Global stability of a predator-prey model with modified Leslie-Gower and Holling-type schemes[1]

Xiong Li[2a], Juan Song[b]

[a]*School of Mathematical Sciences, Beijing Normal University, Laboratory of Mathematics and Complex Systems, Ministry of Education, Beijing 100875, P.R. China*
[b]*School of Mathematical Sciences, Beijing Normal University, Laboratory of Mathematics and Complex Systems, Ministry of Education, Beijing 100875, P.R. China*

Abstract

In this paper we are concerned with a predator-prey model with modified Leslie-Gower and Holling-type schemes. We establish global stability by Dulac's criterion/ Liapunov function, and the existence of limit cycles by Poincaré-Bendixson Theorem, and improve the known results.

Keywords: Global stability, Predator-prey system, Dulac's criterion, Liapunov function, Limit cycles
2000 MSC: 34C35, 92A17

1. Introduction

Predator-prey interaction is one of basic interspecies relations for ecological and social models, and it is also the base block of more complicated food chain, food web and biochemical network structure. Predator-prey models have a long history. One of the first examples of a biological system modelling the interaction between prey and predators was formulated by Lotka in 1925 [13] and Volterra in 1927 [18]:

$$\begin{cases} \dfrac{dx}{dt} = \alpha x - \beta xy, \\ \dfrac{dy}{dt} = -\delta y + \gamma xy. \end{cases} \tag{1.1}$$

[1]Supported by the NSFC (11031002).
[2]Corresponding author.
URL: xli@bnu.edu.cn (Xiong Li)

In this system $x(t)$ and $y(t)$ denote prey and predator densities respectively. Furthermore, all constants are assumed to be positive. Obviously, the attention is restricted to $x \geqslant 0, y \geqslant 0$.

A first generalization of system (1.1) was suggested by Gause in 1934 [10]:

$$\begin{cases} \dfrac{dx}{dt} = \alpha x - p(x)y, \\ \dfrac{dy}{dt} = -\delta y + \gamma p(x)y. \end{cases} \tag{1.2}$$

Here $\alpha > 0$ is the growth rate of the prey in absence of the predator; $\delta > 0$ is the death rate of the predator in absence of the prey; $\gamma > 0$ is the rate of conversion of consumed prey to predator. Finally, $p(x)$ is the capture rate of prey per predator or functional response of a predator.

For most examples that appear in the literature (see the bibliography in [8]) it is assumed that $p(0) = 0$ and $p'(x) > 0$ for all $x > 0$.

The generalized Gause model for the interaction of the two species is (see [8])

$$\begin{cases} \dfrac{dx}{dt} = xg(x) - p(x)y, \\ \dfrac{dy}{dt} = -\delta y + h(x)y. \end{cases} \tag{1.3}$$

System (1.3) incorporates density-dependent prey growth in absence of the predator. This is introduced in the model because it is quite unrealistic to assume that the prey will grow to infinity in absence of predators, as will happen for (1.1) and (1.2). The growth rate $g(x)$ satisfies $g(0) > 0, g'(x) < 0$ for all $x > 0$ and there exists a $K > 0$ such that $g(K) = 0$. K is called the carrying capacity of the prey. A growth rate of this type is thought to model the situation where the food supply for the prey is limited. For high densities of prey they will compete for the resources.

When $h = \gamma p$, system (1.3) is the so-called prey-dependent model:

$$\begin{cases} \dfrac{dx}{dt} = xg(x) - p(x)y, \\ \dfrac{dy}{dt} = -\delta y + \gamma p(x)y. \end{cases} \tag{1.4}$$

Moreover, if we choose $g(x) = 1 - \dfrac{x}{K}$ and $p(x) = \dfrac{cx}{a+x}$, $h = \gamma p$, then system

(1.3) is a model first mentioned by Rosenzweig and McArthur in 1963 [15]:

$$\begin{cases} \dfrac{dx}{dt} = x\Big(1 - \dfrac{x}{K}\Big) - \dfrac{cx}{a+x}y, \\ \dfrac{dy}{dt} = -\delta y + \gamma \dfrac{cx}{a+x}y. \end{cases} \tag{1.5}$$

If p in system (1.3) does not only depend on the prey x, but also on the predator y, and $h = \gamma p$, then system (1.3) in this case is called a predator-dependent model [1]. In other words, a predator-dependent model takes the form of

$$\begin{cases} \dfrac{dx}{dt} = xg(x) - p(x,y)y, \\ \dfrac{dy}{dt} = -\delta y + \gamma p(x,y)y. \end{cases} \tag{1.6}$$

When $p(x,y) = \bar{p}(x/y)$, model (1.6) is called (strictly) ratio-dependent [2]. When $p(x,y) = mx/(a+by+cx)$, model (1.6) is called Beddington-DeAngelis type. This type of functional response was introduced by Beddington [4] and DeAngelis et al. [6].

A slightly different model was suggested by Tanner [17]:

$$\begin{cases} \dfrac{dx}{dt} = x\Big(1 - \dfrac{x}{K}\Big) - \dfrac{cx}{a+x}y, \\ \dfrac{dy}{dt} = sy\Big(1 - h\dfrac{y}{x}\Big). \end{cases} \tag{1.7}$$

In the literature model (1.7) is referred to as the Holling-Tanner model. In (1.7) the predator grows logistically with intrinsic growth rate s and carrying capacity proportional to the size of the prey. The parameter h is the number of prey required to support one predator at equilibrium. Clearly this model incorporates intraspecific competition among the predators. There are some analysis results about this model, for example, see [5], [7], [9], [11], [12], [16] , [19] and the references therein.

In 2003, Aziz-Alaoui et al. [3] proposed the following predator-prey model with modified Leslie-Gower term:

$$\begin{cases} \dfrac{dx}{dt} = \Big(a_1 - b_1 x - \dfrac{c_1 y}{x + k_1}\Big)x, \\ \dfrac{dy}{dt} = \Big(a_2 - \dfrac{c_2 y}{x + k_2}\Big)y \end{cases} \tag{1.8}$$

with $x(0) \geqslant 0$ and $y(0) \geqslant 0$, where x and y represent the population densities of prey and predator at time t; $a_1, a_2, b_1, c_1, c_2, k_1$ and k_2 are positive parameters. These parameters are defined as follows: a_1 is the growth rate of prey x, b_1 measures the strength of competition among individuals of species x, c_1 is the maximum value which per capita reduction rate of x can attain, k_1(respectively, k_2) measures the extent to which environment provides protection to prey x(respectively, to predator y), a_2 describes the growth rate of y, and c_2 is the maximum value which per capita reduction rate of y can attain. In [3] , they analyzed this model and obtained some primary results about boundedness of solutions, existence of an attracting set and global stability of the coexisting interior equilibrium (see also [14]). The aim of this paper is to give some better results about this model than that of [3] and [14].

Rest of this paper is organized as follows. In Section 2 we establish the dissipative result and local stability of the equilibria. Global stabilities are given in Section 3.

2. Basic results

For simplicity, we first nondimensionalizes system (1.8) with the following scaling

$$t \to a_1 t, \quad x \to b_1 x/a_1, \quad y \to b_1 c_1 y/a_1^2, \tag{2.1}$$

then system (1.8) takes the form

$$\begin{cases} \dfrac{dx}{dt} = x(1-x) - \dfrac{xy}{a+x} := f_1(x,y), \\ \dfrac{dy}{dt} = y\Big(\delta - \dfrac{\beta y}{b+x}\Big) := f_2(x,y), \end{cases} \tag{2.2}$$

where

$$a = \frac{k_1 b_1}{a_1}, \quad b = \frac{k_2 b_1}{a_1}, \quad \delta = \frac{a_2}{a_1}, \quad \beta = \frac{c_2}{c_1} \tag{2.3}$$

are positive constants.

When $b = 0$ (that is, $k_2 = 0$), system (2.2) is the so-called Holling-Tanner model. Now we state the phase space for system (2.2) which is meaningful in biology. Define

$$\Omega = \Big\{(x,y) \in \mathbb{R}^2 : 0 < x < 1, 0 < y < (b+1)\delta\beta^{-1}\Big\}. \tag{2.4}$$

Theorem 2.1. Ω *is positively invariant for the semiflow generated by system (2.2). Also all solutions of system (2.2) with the initial values* $x(0) > 0, y(0) > 0$ *will enter* Ω *eventually.*

This is a dissipative result and one can prove it by the standard method, and we omit the details. Back to the original model (1.8), the phase space Ω can be rewritten as

$$\overline{\Omega} = \Big\{(x, y) \in \mathbb{R}^2 : 0 < x < \frac{a_1}{b_1}, 0 < y < \frac{a_2(a_1 + b_1k_2)}{b_1c_2}\Big\}. \tag{2.5}$$

In [3], the phase space is given by

$$\mathcal{A} = \Big\{(x, y) \in \mathbb{R}^2 : 0 < x < \frac{a_1}{b_1}, 0 < x + y < L_1\Big\}, \tag{2.6}$$

where

$$L_1 = \frac{1}{4b_1c_2}\Big[a_1c_2(4 + a_1) + (1 + a_2)^2(a_1 + b_1k_2)\Big]. \tag{2.7}$$

We note that

$$\begin{aligned} L_1 &= \frac{a_1}{b_1} + \frac{1}{4b_1c_2}\Big[a_1^2c_2 + (1 + a_2)^2(a_1 + b_1k_2)\Big] \\ &> \frac{a_1}{b_1} + \frac{1}{4b_1c_2}\Big[4a_2(a_1 + b_1k_2)\Big] \\ &= \frac{a_1}{b_1} + \frac{a_2(a_1 + b_1k_2)}{b_1c_2}. \end{aligned} \tag{2.8}$$

Therefore $\Omega \subset \mathcal{A}$ and Theorem 2.1 here is better than Theorem 4 in [3].

In order to analyze the stability of all equilibria of system (2.2), we first compute the isocline of system (2.2). The prey isoclines are $x = 0$ and $y = g_1(x) := (a + x)(1 - x)$. At the same time, the predator isocline are $y = 0$ and $y = g_2(x) := \beta^{-1}\delta(b + x)$ (see Fig. 1 and Fig. 2 in Section 3). Therefore the boundary equilibria are $E_0(0, 0)$, $E_1(1, 0)$, $E_2(0, \beta^{-1}\delta b)$, respectively.

The variational matrix of system (2.2) takes the form

$$J = \begin{pmatrix} 1 - 2x - \dfrac{ay}{(a + x)^2} & -\dfrac{x}{a + x} \\ \beta\big(\dfrac{y}{a + x}\big)^2 & \delta - \dfrac{2\beta y}{b + x} \end{pmatrix}.$$

At E_0, $J(E_0)$ has the form

$$J = \begin{pmatrix} 1 & 0 \\ 0 & \delta \end{pmatrix},$$

hence E_0 is an unstable node.

At E_1, $J(E_1)$ has the form

$$J = \begin{pmatrix} -1 & -\dfrac{1}{a+1} \\ 0 & \delta \end{pmatrix},$$

thus E_1 is a saddle point with the positive x-axis as its stable manifold.

At E_2, $J(E_2)$ has the form

$$J = \begin{pmatrix} \dfrac{a\beta - \delta b}{\beta} & 0 \\ \dfrac{\delta^2}{\beta} & -\delta \end{pmatrix}.$$

When $a\beta - \delta b < 0$, E_2 is a stable node. Since the intersection point of the prey isocline with the positive y-axis is $(0, a)$, meanwhile the intersection point of the predator isocline with the positive y-axis is $(0, \beta^{-1}\delta b)$, thus in this case system (2.2) has no any internal equilibria, also has no any limit cycles, and hence all solutions with positive initial values will approach to the equilibrium E_2, which is globally asymptotically stable.

When $a\beta - \delta b > 0$, E_2 is an unstable saddle. In this case system (2.2) has a unique internal equilibrium.

When $a\beta - \delta b = 0$, E_2 is a saddle-node. In this case the transcritical bifurcation occurs and all solutions with positive initial values will approach to the equilibrium E_2, which is globally asymptotically stable.

Therefore we arrive at the following result.

Theorem 2.2. *System (2.2) has three boundary equilibria* $E_0(0,0)$, $E_1(1,0)$, $E_2(0, \beta^{-1}\delta b)$. E_0 *is an unstable node, and* E_1 *is a saddle point. When* $a\beta - \delta b \leq 0$, E_2 *is globally asymptotically stable; when* $a\beta - \delta b > 0$, E_2 *is unstable, and system (2.2) has a unique internal equilibrium.*

We first remark that the classification condition $a\beta - \delta b = 0$ is equivalent to that $\frac{a_1 k_1}{c_1} - \frac{a_2 k_2}{c_2} = 0$ in the original model (1.8). From now on we always assume that

$$a\beta - \delta b > 0 \tag{2.9}$$

holds, that is,

$$\frac{a_1 k_1}{c_1} - \frac{a_2 k_2}{c_2} > 0 \tag{2.10}$$

holds in (1.8). In this case system (2.2) has a unique internal equilibrium $E^*(x^*, y^*)$, which satisfies

$$y^* = (1 - x^*)(a + x^*) = \beta^{-1}\delta(b + x^*),$$

that is,

$$y^* = g_1(x^*) = g_2(x^*),$$

and

$$\begin{aligned} x^* &= \frac{1}{2}\Big[1 - a - \beta^{-1} + \sqrt{(1 - a - \beta^{-1})^2 + 4(a - \beta^{-1}\delta b)}\Big], \\ y^* &= (1 - x^*)(a + x^*) = \beta^{-1}\delta(b + x^*). \end{aligned} \tag{2.11}$$

In order to investigate the stability of E^*, we rewrite system (2.2) as

$$\begin{cases} \dot{x} = \dfrac{x}{a + x}\Big[g_1(x) - y\Big], \\ \dot{y} = \dfrac{\beta y}{b + x}\Big[g_2(x) - y\Big]. \end{cases} \tag{2.12}$$

The variational matrix of system (2.12) is

$$J = \begin{pmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{pmatrix},$$

where

$$\begin{aligned} J_{11} &= \frac{a}{(a + x)^2}\Big[g_1(x) - y\Big] + \frac{a}{a + x} g_1'(x), \\ J_{12} &= -\frac{a}{a + x}, \\ J_{21} &= -\frac{\beta y}{(b + x)^2}\Big[g_2(x) - y\Big] + \frac{\beta y}{b + x} g_2'(x), \\ J_{22} &= \frac{\beta}{b + x}\Big[g_2(x) - y\Big] - \frac{\beta y}{b + x}. \end{aligned}$$

Thus, at E^*, $J(E^*)$ has the form

$$J(E^*) = \begin{pmatrix} \dfrac{x^*}{a + x^*} g_1'(x^*) & -\dfrac{x^*}{a + x^*} \\ \beta^{-1}\delta^2 & -\delta \end{pmatrix}.$$

Note that

$$\begin{aligned}\mathrm{Det}J(E^*) &= -\frac{\delta x^*}{a+x^*}g_1'(x^*) + \frac{x^*}{a+x^*}\frac{\delta^2}{\beta} \\ &= \frac{\delta x^*}{a+x^*}\Big[\frac{\delta}{\beta} - g_1'(x^*)\Big] \\ &= \frac{\delta x^*}{a+x^*}\Big[g_2'(x^*) - g_1'(x^*)\Big] > 0,\end{aligned}$$

since at E^* the slope of the predator isocline is larger than that of the prey isocline. Hence, E^* is locally asymptotically stable if and only if

$$\mathrm{Tr}J(E^*) = -\Big(\delta - \frac{x^*}{a+x^*}g_1'(x^*)\Big) < 0,$$

which is equivalent to

$$2(x^*)^2 + (a+\delta-1)x^* + a\delta > 0. \tag{2.13}$$

Define

$$P(x) = 2x^2 + (a+\delta-1)x + a\delta, \tag{2.14}$$

then E^* is locally asymptotically stable if and only if $P(x^*) > 0$. Thus we arrive at the following theorem.

Theorem 2.3. *The equilibrium E^* of system (2.2) is locally asymptotically stable if $P(x^*) > 0$; E^* is unstable if $P(x^*) < 0$.*

We also remark that back to the original model (1.8), the locally asymptotically stability condition is

$$\overline{P}(x^*) = 2b_1 x^{*2} + (a_2 + b_1k_1 - a_1)x^* + a_2k_1 > 0. \tag{2.15}$$

In [3], E^* is locally asymptotically stable provided that

$$a_1 \le a_2, \quad k_1 \ge k_2. \tag{2.16}$$

Also in [14], E^* is locally asymptotically stable provided that

$$a_1 < b_1k_1. \tag{2.17}$$

We note that the conditions (2.16) and (2.17) guarantee that $a_2 + b_1k_1 - a_1 > 0$, which implies that (2.15) holds.

3. Global stability

Now we are going to investigate the global stability of the equilibrium E^*. For this purpose we consider the locally asymptotically stability condition

$$P(x^*) = 2(x^*)^2 + (a + \delta - 1)x^* + a\delta > 0. \tag{3.1}$$

We divide this condition into two cases. One case is that $P(x) \geq 0$ for all $x > 0$, which implies that

$$a + \delta \geq 1, \tag{3.2}$$

or

$$a + \delta < 1 \quad \text{and} \quad (a + \delta - 1)^2 - 8a\delta \leq 0. \tag{3.3}$$

The other case is that

$$a + \delta < 1 \quad \text{and} \quad (a + \delta - 1)^2 - 8a\delta > 0. \tag{3.4}$$

In this case,

$$P(x) = 2(x - \alpha_1)(x - \alpha_2),$$

where $0 < \alpha_1 < \alpha_2 < 1$ are defined by

$$\begin{aligned} \alpha_1 &= \frac{1}{4}\left[1 - a - \delta - \sqrt{(1 - a - \delta)^2 - 8a\delta}\right], \\ \alpha_2 &= \frac{1}{4}\left[1 - a - \delta + \sqrt{(1 - a - \delta)^2 - 8a\delta}\right]. \end{aligned}$$

Thus the equilibrium E^* is locally asymptotically stable if

$$0 < x^* < \alpha_1, \tag{3.5}$$

or

$$\alpha_2 < x^* < 1; \tag{3.6}$$

the equilibrium E^* is unstable if

$$\alpha_1 < x^* < \alpha_2. \tag{3.7}$$

Firstly we remark that if x^* tends to 0 from the right, then the equilibrium E^* collides with the boundary equilibrium E_2, and the transcritical bifurcation occurs as mentioned before; if x^* tends to 1 from the left, then the equilibrium E^* collides with the boundary equilibrium E_1, and also the transcritical bifurcation appears.

Secondly, when $x^* = \alpha_1$ or α_2, the linearized matrix of system (2.2) at the internal equilibrium E^* has a pair of purely imaginary eigenvalues and the stability of the equilibrium E^* depends on the high order terms.

Now we are in a position to state and prove the main results in this section.

Theorem 3.1. *If (3.2) or (3.3) hold, then the equilibrium E^* is globally asymptotically stable (see Fig.1).*

Proof. From Theorem 2.1, all solutions of system (2.2) with positive initial values are positive and bounded. The assumptions implies that the equilibrium E^* is locally asymptotically stable; by Poincaré-Bendixson theorem it suffices to show the global stability of the equilibrium E^*, provided we are able to eliminate the existence of any limit cycles. We prove this by Dulac's criterion. For this purpose, we construct

$$H(x, y) = \left(\frac{x}{a+x}\right)^{-1} \cdot y^{-2}, \quad x > 0, \quad y > 0.$$

Then from (2.2) and the hypothesis, an easy computation yields

$$\frac{\partial(Hf_1)}{\partial x} + \frac{\partial(Hf_2)}{\partial y} = -\frac{H(x, y)}{a+x} P(x) \leq 0, \quad x > 0, \quad y > 0.$$

Hence there are no nontrivial periodic solutions, and we complete the proof. □

Theorem 6 in [3] states that E^* is globally asymptotically stable if

$$L_1 < \frac{a_1 k_1}{2c_1}, \tag{3.8}$$

$$k_1 < 2k_2, \tag{3.9}$$

$$4(a_1 + b_1 k_1) < c_1, \tag{3.10}$$

where L_1 is given by (2.7). We claim that these three conditions are contradictory. Indeed, from (2.8) and (3.8), we have

$$\frac{a_1}{b_1} < L_1 < \frac{a_1 k_1}{2c_1}, \tag{3.11}$$

which implies that

$$2c_1 < b_1 k_1. \tag{3.12}$$

Together with (3.10), we get

$$8(a_1 + b_1 k_1) < b_1 k_1, \tag{3.13}$$

which is contradictory, since all these constants are positive.

Theorem 7 in [14] also states that if

$$a_1 + c_1 < b_1(x^* + k_1) \tag{3.14}$$

and

$$a_1 a_2 < b_1 k_2 (c_2 - a_2) \tag{3.15}$$

hold, E^* is globally asymptotically stable. We note that (3.15) requires that $c_2 > a_2$, which is unreasonable.

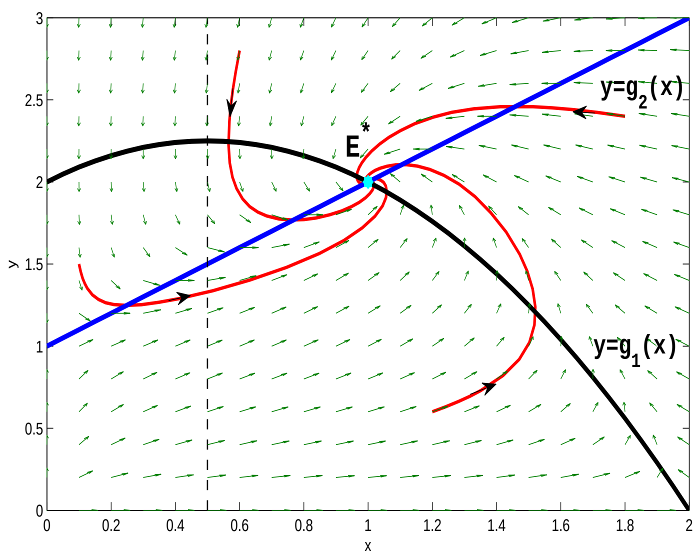

Fig.1. The solutions $(x(t), y(t))$ of (1.8) with the initial conditions $(0.1, 1.5)$, $(0.6, 2.8)$, $(1.2, 0.6)$ and $(1.8, 2.4)$ in Ω will approach to E^*, and E^* is globally asymptotically stable. Here we choose the parameter values as $a_1 = 2, a_2 = 1, c_1 = 1, c_2 = 1, k_1 = 1, k_2 = 1$, and $b_1 = 1$.

Theorem 3.2. *If (3.6) holds, then the equilibrium E^* is globally asymptotically stable.*

Proof. We prove this result also by Dulac's criterion. Let

$$H(x,y)=\ell(x)r(y),\quad x>0,\quad y>0.$$

where $\ell(x)$ and $r(y)$ will be determined later. Then

$$\begin{aligned}\Delta : \;&=\; \frac{\partial(Hf_1)}{\partial x}+\frac{\partial(Hf_2)}{\partial y}\\ &=\; H(x,y)\Big[1+\delta-2x-\frac{ay}{(a+x)^2}-\frac{2\beta y}{b+x}+\\ &\quad \Big(1-x-\frac{y}{a+x}\Big)\frac{x\ell'(x)}{\ell(x)}+\Big(\delta-\frac{\beta y}{b+x}\Big)\frac{yr'(y)}{r(y)}\Big].\end{aligned}$$

Let $r(y)=y^{R-2}$, where R will be determined later. Then

$$\frac{yr'(y)}{r(y)}=R-2$$

and

$$\begin{aligned}\Delta \;&=\; H(x,y)\Big[1+(R-1)\delta-2x-\frac{ay}{(a+x)^2}\\ &\quad +\Big(1-x-\frac{y}{a+x}\Big)\frac{x\ell'(x)}{\ell(x)}-\frac{R\beta y}{b+x})\Big]\\ &=\; H(x,y)\Big\{1+(R-1)\delta-2x+(1-x)x\frac{\ell'(x)}{\ell(x)}\\ &\quad -y\Big[\frac{\beta R}{b+x}+\frac{a}{(a+x)^2}+\frac{x}{a+x}\frac{\ell'(x)}{\ell(x)}\Big]\Big\}.\end{aligned}$$

We choose $\ell(x)=(x+a)\cdot x^{-(1+ab^{-1}\beta R)}\cdot(x+b)^{(a-b)b^{-1}\beta R}$. Then $\ell(x)$ satisfies

$$\frac{\beta R}{b+x}+\frac{a}{(a+x)^2}+\frac{x}{a+x}\frac{\ell'(x)}{\ell(x)}=0,$$

and therefore

$$\begin{aligned}\Delta \;&=\; H(x,y)I(x)\\ :=\;& H(x,y)\Big\{1+(R-1)\delta-2x-\frac{a(1-x)}{a+x}-\frac{\beta R(1-x)(a+x)}{b+x}\Big\}.\end{aligned}$$

We rewrite $I(x)$ as follows:

$$\begin{aligned}
I(x) &= \Big[R\delta - \beta R\frac{(1-x)(a+x)}{b+x}\Big] - \frac{1}{a+x}\Big[a - ax + (a+x)(2x+\delta-1)\Big] \\
&= R\beta\Big[\frac{y^*}{b+x^*} - \frac{(1-x)(a+x)}{b+x}\Big] - \frac{1}{a+x}P(x) \\
&= R\beta\Big[\frac{(1-x^*)(a+x^*)}{b+x^*} - \frac{(1-x)(a+x)}{b+x}\Big] - \frac{1}{a+x}P(x) \\
&= \frac{R\beta}{x+b}\Big\{(x-x^*)\Big[x+b+\frac{(b+1)(a-b)}{x^*+b}\Big]\Big\} - \frac{2}{x+a}(x-\alpha_1)(x-\alpha_2).
\end{aligned}$$

To make $I(x) < 0$ for $0 < x < 1$, we shall determine $R > 0$ satisfying

$$\frac{R\beta}{2}(x+a)(x-x^*)\Big[x+b+\frac{(b+1)(a-b)}{x^*+b}\Big] < (x+b)(x-\alpha_1)(x-\alpha_2) \quad (3.16)$$

for $0 < x < 1$. For this purpose we introduce

$$W(x) = \frac{(x+b)(x-\alpha_1)(x-\alpha_2)}{(x+a)(x-x^*)\Big[x+b+\frac{(b+1)(a-b)}{x^*+b}\Big]}$$

and

$$Q(x) = \frac{(x+b)(x-\alpha_1)}{(x+a)\Big[x+b+\frac{(b+1)(a-b)}{x^*+b}\Big]}.$$

Then

$$W(x) = Q(x) + (x^*-\alpha_2)\frac{(x+b)(x-\alpha_1)}{(x+a)(x-x^*)\Big[x+b+\frac{(b+1)(a-b)}{x^*+b}\Big]}. \quad (3.17)$$

We note that $0 < \alpha_1 < \alpha_2 < x^* < 1$. For $x \in (0, \alpha_1] \cup [\alpha_2, x^*]$, (3.16) holds for any $R > 0$. In order to show that (3.16) holds for $x \in (\alpha_1, \alpha_2] \cup (x^*, 1)$, we choose $R = \frac{2Q(\alpha_2)}{\beta}$, that is, $Q(\alpha_2) = \frac{\beta R}{2}$. If $x \in (\alpha_1, \alpha_2)$, from (3.17) and the fact that $Q(x)$ is monotonically increasing in $(\alpha_1, 1)$, we have

$$W(x) < Q(x) < Q(\alpha_2) = \frac{\beta R}{2}. \quad (3.18)$$

If $x \in (x^*, 1)$, then

$$W(x) > Q(x) > Q(\alpha_2) = \frac{\beta R}{2}. \quad (3.19)$$

From (3.18) and (3.19), it follows that (3.16) holds for $0 < x < 1$. Thus we complete the proof. $\square$

Theorem 3.3. *If $0 < x^* < \hat{x}$ (see (3.22) for the definition of $\hat{x}$), then the equilibrium E^* is globally asymptotically stable.*

Proof. To prove this result, we first reduce system (2.2) to a Gause-type predator-prey system by the following change of variable. Let

$$u = y\ell(x),$$

where $\ell(x)$ will be determined later. Then

$$\begin{aligned} \frac{du}{dt} &= \frac{dy}{dt}\ell(x) + y\ell'(x)\frac{dx}{dt} \\ &= u\Big[\delta + x(1-x)\frac{\ell'(x)}{\ell(x)}\Big] - \frac{\beta u^2}{(b+x)\ell(x)} - \frac{\ell'(x)}{\ell(x)} \cdot \frac{xu^2}{(a+x)\ell(x)}. \end{aligned}$$

We choose $\ell(x)$ such that

$$\delta + x(1-x)\frac{\ell'(x)}{\ell(x)} = 0,$$

that is,

$$\ell(x) = \Big(\frac{1-x}{x}\Big)^{\delta}.$$

Then

$$\frac{du}{dt} = \frac{\beta u^2}{(1-x)(a+x)(b+x)\ell(x)}\Big(x + \frac{a-\beta^{-1}\delta b}{x^*}\Big)(x - x^*).$$

Hence we transform system (2.2) into the following system

$$\begin{cases} \dfrac{dx}{dt} = x(1-x) - \dfrac{x}{a+x}\dfrac{u}{\ell(x)}, \\[2mm] \dfrac{du}{dt} = \dfrac{\beta u^2}{(1-x)(a+x)(b+x)\ell(x)}\Big(x + \dfrac{a-\beta^{-1}\delta b}{x^*}\Big)(x - x^*). \end{cases} \tag{3.20}$$

The x- isocline of systems (3.20) are $x = 0$ and

$$u = h(x) := (1-x)(a+x)\ell(x), \qquad 0 < x \le 1, \tag{3.21}$$

and its derivative is $-\dfrac{\ell(x)}{x}P(x)$. Therefore the prey isocline $u = h(x)$ has a local minimum at α_1 and has a local maximum at α_2, respectively. Also, $\lim_{x\to 0^+} h(x) = +\infty$, and $h(1) = 0$, $h(x)$ is monotonically increasing in the interval $[\alpha_1, \alpha_2]$, monotonically decreasing in $(0, \alpha_1) \cup (\alpha_2, 1]$. Let $\hat{x} \in (0, \alpha_1)$ such that

$$h(\hat{x}) = h(\alpha_2). \tag{3.22}$$

We note that such $\hat{x}$ is unique. Let $0 < x^* < \hat{x}$, then

$$(x - x^*)(h(x) - u^*) < 0$$

for $0 < x < 1$ and $x \neq x^*$, where $u^* = h(x^*)$.

Construct the following Liapunov function

$$V(x,u) = \int_{x^*}^{x} \frac{\eta - x^*}{Q(\eta)} d\eta + \frac{1}{\beta}\int_{u^*}^{u} \frac{\eta - u^*}{\eta^2} d\eta,$$

where

$$Q(x) = x(1-x)(b+x)\Big/\Big(x + \frac{a - \beta^{-1}\delta b}{x^*}\Big).$$

Then

$$\frac{dV}{dt} = \frac{x + \dfrac{a - \beta^{-1}\delta b}{x^*}}{(1-x)(a+x)(b+x)\ell(x)}(x - x^*)(h(x) - u^*) < 0,$$

which implies that the equilibrium E^* is globally asymptotically stable, and we complete the proof. □

Theorem 3.4. *If (3.7) holds, then system (2.2) has at least one limit cycle (see Fig. 2).*

Proof. From Theorem 2.1, all solutions of system (2.2) with positive initial values are positive and bounded. If (3.7) holds, then the equilibrium E^* is unstable, and the result follows directly from Poincaré-Bendixson theorem. □

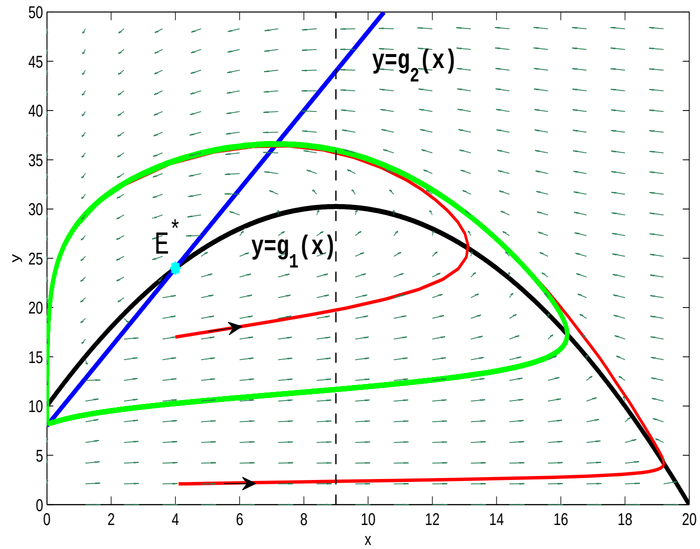

Fig.2. System (1.8) has a limit cycle in $\overline{\Omega}$. The solutions $(x(t), y(t))$ of (1.8) with the initial conditions $(4, 17)$ and $(4.1, 2.1)$ will spirally approach to this limit cycle. Here we choose the parameter values as $a_1 = 10, a_2 = 1, c_1 = 2, c_2 = 0.25, k_1 = 2, k_2 = 2$, and $b_1 = 0.5$.

References

[1] P.A. Abrams, L.R. Ginzburg, The nature of predation: prey dependent, ratio-dependent or neither?, Trends Ecol. Evol. 15 (2000) 337-341.

[2] R. Arditi, L.R. Ginzburg, Coupling in predator-prey dynamics: ratio-dependence, J. Theor. Biol., 139 (1989) 311-326.

[3] M.A. Aziz-Alaoui, M. Daher Okiye, Boundeness and global stability for a predator-prey model with modified Leslie-Gower and Holling-typeII schemes, Appl. Math. Lett. 16 (2003) 1069-1075.

[4] J.R. Beddington, Mutual interference between parasites or predators and its effect on searching efficiency, J. Animal Ecol. 44 (1975) 331-340.

[5] P.A. Braza, The bifurcation structure of the Holling-Tanner model for predator-prey interactions using two-timing, SIAM J. Appl. Math. 63(2003) 889-904.

[6] D.L. DeAngelis, R.A. Goldstein, R.V. O'Neill, A model for trophic interaction, Ecology 56 (1975) 881-892.

[7] M. Falconi, M. Garcia, J. Llibre, Hopf bifurcation in the Holling-Tanner model, Proceedings of the 8th WSEAS international conference on fluid mechanics, 8th WSEAS international conference on Heat and mass transfer. World Scientific and Engineering Academy and Society (WSEAS), 2011, 142-146.

[8] H.I. Freedman, Deterministic mathematical models in population ecology, Marcel Dekker, New York, 1980.

[9] A. Gasull, R.E. Kooij, J. Torregrosa, Limit cycles in the Holling-Tanner model, Publicacions Matemàtiques 41 (1997) 149-167.

[10] G.F. Gause, The struggle for existence, Williams and Wilkins, Baltimore, 1934.

[11] S.B. Hsu, T.W. Huang, Global stability for a class of predator-prey systems, SIAM J. Appl. Math. 55 (1995) 763-783.

[12] S.B. Hsu, T.W. Hwang, Hopf bifurcation analysis for a predator-prey system of Holling and Leslie type, Taiwanese J. Math. 3 (1999) 35-53.

[13] A.J. Lotka, Elements of physical biology, Williams and Wilkins, Baltimore, 1925.

[14] A.F. Nindjin, M.A. Aziz-Alaoui, M. Cadivel, Analysis of a predator-prey model with modified Leslie-Gower and Holling-type II schemes with time delay, Nonlinear Anal. RWA 7(2006) 1104-1118.

[15] M.L. Rosenzweig, R.H. McArthur, Graphical representation and stability conditions of predator-prey interactions, Am. Nat. 47 (1963) 209-223.

[16] E. Sáez, E. González-Olivares, Dynamics of a predator-prey model, SIAM J. Appl. Math. 59 (1999) 1867-1878.

[17] J.T. Tanner, The stability and the intrinsic growth rates of prey and predator populations, Ecology 56 (1975) 855-867.

[18] V. Volterra, Variazioni e fluttuazioni del numero dindividui in specie animai conviventi, in Italian, Mem. R. Com. Tolassogr. Ital. 131 (1927) 1-142.

[19] D. Xiao, Z. Zhang, On the uniqueness and nonexistence of limit cycles for predator-prey systems, Nonlinearity 16 (2003) 1-17.