilibrium $E_5(-\frac{1-bk_2}{bc},0,\frac{1}{b})$ of system (1.5) is classified into the following cases:*

(1) if $\Delta<0$, then $E_5(-\frac{1-bk_2}{bc},0,\frac{1}{b})$ is an unstable saddle-focus point;

(2) if $0\le\Delta<1$, eigenvalues $\lambda_2<0, \lambda_3<0$, then $E_5(-\frac{1-bk_2}{bc},0,\frac{1}{b})$ is an unstable saddle point;

(3) if $\Delta = 1$, eigenvalues $\lambda_2 = -2 < 0, \lambda_3 = 0$, then $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ is an unstable saddle marginal point;

(4) if $\Delta > 1$, eigenvalues $\lambda_2 < 0, \lambda_3 > 0$, then $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ is an unstable saddle point.

Theorem 3.2. *When* $k_2 - ck_1 = \frac{1}{b}$ *so that* $\lambda_1 = 0$*, the prey* R_1*-free equilibrium* $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ *of system* (1.5) *is classified into the following cases:*

(1) if $\Delta < 0$, then $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ is a quasi-stable focus marginal point;

(2) if $0 \leq \Delta < 1$, eigenvalues $\lambda_2 < 0, \lambda_3 < 0$, then $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ is quasi-stable node marginal point;

(3) if $\Delta = 1$, eigenvalues $\lambda_2 = -2 < 0, \lambda_3 = 0$, then $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ is a stable improper node point;

(4) if $\Delta > 1$, eigenvalues $\lambda_2 < 0, \lambda_3 > 0$, then $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ is an unstable saddle marginal point.

Theorem 3.3. *Assume* $k_2 - ck_1 > \frac{1}{b}$ *so that* $\lambda_1 < 0$*, the prey* R_1*-free equilibrium* $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ *of system* (1.5) *is classified into the following cases:*

(1) if $\Delta < 0$, then $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ is a stable node-focus point;

(2) if $0 \leq \Delta < 1$, eigenvalues $\lambda_2 < 0, \lambda_3 < 0$, then $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ is a stable node point;

(3) if $\Delta = 1$, eigenvalues $\lambda_2 = -2 < 0, \lambda_3 = 0$, then $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ is a stable node marginal point;

(4) if $\Delta > 1$, eigenvalues $\lambda_2 < 0, \lambda_3 > 0$, then $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ is an unstable saddle point.

The Jacobian matrix $J(E_6)$ of system (1.5) at $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is

$$J(E_6) = \begin{pmatrix} 0 & -1 + ak_1 & b(-\frac{1}{a} + k_1) \\ -\frac{1}{a} & -\frac{1}{a} & 0 \\ 0 & 0 & \frac{c}{a} - ck_1 + k_2 \end{pmatrix}. \tag{3.10}$$

The corresponding characteristic equation of $J(E_6)$ is

$$\begin{aligned} &\lambda^3 - \frac{\lambda\left(-\left(ak_1(a+c)\right) + ak_2 + a + c\right)}{a^2} + \frac{(ak_1 - 1)\left(ack_1 - ak_2 - c\right)}{a^2} \\ &+ \frac{\lambda^2\left(ack_1 - ak_2 - c + 1\right)}{a} = 0. \end{aligned} \tag{3.11}$$

The eigenvalues of (3.11) are $\lambda_1 = \frac{-\sqrt{-4a^2k_1+4a+1}-1}{2a}, \lambda_2 = \frac{\sqrt{-4a^2k_1+4a+1}-1}{2a}, \lambda_3 = \frac{-ack_1+ak_2+c}{a}$.

Similarly, we consider the stability of equilibrium E_6 under three different cases, $\lambda_3 > 0, \lambda_3 = 0$ and $\lambda_3 < 0$. Let $\Delta = -4a^2k_1 + 4a + 1$.

Theorem 3.4. *When* $ck_1 - k_2 > \frac{c}{a}$*, the prey* R_2*-free equilibrium* $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ *of system* (1.5) *is classified into the following cases:*

(1) if $\Delta < 0$, then $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is an unstable saddle-focus point;

(2) if $0 \leq \Delta < 1$, $\lambda_1 < 0, \lambda_2 < 0$, then $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is an unstable saddle point;

(3) if $\Delta = 1$, then $\lambda_1 = -2 < 0, \lambda_2 = 0$, and $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is an unstable saddle marginal point;

(4) if $\Delta > 1$, $\lambda_1 < 0, \lambda_2 > 0$, then $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is an unstable saddle point.

Theorem 3.5. *When $ck_1 - k_2 = \frac{c}{a}$, the prey R_2-free equilibrium $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ of system (1.5) is classified into the following cases:*

(1) if $\Delta < 0$, then $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is a quasi-stable focus marginal;

(2) if $0 \leq \Delta < 1$, $\lambda_1 < 0, \lambda_2 < 0$, then $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is quasi-stable node marginal;

(3) if $\Delta = 1$, then $\lambda_1 = -2 < 0, \lambda_2 = 0$, and $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is a stable improper node;

(4) if $\Delta > 1$, $\lambda_1 < 0, \lambda_2 > 0$, then $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is an unstable saddle marginal point.

Theorem 3.6. *When $ck_1 - k_2 < \frac{c}{a}$, the prey R_2-free equilibrium $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ of system (1.5) is classified into the following cases:*

(1) if $\Delta < 0$, then $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is a stable node-focus;

(2) if $0 \leq \Delta < 1$, $\lambda_1 < 0, \lambda_2 < 0$, then $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is a stable node;

(3) if $\Delta = 1$, then $\lambda_1 = -2 < 0, \lambda_2 = 0$, and $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is a stable node marginal;

(4) if $\Delta > 1$, $\lambda_1 < 0, \lambda_2 > 0$, then $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ is an unstable saddle point.

3.2. Stability of positive equilibrium

3.2.1. Local stability analysis

Now, we consider the local stability of the positive equilibrium $E^*(x^*, y^*, z^*)$ of system (1.5).

To reduce the amount of computation, we perform a translation transformation for system (1.5). Let $u = x - x^*, v = y - y^*, w = w - w^*$, then system (1.5) is transformed into

$$\begin{aligned} \frac{\mathrm{d}u}{\mathrm{d}\tau} &= (u + x^*)(av + bw), \\ \frac{\mathrm{d}v}{\mathrm{d}\tau} &= -(v + y^*)(u + v), \\ \frac{\mathrm{d}w}{\mathrm{d}\tau} &= -(w + z^*)(cu + w). \end{aligned} \tag{3.12}$$

The Jacobian matrix of system (3.12) at $E_0(0, 0, 0)$ is

$$J(E_0) = \begin{pmatrix} 0 & ax^* & bx^* \\ -y^* & -y^* & 0 \\ -cz^* & 0 & -z^* \end{pmatrix}.$$

Similarly, the characteristic polynomial of system (3.12) at $E_0(0,0,0)$ is

$$\begin{aligned} G(\lambda) =& (\lambda + z^*)\left(ax^*y^* + \lambda^2 + \lambda y^*\right) + cz^*\left(b\lambda x^* + bx^*y^*\right) \\ =& \lambda^3 + A_2\lambda^2 + A_1\lambda + A_0, \end{aligned}$$

where

$$\begin{aligned} A_2 =& y^* + z^*, \\ A_1 =& x^*\left(ay^* + bcz^*\right) + y^*z^*, \\ A_0 =& (a+bc)x^*y^*z^* = -\det(J(E_0)). \end{aligned}$$

Theorem 3.7. *The positive equilibrium $E^*(x^*, y^*, z^*)$ of system (1.5) is locally asymptotically stable if the equilibrium E^* exists, i.e., the condition (2.1) hold.*

Proof. By simple calculation, we get

$$A_2A_1 - A_0 = ax^*(y^*)^2 + (y^*)^2z^* + bcx^*(z^*)^2 + y^*(z^*)^2 > 0.$$

Thus, by Routh-Hurwitz criteria [32], we know that the positive equilibrium $E_0(0,0,0)$ of system (3.12) is locally asymptotically stable if $A_2A_1 - A_0 > 0$. So the equilibrium $E_0(0,0,0)$ of system (3.12) is locally asymptotically stable. That is to say, the positive equilibrium $E^*(\frac{-1+ak_1+bk_2}{a+bc}, \frac{1+bck_1-bk_2}{a+bc}, \frac{c-ack_1+ak_2}{a+bc})$ of system (1.5) is locally asymptotically stable. That is to say, system (1.5) can not go through Hopf bifurcation at the positive equilibrium E^*. □

3.2.2. Global stability of the positive equilibrium

In this section, we investigate the global stability of the unique positive equilibrium $E^*(\frac{-1+ak_1+bk_2}{a+bc}, \frac{1+bck_1-bk_2}{a+bc}, \frac{c-ack_1+ak_2}{a+bc})$ of system (1.5). By using the Lyapunov-LaSalle theorem, we obtain the following results by equivalently considering the global stability of the equilibrium $E_0(0,0,0)$ of the shifted system (3.12).

Theorem 3.8. *The positive equilibrium $E^*(x^*, y^*, z^*)$ of system (1.5) is globally asymptotically stable if the condition (2.1) holds.*

Proof. Consider the following Lyapunov function:

$$V = (u - x^*\ln\frac{u+x^*}{x^*}) + a(v - y^*\ln\frac{v+y^*}{y^*}) + \frac{b}{c}(w - z^*\ln\frac{w+z^*}{z^*}).$$

We prove that the function $V(u,v,w)$ is non-negative. Let $f(x) = x - a\ln\frac{x+a}{a}$ $(a > 0, x > -a)$. Obviously, $f(0) = 0$, and

$$\frac{df}{dx} = 1 - \frac{a}{x+a} = \frac{x}{x+a}.$$

We obtain $f'(0) = 0$, $f'(x) > 0$ for $x > 0$, and $f'(x) < 0$ for $-a < x < 0$. Therefore, $f(x) \geq 0$ and the function $V(u,v,w)$ is non-negative.

Differentiating V with respect to t and using system (3.12) yield

$$\left.\frac{dV}{dt}\right|_{(3.12)} = u'\frac{u}{u+x^*} + av'\frac{v}{v+y^*} + \frac{b}{c}w'\frac{w}{w+z^*}$$

$$
\begin{aligned}
&= u(av + bw) - av(u + v) - \frac{b}{c}w(cu + w) \\
&= -av^2 - \frac{b}{c}w^2 \\
&< 0.
\end{aligned}
$$

Therefore, the equilibrium $E_0(0, 0, 0)$ of system (3.12) is globally asymptotically stable. It is easy to know that $\frac{dV}{dt}|_{(3.12)} \le 0$, and $\frac{dV}{dt}|_{(3.12)} = 0$ at E_0 of system (3.12). According to the Lyapunov-LaSalle theorem [16], E_0 of system (3.12) is globally asymptotically stable. That is to say, the positive equilibrium $E^*(x^*, y^*, z^*)$ of system (1.5) is globally asymptotically stable if the condition (2.1) holds. □

4. Bifurcation analysis

In this section, we will study bifurcation and conduct numerical simulations of system (1.5). System (1.5) undergoes transcritical bifurcation at the boundary equilibria $E_4(0, k_1, k_2)$, $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$, and $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$. For $E_4(0, k_1, k_2)$, a forward bifurcation curve appears if $a > a^*$, and the bifurcation direction at the non-predator equilibrium point is positive, while there is no positive equilibrium at $a < a^*$. If there is a positive bifurcation balance in the case of $a < a^*$, we call it backward bifurcation [4]. The scenarios for boundary equilibrium points $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ and $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ are similar to E_4.

Theorem 4.1. *System* (1.5) *will go through a forward bifurcation at* $E_4(0, k_1, k_2)$ *if* $0 < a \le \frac{1}{k_1}$, $bk_2 < 1$ *and* $c > 0$.

Proof. Part I. When $a = a^*$, there is one zero eigenvalue for the Jacobian matrix of the model (1.5) at the predator-free equilibrium (PFE) E_4.

The Jacobian matrix of model (1.5) at E_4 is

$$
J(E_4) = \begin{pmatrix} -1 + ak_1 + bk_2 & 0 & 0 \\ -k_1 & -k_1 & 0 \\ -ck_2 & 0 & -k_2 \end{pmatrix}, \tag{4.1}
$$

and the corresponding eigenvalues of $J(E_4)$ are as follows:

$$
\begin{aligned}
\lambda_1 &= -k_1 < 0, \\
\lambda_2 &= -k_2 < 0, \\
\lambda_3 &= -1 + ak_1 + bk_2.
\end{aligned}
$$

It's clear that the eigenvalues λ_1 and λ_2 are negative. If $\lambda_3 = 0$, then

$$
a^* = \frac{1 - bk_2}{k_1} > 0.
$$

We find that at $a = a^*$, the Jacobian matrix $J(E_4)$ has a zero characteristic root and all other eigenvalues are negative. Therefore, the center manifold theory can be used to analyze the dynamics of the model near $a = a^*$. Moreover, the predator-free equilibrium is locally stable when $a < a^*$ and unstable when $a > a^*$. The critical value $a = a^*$ is a bifurcation value.

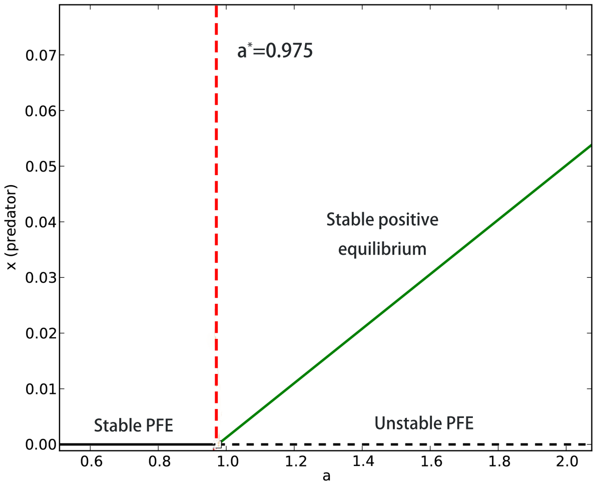


Figure 2. Forward bifurcation diagram of the concentration of predator with respect to a when $0 < a \le \frac{1}{k_1}$ and $c > \frac{bk_2-1}{bk_1}$. Here the solid and dotted curves represent, respectively, the stable and unstable branches.

Part II. The existence and stability of $E^*(x^*, y^*, z^*)$ of system (1.5) as a varies.

When $a \le a^*$, we have $x^* = \frac{-1+ak_1+bk_2}{a+bc} \le 0$. This means no positive equilibrium exists. As $a^* = \frac{1-bk_2}{k_1} < a \le \frac{1}{k_1}$, $bk_2 < 1$ and $c > 0$, the positive equilibrium E^* exists. Therefore, we conclude that when $a < a^*$, the boundary equilibrium E_4 is stable, and there is no positive equilibrium E^*. When $a > a^*$, the boundary equilibrium E_4 loses stability, and a positive equilibrium E^* exists in system (1.5). Thus, system (1.5) undergoes a forward bifurcation. ☐

Numerically, in system (1.5), we choose parameter values $b = 3.5, c = 0.5, k_1 = 0.2$ and $k_2 = 0.23$. When $0 < a \le \frac{1}{k_1}$, $bk_2 < 1$ and $c > 0$, system (1.5) undergoes a forward bifurcation, shown in Figure 2, with $a^* = 0.975$. The solid curve and the dotted curve indicate the stable and unstable equilibrium points, respectively. Moreover, when $0 < a < a^*$, the predator-free equilibrium (PFE) $E_4(0, k_1, k_2)$ of system (1.5) is stable, and there is no positive equilibrium point in system (1.5). When $a^* < a < \frac{1}{k_1}$, the predator-free equilibrium (PFE) E_4 of system (1.5) is unstable, and the positive equilibrium E^* of system (1.5) exists.

Theorem 4.2. *When $bk_2 > 1$, system (1.5) will go through a forward bifurcation at $E_5(\frac{bk_2-1}{bc}, 0, \frac{1}{b})$ if one of the following conditions holds:*

(1) $0 < a \le \frac{1}{k_1}$ and $c > 0$;

(2) $a > \frac{1}{k_1}$ and $0 < c < \frac{ak_2}{ak_1-1}$.

Proof. Part I. When $c = c^*$, there is one zero eigenvalue for the Jacobian matrix of the model at the prey R_1-free equilibrium (R1FE) E_5.

The Jacobian matrix of model (1.5) at E_5 is

$$J(E_5) = \begin{pmatrix} 0 & -\frac{a(1-bk_2)}{bc} & -\frac{1-bk_2}{c} \\ 0 & k_1 + \frac{1-bk_2}{bc} & 0 \\ -\frac{c}{b} & 0 & -\frac{1}{b} \end{pmatrix}. \tag{4.2}$$

The corresponding eigenvalues of $J(E_5)$ are as follows:

$$\lambda_1 = \frac{bck_1 - bk_2 + 1}{bc},$$
$$\lambda_2 = \frac{-\sqrt{-4b^2k_2 + 4b + 1} - 1}{2b},$$
$$\lambda_3 = \frac{\sqrt{-4b^2k_2 + 4b + 1} - 1}{2b}.$$

The Jacobian matrix $J(E_5)$ has a zero characteristic root and all other eigenvalues are negative if $bk_2 > 1$. Then we obtain

$$c^* = \frac{bk_2 - 1}{bk_1} > 0.$$

We find that at $c = c^*$, the Jacobian matrix $J(E_5)$ has a zero characteristic root and all other eigenvalues are negative. Therefore, the center manifold theory can be used to analyse the dynamics of the model near $c = c^*$ [36]. The prey R_1-free equilibrium is locally stable when $c < c^*$ and locally unstable when $c > c^*$. The critical value $c = c^*$ is a bifurcation value.

Part II. The existence and stability of $E^*(x^*, y^*, z^*)$ of system (1.5) as c varies.

When $c \leq c^*$ and $y^* = \frac{bck_1 - bk_2 + 1}{a + bc} \leq 0$, there is no positive equilibrium. From Theorem 2.3, we know that positive equilibrium E^* exists if case 1: $0 < a < \frac{1}{k_1}$ and $c > 0$ or case 2: $a > \frac{1}{k_1}$ and $0 < c < \frac{ak_2}{ak_1 - 1}$ are satisfied. Therefore, we conclude that when $c < c^*$, the boundary equilibrium E_5 is stable, and there is no positive equilibrium E^*. When $c > c^*$, the boundary equilibrium E_5 is unstable, and there is a positive equilibrium E^* in the system (1.5). Thus, the system (1.5) undergoes a forward bifurcation at $c = c^*$. □

In system (1.5), because the change in the value of a in case 2 does not affect c^*, here we only simulate case 1 numerically. We choose parameter values $a = 2, b = 2, k_1 = 0.4$ and $k_2 = 1$. When $0 < a \leq \frac{1}{k_1}$ and $c > 0$, system (1.5) undergoes a forward bifurcation at $c^* = 1.25$, as shown in Figure 3. The solid curve and the dotted curve indicate the stable equilibrium and unstable equilibrium points, respectively. Moreover, when $0 < c < c^*$, the prey R_1-free equilibrium (R1FE) $E_5(-\frac{1-bk_2}{bc}, 0, \frac{1}{b})$ of the system (1.5) is stable, and there is no positive equilibrium point in the system (1.5). When $c > c^*$, the prey R_1-free equilibrium (R1FE) E_5 of the system (1.5) is unstable, and the positive equilibrium E^* of the system (1.5) exists.

Theorem 4.3. *Assume $ak_1 > 1$ and $c > \frac{bk_2 - 1}{bk_1}$. System (1.5) goes through a forward bifurcation at $E_6(\frac{ak_1 - 1}{a}, \frac{1}{a}, 0)$.*

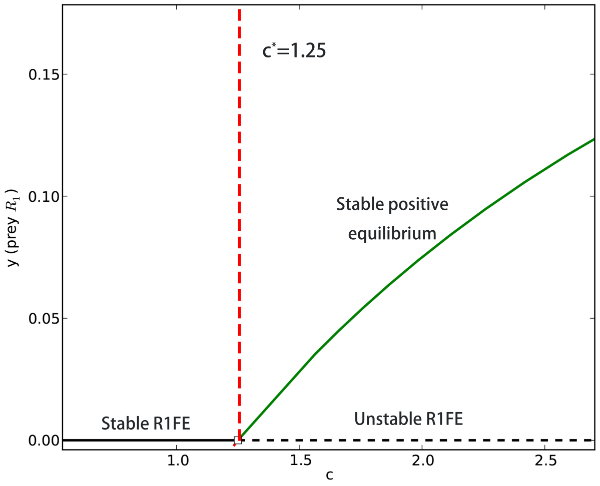


Figure 3. Forward bifurcation diagram of the concentration of predator with respect to c when $0 < a \le \frac{1}{k_1}$ and $c > 0$. Here, the solid and dotted curves represent, respectively, the stable and unstable branches.

Proof. Part I. When $k_2 = k_2^*$, there is one zero eigenvalue for the Jacobian matrix of the model (1.5) at the prey R_2-free equilibrium (R2FE) E_6.

The Jacobian matrix of model (1.5) at E_6 is

$$J(E_6) = \begin{pmatrix} 0 & -1 + ak_1 & b(-\frac{1}{a} + k_1) \\ -\frac{1}{a} & -\frac{1}{a} & 0 \\ 0 & 0 & \frac{c}{a} - ck_1 + k_2 \end{pmatrix}. \tag{4.3}$$

The corresponding eigenvalues of $J(E_6)$ are as follows:

$$\lambda_1 = \frac{-\sqrt{-4a^2k_1 + 4a + 1} - 1}{2a},$$
$$\lambda_2 = \frac{\sqrt{-4a^2k_1 + 4a + 1} - 1}{2a},$$
$$\lambda_3 = \frac{-ack_1 + ak_2 + c}{a}.$$

The Jacobian matrix $J(E_6)$ has a zero characteristic root and all other eigenvalues are negative if $ak_1 > 1$. Clearly, the eigenvalue $\lambda_3 = 0$ is equivalent to

$$k_2^* = \frac{c(ak_1 - 1)}{a} > 0.$$

At $k_2 = k_2^*$, the Jacobian matrix $J(E_6)$ has a zero characteristic root and all other eigenvalues are negative. Therefore, the center manifold theory can be used to analyse the dynamics of the model near $k_2 = k_2^*$ [36]. Moreover, The prey R_2-free equilibrium is locally stable when $k_2 < k_2^*$ and unstable when $k_2 > k_2^*$. The critical value $k_2 = k_2^*$ is a bifurcation value.

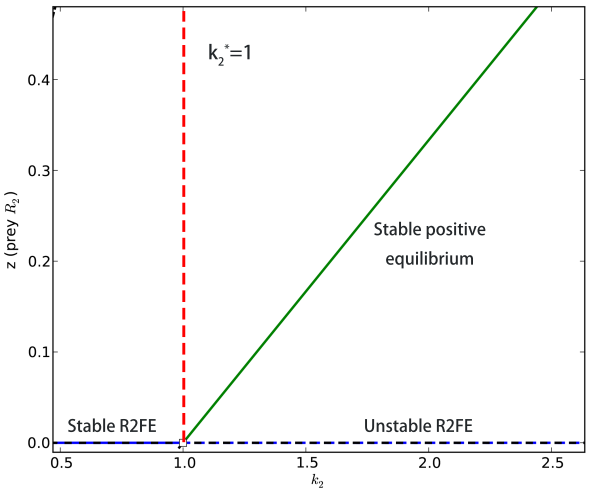


Figure 4. Forward bifurcation diagram of the concentration of predator with respect to a when $c > \frac{bk_2-1}{bk_1}$ and $ak_1 > 1$. Here the solid and dotted curves represent, respectively, the stable and unstable branches as $a = 1, b = 2, c = 1$, and $k_1 = 2$.

Part II. The existence and stability of $E^*(x^*, y^*, z^*)$ of system (1.5) as the parameter k_2 varies.

When $k_2 \leq k_2^*$, $z^* = \frac{-ack_1+ak_2+c}{a+bc} \leq 0$, there is no positive equilibrium. We know from the existence conditions of the positive equilibrium that the positive equilibrium E^* exists if $ak_1 > 1$ and $c > \frac{bk_2-1}{bk_1}$. Therefore, we conclude that when $k_2 < k_2^*$, the boundary equilibrium E_6 is stable, and there is no positive equilibrium E^*. When $k_2 > k_2^*$, the boundary equilibrium E_6 is unstable, and there is a positive equilibrium E^* in the system (1.5). Thus, the system (1.5) undergoes a forward bifurcation at $k_2 = k_2^*$. □

As a numerical illustration, in system (1.5), we choose parameter values $a = 1, b = 2, c = 1$ and $k_1 = 2$. When $c > \frac{bk_2-1}{bk_1}$ and $ak_1 > 1$, the system (1.5) undergoes a forward bifurcation, as shown in Figure 4, with $k_2^* = 1$. The solid curve and the dotted curve indicate the stable and unstable equilibrium points, respectively. Moreover, when $0 < k_2 < k_2^*$, the prey R_2-free equilibrium (R2FE) $E_6(-\frac{1-ak_1}{a}, \frac{1}{a}, 0)$ of the system (1.5) is stable, and there is no positive equilibrium point in the system (1.5). When $k_2 > k_2^*$, the prey R_2-free equilibrium (R2FE) E_6 of the system (1.5) is unstable, and the positive equilibrium E^* of the system (1.5) exists.

5. Conclusion

In this paper, we studied the existence, stability, and bifurcation of equilibrium points in a three-dimensional predator-prey system consisting of two prey and one predator. The existence and stability of boundary equilibrium and positive equilibrium were examined. Applying the Lyapunov-LaSalle theorem, we found that the positive equilibrium is globally asymptotically stable. That is to say, the system can not undergo Hopf bifurcation. Seen from the forward bifurcation, we found that the densities of predator and the prey will increase when the predator's foraging effort for the prey group R_1 or R_2 increase. From a biological perspective, the unobvious predator discrimination greatly benefits the coexistence of prey and predator.

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