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STABILITY ANALYSIS AND HOPF BIFURCATION OF DENSITY-DEPENDENT PREDATOR-PREY SYSTEMS WITH BEDDINGTON-DEANGELIS FUNCTIONAL RESPONSE

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Abstract. In this article, we study a density-dependent predator-prey system with the Beddington-DeAngelis functional response for stability and Hopf bifurcation under certain parametric conditions. We start with the condition of the existence of the unique positive equilibrium, and provide two sufficient conditions for its local stability by the Lyapunov function method and the Routh-Hurwitz criterion, respectively. Then, we establish sufficient conditions for the global stability of the positive equilibrium by proving the non-existence of closed orbits in the first quadrant $\mathbb{R}^2_+$. Afterwards, we analyze the Hopf bifurcation geometrically by exploring the monotonic property of the trace of the Jacobean matrix with respect to r and analytically verifying that there is a unique r^* such that the trace is equal to 0. We also introduce an auxiliary map by restricting all the five parameters to a special one-dimensional geometrical structure and analyze the Hopf bifurcation with respect to all these five parameters. Finally, some numerical simulations are illustrated which are in agreement with our analytical results.

1. Introduction

The dynamic relationship between predators and their preys is one of the dominant themes in both mathematical biology and theoretical ecology. Better understanding exact trends of population dynamics can contribute to the environmental protection and resource utilization. In the past decades, considerable attention has been dedicated to various predator-prey models [5, 8, 10, 11, 14, 19, 22, 24, 25, 28, 29], of which the following predator-prey system with the Beddington-DeAngelis functional response, originally proposed by Beddington [4] and DeAngelis [9], independently, has been extensively studied by applied mathematicians and biologists theoretically and experimentally:

$$\begin{aligned}\frac{dx(t)}{dt} &= x(t)\Big(c - bx(t) - \frac{sy(t)}{m_1 + m_2x(t) + m_3y(t)}\Big),\\ \frac{dy(t)}{dt} &= y(t)\Big(-d + \frac{fx(t)}{m_1 + m_2x(t) + m_3y(t)}\Big),\end{aligned} \tag{1.1}$$

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where $c, b, s, m_1, m_2, m_3, d$ and f are positive constants, $x(t)$ and $y(t)$ represent the population density of the prey and the predator at time t respectively, c is the intrinsic growth rate of the prey, d is the death rate of the predator, and b stands for the mutual interference between preys. The predator consumes the prey with the functional response of Beddington-DeAngelis type $\frac{sx(t)y(t)}{m_1+m_2x(t)+m_3y(t)}$ and contributes to its growth with the rate $\frac{fx(t)y(t)}{m_1+m_2x(t)+m_3y(t)}$. This is similar to the well-known Holling type II model with an extra term $m_3y(t)$ in the denominator.

System (1.1) is a population model which has received much attention in biology and ecology. Cantrell and Cosner [6] presented qualitative analysis of system (1.1) on permanence, which implies the existence of a locally asymptotically stable positive equilibrium or periodic orbits. Hwang [15] considered the local and global asymptotic stability of the positive equilibrium $(\hat{x}, \hat{y})$ by the divergence criterion. That is, for system (1.1), under the conditions $(f - dm_2)\frac{c}{b} > dm_1$ and $tr(J(\hat{x}, \hat{y})) \le 0$, $(\hat{x}, \hat{y})$ is globally asymptotically stable. Recently, Hwang [16] presented the condition $(f - dm_2)\frac{c}{b} > dm_1$ and $tr(J(\hat{x}, \hat{y})) > 0$ to ensure the uniqueness of the limit cycle of system (1.1). For more details about biological background of system (1.1), we refer the reader to [1, 6, 7, 9, 15].

However, abundant evidence suggests that predators do interfere with each other's activities so as to result in competition efforts and that the predator may be of density dependence because of the environmental factors [2, 3]. Kratina et al have demonstrated a fact that the predator density dependence is significant at both high predator densities and low predator densities [17]. Hence, the following more realistic predator and prey density-dependent model with the Beddington-DeAngelis functional response was proposed [18, 21]:

$$\begin{aligned} \frac{dx(t)}{dt} &= x(t)\Big(c - bx(t) - \frac{sy(t)}{m_1 + m_2x(t) + m_3y(t)}\Big), \\ \frac{dy(t)}{dt} &= y(t)\Big(-d - ry(t) + \frac{fx(t)}{m_1 + m_2x(t) + m_3y(t)}\Big), \end{aligned} \tag{1.2}$$

where r represents the rate of predator density dependence. Compared with system (1.1), system (1.2) contains not only $bx^2(t)$ which stands for intraspecific action of prey species, but also $ry^2(t)$ which stands for intraspecific action of predator species.

Li and She [18] considered dynamics of system (1.2) by showing $(f - dm_2)\frac{c}{b} > dm_1$ as the sufficient and necessary condition for the permanence and existence of the unique positive equilibrium, and $(f - dm_2)\frac{c}{b} \le dm_1$ as the sufficient and necessary condition for the global asymptotical stability of boundary solution. Furthermore, the dynamics of the stage-structured model of system (1.2) was studied in [23] and the non-autonomous case of system (1.2) was tackled in [20].

From the point of view of ecological managers, it may be desirable to have a unique positive equilibrium which is globally asymptotically stable. Although considerable attention has been undertaken on system (1.2), it seems that sufficient and necessary conditions for local stability and even global stability of the positive equilibrium have not been comprehensively presented yet. In addition, the existence of (stable or unstable) limit cycles and Hopf bifurcation with respect to the parameters are rarely discussed.

In this article, we will discuss the local and global stability of the positive equilibrium and analyze the Hopf bifurcation of system (1.2) in the first quadrant. For simplicity, by the re-scaling $t \to ct$, $x \to \frac{b}{c}x$, $y \to \frac{bm_3}{cm_2}y$, $s = \frac{s}{cm_3}$, $a = \frac{bm_1}{cm_2}$, $b = \frac{f}{cm_2}$,

$d = \frac{m_2 d}{f}$ and $r = \frac{crm_2^2}{bfm_3}$, system (1.2) is nondimensionalized to

$$\begin{aligned} \frac{dx(t)}{dt} &= P(x(t), y(t)) := x(t)(1 - x(t)) - \frac{sx(t)y(t)}{x(t) + y(t) + a}, \\ \frac{dy(t)}{dt} &= Q(x(t), y(t)) := by(t)\Big(- d - ry(t) + \frac{x(t)}{x(t) + y(t) + a}\Big). \end{aligned} \tag{1.3}$$

We start with the existence of the unique positive equilibrium of system (1.3) and show that this unique positive equilibrium cannot be a saddle under the given conditions. To ensure the local stability of this positive equilibrium, we first provide a sufficient condition by constructing a Lyapunov function, and then give a concrete condition depending only on the parameters by the Routh-Hurwitz criterion. By virtue of two classical criteria, we discuss the global asymptotic stability of the positive equilibrium and present several nonequivalent sufficient conditions. That is, under the permanence condition, we firstly present a condition by Dulac's criterion for the global attractiveness of the positive equilibrium. Secondly, by the divergency criterion, we provide a sufficient condition for the stability of all possibly existing closed orbits, under which we prove that the positive equilibrium is locally and globally asymptotic stable because of the non-existence of stable closed orbits. Thirdly, under a stronger permanence condition for providing concrete bounds of all possible closed orbits, we apply Grammer's rule and Green's theorem to present the divergency integral, and obtain another sufficient condition on global asymptotical stability of the positive equilibrium.

Afterwards, we explore the Hopf bifurcation with respect to the parameter r. We first geometrically explore the monotonic property of the trace of the Jacobian matrix with respect to r, and then analytically verify that there is a unique r^* such that the trace is equal to 0. Based on these arguments, we analyze the Hopf bifurcation with respect to the parameter r. Moreover, in order to generalize our conclusion on the Hopf bifurcation, we consider the Hopf bifurcation with respect to all five parameters by introducing an auxiliary map and restrict the five parameters to a special one-dimensional geometrical structure. Some numerical simulations are performed to illustrate our analytical results.

Note that Hwang [15] verified that for system (1.1), the local stability and global stability of the positive equilibrium coincide. However, from the Hopf bifurcation analysis, we find that for system (1.3), the coincidence between local stability and global stability does not hold due to the existence of the parameter r. Consequently, the analysis results show that the rate r of predator density dependence has a significant effort on the global dynamics of system (1.3).

The rest of this paper is organized as follows. In Section 2, we consider the local stability of the positive equilibrium. In Section 3, we establish several sufficient conditions for the global stability of the positive equilibrium by two classical criteria. In Section 4, we analyze Hopf bifurcations with respect to the parameter r and all five parameters, respectively. Section 5 presents some numerical simulations and Section 6 is a brief conclusion.

2. Local stability of positive equilibrium

We know from [18] that system (1.3) has a unique positive equilibrium if and only if the condition

$$ad < 1 - d \tag{2.1}$$

holds, which is the sufficient and necessary condition for permanence of the system. This unique positive equilibrium cannot be a saddle point. According to the definition of permanence [18] and the Poincáre-Bendixson theorem [13], for any trajectory starting in $\mathbb{R}^2_+ := \{(x,y) \in \mathbb{R}^2 : x > 0, y > 0\}$, there are three cases for its ω-limit set in $\mathbb{R}^2_+$: the positive equilibrium which is not a saddle, a closed orbit or a saddle together with possible homoclinic orbits. For the third case, in addition to this saddle, there exists at least another positive equilibrium inside the region enclosed by the homoclinic orbit simultaneously.

Since the unique positive equilibrium is not a saddle, we now explore the conditions to guarantee the local asymptotic stability of this positive equilibrium. Let (x^*, y^*) be the unique positive equilibrium, which is short for the expression $(x^*(a,b,d,r,s), y^*(a,b,d,r,s))$ and satisfies

$$\begin{gathered} 1 - x^* - \frac{sy^*}{x^*+y^*+a} = 0, \\ -d - ry^* + \frac{x^*}{x^*+y^*+a} = 0. \end{gathered} \tag{2.2}$$

Clearly, $0 < x^* < 1$ and $0 < y^* < \frac{1-d}{r}$. By [27, Theorem 1.2], (x^*, y^*) smoothly depends on the parameters a, s, r and d. Let $x(t) \to x^* + x(t)$ and $y(t) \to y^* + y(t)$. Then system (1.3) is equivalent to

$$\begin{aligned} \frac{dx}{dt} &= F_x^* x^* x + F_y^* x^* y + g^1(x,y), \\ \frac{dy}{dt} &= G_x^* y^* x + G_y^* y^* y + g^2(x,y), \end{aligned} \tag{2.3}$$

where

$$\begin{aligned} F_x^* &= \frac{sy^*}{(x^*+y^*+a)^2} - 1, \quad F_y^* = -\frac{s(x^*+a)}{(x^*+y^*+a)^2}, \\ G_x^* &= \frac{b(y^*+a)}{(x^*+y^*+a)^2}, \quad G_y^* = -\frac{bx^*}{(x^*+y^*+a)^2} - br, \end{aligned} \tag{2.4}$$

and both $g^1(x,y)$ and $g^2(x,y)$ are of $o(x,y)$, given by:

$$\begin{aligned} g^1(x,y) &= -F_x^* x^* x - F_y^* x^* y + \Big(x - x^2 - \frac{sxy}{x+y+a}\Big), \\ g^2(x,y) &= -G_x^* y^* x - G_y^* y^* y + \Big(-bdy - bry^2 + \frac{bxy}{x+y+a}\Big). \end{aligned}$$

Applying the Lyapunov stability theorem [26], we can find a condition to ensure the local asymptotic stability of $(0,0)$ for system (2.3) as follows:

Theorem 2.1. *If condition* (2.1) *holds and* $F_x^* < 0$, *then the positive equilibrium* (x^*, y^*) *of system* (1.3) *is locally asymptotically stable.*

Proof. Let $V(x,y) = \frac{1}{2}x^2 - \frac{x^* F_y^*}{2y^* G_x^*} y^2$. For system (2.3), we have

$$\begin{aligned} \frac{dV}{dt}(x,y) &:= \frac{\partial V}{\partial x}\frac{dx}{dt} + \frac{\partial V}{\partial y}\frac{dy}{dt} \\ &= x^* F_x^* x^2 - \frac{x^* F_y^* G_y^*}{G_x^*} y^2 + o(x^2, xy, y^2). \end{aligned}$$

Obviously, $V(x,y) \geq 0$ and $V(x,y) = 0$ if and only if $(x,y) = (0,0)$. Under the condition $F_x^* < 0$, there exists a neighborhood N of the origin such that $\frac{dV}{dt}(x,y) \leq$

0 holds in N and $\frac{dV}{dt}(x,y) = 0$ if and only if $x(t) = y(t) = 0$. This implies that $V(x,y)$ is a Lyapunov function for system (2.3), and thus $(0,0)$ is locally asymptotical stable. That is, the positive equilibrium (x^*,y^*) of system (1.3) is locally asymptotically stable. □

Remark 2.2. Since $|x^*F_y^* + y^*G_x^*| < \min\{-2y^*G_y^*, -2x^*F_x^*\}$ implies that $F_x^* < 0$, we here obtain a weaker local asymptotic stability condition than the one in [18].

Note that the condition of local stability in Theorem 2.3 depends on x^* and y^*, and the positive equilibrium (x^*,y^*) usually needs to be solved numerically at first. It is evident that the condition $F_x^* < 0$ can be directly derived by $s \le 2a$. So, in the following, we attempt to seek a weaker condition than $s \le 2a$ by applying the Routh-Hurwitz criterion for the linerization of system (2.3) instead of constructing a Lyapunov function.

Clearly, the characteristic equation of the linerization of system (2.3) is

$$\lambda^2 + a_1\lambda + a_2 = 0, \tag{2.5}$$

where

$$\begin{gathered} a_1 = x^* + bry^* + \frac{(b-s)x^*y^*}{(x^*+y^*+a)^2}, \\ a_2 = \big[r + \frac{x^* - rsy^*}{(x^*+y^*+a)^2} + \frac{as}{(x^*+y^*+a)^3}\big]bx^*y^*. \end{gathered} \tag{2.6}$$

Since $a_1 \le 0$ is equivalent to $x^* + bry^* + \frac{(b-s)x^*y^*}{(x^*+y^*+a)^2} \le 0$, it follows from the first equation in (2.2) that

$$a_1 \le 0 \Leftrightarrow \frac{s}{1-x^*} \le \frac{(s-b)x^*(x^*+s-1)}{s(x^*+bry^*)(x^*+a)}.$$

Because of the relation $s > \frac{sy^*}{x^*+y^*+a} = 1 - x^*$, $a_1 \le 0$ implies that $s > b$ and $s > 1 + a$. Thus, if $s \le b$ or $s \le 1 + a$, then $a_1 > 0$, i.e. the trace of the Jacobian matrix at (x^*,y^*) is negative.

From (2.2), we have $x^* - rsy^* = 1 + sd - \frac{s(x^*+y^*)}{x^*+y^*+a} > 1 + sd - s$. According to

$$a_2 > 0 \Leftrightarrow \big[r + \frac{x^* - rsy^*}{(x^*+y^*+a)^2} + \frac{as}{(x^*+y^*+a)^3}\big]bx^*y^* > 0,$$

then $r + \frac{1+sd-s}{(x^*+y^*+a)^2} + \frac{as}{(x^*+y^*+a)^3} > 0$ implies $a_2 > 0$. Since $r + \frac{1+sd-s}{(x^*+y^*+a)^2} + \frac{as}{(x^*+y^*+a)^3} > 0$ can be derived by $s \le 1 + sd + ra^2$, we see that, if $s \le 1 + sd + ra^2$, then $a_2 > 0$. Especially, when $s \le \frac{1}{1-d}$, then $a_2 > 0$, i.e. the determinant of the Jacobian matrix at (x^*,y^*) is positive.

Let $S_1 = \max\{2a, b, 1 + a\}$ and $S_2 = \max\{2a, \frac{1+ra^2}{1-d}\}$. By the Routh-Hurwitz criterion, it is straightforward to reach a condition, depending only on parameters, for the local stability of (x^*,y^*) as follows:

Theorem 2.3. *If condition* (2.1) *and*

$$s \le \min\{S_1, S_2\} \tag{2.7}$$

hold, then the unique positive equilibrium (x^*,y^*) *of system* (1.3) *is locally asymptotically stable.*

Remark 2.4. In [21], it shows that for system (1.3), the positive equilibrium is locally asymptotically stable if $d < 1 \wedge ad < (1-d)\left(1 - s - \frac{d}{r}\right)$ or $s + \frac{d}{r} < 1 \wedge ad < (1-d)\left(1 - s - \frac{d}{r}\right)$. Clearly, this condition can also generate condition (2.7), but (2.7) looks succinct.

Remark 2.5. Notice that the unique positive equilibrium is not a saddle under condition (2.1) and we have derived that when $s \le \frac{1}{1-d}$ (and even $s \le S_2$), then $a_2 > 0$, which will be used for analyzing Hopf bifurcation in Section 4. Here it is still of our interest whether $a_2 > 0$ always holds or not while we analyze Hopf bifurcation.

3. Global stability of the positive equilibrium

In the previous section, we have presented conditions for local asymptotic stability of the positive equilibrium. In this section, we try to establish sufficient conditions for its global asymptotic stability. For this, by [18, Theorem 4.3], we need to provide conditions to ensure that there is no closed orbit except for the positive equilibrium (x^*, y^*) in the first quadrant $\mathbb{R}_+^2$. We will use Dulac's criterion and the divergency criterion for analyzing the global attractiveness of (x^*, y^*), respectively.

Theorem 3.1. *For system* (1.3)*, if condition* (2.1) *and*

$$\min\{bd, 2a - b\} \ge 1 \tag{3.1}$$

hold, then the positive equilibrium is globally asymptotically stable.

Proof. For system (1.3), by choosing $B(x, y) = x + y + a$, there holds

$$\begin{aligned} &\frac{\partial BP}{\partial x} + \frac{\partial BQ}{\partial y} \\ &= (x + y + a)(1 - bd - 2x - 2bry) + (1 + b)x - (x^2 + bry^2 + sy + bdy) < 0 \end{aligned}$$

in the simply connected region $\mathbb{R}_+^2$ due to conditions (2.1) and (3.1). Thus, by Dulac's criterion [13], there is no periodic solution in $\mathbb{R}_+^2$, and this implies that the positive equilibrium (x^*, y^*) is globally asymptotically stable. □

Lemma 3.2 (divergency criterion [13])**.** *Assume that L is a closed orbit with period T. If the condition*

$$\oint_0^T \operatorname{div}(x, y)dt < 0 \quad (> 0)$$

holds, then L is a single stable (unstable) limit cycle.

Based on Lemma 3.2, we obtain the following result.

Theorem 3.3. *For system* (1.3)*, if condition* (2.1) *and*

$$s \le \max\{b + 4abr, b + 4a\} \tag{3.2}$$

hold, then the local and global asymptotic stability of the positive equilibrium (x^*, y^*) coincide.

Proof. For system (1.3), the Jacobian matrix is

$$J(x(t), y(t)) = \begin{pmatrix} J_1 & J_2 \\ J_3 & J_4 \end{pmatrix},$$

where

$$J_1 = 1 - 2x(t) - \frac{sy(t)}{x(t)+y(t)+a} + \frac{sx(t)y(t)}{(x(t)+y(t)+a)^2}, \quad J_2 = -\frac{sx(t)(x(t)+a)}{(x(t)+y(t)+a)^2},$$
$$J_3 = \frac{by(t)(y(t)+a)}{(x(t)+y(t)+a)^2}, \quad J_4 = b[-d - 2ry + \frac{x(t)}{x(t)+y(t)+a} - \frac{x(t)y(t)}{(x(t)+y(t)+a)^2}].$$

Assume that $l(t) = (x(t), y(t))$ is an arbitrary but fixed nontrivial periodic orbit of system (1.3) with period $T > 0$, then there holds

$$\oint_0^T \frac{x'(t)}{x(t)} dt = \oint_0^T \big[1 - x(t) - \frac{sy(t)}{x(t)+y(t)+a}\big] dt = 0,$$
$$\oint_0^T \frac{y'(t)}{y(t)} dt = \oint_0^T b\big[- d - ry(t) + \frac{x(t)}{x(t)+y(t)+a}\big] dt = 0.$$

If $s \le b$, then

$$\oint_0^T trJ(x(t), y(t)) dt = \oint_0^T [-x(t) - bry(t) + \frac{(s-b)x(t)y(t)}{(x(t)+y(t)+a)^2}] dt < 0.$$

If $s > b$, then

$$\oint_0^T trJ(x(t), y(t)) dt \le \oint_0^T [-x(t) - \frac{(s-b)y(t)}{4a} + \frac{(s-b)y(t)}{4a}] dt < 0$$

because of the condition $s \le b + 4abr$ and $\oint_0^T trJ(x(t), y(t)) dt \le \oint_0^T [-x(t) + \frac{(s-b)x(t)}{4a} - bry(t)] dt < 0$ by the condition $s \le b + 4a$.

Consequently, by the divergency criterion, the closed orbit $l(t)$ is stable, which yields a contradiction with the local asymptotic stability of the positive equilibrium. So, if (x^*, y^*) is locally asymptotically stable, system (1.3) has no nontrivial periodic orbit in $\mathbb{R}_+^2$. This indicates that the positive equilibrium must be also globally asymptotically stable. □

Then, from Theorems 2.3 and 3.3, we can directly obtain the following corollary.

Corollary 3.4. *For system* (1.3)*, if conditions* (2.1)*,* (2.7) *and* (3.2) *hold, then the unique positive equilibrium is globally asymptotically stable.*

Remark 3.5. Provided that conditions (2.1) and (3.2) hold, we can additionally obtain that system (1.3) has the unique (stable) limit cycle in the first quadrant if the positive equilibrium is unstable, which will be described as Corollary 4.5.

Note that in the proof of Theorem 3.3, we simply apply the mean inequality to assure the negativeness of the divergency integral. In fact, the divergency integral can be further expanded by applying Grammer's rule and Green's theorem. However, this requires boundary values of periodic orbits of system (1.3). For this, similar to [19, Theorem 2.2], by defining a set

$$\Gamma := \{(x, y) \in \mathbb{R}_+^2 : \underline{x} \le x \le \overline{x}, \underline{y} \le y \le \overline{y}\},$$

where $\underline{x} = 1 - s$, $\overline{x} = 1$,

$$\underline{y} = \frac{1}{2}[-\frac{d + r(a+1-s)}{r} + \sqrt{[\frac{d + r(a+1-s)}{r}]^2 + 4\frac{(1-d)(1-s) - da}{r}}]$$

and $\overline{y} = \frac{1-d(a+1)}{d+r(a+1)}$, we have the following stronger permanent condition for providing concrete boundary values.

Theorem 3.6. *Suppose that system* (1.3) *satisfies the condition*

$$ad < (1-d)(1-s) \quad \text{and} \quad s < 1. \tag{3.3}$$

Then for any solution $(x(t), y(t))$ *of system* (1.3) *with the positive initial condition (i.e.* $x(0) > 0$ *and* $y(0) > 0$*), there is a* $T_0 > 0$ *such that for all* $t > T_0$, $(x(t), y(t)) \in \Gamma$ *holds.*

Obviously, since $ad < (1-d)(1-s)$ implies that condition (2.1) holds, and $s < 1$ implies that condition (2.7) holds, by combining Theorem 2.3 and Corollary 3.4, we directly have the following corollary.

Corollary 3.7. *If condition* (3.3) *holds, then the unique positive equilibrium is locally asymptotically stable. If conditions* (3.2) *and* (3.3) *hold, then the unique positive equilibrium is globally asymptotically stable.*

From Theorem 3.3 and Corollary 3.7, we know that if conditions (3.3) holds and $s \leq b$, the unique positive equilibrium of system (1.3) is globally asymptotically stable. Further, we can derive from Theorem 3.6 that if condition (3.3) holds, all possible periodic orbits must lie in Γ. Thus, instead of (2.1), we attempt to employ condition (3.3) for the case of $s > b$ to derive the divergency integral and obtain the following theorem.

Theorem 3.8. *For system* (1.3)*, if the condition*

$$\begin{gathered}
(s-b)(1-x^*) - sb = 0, \\
r < \min\{\frac{as}{(\overline{x}+\overline{y}+a)^2(x^*+y^*+a)}, \frac{s\underline{x}}{b(\overline{x}+\overline{y}+a)^2}\}, \\
\text{or} \\
(s-b)(1-x^*) - sb > 0, \\
r < \min\Big\{\frac{as}{(\overline{x}+\overline{y}+a)^2(x^*+y^*+a)}, \frac{s\underline{x}}{b(\overline{x}+\overline{y}+a)^2}\Big\}, \\
\underline{x}(x^*+\underline{x}+\underline{y}+a-1) > b\overline{y}(1-d-ry^*),
\end{gathered} \tag{3.4}$$

holds, then the unique positive equilibrium (x^*, y^*) *is globally asymptotically stable, provided that condition* (3.3) *holds.*

Proof. Assume that $l(t) = (x(t), y(t))$ is an arbitrary but fixed nontrivial periodic orbit of system (1.3) with period $T > 0$. Similar to the proof of Theorem 3.3, it suffices to show that under conditions (3.3) and (3.4), $\oint_0^T trJ(x(t), y(t))dt < 0$.

Since $(x(t), y(t))$ is an orbit of system (1.3) and

$$\oint_0^T trJ(x(t), y(t))dt = \oint_0^T \Big[-x(t) - bry(t) + \frac{(s-b)x(t)y(t)}{(x(t)+y(t)+a)^2}\Big]dt,$$

we have

$$\begin{aligned}
&\oint_0^T trJ(x(t), y(t))dt \\
&= \oint_0^T \Big[-x(t) - bry(t) + (s-b)d\frac{y(t)}{x(t)+y(t)+a}\Big]dt \\
&\quad + \oint_0^T \Big[(s-b)\frac{y(t)}{x(t)+y(t)+a}(\frac{x(t)}{x(t)+y(t)+a} - d)\Big]dt
\end{aligned}$$

$$
\begin{aligned}
&= \oint_0^T \Big[- x(t) - bry(t) + (s-b)\frac{d}{s}(1 - x(t) - \frac{x'(t)}{x(t)})\Big] dt \\
&\quad + \oint_0^T \Big[(s-b)\frac{y(t)}{x(t)+y(t)+a}(ry(t) + \frac{y'(t)}{by(t)})\Big] dt \\
&= \oint_0^T \Big[- x(t) - bry(t) + (s-b)\frac{d}{s}(1 - x(t))\Big] dt \\
&\quad + \oint_0^T \Big[(s-b)\frac{ry(t)^2}{x(t)+y(t)+a} + \frac{s-b}{b}\frac{y'(t)}{x(t)+y(t)+a}\Big] dt \\
&= \oint_0^T \Big[- x(t) - bry(t) + (s-b)\frac{1}{s}(1 - x(t))(d + ry(t))\Big] dt \\
&\quad + \oint_0^T \Big[- (s-b)\frac{ry(t)}{s}\frac{x'(t)}{x(t)} + \frac{s-b}{b}\frac{y'(t)}{x(t)+y(t)+a}\Big] dt.
\end{aligned}
$$

Further, since

$$
\oint_0^T trJ(x^*, y^*) dt = - \oint_0^T [x^* + bry^* - \frac{1}{s}(s-b)(1-x^*)(d+ry^*)] dt,
$$

it is easy to show that

$$
\begin{aligned}
&\oint_0^T trJ(x(t), y(t)) dt \\
&= \oint_0^T trJ(x^*, y^*) dt \\
&\quad + \oint_0^T \Big[\frac{s-b}{b}\frac{y'(t)}{x(t)+y(t)+a} - \frac{s-b}{s} ry(t)\frac{x'(t)}{x(t)}\Big] dt \\
&\quad + \oint_0^T \big[(-(x(t)-x^*) - br(y(t)-y^*)) \big] dt \\
&\quad + \oint_0^T \Big[\frac{s-b}{s}\,((d+ry(t))(1-x(t)) - (d+ry^*)(1-x^*)) \Big] dt \qquad (3.5) \\
&= \oint_0^T trJ(x^*, y^*) dt \\
&\quad + \oint_0^T \Big[\frac{s-b}{b}\frac{y'(t)}{x(t)+y(t)+a} - \frac{s-b}{s} ry(t)\frac{x'(t)}{x(t)}\Big] dt \\
&\quad + \oint_0^T \Big[\Big(-1 - \frac{1}{s}(s-b)(d+ry(t))\Big)(x(t)-x^*)\Big] dt \\
&\quad + \oint_0^T \Big[r\Big(\frac{1}{s}(s-b)(1-x^*) - b\Big)(y(t)-y^*)\Big] dt.
\end{aligned}
$$

Clearly,

$$
\begin{aligned}
&\oint_0^T \Big[\frac{s-b}{b}\frac{y'(t)}{x(t)+y(t)+a} - \frac{s-b}{s} ry(t)\frac{x'(t)}{x(t)}\Big] dt \\
&= \frac{s-b}{bs}\Big(\oint_l -\frac{bry}{x} dx + \frac{s}{x+y+a} dy\Big).
\end{aligned}
$$

Moreover, since $(x(t),y(t))$ satisfies system (1.3) and (x^*,y^*) satisfies system (2.2), we can obtain that

$$\begin{aligned}\frac{x'(t)}{x(t)} &= 1-x(t)-\frac{sy(t)}{x(t)+y(t)+a}\\ &= x^*+\frac{sy^*}{x^*+y^*+a}-x(t)-\frac{sy(t)}{x(t)+y(t)+a}\\ &= \Big[-1+\frac{sy^*}{(x^*+y^*+a)(x(t)+y(t)+a)}\Big](x(t)-x^*)\\ &\quad -\frac{(x^*+a)s}{(x^*+y^*+a)(x(t)+y(t)+a)}(y(t)-y^*),\end{aligned}$$

and

$$\begin{aligned}\frac{y'(t)}{by(t)} &= -d-ry(t)+\frac{x(t)}{x(t)+y(t)+a}\\ &= ry^*-\frac{x^*}{x^*+y^*+a}-ry(t)+\frac{x(t)}{x(t)+y(t)+a}\\ &= \frac{y^*+a}{(x^*+y^*+a)(x(t)+y(t)+a)}(x(t)-x^*)\\ &\quad -\Big[r+\frac{x^*}{(x^*+y^*+a)(x(t)+y(t)+a)}\Big](y(t)-y^*).\end{aligned}$$

Thus, by Crammer's Rule, we have

$$\begin{aligned} x-x^* &= \frac{[\frac{x^*}{x^*+y^*+a}+r(x(t)+y(t)+a)]\frac{x'(t)}{x(t)}-[\frac{(x^*+a)s}{x^*+y^*+a}]\frac{y'(t)}{by(t)}}{\frac{rsy^*-x^*}{x^*+y^*+a}-r(x(t)+y(t)+a)-\frac{as}{(x(t)+y(t)+a)(x^*+y^*+a)}},\\ y-y^* &= \frac{[\frac{y^*+a}{x^*+y^*+a}]\frac{x'(t)}{x(t)}-[\frac{sy^*}{x^*+y^*+a}-(x(t)+y(t)+a)]\frac{y'(t)}{by(t)}}{\frac{rsy^*-x^*}{x^*+y^*+a}-r(x(t)+y(t)+a)-\frac{as}{(x(t)+y(t)+a)(x^*+y^*+a)}}.\end{aligned}\tag{3.6}$$

Let D denote the region encloused by the periodic orbit $l(t)$ and

$$\begin{aligned} M_1(x,y) &= \frac{-1-\frac{1}{s}(s-b)(d+ry(t))}{-r(x(t)+y(t)+a)+\frac{rsy^*-x^*}{x^*+y^*+a}-\frac{as}{(x^*+y^*+a)(x(t)+y(t)+a)}},\\ M_2(x,y) &= \frac{r[\frac{1}{s}(s-b)(1-x^*)-b]}{-r(x(t)+y(t)+a)+\frac{rsy^*-x^*}{x^*+y^*+a}-\frac{as}{(x^*+y^*+a)(x(t)+y(t)+a)}},\\ M_3(x,y) &= \frac{-r+\frac{as}{(x(t)+y(t)+a)^2(x^*+y^*+a)}}{bxy\big(-r(x(t)+y(t)+a)+\frac{rsy^*-x^*}{x^*+y^*+a}-\frac{as}{(x^*+y^*+a)(x(t)+y(t)+a)}\big)^2}.\end{aligned}$$

Then, from (3.5) and (3.6), we obtain

$$\begin{aligned}&\oint_0^T\Big[-1-\frac{1}{s}(s-b)(d+ry(t))\Big](x(t)-x^*)dt\\ &+\oint_0^T r\Big[\frac{1}{s}(s-b)(1-x^*)-b\Big](y(t)-y^*)dt\\ &=\oint_0^T M_1(x,y)\Big[\Big(\frac{x^*}{x^*+y^*+a}+r(x(t)+y(t)+a)\Big)\frac{x'(t)}{x(t)}\Big]dt\end{aligned}$$

$$
\begin{aligned}
&- \oint_0^T M_1(x,y)\Big[\frac{(x^*+a)s}{x^*+y^*+a}\frac{y'(t)}{by(t)}\Big]dt \\
&- \oint_0^T M_2(x,y)\Big[\Big(\frac{sy^*}{x^*+y^*+a} - (x(t)+y(t)+a)\Big)\frac{y'(t)}{by(t)}\Big]dt \\
&+ \oint_0^T M_2(x,y)\Big[\frac{y^*+a}{x^*+y^*+a}\frac{x'(t)}{x(t)}\Big]dt \\
&= \oint_l \Big[M_1(x,y)\Big(\frac{x^*}{x^*+y^*+a} + r(x+y+a)\Big)\Big]\frac{dx}{x} \\
&+ \oint_l \Big[M_2(x,y)\frac{y^*+a}{x^*+y^*+a}\Big]\frac{dx}{x} \\
&+ \oint_l \Big[M_2(x,y)\Big((x+y+a) - \frac{sy^*}{x^*+y^*+a}\Big)\Big]\frac{dy}{by} \\
&- \oint_l \Big[M_1(x,y)\frac{(x^*+a)s}{x^*+y^*+a}\Big]\frac{dy}{by}.
\end{aligned}
$$

In the following, we denote that

$$
K_1 = -1 - \frac{1}{s}(s-b)(d+ry), \quad K_2 = r(\frac{1}{s}(s-b)(1-x^*) - b).
$$

Then by applying Green's theorem, we deduce that

$$
\begin{aligned}
&\oint_0^T trJ(x(t),y(t))dt \\
&= \oint_0^T trJ(x^*,y^*)dt + \iint_D \frac{s-b}{bs}(-\frac{s}{(x+y+a)^2} + \frac{br}{x})\,dx\,dy \\
&+ \iint_D K_1 M_3(x,y)\Big[\frac{sx(x^*+a)}{x^*+y^*+a}\Big]\,dx\,dy \\
&+ \iint_D K_1 M_3(x,y)\Big[by(\frac{x^*}{x^*+y^*+a} + r(x+y+a))\Big]\,dx\,dy \\
&+ \iint_D K_2 M_3(x,y)\Big[\frac{by(y^*+a)}{x^*+y^*+a}\Big]\,dx\,dy \\
&+ \iint_D K_2 M_3(x,y)\Big[x(\frac{sy^*}{x^*+y^*+a} - (x+y+a))\Big]\,dx\,dy \\
&+ \iint_D \frac{\frac{r}{by}[\frac{1}{s}(s-b)(1-x^*) - b]}{-r(x+y+a) + \frac{rsy^*-x^*}{x^*+y^*+a} - \frac{as}{(x^*+y^*+a)(x+y+a)}}\,dx\,dy \\
&+ \iint_D \frac{\frac{r}{sx}(s-b)[\frac{x^*}{x^*+y^*+a} + r(x+y+a)]}{-r(x+y+a) + \frac{rsy^*-x^*}{x^*+y^*+a} - \frac{as}{(x^*+y^*+a)(x+y+a)}}\,dx\,dy \\
&+ \iint_D \frac{\frac{r}{x}[1 + \frac{1}{s}(s-b)(d+ry)]}{-r(x+y+a) + \frac{rsy^*-x^*}{x^*+y^*+a} - \frac{as}{(x^*+y^*+a)(x+y+a)}}\,dx\,dy.
\end{aligned}
$$

It is easy to see that

- $\oint_0^T trJ(x^*,y^*)dt < 0$ since (x^*,y^*) is locally asymptotically stable under conditions (3.3).
- $\iint_D(-\frac{s}{(x+y+a)^2} + \frac{br}{x})\,dx\,dy < 0$ because of the condition $r < \frac{sx}{b(\overline{x}+\overline{y}+a)^2}$.
- $M_3(x,y) > 0$ because of $r < \frac{as}{(\overline{x}+\overline{y}+a)^2(x^*+y^*+a)}$.

- the denominator in M_1 is negative since condition (3.3) implies that $x^* - rsy^* > 1 + sd - s > 0$.

Thus, if $(s-b)(1-x^*) - sb = 0$, then $s > b$ and we have $\oint_0^T trJ(x(t), y(t))dt < 0$. And if $(s-b)(1-x^*) - sb > 0$, then $s > b$ and we have

$$\frac{by(y^*+a)}{x^*+y^*+a} + x\Big(\frac{sy^*}{x^*+y^*+a} - (x+y+a)\Big) < 0$$

by the inequality $\underline{x}(x^* + \underline{x} + \underline{y} + a - 1) > b\overline{y}(1 - d - ry^*)$, which also implies that $\oint_0^T trJ(x(t), y(t))dt < 0$.

Consequently, under conditions (3.3) and (3.4), the positive equilibrium (x^*, y^*) is globally asymptotically stable. □

Remark 3.9. From the proof of Theorem 3.8, we can find that when $r = 0$, $\oint_0^T trJ(x(t), y(t))dt < 0$ always holds. Thus, for system (1.3) with $r = 0$, the local and global asymptotic stability of the positive equilibrium coincide, which was also proved in [15].

Remark 3.10. Similarly, it is also interesting to find conditions to ensure that $\oint_0^T trJ(x(t), y(t))dt > 0$; that is,

$$\oint_0^T \Big[- x(t) - bry(t) + \frac{(s-b)x(t)y(t)}{(x(t)+y(t)+a)^2}\Big] dt > 0, \tag{3.7}$$

such that the local and global asymptotic stability of the positive equilibrium (x^*, y^*) coincide.

In Theorem 3.8, we obtained a sufficient condition for global stability of the positive equilibrium based on the permanence condition (3.3) which is also the local asymptotic stability condition. But, this condition contains x^* and y^* which we need to numerically solve the positive equilibrium first. Intuitively, condition (3.4) can be simplified by replacing x^* and y^* with boundary values defined in Γ. However, for the case of $s > b$, the sub-condition $(s-b)(1-x^*) - sb > 0$ in condition (3.4) can not be simplified further since $\overline{x} = 1$.

4. Hopf bifurcations with respect to one parameter r and all five parameters

Compared to the systems studied in [6, 15, 16], system (1.3) involves the density dependence of the predators and thus has the extra term ry^2 with $r > 0$. In this section, we will first focus on the Hopf bifurcation with respect to the parameter r, and then extend our discussions to all other parameters.

From [6], we know that system (1.3) with $r = 0$ has a unique positive equilibrium if and only if condition (2.1) holds. Thus, system (1.3) with $r \geq 0$ has a unique positive equilibrium if and only if condition (2.1) holds. Following [27], one can see that this positive equilibrium (x^*, y^*) must smoothly depend on the parameters $a > 0$, $d > 0$, $s > 0$, $b > 0$ and $r \geq 0$.

For the Hopf bifurcation, we perform two different choices of parameters to analyze the change of $Sign(a_1)$ by following the ideas in [26].

Lemma 4.1. *For system* (1.3) *with* $r = 0$, *if* (2.1) *holds and* $s > \max\{b, \frac{bd}{1+d} + \frac{1}{1-d^2}\}$, *then we have* $a_1 < 0$ *if and only if*

$$a < \frac{1}{s}\frac{s-b}{s+(s-b)d}\Big[\frac{(s-b)d}{s+(s-b)d} + s - 1 - sd\Big].$$

Proof. Let $\rho = \frac{(s-b)d}{s+(s-b)d}$ and $\hat{a} = \frac{\rho}{sd}(\rho + s - 1 - sd)$. Then we see $\hat{a} > 0$ if and only if $s > \frac{bd}{1+d} + \frac{1}{1-d^2}$. As $r = 0$ in system (2.2), it gives $ads = x^*(x^* + s - 1 - sd)$. Namely, when $a = \hat{a}$, it has $x^* = \rho$.

As $r = 0$ in system (1.3), if $s > b$, we have $a_1 = [1 + (1 - \frac{b}{s})](x^* - \rho)$. Because $x^* = \frac{1}{2}[1 + sd - s + \sqrt{(1 + sd - s)^2 + 4ads}]$, x^* increases as a increases. So, we see that $a_1 < 0$ if and only if $a < \hat{a}$. □

Lemma 4.2. *Under condition* (2.1), *if* $s > S_1$ *and* $b + \frac{b}{s} - 1 \geq 0$, *then* $\frac{\partial a_1}{\partial r} > 0$.

Proof. According to the equation $x^* = rsy^* + as\frac{d+ry^*}{x^*} + 1 + sd - s$, ry^* increases as x^* increases. Moreover, with the condition $b + \frac{b}{s} - 1 \geq 0$, a_1 increases as x^* increases since

$$a_1 = [1 + d(1 - \frac{b}{s})]x^* + (b + \frac{b}{s} - 1)ry^* + (1 - \frac{b}{s})rx^*y^* - d(1 - \frac{b}{s}).$$

Hence, it suffices to prove that x^* increases as r increases.

Since (x^*, y^*) satisfies system (2.2), under the condition $s > S_1$, (x^*, y^*) can be determined by the two hyperbolic equations, whose corresponding locations can be roughly shown in Figure 1 (left) and Figure 1 (middle) by the classifications provided in [18]. Notice that the hyperbolic curves in Figure 1 (left) do not depend on the parameter r and $(\frac{ad}{1-d}, 0)$ lies on the right hyperbolic curve in Figure 1 (middle). Further, for the second equation in system (2.2), $\frac{dy}{dx} = \frac{1-d-ry}{r(x+2y+a)+d} > 0$ holds for the right curve in the first quadrant, especially for $r_1 < r_2$, $(x, y) = (\frac{ad}{1-d}, 0)$, and $\frac{1-d-r_1 y}{r_1(x+2y+a)+d} > \frac{1-d-r_2 y}{r_2(x+2y+a)+d}$. Moreover, in the first quadrant, when $r_1 < r_2$, the curve corresponding to r_1 lies above the curve corresponding to r_2, which is shown in Figure 1 (right). Otherwise, the curve corresponding to r_1 must intersect with the curve corresponding to r_2 at a point (x_0, y_0) in the first quadrant. However, since $\frac{1-d-r_1 y_0}{r_1(x_0+2y_0+a)+d} < \frac{1-d-r_2 y_0}{r_2(x_0+2y_0+a)+d}$, it arrives at a contradiction. As shown in Figure 1 (left) and Figure 1 (right), as r increases, we see that x^* increases. Thus, we complete the proof. □

Based on the above two lemmas, let us first focus on the Hopf bifurcation with respect to the parameter r, regarding other parameters as fixed constants. Under condition (2.1), if $s > S_1$ and $b + \frac{b}{s} - 1 \geq 0$, then $\frac{da_1(r)}{dr} > 0$ holds for system (1.3) with $r \geq 0$. Furthermore, by Lemmas 4.1 and 4.2, we have the following result:

Lemma 4.3. *For system* (1.3), *under the same conditions as shown in Lemmas 4.1 and 4.2, there exists a unique* r^* *such that* $a_1(r^*) = 0$. *Moreover,* $a_1(r) < 0$ *if* $r < r^*$ *and* $a_1(r) > 0$ *if* $r > r^*$.

Proof. Let (x_0, y_0) be the point in Figure 1 (left) with $x_0 = \frac{d(1-\frac{b}{s})}{1+d(1-\frac{b}{s})}$. Under the conditions shown in Lemmas 4.1 and 4.2, we can obtain that for the sufficiently large r, $x^* \geq x_0$ holds, and hence $a_1(r) = [1 + d(1 - \frac{b}{s})]x^* + (b + \frac{b}{s} - 1)ry^* + (1 - \frac{b}{s})rx^*y^* - d(1 - \frac{b}{s}) > 0$ holds. Otherwise, for all $r \geq 0$ and $x^* < x_0$, due to the

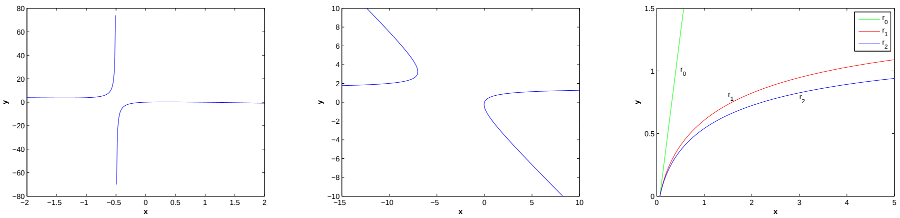

FIGURE 1. Left: Curves for the hyperbolic equation $sy = (1 - x)(x + y + a)$. Middle: Curves for the hyperbolic equation $x = (d + ry)(x + y + a)$. Right: Curves for $x = (d + ry)(x + y + a)$ with $r_2 > r_1 > r_0 = 0$.

hyperbolic curves in Figure 1 (left) and Figure 1 (middle), $y^* > y_0$ as $r \to +\infty$ and so $ry^* \to +\infty$ as $r \to +\infty$. This contradicts the fact that $ry^* < 1 - d$.

From Lemmas 4.1 and 4.2, there exists one unique r^* such that $a_1(r^*) = 0$ and $a_1(r) < 0$ if and only if $r < r^*$. □

From Lemma 4.3, $a_1(r^*) = 0$ under the conditions shown in Lemmas 4.1 and 4.2. Moreover, recalling from Section 2 that when $s \le \frac{1}{1-d}$, we have $a_2(r) > 0$, and thus $a_2(r^*) > 0$. Since a_1 and a_2 smoothly depend on the parameters $a > 0$, $b > 0$, $d > 0$, $s > 0$ and $r \ge 0$, there exists a neighborhood W of r^* such that for all $r \in W$, there holds $a_1^2(r) < 4a_2(r)$. This implies that the characteristic equation (2.5) has conjugate complex roots for all $r \in W$, denoted as $\lambda := \alpha(r) \pm i\omega(r) = \frac{-a_1}{2} \pm \frac{\sqrt{4a_2 - a_1^2}}{2} i$.

Notice that $\alpha(r^*) = 0$ and $\omega(r^*) > 0$. Hence the characteristic equation (2.5) has one pair of conjugated pure imaginary roots $\lambda = \pm i\omega(r^*)$. By the center manifold theorem [26], the orbit structure near $(x, y, r) = (x^*, y^*, r^*)$ can be determined by the vector field (2.3) restricted to the center manifold, which has the following form

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = \begin{pmatrix} \alpha(r) & -\omega(r) \\ \omega(r) & \alpha(r) \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} f^1(x, y, r) \\ f^2(x, y, r) \end{pmatrix}$$

where f^1 and f^2 are nonlinear in x and y. Then, by the Hopf bifurcation theory [26], we can directly obtain the following result on Hopf bifurcation for system (1.3).

Theorem 4.4. *For system* (1.3), *if the following conditions* $ad < 1 - d$, $s \le \frac{1}{1-d}$, $b + \frac{b}{s} - 1 \ge 0$, $s > \max\{b, 2a, 1 + a, \frac{bd}{1+d} + \frac{1}{1-d^2}\}$ *and*

$$a < \frac{1}{s} \frac{s - b}{s + (s - b)d} \Big[\frac{(s - b)d}{s + (s - b)d} + s - 1 - sd \Big]$$

hold, then the positive equilibrium (x^*, y^*) *is an unstable focus for* $0 < r^* - r \ll 1$ *and an asymptotically stable focus for* $0 < r - r^* \ll 1$. *Moreover, when* $u(r^*) > 0$, *there exists a neighborhood* U *of the positive equilibrium* (x^*, y^*) *such that the system has a unique unstable periodic orbit in* U *for* $0 < r - r^* \ll 1$ *(and hence a stable periodic orbit exists outside this unstable periodic orbit). When* $u(r^*) < 0$, *there exists a neighborhood* U *of the positive equilibrium* (x^*, y^*) *such that the system has a unique stable periodic orbit in* U *for* $0 < r^* - r \ll 1$, *where* $u(r^*)$ *is given in* [26] *as:*

$$
\begin{aligned}
u(r^*) = \frac{1}{16}[f^1_{xxx} + f^1_{xyy} + f^2_{xxy} + f^2_{yyy}] + \frac{1}{16\omega(r^*)}\Big[f^1_{xy}(f^1_{xx} + f^1_{yy}) \\
- f^2_{xy}(f^2_{xx} + f^2_{yy}) - f^1_{xx}f^2_{xx} + f^1_{yy}f^2_{yy}\Big].
\end{aligned}
$$

In Theorem 4.4, we have discussed the existence of limit cycles for sufficiently small $|r - r^*|$. In fact, combining Lemmas 4.3 and 3.2 with the proof of Theorem 3.3, it is straightforward to obtain the following corollary.

Corollary 4.5. *For system* (1.3)*, if the conditions shown in Theorem 4.4 hold, then there is at least one stable limit cycle when $r < r^*$. Moreover, the limit cycle is unique if condition* (3.2) *is also satisfied.*

Additionally, we have the following stability results on the positive equilibrium.

Corollary 4.6. *For system* (1.3)*, if the conditions shown in Theorem 4.4 hold, then the positive equilibrium is unstable if $r < r^*$ and locally asymptotically stable if $r > r^*$. Moreover, the positive equilibrium is globally asymptotically stable when $r > r^*$ and condition* (3.2) *holds.*

Up to now, we have discussed the Hopf bifurcation only with respect to the parameter r. It is also interesting to discuss the Hopf bifurcation with respect to all parameters. In the rest of this section, we would like to set a special geometrical structure such that the analysis process can be simplified by applying the classical Hopf bifurcation theory on systems with one single parameter.

For this, let $\mu = \frac{(b-s)x^*y^*}{(x^*+y^*+a)^2} + x^* + bry^*$ be an auxiliary map, which can be also regarded as an auxiliary parameter and will be used to analyze the Hopf bifurcation. Intuitively, by this parameter μ, we restrict the five parameters of system (1.3) to a special geometrical structure such that the five-dimensional parameters can be simply mapped to one-dimensional parameter. Thus, it enables us to consider the Hopf bifurcation along with this special geometrical structure, where the five parameters to some extent affect together as one parameter μ. Note that from Lemmas 4.1 and 4.3, there certainly exist conditions on the five parameters a, b, d, r, s to assure the possibilities of $\mu > 0$, $\mu < 0$ and $\mu = 0$, respectively.

Moreover, since a_1 and a_2 smoothly depend on the five parameters, $a_2 > 0$ if $s \le \frac{1}{1-d}$ and μ can be regarded as a continuous map of the five parameters. For the parameters a, b, d, r, s satisfying $\mu(a, b, d, r, s) = 0$, there exists a neighborhood $K \subsetneq \mathbb{R}^5$ of (a, b, d, r, s) (and thus a neighborhood $\Omega \subsetneq \mathbb{R}$ of $\mu = 0$) such that for all $(a, b, d, r, s) \in K$ (and thus $\mu \in \Omega$), $a_1^2(a, b, d, r, s) < 4a_2(a, b, d, r, s)$ holds. This implies that the characteristic equation (2.5) has conjugate complex roots in K, denoted as $\lambda := \beta(\mu) \pm i\varphi(\mu) = \frac{-a_1}{2} \pm \frac{\sqrt{4a_2 - a_1^2}}{2} i$.

Clearly, when $\mu = 0$, $\beta(0) = 0$, $\beta'(0) = -\frac{1}{2} < 0$ and $\varphi(0) > 0$, the characteristic equation (2.5) has one pair of conjugated pure imaginary roots $\lambda = \pm i\varphi(0)$. By the center manifold theorem [26], we can see that the orbit structure near $(x^*, y^*, a, b, d, r, s)$ with $\mu(a, b, d, r, s) = 0$ (i.e. near (x^*, y^*, μ) with $\mu = 0$) is determined by the vector field (2.3) restricted to the center manifold, which has the form

$$
\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = \begin{pmatrix} \beta(\mu) & -\varphi(\mu) \\ \varphi(\mu) & \beta(\mu) \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} f^1(x, y, \mu) \\ f^2(x, y, \mu) \end{pmatrix}
$$

where f^1 and f^2 are nonlinear in x and y.

Since $\beta'(0) = -\frac{1}{2} < 0$, by the classical Hopf bifurcation theory on dynamical systems with one single parameter [26], we can obtain the following theorem on the Hopf bifurcation with respect to all the five parameters along with the special geometrical structure $\mu = \frac{(b-s)x^*y^*}{(x^*+y^*+a)^2} + x^* + bry^*$.

Theorem 4.7. *For system* (1.3)*, if $s \le \frac{1}{1-d}$, then the positive equilibrium (x^*, y^*) is an unstable focus for $-1 \ll \mu < 0$, or an locally asymptotically stable focus for $0 < \mu \ll 1$. Moreover, when $\psi(0) > 0$, there exists a neighborhood $\bar{U}$ of the positive equilibrium (x^*, y^*) such that the system has a unique unstable periodic orbit in $\bar{U}$ for $0 < \mu \ll 1$ (and hence a stable periodic orbit exists outside this unstable periodic orbit). When $\psi(0) < 0$, there exists a neighborhood $\bar{U}$ of the positive equilibrium (x^*, y^*) such that the system has a unique stable periodic orbit in $\bar{U}$ for $-1 \ll \mu < 0$, where the coefficient $\psi(0)$ is given as in* [26]*:*

$$\begin{aligned}\psi(0) = \frac{1}{16}[f^1_{xxx} + f^1_{xyy} + f^2_{xxy} + f^2_{yyy}] + \frac{1}{16\varphi(0)}\Big[f^1_{xy}(f^1_{xx} + f^1_{yy}) \\ - f^2_{xy}(f^2_{xx} + f^2_{yy}) - f^1_{xx}f^2_{xx} + f^1_{yy}f^2_{yy}\Big].\end{aligned}$$

5. Numerical simulations

In this section, we illustrate some numerical examples.

Example 5.1. Let $a = 3$, $b = 5$, $s = 1$, $d = 0.2$ and $r = 1$, then system (1.3) becomes

$$\begin{aligned}x'(t) &= x(t)(1 - x(t)) - \frac{x(t)y(t)}{x(t) + y(t) + 3}, \\ y'(t) &= 5y(t)\big(- 0.2 - y(t) + \frac{x(t)y(t)}{x(t) + y(t) + 3}\big).\end{aligned} \tag{5.1}$$

Since $0.6 = ad < 1 - d = 0.8$ and $1 = s < 2a = 6$, according to Theorem 2.3, the positive equilibrium $(x^*, y^*) \approx (0.9888, 0.0451)$ of system (5.1) is locally asymptotically stable. In fact, the positive equilibrium is globally asymptotically stable too, since $1 = bd \ge 1$ and $1 = 2a - b \ge 1$, and condition (3.1) in Theorem 3.1 holds. The global asymptotic stability can be seen from Figure 2 (left). Note that in Figure 2 (left), all six orbits go to $(0.9888, 0.0451)$ as t tends to $+\infty$, starting from initial points $(0.1, 0.2)$, $(0.5, 0.3)$, $(0.7, 0.6)$, $(0.9, 1.0)$, $(1.2, 1.05)$ and $(1.5, 1.35)$, respectively.

Example 5.2. Let $a = 1$, $b = 1$, $s = 0.5$, $d = 0.1$ and $r = 1$, then system (1.3) becomes

$$\begin{aligned}x'(t) &= x(t)(1 - x(t)) - \frac{0.5x(t)y(t)}{x(t) + y(t) + 1}, \\ y'(t) &= y(t)\Big(- 0.1 - y(t) + \frac{x(t)y(t)}{x(t) + y(t) + 1}\Big).\end{aligned} \tag{5.2}$$

Since $0.1 = ad < (1 - d)(1 - s) = 0.45$ and $0.5 = s < 1$, according to Theorem 3.6, the positive equilibrium $(x^*, y^*) \approx (0.9300, 0.3144)$ of system (5.2) is locally asymptotically stable. In fact, by Theorem 3.3, the positive equilibrium is globally asymptotically stable too, since $0.5 = s < b = 1$. The global asymptotic stability can be seen from Figure 2 (right). Note that in Figure 2 (right), all six orbits all go to $(0.9300, 0.3144)$ as t tends to $+\infty$, starting from initial points $(0.1, 0.2)$, $(0.5, 0.3)$, $(0.7, 0.6)$, $(0.9, 1.0)$, $(1.2, 1.05)$ and $(1.5, 1.35)$, respectively.

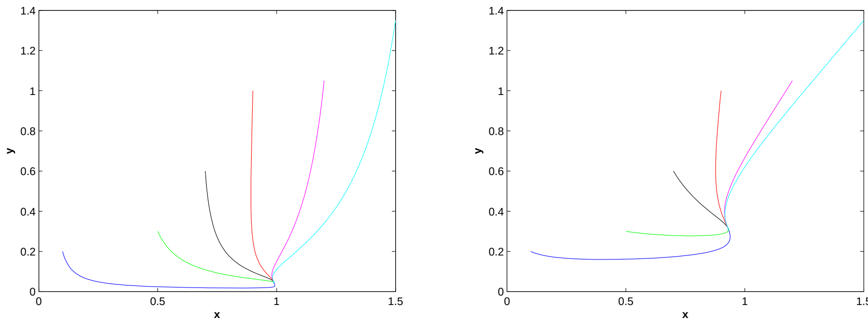

FIGURE 2. Left: Evolutions of six orbits for system (5.1). Right: Evolutions of six orbits for system (5.2).

Example 5.3. Let $a = 2$, $b = 1/20$, $s = 1/2$, $d = 1/6$, and $r = 1/750$, then system (1.3) becomes

$$
\begin{aligned}
x'(t) &= x(t)(1 - x(t)) - \frac{\frac{1}{2}x(t)y(t)}{x(t) + y(t) + 2},\\
y'(t) &= \frac{1}{20}y(t)\Big(-\frac{1}{6} - \frac{1}{750}y(t) + \frac{x(t)y(t)}{x(t) + y(t) + 2}\Big).
\end{aligned} \tag{5.3}
$$

The positive equilibrium is $(x^*, y^*) \approx (0.7969, 1.9126)$. A straightforward calculation gives that $\frac{1}{2} = s < 1$, $\frac{1}{3} = ad < (1-d)(1-s) = \frac{5}{12}$, $(s-b)(1-x^*) - sb \approx 0.0664 > 0$, $\frac{1}{750} = r < \frac{as}{(a+1+\frac{1}{d})^3} = \frac{1}{729}$, $\frac{1}{750} = r < \frac{s(1-s)}{(a+1+\frac{1}{d})^2} = \frac{1}{324}$, and $\frac{1}{20} = b < d(a-1)(1-s) = \frac{1}{12}$. This implies that conditions (3.3) and (3.4) in Theorem 3.8 are satisfied. Thus, (x^*, y^*) is globally attractive, which can be seen from Figure 3. Note that in Figure 3, the six orbits starting from initial points $(0.1, 1.7)$, $(0.3, 3.5)$, $(0.5, 0.3)$, $(1, 2.7)$, $(1.2, 1.05)$, $(1.5, 3)$, respectively, go to $(0.7969, 1.9126)$ as t tends to $+\infty$.

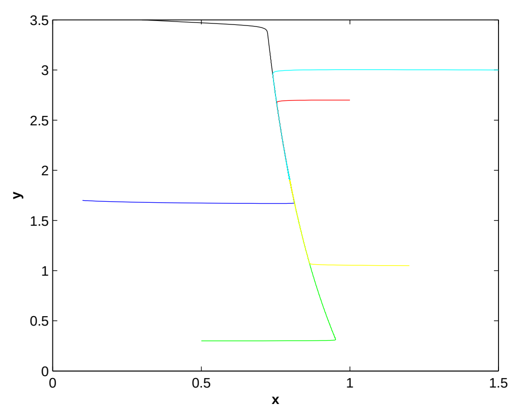

FIGURE 3. Evolutions of six orbits for system (5.3).

Example 5.4. *Let* $a = \frac{1}{1000}$, $b = 1$, $s = \frac{4}{3}$, *and* $d = 1/4$, *then system* (1.3) *becomes*

$$
\begin{aligned}
x'(t) &= x(t)(1 - x(t)) - \frac{\frac{4}{3}x(t)y(t)}{x(t) + y(t) + \frac{1}{1000}},\\
y'(t) &= y(t)\Big(- \frac{1}{4} - ry(t) + \frac{x(t)}{x(t) + y(t) + \frac{1}{1000}}\Big).
\end{aligned} \tag{5.4}
$$

A direct calculation shows that $\frac{1}{4000} = ad < 1 - d = \frac{3}{4}$, $\frac{4}{3} = s > \max\{b, 1 + a, 2a, \frac{bd}{1+d} + \frac{1}{1-d^2}\} = \frac{19}{15}$,

$$
\frac{1}{1000} = a < \frac{1}{s}\frac{s-b}{s+(s-b)d}\big(\frac{(s-b)d}{s+(s-b)d} + s - 1 - sd\big) = \frac{3}{289},
$$

and $\frac{3}{4} = b + \frac{b}{s} - 1 \geq 0$. *This indicates that the conditions in Lemmas 4.1 and 4.2 hold, and the condition* $\frac{4}{3} = s \leq \frac{1}{1-d} = \frac{4}{3}$ *also holds. Hence, there is one unique* r^*, *which can be calculated numerically as* $r^* \approx 0.2250395$, *and then* $u(r^*) \approx 9929481 > 0$. *We can choose* $r = 0.228 > r^*$, *and find* $0.0045 = a_2 > 0.0001 > \frac{1}{4}a_1^2$. *By Theorem 4.4, the positive equilibrium* $(x^*, y^*) \approx (0.0422, 0.1101)$ *is locally asymptotically stable and there is at least one unstable closed orbit and one stable closed orbit in the first quadrant. Note that in Figure 4 (left), the orbit starting from initial points* $(0.0416, 0.109)$ *and* $(0.0413, 0.1081)$ *tends to a stable limit cycle as* t *approaches* $+\infty$; *and in Figure 4 (middle) and 4 (right),* $(x(t), y(t))$ *starting from initial points* $(0.0416, 0.109)$ *tends to a periodic form as* t *approaches* $+\infty$. *Note that the unstable limit cycle in the region enclosed by the stable limit cycle is very close to the positive equilibrium and thus has not been shown in Figure 4 (left).*

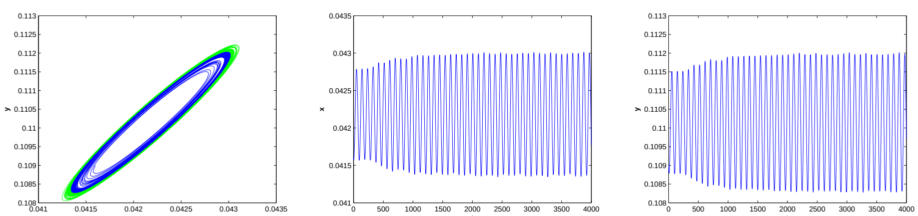

FIGURE 4. Phase diagram (left) for system (5.4) with evolution of $x(t)$ (middle) and $y(t)$ (right) as $t \to +\infty$.

Conclusions and future works. In this article, we considered the stability of the unique positive equilibrium and Hopf bifurcation with respect to parameters in a density-dependent predator-prey system with the Beddington-DeAngelis functional response. We started with the existence and uniqueness of the positive equilibrium, which can not be a saddle, and provided first a weaker sufficient condition by the Lyapunov function method and then a concrete condition only depending on parameters by the Routh-Hurwitz criterion for local stability.

Moreover, we presented several sufficient conditions for global stability of the positive equilibrium by two classical criteria. That is, by Dulac's criterion, we directly obtained (2.1) and (3.1) for global stability. By the divergency criterion, we established (2.1), (2.7) and (3.2) as the sufficient conditions of global attractiveness.

By Grammer's rule and Green's theorem, we derived the divergency integral and further obtained (3.3) and (3.4) as the sufficient conditions of global attractiveness.

Afterwards, we analyzed the Hopf bifurcation with respect to the parameter r by exploring the monotonicity of $a_1(r)$ and successively obtaining a unique r^* such that $a_1(r^*) = 0$. Furthermore, we introduced an auxiliary map $\mu = \frac{(b-s)x^*y^*}{(x^*+y^*+a)^2} + x^* + bry^*$ to restrict the five parameters to a special one-dimensional geometrical structure and analyzed the Hopf bifurcation with respect to all five parameters along with this geometrical restriction.

Note that Hwang verified that for system (1.1), the local stability and global stability of the positive equilibrium coincide in [15]. However, from analysis in Section 4, we find that for system (1.3), the coincidence between local stability and global stability does not hold because of the occurrence of the parameter r. Consequently, the analysis results show that the predator density dependence rate r has a significant effort on the global dynamics of system (1.3).

Finally, some numerical simulations have been performed to illustrate our analytical results.

Notice that from the analysis in Section 4, system (1.3) has limit cycles under certain conditions. However, the problem on the number of limit cycles is not involved at this stage. So, it is interesting to further explore the number of the limit cycles with their location estimate in our future work, as well as the necessary and sufficient conditions for the uniqueness of limit cycles.

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