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Global dynamics of a predator–prey model [☆]

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ABSTRACT

This paper deals with the dynamics of a predator–prey model with Hassell–Varley–Holling functional response. First, we show that the predator coexists with prey if and only if predator's growth ability is greater than its death rate. Second, using a blow-up technique, we prove that the origin equilibrium point is repelling and extinction of both predator and prey populations is impossible. Third, the local and global stability of the positive steady state coincide when the predator interference is large. Finally, for a typical biological case, we show instability of the positive equilibrium implies global stability of the limit cycle. Numerical simulations are carried out for a hypothetical set of parameter values to substantiate our analytical findings.

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1. Introduction

Predator–prey interactions have long been the subject of wild interest in the biomathematical literature. The classical Gause type model for a prey population of density N and a predator population of density P may be written as

$$\begin{cases} \frac{dN}{dt} = B(N) - \varphi(N, P)P, \\ \frac{dP}{dt} = e\varphi(N, P)P - dP, \end{cases} \quad (1.1)$$

where $B(N)$ is the growth rate of the prey population in the absence of predation. The functional response $\varphi(N, P)$ represents the instantaneous rate of prey depletion per predation. The constant e describes the efficiency of the predator in converting consumed prey into predator offspring, while d denotes the food independent predator mortality rate.

Since the famous work of Lotka [21] and Volterra [26], there has been extensively investigation on the dynamics of predator–prey models (see, e.g., [7,10–14,18–20,22,27,29] and references therein). In these works, the functional response, quantifying the amount of prey consumed per predator per unit time, plays an important role in predator–prey dynamics. Functional responses are conventionally modeled as prey-dependent, where the prey consumption rate by an average predator is only a function of prey density alone, that is, $\varphi(N, P) = \varphi(N)$. Different prey-dependent response types (for example, the mass-action approach in Lotka–Volterra model and Holling types I–III) have been used to model the prey–predator interactions and get success in describing some ecological communities. As noted in [5], the derived functional response

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maybe prey-dependent under the assumption of spatially homogeneous distributions of both predators and prey. However, when the spatial structure of one or both of the interacting populations are involved, it would be more plausible to take the predator-dependent functional form, where both predator and prey densities affect the response. Recently, predator-dependent responses, a terminology taken from [2], have received increasing support from theoretical and empirical study in ecology (see, e.g., [2,5,16,17]). In 1969, Hassell and Varley [8] proposed a trophic function

$$\varphi_1(N, P) = \frac{\alpha N}{P\sigma},$$

based on the empirical evidence for an adverse influence of predator abundance on the predator ration. In this functional response, α quantifies the searching efficiency and σ presents the predator interference, which is called the Hassell–Varley constant. This type of response is referred as the Hassell–Varley response. After that, extended study has been done on Hassell–Varley response, see, e.g., [1,5,12,24]. In [5], Cosner et al. gave a unified mechanistic approach for Hassell–Varley response. If predators do not form groups, one can assume $\sigma = 1$, which is so-called ratio-dependence and studied by many authors, see, e.g., [10,11,18,19]. As pointed in [5,12], $\sigma = 1/2$ is suitable for terrestrial predators that form a fixed number of tight groups, $\sigma = 1/3$ for aquatic predators that form a fixed number of tight groups, and for most realistic predator–prey interactions, it can be argued that $\sigma \in [1/2, 1)$ since most predators do not form a fixed number of tight groups. Recently, by manipulating prey density of paper wasps against larvae of the shield beetle in the field, Schenk et al. [23] derived the following functional response

$$\varphi_2(N, P) = \frac{\alpha \left(\frac{N}{P\sigma}\right)^2}{1 + \alpha h \left(\frac{N}{P\sigma}\right)^2},$$

which is the Hassell–Varley functional response, adapted for the Holling type III response [17]. Here h is the handling time. Moreover, it is pointed out in [23] that their study provided the first experimental evidence discriminating between ratio- and prey-dependence in a natural setting with unconfined predators and prey. It is worthy for us to further study the dynamics of a predator–prey system with this specific functional response.

The main objective of this paper is to consider a Gause type predator–prey model with Hassell–Varley–Holling functional response. Suppose the prey population grows logistically in the absence of predation, with the intrinsic growth rate r and carrying capacity K , that is $B(N) = rN(1 - \frac{N}{K})$. Therefore, we focus on the dynamics of the following model

$$\begin{cases} \frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - \frac{\alpha N^2 P}{\alpha h N^2 + P^2 \sigma}, \\ \frac{dP}{dt} = -dP + \frac{e \alpha N^2 P}{\alpha h N^2 + P^2 \sigma}, \end{cases} \quad (1.2)$$

with r, K, d, e, α, h being positive and $\sigma \in (0, 1)$ the Hassell–Varley constant.

For the sake of simplicity it is convenient to scale the model to nondimensional form. Thus, in (1.2), we take

$$\bar{t} = rt, \quad x = N/K, \quad y = 1/(K\sqrt{\alpha h})^{\frac{1}{\sigma}} P,$$

and rescale the parameters via

$$a = \frac{(K\sqrt{\alpha h})^{\frac{1}{\sigma}}}{rhK}, \quad b = \frac{d}{r}, \quad c = \frac{e}{rh}.$$

This leads to (after dropping the bar on t) the following dimensionless system

$$\begin{cases} \frac{dx}{dt} = x(1-x) - \frac{ax^2y}{x^2 + y^{2\sigma}} := F_1(x, y), \\ \frac{dy}{dt} = -by + \frac{cx^2y}{x^2 + y^{2\sigma}} := F_2(x, y), \end{cases} \quad (1.3)$$

where a, b and c are positive constants. Note that when $\sigma = 0$, system (1.3) reduces to a predator–prey model with Holling III functional response while it is a model with ratio-dependent response when $\sigma = 1$. We may say that the prey-dependent and ratio-dependent models are extremes of system (1.3).

In this paper, we shall give an almost complete classification for the asymptotic behavior of the solutions for system (1.3). According to [15] and our numerical simulations, in the ratio-dependent predator–prey models (with $\sigma = 1$), the origin has its own basin of attraction in phase space and deterministic extinction of both predator and prey populations can occur. However, our result shows that $(0, 0)$ must be a repeller when $\sigma < 1$. Moreover, we have a threshold result. The predator coexists with prey permanently if and only if the predator's growth ability is greater than its death rate. When the predator's growth ability is less than or equal to its death rate, the predator will become extinction and the prey can survive from predation. Furthermore, a large degree of predator interference may guarantee that local stability of positive equilibrium implies its global stability. For terrestrial predators that form a fixed number of tight groups, it is often reasonable to assume

that $\sigma = \frac{1}{2}$. In this special case, we show that the system admits a unique stable limit cycle if the positive equilibrium is unstable. The choice of suitable Hassell–Varley constant σ is of crucial importance, calling for both empirical and theoretical studies.

The remainder of this paper is organized as follows. The next section deals with the coexistence and extinction. Local and global stability analysis of equilibria is established in Sections 3 and 4, respectively. Section 5 focuses on the study of limit cycles. Each section ends with some carefully designed numerical simulations. Finally, a brief discussion completes the paper.

2. Coexistence and extinction

In this section, we shall present some preliminary results, including the boundedness of solutions, and try to find conditions to ensure predator–prey coexistence. Observing that $\lim_{(x,y) \rightarrow (0,0)} F_1(x, y) = \lim_{(x,y) \rightarrow (0,0)} F_2(x, y) = 0$, we may define that $F_1(0, 0) = F_2(0, 0) = 0$. Clearly, with this extended definition, both F_1 and F_2 are continuous functions on \mathbb{R}_+^2 . It is easy to see that a solution with non-negative initial value exists and is unique. Moreover, it stays non-negative. Our next task is to show the boundedness of solutions.

Lemma 2.1. *Let $(x(t), y(t))$ be any solution of (1.3) with non-negative initial condition $(x(0), y(0))$, then*

$$\limsup_{t \rightarrow \infty} \left(x(t) + \frac{a}{c}y(t) \right) \leq \frac{(1+b)^2}{4b}.$$

Proof. Let $V(t) = x(t) + ay(t)/c$. Differentiating V , one yields

$$V'(t) = x(t)(1 + b - x(t)) - bV(t) \leq \frac{(1+b)^2}{4} - bV(t).$$

Thus, we have $\limsup_{t \rightarrow \infty} V(t) \leq \frac{(1+b)^2}{4b}$ and system (1.3) is dissipative. \square

Before proving the main result of this section, we need some preliminaries. First, we consider the following ordinary differential equation

$$x'(t) = xh(x), \tag{2.1}$$

where $h \in C(\mathbb{R}_+, \mathbb{R})$ with $h(0) > 0$ and $h'(x) < 0$ for all $x > 0$. In addition, there exists $M > 0$ such that $h(M) < 0$. It then follows from [28, Theorem 5.2.1] that the following statement holds.

Lemma 2.2. *The scalar ordinary differential equation (2.1) has a unique positive equilibrium, which is globally attractive in $\mathbb{R}_+ \setminus \{0\}$.*

Consider an auxiliary function

$$G(z) = \frac{z}{\lambda + z^{2\sigma}}$$

which is defined on $[0, \infty)$ with $\lambda > 0$ and $\sigma \in (0, 1)$, its monotonicity is given by the following lemma.

Lemma 2.3. *If $\sigma \in (0, 1/2]$, then $G'(z) > 0$ for $z \in [0, \infty)$. If $\sigma \in (1/2, 1)$, then $G'(z) > 0$ for $z \in [0, z_*)$ and $G'(z) < 0$ for $z \in (z_*, \infty)$, where $z_* = (\frac{\lambda}{2\sigma-1})^{1/(2\sigma)}$.*

Now, we are in a position to state the main result of this section. It gives conditions which are both necessary and sufficient conditions for predator–prey coexistence or predator extinction.

Theorem 2.1. *Suppose that $(x(t), y(t))$ is the solution of (1.3) through the initial value $(x(0), y(0)) \in \text{int}(\mathbb{R}_+^2)$. Then the following statements are valid:*

- (i) *If $c \leq b$, then $\lim_{t \rightarrow \infty} (x(t), y(t)) = (1, 0)$;*
- (ii) *If $c > b$, then system (1.3) is uniform persistence in the sense that there exists an $\eta > 0$ such that $\liminf_{t \rightarrow \infty} x(t) \geq \eta$ and $\liminf_{t \rightarrow \infty} y(t) \geq \eta$.*

Proof. Since $(x(t), y(t)) \in \mathbb{R}_+^2, \forall t \geq 0$, we have $y'(t) < (-b + c)y \leq 0$. Suppose $y(t) \rightarrow \varepsilon > 0$ as $t \rightarrow \infty$, then $y(t) \geq \varepsilon, \forall t \geq 0$ and there exists some t_0 such that $x(t) \leq 1 + \varepsilon$ when $t \geq t_0$. Therefore,

$$\frac{dy}{dt} = -by + \frac{cx^2y}{x^2 + y^{2\sigma}} \leq y \left[-b + \frac{c(1 + \varepsilon)^2}{(1 + \varepsilon)^2 + \varepsilon^{2\sigma}} \right], \quad \forall t \geq t_0.$$

Hence, we have $y(t) \rightarrow 0$ as $t \rightarrow \infty$, a contradiction. Then, $y(t) \rightarrow 0$ as $t \rightarrow \infty$, and the equation for x is asymptotic to the following one

$$\frac{dx}{dt} = x(1 - x).$$

By the theory of asymptotically autonomous semiflows (see [25]),

$$\lim_{t \rightarrow \infty} x(t) = 1, \quad \forall x(0) > 0.$$

To prove the uniform persistence, we consider two different cases: $1 - 2\sigma \geq 0$ and $1 - 2\sigma < 0$.

In the case where $1 - 2\sigma \geq 0$, it then follows from Lemma 2.1 that there exist $M > 0$ and $t_1 > 0$ such that $(y(t))^{1-2\sigma} \leq M$ for $t \geq t_1$. Hence, Lemma 2.3 implies that

$$\frac{dx}{dt} \geq x(1 - x - aMx), \quad \forall t \geq t_1.$$

According to the comparison principle and Lemma 2.2, there exists an $\eta_1 > 0$ such that $\liminf_{t \rightarrow \infty} x(t) > \eta_1$.

In the case where $1 - 2\sigma < 0$, according to Lemma 2.3, we have

$$\frac{dx}{dt} \geq x\left(1 - x - \mu x^{\frac{1-\sigma}{\sigma}}\right),$$

where $\mu = \frac{a}{2\sigma}(2\sigma - 1)^{\frac{2\sigma-1}{2\sigma}}$. By the comparison principle and Lemma 2.2 again, we can show there exists an $\eta_1 > 0$ such that $\liminf_{t \rightarrow \infty} x(t) > \eta_1$.

Therefore, there exists an $\eta_1 > 0$ such that $\liminf_{t \rightarrow \infty} x(t) > \eta_1$ for both cases. Consequently, for the predator equation, there exists a $t_0 > 0$ such that

$$\frac{dy}{dt} \geq y\left(-b + \frac{c\eta_1^2}{\eta_1^2 + y^{2\sigma}}\right), \quad \forall t > t_0.$$

It then follows from Lemma 2.2 and the comparison principle that there exists an $\eta_2 > 0$ such that $\liminf_{t \rightarrow \infty} y(t) > \eta_2$. The proof of theorem is completed. \square

3. Boundary equilibria

By setting $F_1(x, y) = 0$ and $F_2(x, y) = 0$, we obtain two boundary equilibria $E_0(0, 0)$ and $E_1(1, 0)$ for any positive parameters (a, b, c) and $\sigma \in (0, 1)$. In addition, there exists a positive equilibrium $E_*(x_*, y_*)$ if and only if $c > b$. In this section, we will investigate two boundary steady states.

Since the variational matrix at E_1 is given by

$$J(E_1) = \begin{pmatrix} -1 & -a \\ 0 & -b + c \end{pmatrix},$$

it is clear that the following result holds.

Proposition 3.1. *If $c > b$, then E_1 is a saddle.*

Since the functional response is undefined at the origin, as a sequence, the origin is a so-called “complicated equilibrium”, and the standard local stability analysis method cannot be applied to E_0 . To study the behavior of the model system around E_0 , we follow the blow-up technique developed by Berezovskaya et al. [4]. For this purpose, we first introduce some basic notations.

Consider a system of differential equations

$$\begin{cases} \frac{dx}{dt} = P(x, y) = P_n(x, y) + P^*(x, y), \\ \frac{dy}{dt} = Q(x, y) = Q_n(x, y) + Q^*(x, y), \end{cases} \tag{3.1}$$

where $P_n(x, y)$, $Q_n(x, y)$ are homogeneous polynomials of the n th order, and

$$P^*(x, y) = o(|(x, y)|^n), \quad Q^*(x, y) = o(|(x, y)|^n).$$

Define the corresponding vector field

$$W(x, y) = \frac{\partial}{\partial x} P(x, y) + \frac{\partial}{\partial y} Q(x, y). \tag{3.2}$$

We assume that the origin is an isolated singular point of (3.1), and let $H(x, y) = xQ_n(x, y) - yP_n(x, y)$.

Definition 3.1. A vector field $W(x, y)$ is non-degenerate if it satisfies the following two conditions:

- (C1) polynomials $P_n(x, y), Q_n(x, y)$ have no common factors of the form $Ax + By$, where at least one of the constants A, B is non-zero;
- (C2) polynomials $H(x, y)$ has no factors of the form $(Ax + By)^k$, where $k > 1$.

Making change of variables with $x \rightarrow x, y \rightarrow y^\sigma$, system (1.3) takes the form

$$\begin{cases} \frac{dx}{dt} = x(1-x) - \frac{ax^2y^{\frac{1}{\sigma}}}{x^2+y^2}, \\ \frac{dy}{dt} = -\sigma by + \frac{\sigma cx^2y}{x^2+y^2}. \end{cases}$$

Through time scale change $dt \rightarrow dt/(x^2 + y^2)$, it becomes

$$\begin{cases} \frac{dx}{dt} = x^3 + xy^2 - ax^2y^{\frac{1}{\sigma}} - x^4 - x^2y^2, \\ \frac{dy}{dt} = \sigma(c-b)x^2y - \sigma by^3. \end{cases} \tag{3.3}$$

Let $P_3(x, y) = x^3 + xy^2, Q_3(x, y) = \sigma(c-b)x^2y - \sigma by^3$, then

$$H(x, y) = xQ_3(x, y) - yP_3(x, y) = xy[(\sigma c - \sigma b - 1)x^2 - (\sigma b + 1)y^2].$$

Obviously, the vector field of (3.3) is non-degenerate. After transformations $(x, y) \rightarrow (x, u)$ with

$$u = \frac{y}{x}, \quad x \neq 0,$$

and the time change $dt \rightarrow x^2 dt$, we obtain the following system

$$\begin{cases} \frac{dx}{dt} = xP_3(1, u) + G_1(x, u), \\ \frac{du}{dt} = H_1(u) + G_2(x, u), \end{cases} \tag{3.4}$$

with

$$H_1(u) = H(1, u) = u[(\sigma c - \sigma b - 1) - (\sigma b + 1)u^2],$$

$$G_1(x, u) = P^*(x, u)/x^2, \quad G_2(x, u) = (Q^*(x, ux) - P^*(x, ux)u)/x^3.$$

Thus, if $(c-b)\sigma > 1, H_1(u)$ has two non-negative roots: $u_1 = 0, u_2 = \sqrt{\frac{(c-b)\sigma - 1}{\sigma b + 1}}$ and hence (3.4) has two equilibria $O_1(0, u_1)$ and $O_2(0, u_2)$ on u -axis. If $(c-b)\sigma < 1, H_1(u)$ has only one non-negative roots $u_1 = 0$, and consequently, (3.4) has one equilibrium $O_1(0, u_1)$. Therefore, we have the following lemma.

Lemma 3.1. *If $(c-b)\sigma > 1, O_1(0, u_1)$ is an instable node whereas $O_2(0, u_2)$ is a saddle respectively. If $(c-b)\sigma < 1, O_1$ is a saddle.*

Proof. It is easy to see that $P_3(1, u_1) = 1$ and $P_3(1, u_2) = 1 + u_2^2 > 0$. If $(c-b)\sigma > 1$, then $H'_1(u_1) = (c-b)\sigma - 1 > 0$ and $H'_1(u_2) = -[(c-b)\sigma - 1] < 0$. It then follows from [4, Proposition 3] that O_1 is an instable node and O_2 is a saddle, respectively. If $(c-b)\sigma < 1$, then $H'_1(u_1) = (c-b)\sigma - 1 < 0$, which implies O_1 is a saddle. \square

Similarly, after transformations $(x, y) \rightarrow (x, v)$ with

$$v = \frac{x}{y}, \quad y \neq 0,$$

and the time change $dt \rightarrow y^2 dt$, we obtain the system

$$\begin{cases} \frac{dv}{dt} = H_2(v) + K_1(v, y), \\ \frac{dy}{dt} = yQ_3(v, 1) + K_2(v, y), \end{cases} \tag{3.5}$$

where

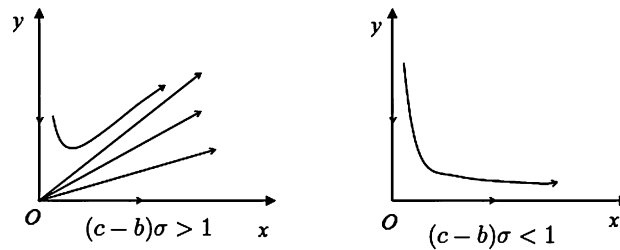


Fig. 1. Structure of the neighborhood of the origin point O in the first quadrant.

$$H_2(v) = -H(v, 1) = -v((c - b)\sigma - 1)v^2 - (\sigma b + 1),$$

$$K_1(v, y) = (P^*(vy, y) - Q^*(vy, y)v)/y^3,$$

$$K_2(v, y) = Q^*(vy, y)/y^2.$$

Thus, system (3.5) has two equilibria $O_1^*(0, 0)$ and $O_2^*(v_2, 0)$ on the v -axis. Point O_1^* is a new equilibrium and it does not exist in the (x, u) -plane. However, point O_2^* corresponds to point O_2 , and we do not need to study it again.

Note that $H'_2(0) = \sigma b + 1 > 0$ and $Q_3(0, 1) = -\sigma b < 0$. It is clear from [4, Proposition 3] that the next conclusion is valid.

Lemma 3.2. O_1^* is a saddle.

According to Lemmas 3.1 and 3.2, it then follows from [4, Proposition 3] that the following result holds for the singular equilibrium $(0, 0)$ of system (1.3).

Theorem 3.1. If $(c - b)\sigma > 1$, then the neighborhood of $(0, 0)$ in the first quadrant has a saddle sector and a repelling node sector. If $(c - b)\sigma < 1$, then the neighborhood of $(0, 0)$ in the first quadrant has only a saddle sector.

Remark 3.1. Theorem 3.1 implies that the origin equilibrium E_0 is repelling, which is illustrated in Fig. 1. If $(c - b)\sigma = 1$, O_i ($i = 1, 2$) are also complicated equilibria and need to use blow-up again. However, Theorem 4.3 in Section 4 indicates the positive equilibrium is global asymptotical stable for this case. Hence, when $\sigma < 1$, the possibility of predator-prey extinction is excluded. This is also consistent with our threshold result (Theorem 2.1).

4. Positive equilibrium

In the previous section, we have observed that instability of the boundary equilibrium point $E_1(1, 0)$ gives support for the existence of a positive interior equilibrium E_* . The parametric condition for the existence of positive equilibrium E_* is $b < c$. Now we try to find conditions under which the positive equilibrium E_* is globally stable. Hence, in this section, we always assume $c > b$.

According to Theorem 2.1, system (1.3) is uniformly persistent and there exists a positive equilibrium $E_*(x_*, y_*)$ satisfying

$$\begin{cases} 1 - x_* - \frac{ax_*y_*}{x_*^2 + y_*^{2\sigma}} = 0, \\ \frac{cx_*^2}{x_*^2 + y_*^{2\sigma}} = b, \end{cases}$$

which is equivalent to

$$\begin{cases} y_* = \frac{c}{ab}x_*(1 - x_*), & x_* > 0, \\ y_* = \left(\sqrt{\frac{c}{b}} - 1\right)^{\frac{1}{\sigma}} x_*^{\frac{1}{\sigma}}. \end{cases} \tag{4.1}$$

We first study the local stability of the positive equilibrium E_* .

4.1. Local stability

The variational matrix of system (1.3) is given by

$$J(x, y) = \begin{pmatrix} 1 - 2x - \frac{2axy}{x^2 + y^{2\sigma}} + \frac{2ax^3y}{(x^2 + y^{2\sigma})^2} & -\frac{ax^2[x^2 + (1 - 2\sigma)y^{2\sigma}]}{(x^2 + y^{2\sigma})^2} \\ \frac{2cxy^{2\sigma+1}}{(x^2 + y^{2\sigma})^2} & -b + \frac{cx^2[x^2 + (1 - 2\sigma)y^{2\sigma}]}{(x^2 + y^{2\sigma})^2} \end{pmatrix}.$$

Hence, the variational matrix of system (1.3) at E_* becomes

$$J(E_*) = \begin{pmatrix} x_* \left[-1 + \frac{a(x_*^{2\sigma} - y_*^{2\sigma})y_*}{(x_*^2 + y_*^{2\sigma})^2} \right] & -\frac{ax_*^2[x_*^2 + (1-2\sigma)y_*^{2\sigma}]}{(x_*^2 + y_*^{2\sigma})^2} \\ \frac{2cx_*y_*^{2\sigma+1}}{(x_*^2 + y_*^{2\sigma})^2} & -\frac{2\sigma cx_*^2y_*^{2\sigma}}{(x_*^2 + y_*^{2\sigma})^2} \end{pmatrix}.$$

A straightforward calculation leads that

$$\begin{aligned} \det(J(E_*)) &= -x_* \left[-1 + \frac{a(x_*^{2\sigma} - y_*^{2\sigma})y_*}{(x_*^2 + y_*^{2\sigma})^2} \right] \cdot \frac{2\sigma cx_*^2y_*^{2\sigma}}{(x_*^2 + y_*^{2\sigma})^2} + \frac{ax_*^2[x_*^2 + (1-2\sigma)y_*^{2\sigma}] \cdot 2cx_*y_*^{2\sigma+1}}{(x_*^2 + y_*^{2\sigma})^4} \\ &= \frac{2\sigma cx_*^3y_*^{2\sigma}}{(x_*^2 + y_*^{2\sigma})^2} + \frac{2acx_*^3y_*^{2\sigma+1}}{(x_*^2 + y_*^{2\sigma})^4} \left[-\sigma(x_*^2 - y_*^{2\sigma}) + x_*^2 + (1-2\sigma)y_*^{2\sigma} \right] \\ &= \frac{2\sigma cx_*^3y_*^{2\sigma}}{(x_*^2 + y_*^{2\sigma})^2} + \frac{2ac(1-\sigma)x_*^3y_*^{2\sigma+1}}{(x_*^2 + y_*^{2\sigma})^4} (x_*^2 + y_*^{2\sigma}) > 0, \end{aligned}$$

and

$$\text{tr}(J(E_*)) = \frac{x_*}{(x_*^2 + y_*^{2\sigma})^2} [a(x_*^2 - y_*^{2\sigma})y_* - 2\sigma cx_*y_*^{2\sigma} - (x_*^2 + y_*^{2\sigma})^2].$$

Notice that $x_*^{2\sigma} + y_*^{2\sigma} = \frac{c}{b}x_*^2$. By the first equation of (4.1), we get

$$\begin{aligned} \text{tr}(J(E_*)) &= \frac{x_*}{(x_*^2 + y_*^{2\sigma})^2} \left(a \left[x_*^2 - \left(\frac{c}{b} - 1 \right) x_*^2 \right] \cdot \frac{c}{ab} x_* (1 - x_*) - \sigma cx_* \left(\frac{c}{b} - 1 \right) x_*^2 - \left(\frac{c}{b} \right)^2 x_*^4 \right) \\ &= \frac{cx_*^4}{b(x_*^2 + y_*^{2\sigma})^2} \left[\left(2 - \frac{c}{b} \right) (1 - x_*) - 2b\sigma \left(\frac{c}{b} - 1 \right) - \left(\frac{c}{b} \right) x_* \right] \\ &= \frac{cx_*^4}{b^2(x_*^2 + y_*^{2\sigma})^2} [2b(1 - x_*) - c - 2b(c - b)\sigma]. \end{aligned}$$

Thus, the stability of E_* is determined by the sign of $\text{tr}(J(E_*))$. In other words, E_* is locally asymptotically stable (or instable) if $\text{tr}(J(E_*)) < 0$ (> 0).

Define

$$\delta := [2b(1 - x_*) - c] / [2b(c - b)],$$

then the following conclusion holds.

Theorem 4.1. *The following statements are valid for system (1.3):*

- (a) E_* is locally asymptotically stable if $\sigma > \delta$.
- (b) E_* is instable if $\sigma < \delta$.

Moreover, we have the following corollary since $2b(1 - x_*) - c < 0$ ($\delta < 0$) whenever $x_* \geq \frac{1}{2}$.

Corollary 4.1. *If $x_* \geq \frac{1}{2}$, then E_* is locally asymptotically stable.*

Next, we study the global stability of E_* .

4.2. Global stability

In this subsection, we consider the global asymptotical stability of the positive equilibrium. The techniques used here are similar to those in [12]. Using the change of variables $(x, y) \rightarrow (u, v)$ with $u = x/y^\sigma$, $v = y^\gamma$, where $\gamma > 0$ will be chosen later, we reduce system (1.3) into the following form

$$\begin{cases} u'(t) = g(u) - \phi_1(u)v^{\gamma_1} - \phi_2(u)v^{\gamma_2} := f_1(u, v), \\ v'(t) = \varphi(u)v := f_2(u, v), \\ u(0) > 0, \quad v(0) > 0, \end{cases} \tag{4.2}$$

where

$$g(u) = \frac{u[(1 + \sigma b) + (1 + \sigma b - \sigma c)u^2]}{1 + u^2},$$

$$\phi_1(u) = u^2,$$

$$\phi_2(u) = \frac{au^2}{1 + u^2},$$

$$\varphi(u) = \gamma \left(-b + \frac{cu^2}{1 + u^2} \right),$$

with $\gamma_1 = \sigma/\gamma$ and $\gamma_2 = (1 - \sigma)/\gamma$.

If $\sigma \in (0, 1/2)$, then we set $\gamma = \sigma$. In this case, $\gamma_1 = 1$ and $\gamma_2 \geq 1$. If $\sigma \in [1/2, 1)$, then we choose $\gamma = 1 - \sigma$. Hence $\gamma_1 = \sigma/(1 - \sigma) \geq 1$ and $\gamma_2 = 1$. Therefore, the vector field (f_1, f_2) is C^1 smooth in \mathbb{R}_+^2 . That is, (4.2) has better smoothness than (1.3). Moreover, the following remark remains valid.

Remark 4.1. The above change of variables does not change the numbers of positive equilibria and periodic orbits (if any) of system (1.3). The positive equilibrium $E_*(x_*, y_*)$ of (1.3) changes into (u_*, v_*) of (4.2), where $u_* = \sqrt{\frac{b}{c-b}}$ and $f_1(u_*, v_*) = 0$. In addition,

$$\varphi(u) = \frac{\gamma(c - b)(u^2 - u_*^2)}{1 + u^2}.$$

Clearly, system (4.2) has a trivial equilibrium $\tilde{E}_0(0, 0)$ and a positive equilibrium $\tilde{E}(u_*, v_*)$. Moreover, system (4.2) admits a boundary equilibrium $\tilde{E}_1(u_0, 0)$ with $u_0 = (1 + \sigma b)/[\sigma(c - b) - 1]$ if and only if $1 + \sigma(b - c) < 0$. In fact, under the change of variables, the boundary equilibrium E_1 in system (1.3) is transformed to $(\infty, 0)$ and E_0 splits into two equilibria \tilde{E}_0 and \tilde{E}_1 . Here we only need to investigate the positive equilibrium $\tilde{E}(u_*, v_*)$, and its stability is given by the following lemma.

Lemma 4.1. *The following statements are true for system (4.2):*

- (i) *If $\sigma < \delta$, \tilde{E}_* is an instable focus or node;*
- (ii) *If $\delta < \sigma$, \tilde{E}_* is locally asymptotically stable.*

Proof. For the sake of simplicity, we denote $A = 1 + \sigma b$ and $B = 1 + \sigma b - \sigma c$. Note that the variational matrix of system (4.2) at \tilde{E}_* is given by

$$J(\tilde{E}_*) = \begin{pmatrix} \frac{\partial f_1}{\partial u}(\tilde{E}_*) & \frac{\partial f_1}{\partial v}(\tilde{E}_*) \\ \frac{2c\gamma u_* v_*}{(1 + u_*^2)^2} & 0 \end{pmatrix}.$$

Since $\frac{\partial f_1}{\partial v}(\tilde{E}_*) < 0$, $\det(J(\tilde{E}_*)) > 0$ and the stability of \tilde{E}_* is determined by the sign of the trace of $J(\tilde{E}_*)$.

Our next task is to show $\text{tr}(J(\tilde{E}_*)) = \text{tr}(J(E_*))$. Note that

$$\frac{A + Bu_*^2}{u_*^2 + 1} - u_* v_*^{\gamma_1} - \frac{au_*}{u_*^2 + 1} v_*^{\gamma_2} = 0.$$

Hence one has

$$\begin{aligned} \text{tr}(J(\tilde{E}_*)) &= g'(u_*) - \phi_1'(u_*)v_*^{\gamma_1} - \phi_2'(u_*)v_*^{\gamma_2} \\ &= B + \frac{(B - A)(u_*^2 - 1)}{(u_*^2 + 1)^2} - 2u_* v_*^{\gamma_1} - \frac{2au_*}{(u_*^2 + 1)^2} v_*^{\gamma_2} \\ &= B + \frac{(B - A)(u_*^2 - 1)}{(u_*^2 + 1)^2} - u_* v_*^{\gamma_1} - \frac{2au_* - au_*(1 + u_*^2)}{(u_*^2 + 1)^2} v_*^{\gamma_2} - \frac{(A + Bu_*^2)(1 + u_*^2)}{(u_*^2 + 1)^2} \\ &= -u_* v_*^{\gamma_1} + \frac{2(A - B)u_*^2}{(u_*^2 + 1)^2} - \frac{au_*(1 - u_*^2)}{(u_*^2 + 1)^2} v_*^{\gamma_2} \\ &= -x_* + \frac{a(x_*^2 - y_*^{2\sigma})y_*}{(x_*^2 + y_*^{2\sigma})^2} - \frac{2\sigma c x_*^2 y_*^{2\sigma}}{(x_*^2 + y_*^{2\sigma})^2} = \text{tr}(J(E_*)). \end{aligned}$$

Thus the local stability of E_* and \tilde{E}_* are the same. By Theorem 4.1, \tilde{E}_* is an instable focus or node if $\sigma < \delta$ and locally asymptotically stable if $\sigma > \delta$. \square

The above lemma tells us that \tilde{E}_* is locally asymptotically stable if $\sigma > \delta$. An interesting problem naturally arise: whether E_* is also globally asymptotically stable? We will first answer this problem partially under the most biologically interesting case of $\sigma \geq 1/2$.

Let us consider the following function

$$q(v, \iota) = \begin{cases} \frac{v^\iota - v_*^\iota}{v - v_*}, & \text{if } v \neq v_*, \\ \iota v_*^{\iota-1}, & \text{if } v = v_*, \end{cases} \tag{4.3}$$

with $\iota > 0$. Clearly, $q(\cdot, \iota)$ is a positive C^1 function on $[0, \infty)$ and $q(v, 1) = 1$ for $v \geq 0$. Additionally, $\frac{\partial q(v, \iota)}{\partial v} > 0$ (< 0) for $v > 0$ if $\iota > 1$ (< 1). Since we consider the case where $\sigma \geq \frac{1}{2}$, we have $\gamma_1 = \frac{\sigma}{1-\sigma} \geq \gamma_2 = 1$. Denote $q(v) = q(v, \gamma_1)$, then $q'(v) \geq 0$ for $v > 0$.

Lemma 4.2. Assume that (u, v) is a solution of system (4.2) with $u(0) > 0, v(0) > 0$, then

$$v(t) - v_* = \frac{-\sigma c + auv - (\theta_1 v^{\gamma_1} + av)\kappa(u)}{\gamma c u_* [q(v) + \theta_2]} \cdot \frac{v'(t)}{v(t)} - \frac{1}{u_* [q(v) + \theta_2]} \cdot \frac{u'(t)}{u(t)},$$

where $\kappa(u) = \frac{1+u^2}{u+u_*}, \theta_1 = \frac{c}{c-b}$ and $\theta_2 = \frac{a(c-b)}{c}$.

Proof. It is easy to see that

$$\frac{v'(t)}{v(t)} = \frac{\gamma(c-b)(u^2 - u_*^2)}{1 + u^2}$$

and

$$\frac{u'(t)}{u(t)} = \left(\frac{A + Bu^2}{1 + u^2} - \frac{A + Bu_*^2}{1 + u_*^2} \right) - (uv^{\gamma_1} - u_* v_*^{\gamma_1}) - \left(\frac{auv}{1 + u^2} - \frac{au_* v_*}{1 + u_*^2} \right),$$

where $A = 1 + \sigma b, B = 1 + \sigma b - \sigma c$. A direct computation produces that

$$\frac{A + Bu^2}{1 + u^2} - \frac{A + Bu_*^2}{1 + u_*^2} = \frac{(B - A)(u^2 - u_*^2)}{(1 + u^2)(1 + u_*^2)} = -\frac{\sigma}{\gamma} \cdot \frac{v'(t)}{v(t)}.$$

Moreover, we have

$$\begin{aligned} uv^{\gamma_1} - u_* v_*^{\gamma_1} &= (u - u_*)v^{\gamma_1} + u_*(v^{\gamma_1} - v_*^{\gamma_1}) \\ &= \frac{(1 + u^2)v^{\gamma_1}}{\gamma(c-b)(u + u_*)} \cdot \frac{v'(t)}{v(t)} + u_* q(v)(v - v_*), \end{aligned} \tag{4.4}$$

and

$$\begin{aligned} \frac{auv}{1 + u^2} - \frac{au_* v_*}{1 + u_*^2} &= \frac{a[u(u_*^2 - u^2)v + (1 + u^2)(uv - u_* v_*)]}{(1 + u^2)(1 + u_*^2)} \\ &= \frac{a(u - u_*)v}{1 + u_*^2} + \frac{au_*(v - v_*)}{1 + u_*^2} - \frac{au(u^2 - u_*^2)v}{(1 + u^2)(1 + u_*^2)} \\ &= \frac{a(1 + u^2)v}{\gamma c(u + u_*)} \cdot \frac{v'(t)}{v(t)} - \frac{auv}{\gamma c} \cdot \frac{v'(t)}{v(t)} + \frac{au_*(c-b)}{c}(v - v_*). \end{aligned}$$

Therefore, it follows that

$$\begin{aligned} \frac{u'(t)}{u(t)} &= \frac{v'(t)}{v(t)} \left[-\frac{\sigma}{\gamma} + \frac{auv}{\gamma c} - \frac{(1 + u^2)v^{\gamma_1}}{\gamma(c-b)(u + u_*)} - \frac{a(1 + u^2)v}{\gamma c(u + u_*)} \right] - u_*(v - v_*) \left[q(v) + \frac{a(c-b)}{c} \right] \\ &= \frac{v'(t)}{v(t)} \cdot \frac{-\sigma c + auv - (\theta_1 v^{\gamma_1} + av)\kappa(u)}{\gamma c} - u_*(v - v_*) [q(v) + \theta_2], \end{aligned}$$

where $\kappa(u) = \frac{1+u^2}{u+u_*}, \theta_1 = \frac{c}{c-b}$ and $\theta_2 = \frac{a(c-b)}{c}$. Hence, we obtain

$$v(t) - v_* = \frac{-\sigma c + auv - (\theta_1 v^{\gamma_1} + av)\kappa(u)}{\gamma c u_* [q(v) + \theta_2]} \cdot \frac{v'(t)}{v(t)} - \frac{1}{u_* [q(v) + \theta_2]} \cdot \frac{u'(t)}{u(t)}.$$

This completes the proof. \square

Lemma 4.3. Let $\Gamma(t) = (u(t), v(t))$ be any positive T -periodic solution of system (4.2), then

$$\int_0^T \text{tr}(J(\Gamma(t))) \, dt = \int_0^T \left[\left(B - \frac{A+B}{1+u^2} \right) - 2 \left(u - \frac{u}{1+u^2} \right) v^{\gamma_1} \right] \, dt.$$

Proof. Assume that $\Gamma(t) = (u(t), v(t))$ is a T -periodic solution of system (4.2), one has

$$\begin{aligned} \text{tr}(J(\Gamma(t))) &= g'(u) - \phi_1'(u)v^{\gamma_1} - \phi_2'(u)v^{\gamma_2} + \frac{v'(t)}{v(t)} \\ &= \frac{v'(t)}{v(t)} + g'(u) - \phi_1'(u)v^{\gamma_1} - \frac{\phi_2'(u)}{\phi_2(u)} [g(u) - \phi_1(u)v^{\gamma_1} - u'(t)] \\ &= \frac{v'(t)}{v(t)} + \frac{\phi_2'(u)}{\phi_2(u)} u'(t) + \phi_2(u) \left[\left(\frac{g(u)}{\phi_2(u)} \right)' - \left(\frac{\phi_1(u)}{\phi_2(u)} \right)' v^{\gamma_1} \right]. \end{aligned}$$

Since

$$\int_0^T \frac{v'(t)}{v(t)} \, dt = 0 \quad \text{and} \quad \int_0^T \frac{\phi_2'(u(t))}{\phi_2(u(t))} u'(t) \, dt = 0,$$

we get

$$\begin{aligned} \int_0^T \text{tr}(J(\Gamma(t))) \, dt &= \int_0^T \phi_2(u) \left[\left(\frac{g(u)}{\phi_2(u)} \right)' - \left(\frac{\phi_1(u)}{\phi_2(u)} \right)' v^{\gamma_1} \right] \, dt \\ &= \int_0^T \frac{au^2}{1+u^2} \left(\frac{Bu^2-A}{au^2} - \frac{2u}{a} v^{\gamma_1} \right) \, dt \\ &= \int_0^T \left(\frac{Bu^2-A}{1+u^2} - \frac{2u^3}{1+u^2} v^{\gamma_1} \right) \, dt \\ &= \int_0^T \left[\left(B - \frac{A+B}{1+u^2} \right) - 2 \left(u - \frac{u}{1+u^2} \right) v^{\gamma_1} \right] \, dt. \end{aligned}$$

Hence, the lemma holds. \square

Lemma 4.4. Let $\Gamma(t) = (u(t), v(t))$ be any T -periodic solution of system (4.2), then

$$\int_0^T \text{tr}(J(\Gamma(t))) \, dt = \text{tr}(J(\tilde{E}_*))T - \iint_{\Omega} \Phi(u, v) \, du \, dv,$$

where Ω is the bounded region enclosed by Γ and

$$\Phi(u, v) = \frac{2bcv^{\gamma_1}\theta_2\kappa'(u) + 2abv(c-b)q(v)(1-\kappa'(u))}{\gamma c^2v(c-b)[q(v) + \theta_2]} + \frac{2b\theta_2q'(v)}{uc[q(v) + \theta_2]^2}.$$

Proof. By Lemma 4.3, one has

$$\begin{aligned} &\int_0^T (\text{tr}(J(\Gamma(t))) - \text{tr}(J(\tilde{E}_*))) \, dt \\ &= - \int_0^T \left(\frac{A+B}{1+u^2} - \frac{A+B}{1+u_*^2} \right) \, dt - 2 \int_0^T (uv^{\gamma_1} - u_*v_*^{\gamma_1}) \, dt + 2 \int_0^T \left(\frac{uv^{\gamma_1}}{1+u^2} - \frac{u_*v_*^{\gamma_1}}{1+u_*^2} \right) \, dt. \end{aligned}$$

A straightforward calculation leads to

$$\int_0^T \left(\frac{A+B}{1+u^2} - \frac{A+B}{1+u_*^2} \right) dt = \int_0^T \frac{(A+B)(u^2 - u_*^2)}{(1+u_*^2)(1+u^2)} dt = -\frac{A+B}{\gamma c} \int_0^T \frac{v'(t)}{v(t)} dt = 0.$$

On the other hand,

$$\begin{aligned} & 2 \int_0^T \left(\frac{uv^{\gamma_1}}{1+u^2} - \frac{u_*v_*^{\gamma_1}}{1+u_*^2} \right) dt - 2 \int_0^T (uv^{\gamma_1} - u_*v_*^{\gamma_1}) dt \\ &= 2 \int_0^T \frac{-u(u^2 - u_*^2)v^{\gamma_1} + (1+u^2)(uv^{\gamma_1} - u_*v_*^{\gamma_1})}{(1+u_*^2)(1+u^2)} dt - 2 \int_0^T (uv^{\gamma_1} - u_*v_*^{\gamma_1}) dt \\ &= -2 \int_0^T \frac{u(u^2 - u_*^2)v^{\gamma_1}}{(1+u^2)(1+u_*^2)} dt - 2 \int_0^T \frac{u_*^2}{1+u_*^2} (uv^{\gamma_1} - u_*v_*^{\gamma_1}) dt \\ &= -2 \int_0^T \frac{uv^{\gamma_1}}{\gamma c} \cdot \frac{v'(t)}{v(t)} dt - \frac{2b}{c} \int_0^T (uv^{\gamma_1} - u_*v_*^{\gamma_1}) dt. \end{aligned}$$

Using (4.4) we have

$$\int_0^T (uv^{\gamma_1} - u_*v_*^{\gamma_1}) dt = \int_0^T \frac{(1+u^2)v^{\gamma_1}}{\gamma(c-b)(u+u_*)} \cdot \frac{v'(t)}{v(t)} dt + \int_0^T u_*q(v)(v - v_*) dt.$$

It then follows from Lemma 4.3 that

$$\begin{aligned} & \int_0^T (\text{tr}(J(\Gamma(t))) - \text{tr}(J(\tilde{E}_*))) dt \\ &= - \int_0^T \left\{ \frac{2bv^{\gamma_1}\kappa(u)}{\gamma c(c-b)} + \frac{2uv^{\gamma_1}}{\gamma c} + \frac{2bq(v)[- \sigma c + auv - (\theta_1 v^{\gamma_1} + av)\kappa(u)]}{\gamma c^2[q(v) + \theta_2]} \right\} \cdot \frac{v'(t)}{v(t)} dt + \int_0^T \frac{2bq(v)}{c[q(v) + \theta_2]} \cdot \frac{u'(t)}{u(t)} dt \\ &= \oint_{\Gamma} M(u, v) du + N(u, v) dv, \end{aligned}$$

where

$$\begin{aligned} M(u, v) &= \frac{2bq(v)}{uc[q(v) + \theta_2]}, \quad \text{and} \\ N(u, v) &= -\frac{1}{v} \left\{ \frac{2bv^{\gamma_1}\kappa(u)}{\gamma c(c-b)} + \frac{2uv^{\gamma_1}}{\gamma c} + \frac{2bq(v)[- \sigma c + auv - (\theta_1 v^{\gamma_1} + av)\kappa(u)]}{\gamma c^2[q(v) + \theta_2]} \right\}. \end{aligned}$$

The Green's Theorem implies that

$$\begin{aligned} \int_0^T (\text{tr}(J(\Gamma(t))) - \text{tr}(\tilde{E}_*)) dt &= \iint_{\Omega} \left(\frac{\partial N}{\partial u} - \frac{\partial M}{\partial v} \right) du dv \\ &= - \iint_{\Omega} \left\{ \frac{2bcv^{\gamma_1}\theta_2\kappa'(u) + 2abv(c-b)q(v)(1 - \kappa'(u))}{\gamma c^2 v(c-b)[q(v) + \theta_2]} + \frac{2b\theta_2q'(v)}{uc[q(v) + \theta_2]^2} \right\} du dv \\ &= - \iint_{\Omega} \Phi(u, v) du dv, \end{aligned}$$

where Ω is the bounded region enclosed by Γ . This proves the lemma. \square

Lemma 4.5. *Let $\sigma \geq \frac{1}{2}$. If \tilde{E}_* is locally asymptotically stable, then system (4.2) has no nontrivial periodic orbit in $\text{int}(\mathbb{R}_+^2)$.*

Proof. For any $u \geq 0$ and $v \geq 0$, we have $q'(v) \geq 0$ and $\kappa'(u) = \frac{u^2 + 2uu_* - 1}{(u + u_*)^2} < 1$. Hence $\Phi(u, v) > 0$ for $u > 0$ and $v > 0$. Assume, by contradiction, there exists a nontrivial periodic orbit of (4.2) with period $T > 0$. It then follows from Lemma 4.4 that $\int_0^T \text{tr}(J(\Gamma(t))) dt < 0$, a contradiction with the fact that \tilde{E}_* is locally asymptotically stable. The proof is completed. \square

By Remark 4.1, we obtain the following theorem for system (1.3).

Theorem 4.2. *Let $\sigma \geq \frac{1}{2}$, then local and global stability of E_* coincide for system (1.3).*

Note that Theorem 4.2 is not applicable for $\sigma < \frac{1}{2}$ since we cannot determine the sign of $\Phi(u, v)$ for $\frac{\partial q(v, \gamma_1)}{\partial v} < 0$ in this case. However, we can show that it is globally stable when $\sigma \geq 1/(c - b)$ by Lyapunov function and LaSalle’s invariance principle.

Lemma 4.6. *Let $\sigma \in [\frac{1}{c-b}, 1)$, then \tilde{E}_* is globally asymptotically stable for system (4.2) in $\text{int}(\mathbb{R}_+^2)$.*

Proof. Note that $\delta = \frac{2b(1-x_*)-c}{2b(c-b)} < \frac{1}{c-b}$. Hence \tilde{E}_* is locally asymptotically stable if $\sigma \in [\frac{1}{c-b}, 1)$. Consider the following Lyapunov function

$$V(u, v) = v^{-\frac{g(u_*)}{\phi_2(u_*)}} \exp\left(\frac{\phi_1(u_*)}{\phi_2(u_*)} \cdot \frac{v^{\gamma_1}}{\gamma_1} + \frac{v^{\gamma_2}}{\gamma_2} + \int_{u_*}^u \frac{\varphi(\tau)}{\phi_2(\tau)} d\tau\right)$$

for $(u, v) \in \text{int}(\mathbb{R}_+^2)$. The derivative of V along the solution of system (4.2) satisfies

$$\begin{aligned} \frac{\dot{V}(u, v)}{V(u, v)} &= -\frac{g(u_*)}{\phi_2(u_*)} \varphi(u) + \frac{\phi_1(u_*)}{\phi_2(u_*)} \varphi(u) v^{\gamma_1} + \varphi(u) v^{\gamma_2} + \frac{\varphi(u)}{\phi_2(u)} [g(u) - \phi_1(u) v^{\gamma_1} - \phi_2(u) v^{\gamma_2}] \\ &= \left(\frac{g(u)}{\phi_2(u)} - \frac{g(u_*)}{\phi_2(u_*)}\right) \varphi(u) - \left(\frac{\phi_1(u)}{\phi_2(u)} - \frac{\phi_1(u_*)}{\phi_2(u_*)}\right) \varphi(u) v^{\gamma_1} \\ &= \frac{1}{a} \varphi(u) (u - u_*) \left[(1 + \sigma(b - c)) - \frac{1 + \sigma b}{uu_*} - (u + u_*) v^{\gamma_1} \right]. \end{aligned}$$

Clearly, $(c - b)\sigma \geq 1$ implies that $\dot{V}(u, v) \leq 0$ for $(u, v) \in \text{int}(\mathbb{R}_+^2)$. Therefore, the lemma follows from LaSalle’s invariance principle. \square

For the positive equilibrium E_* of system (1.3), we have the following result.

Theorem 4.3. *Let $\sigma \in [\frac{1}{c-b}, 1)$, then E_* is globally asymptotically stable for system (1.3) in $\text{int}(\mathbb{R}_+^2)$.*

Fig. 2 shows that when $\sigma \geq \frac{1}{2}$ or $\sigma \geq \frac{1}{c-b}$, local stability of positive equilibrium implies its global stability.

5. Limit cycles

If $\sigma < \delta$ and $c > b$, then the positive equilibrium E_* is instable and the system is uniformly persistent. According to the Poincaré–Bendixson Theorem, there will be at least one limit cycle in the positive quadrant of the xy -plane. Now we can state the following lemma.

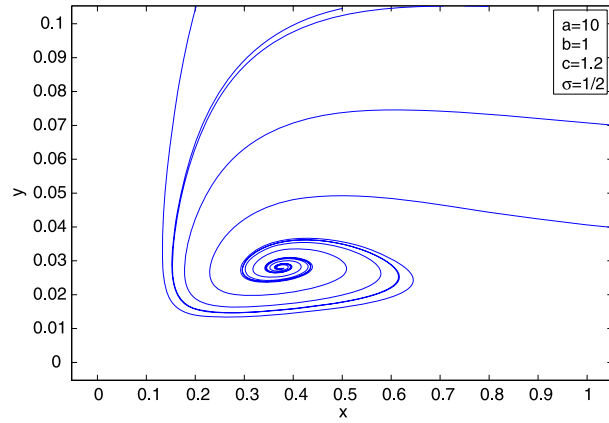
Lemma 5.1. *If $c > b$ and $\sigma < \delta$, there is at least one limit cycle in system (1.3).*

The above result establishes the existence of a periodic solution. Our next task is to find the conditions for uniqueness of the limit cycle. To do this, we will study a special case where terrestrial predator form a fixed number of tight group, that is $\sigma = \frac{1}{2}$. In this case, one has $\gamma_1 = \gamma_2 = 1$, and system (4.2) becomes

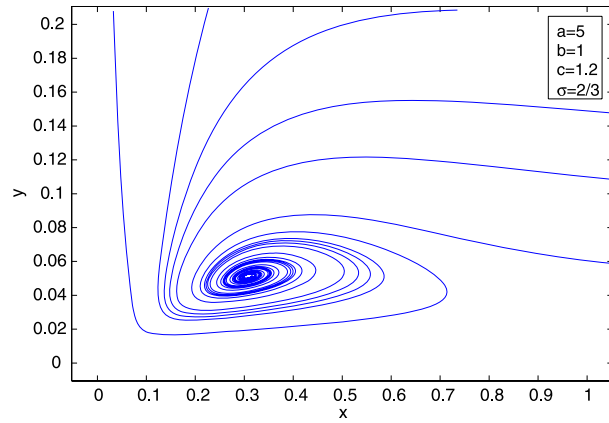
$$\begin{cases} u'(t) = \phi(u)[h(u) - v], \\ v'(t) = \varphi(u)v, \\ u(0) > 0, \quad v(0) > 0 \end{cases} \tag{5.1}$$

with

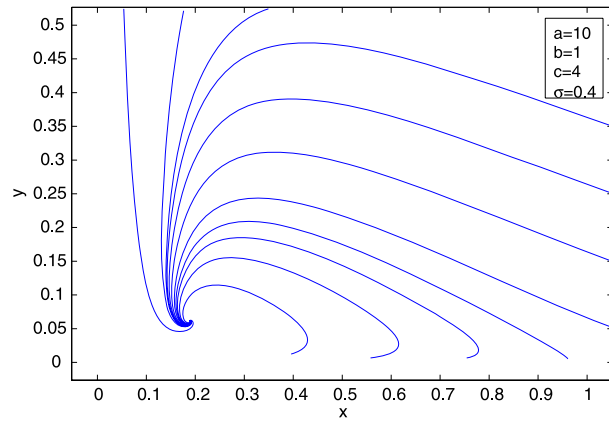
$$\phi(u) = u^2 + \frac{au^2}{1 + u^2} \quad \text{and} \quad h(u) = g(u)/\phi(u).$$



(a) $\sigma = \frac{1}{2}$



(b) $\sigma = \frac{2}{3}$



(c) $\sigma = 0.4 > \frac{1}{c-b} = \frac{1}{3}$

Fig. 2. Local and global stability of E_* coincide if $\sigma \geq \frac{1}{2}$ or $\sigma \geq \frac{1}{c-b}$.

By Theorems 4.2 and 4.3, the limit cycle exists only when positive equilibrium is not globally stable, that is, $B = 1 + \sigma b - \sigma c > 0$ and $h'(u_*) > 0$. Note that system (5.1) is similar to those discussed in Ref. [14], and the assumptions (A1)–(A5) in [14, Theorem 2.2] are satisfied except the latter part of assumption (A3), i.e., there exists $K > 0$ such that $g'(K) < 0$ and $(x - K)g(x) < 0$ for $x \in (0, \infty) \setminus \{K\}$. Hence, we cannot directly use [14, Theorem 2.2] to prove the uniqueness of limit cycle. In this subsection, we follow the proof idea developed in [6,14] to overcome it. For this purpose we need to prove the following lemma first.

Lemma 5.2. *If $c > b$ and $h'(u_*) > 0$, then*

$$\frac{d}{du} \left(\frac{\phi(u)h'(u)}{\varphi(u)h(u)} \right) < 0 \quad (5.2)$$

for $u \in (0, \infty) \setminus \{u_*\}$.

Proof. It is easy to obtain

$$h'(u) = \left[\frac{A + Bu^2}{u^3 + (a+1)u} \right]' = \frac{-Bu^4 + Cu^2 - D}{u^2(u^2 + a + 1)^2},$$

where

$$C = B(a+1) - 3A = (a-2)(1+\sigma b) - \sigma c(a+1),$$

and

$$D = (1 + \sigma b)(a + 1).$$

Denote $\beta(u) = -Bu^4 + Cu^2 - D$, then $\beta(u_*) = h'(u_*)(u_*^2(u_*^2 + a + 1)^2) > 0$. Moreover,

$$\phi(u)h'(u) = \frac{\beta(u)}{(u^2 + 1)(u^2 + a + 1)}$$

and

$$\varphi(u)h(u) = \frac{\gamma(c-b)(u^2 - u_*^2)(A + Bu^2)}{u(1+u^2)[u^2 + (a+1)]}.$$

Hence, we have

$$\frac{\phi(u)h'(u)}{\varphi(u)h(u)} = \frac{u\beta(u)}{\gamma(c-b)(u^2 - u_*^2)(A + Bu^2)}.$$

Note that

$$u\beta(u) = u\beta(u_*) + u[\beta(u) - \beta(u_*)] = u\beta(u_*) - u(u^2 - u_*^2)[B(u^2 + u_*^2) - C].$$

Consequently, we obtain

$$\begin{aligned} \frac{\phi(u)h'(u)}{\varphi(u)h(u)} &= \frac{1}{\gamma(c-b)} \left\{ \frac{\beta(u_*)u}{(u^2 - u_*^2)(A + Bu^2)} - \frac{u[B(u^2 + u_*^2) - C]}{A + Bu^2} \right\} \\ &:= \frac{1}{\gamma(c-b)} [\beta(u_*)P_1(u) - P_2(u)]. \end{aligned}$$

Since

$$\begin{aligned} P_1'(u) &= \frac{(u^2 - u_*^2)(A + Bu^2) - 2u^2[A + Bu^2 - B(u^2 - u_*^2)]}{[(u^2 - u_*^2)(A + Bu^2)]^2} \\ &= \frac{-3Bu^4 + Buu^2u_*^2 - Au^2 - Au_*^2}{[(u^2 - u_*^2)(A + Bu^2)]^2} \\ &= \frac{-\frac{11}{4}Bu^4 - B(\frac{u^2}{2} - u_*)^2 - Au^2 - \sigma cu_*^2}{[(u^2 - u_*^2)(A + Bu^2)]^2} < 0, \end{aligned}$$

and note that $\beta(u_*) > 0$ implies $C > Bu_*^2 + D/u_*^2$,

$$P_2'(u) = \frac{B^2u^4 + B(3A + C - Bu_*^2)u^2 + A(C - Bu_*^2)}{(A + Bu^2)^2} > 0,$$

we proved $\frac{d}{du} \left(\frac{\phi(u)h'(u)}{\varphi(u)h(u)} \right) < 0$ for $u \in (0, \infty) \setminus \{u_*\}$. \square

By replacing $(0, K) \setminus \{u_*\}$ with $(0, \infty) \setminus \{u_*\}$, we can see that the proof of [14, Theorem 2.2] still holds. It then follows from [14, Theorem 2.2] and Lemma 5.2 that system (1.3) admits a unique limit cycle provided that the positive equilibrium is instable.

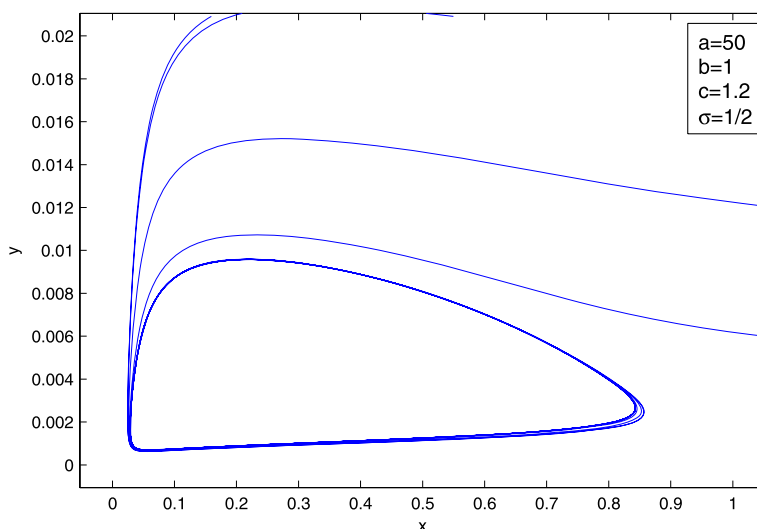


Fig. 3. When $\sigma = \frac{1}{2}$, the limit cycle is globally stable in $int(\mathbb{R}_+^2)$ provided that the positive equilibrium is instable.

Theorem 5.1. *If $\delta > \sigma = 1/2$, then there exists a unique stable limit cycle.*

Remark 5.1. By the threshold result (Theorem 2.1), combined with the Poincaré–Bendixson Theorem, we can see that this unique limit cycle is globally stable in $int(\mathbb{R}_+^2)$.

Fig. 3 numerically shows that when $\sigma = \frac{1}{2}$, instability of the positive equilibrium implies the global stability of the limit cycle.

6. Discussion

In some predator–prey models, it is a classical assumption that the consumption rate of a single predator (so-called functional response) is prey-dependent, that is, predators encounter prey at random and that the response function depends solely on prey abundance. However, it is clear that predator abundance can influence the functional response and hence, it is reasonable to assume that the response function depends not only on prey abundance but also on predator abundance. One special form of predator-dependent response is ratio-dependent, i.e., the functional response depends on the ratio of prey to predator abundance. Quite a good number of works have already performed on the ratio-dependent predator–prey models, see e.g., [3,4] and references therein. However, other kinds of predator-dependent functional responses have also been approved by field and laboratory observations (see [8,17,23]).

In this paper, we have considered a nonlinear predator–prey system with Hassell–Varley–Holling functional response. Actually, prey-dependent and ratio-dependent models are extremes or limiting cases for this functional response: when $\sigma = 1$, our system is a ratio-dependent predator–prey model while $\sigma = 0$, it is a prey-dependent one. First, we show that the relationship between predator’s growth ability (c) and death rate (b) plays a major role in the long-term behavior of the system. Using the similar idea as in [9], we can define the predator demographic reproduction number $\mathcal{R}_p = \frac{c}{b}$. This number has clear ecological interpretation. Assume that the prey are at carrying capacity, then the maximum predator birth rate is c , with an expected life span of $\frac{1}{b}$. Subsequently, the product of these two terms gives the averaged number of offspring a predator individual has in its lifetime. Furthermore, the threshold result indicates that if the predator demographic reproduction number $\mathcal{R}_p \leq 1$ ($b \geq c$), then the predator species will become extinct and the prey species will go to the carrying capacity, surviving from predation. If $\mathcal{R}_p > 1$ ($c > b$), then the predator and prey will coexist in the environments.

Second, we studied the local behavior of two x -axis equilibria: $E_0(0, 0)$ and $E_1(1, 0)$. Since the origin E_0 is a complicated equilibrium, it is impossible to determine its stability by conventional procedure. To overcome this situation, we employed the blow-up method introduced in [4]. Our analysis shows that the origin is repelling and both the populations cannot become extinction. Because extinction of both populations can be explained as a simple deterministic process ([15] and Fig. 4) in the ratio-dependent models, the dynamics of our model system is significantly different with its limiting case ($\sigma = 1$).

Next, we have considered the local and global stability of interior equilibrium E_* . For a large degree of predator interference ($\sigma \geq \min\{\frac{1}{c-b}, \frac{1}{2}\}$) which is applicable for most biological realistic cases, local stability of the positive equilibrium E_*

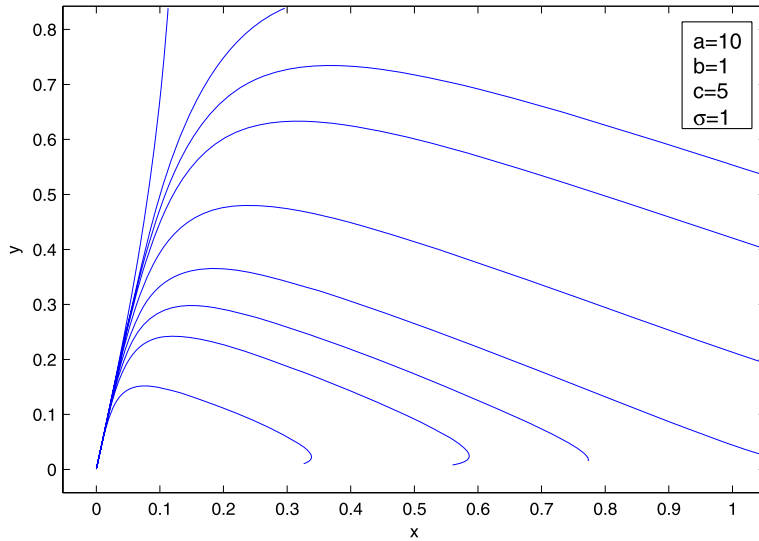


Fig. 4. When $\sigma = 1$, both prey and predator populations may go to extinction.

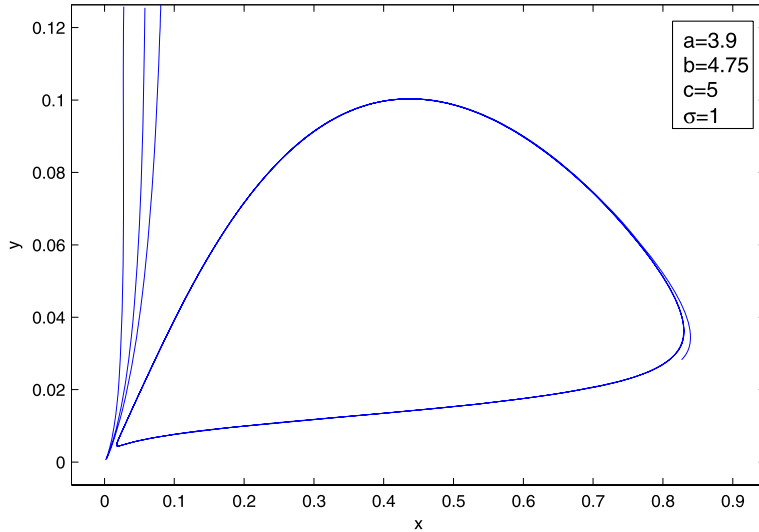


Fig. 5. When $\sigma = 1$, a stable limit cycle can coexist with an “attracting” origin equilibrium.

implies its global stability. In this case, both prey and predator populations coexist at their steady value E_* . It is crucial to accurately determine the predator interference (Hassell–Varley constant σ) in field work.

On the other hand, instability of the interior equilibrium E_* implies the existence of limit cycles. Since when terrestrial predator is forming a fixed number of tight groups, it is biologically reasonable to assume $\sigma = \frac{1}{2}$. Mathematically, we formally proved that when $\sigma = \frac{1}{2}$, the limit cycle is globally stable provided that the interior equilibrium E_* is unstable. In this scenario, we can conclude that both prey and predator populations coexist and oscillates, generating a balanced dynamics. As mentioned in Schenk et al. [23], the functional response in this paper is neither prey-dependent nor ratio-dependent. However, for the ratio-dependence functional response ($\sigma = 1$), Ref. [15] and our numerical simulation (Fig. 5) show that the stable limit cycle can coexist with the partially attractive origin equilibrium point. Hence, there are significantly different dynamics between $\sigma = \frac{1}{2}$ and $\sigma = 1$.

Finally, we remark that there are quite a few space to improve and generalize our work. Although in Figs. 6 and 7, we have shown numerically that the limit cycle is still unique when $\sigma \neq \frac{1}{2}$ and E_* is unstable, and E_* is globally stable when $\delta < \sigma < \min\{\frac{1}{2}, \frac{1}{c-b}\}$, it is mathematically interesting to rigorously validate that these statements hold or not. Biologically, it is well known that the seasonal fluctuation has impact on the dynamics of both predator and prey populations. It would also be interesting to incorporate seasonal effects into the current model. We leave these problems for further investigation.

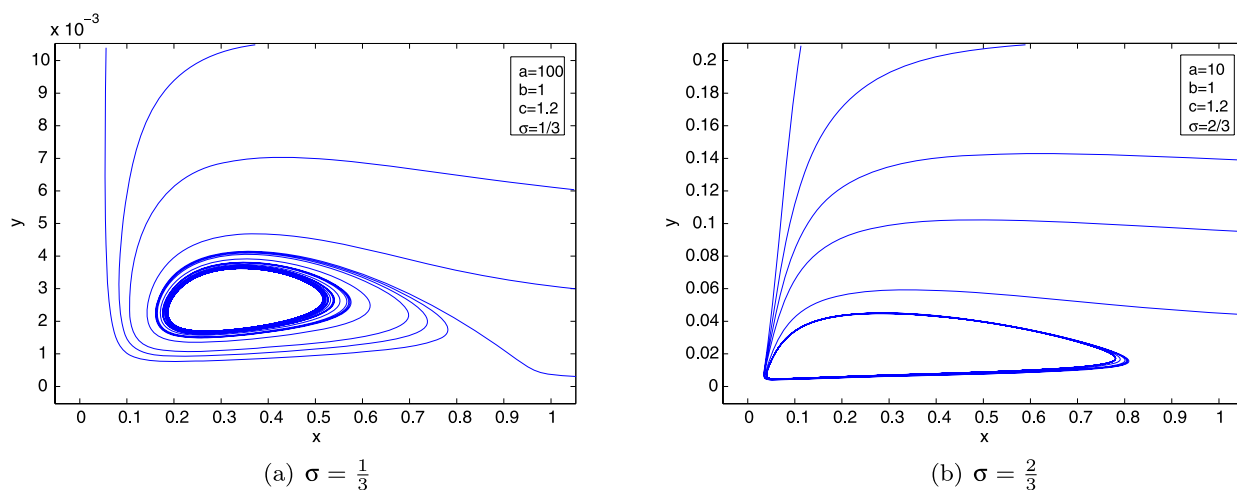


Fig. 6. When $\sigma \neq \frac{1}{2}$ and E_* is unstable, there is still a “unique” limit cycle.

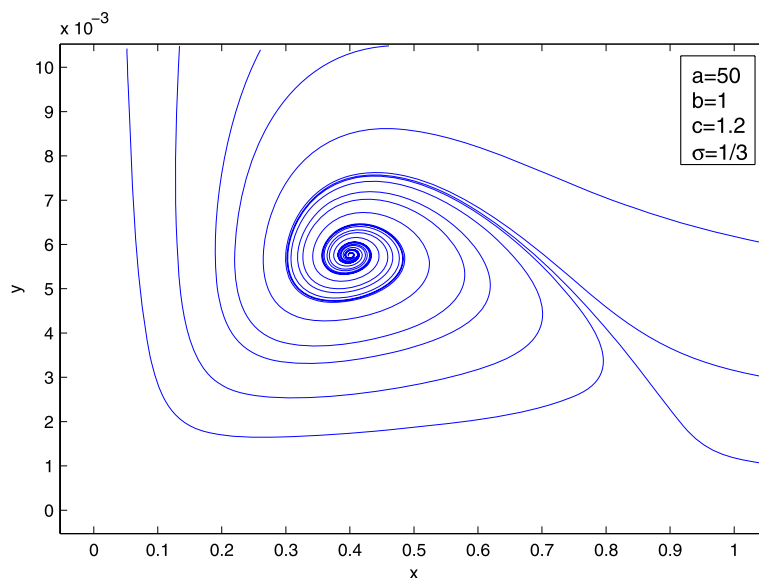


Fig. 7. When $\delta = -0.4 < \sigma = \frac{1}{3} < \min\{\frac{1}{2}, \frac{1}{c-b}\}$, E_* is locally stable. Moreover, it is also “globally stable”.

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