ON THE DYNAMICS OF PREDATOR-PREY MODELS WITH IVLEV'S FUNCTIONAL RESPONSE

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ABSTRACT. In this paper, we study the existence and the stability of equilibria of predator-prey models with Ivlev's functional response. We give a simple proof for the uniqueness of limit cycles of the predator-prey system. The existence and the stability at the origin and a boundary equilibrium point(including the positive equilibrium point) are also investigated.

1. Introduction

In this paper, we consider the predator-prey system with Ivlev's functional response:

$$(1.1) \qquad \begin{cases} \frac{dx}{dt} = rx(1-x) - (1-e^{-ax})y, \\ \frac{dy}{dt} = y((1-e^{-ax}) - D), \\ x(0) > 0, \ y(0) > 0 \end{cases}$$

where r, a and D are positive constants that stand for the prey's intrinsic growth rate, the efficiency of the predator for capturing prey and the predator death rate, respectively. Here $x(t)$ and $y(t)$ are the population densities of prey and predator at time t, respectively.

Predator-prey systems with Ivlev's functional response have been studied on the existence and the uniqueness of limit cycles(one can refer [1, 2, 4, 5] and the references therein). In [4], J. Sugie gave a necessary and sufficient condition for the uniqueness of limit cycles for system (1.1). To prove the result, after transforming system (1.1) into a Liénard

system when $D < 1 - e^{-a}$, the author applied the Poincaré-Bendixson theorem and the result by R. E. Kooij and A. Zegeling [2].

The purpose of this paper is to study the existence and the stability of the three equilibria $(0,0)$, $(1,0)$ and (x^*, y^*) of system (1.1), where (x^*, y^*) is a positive equilibrium. We point out that the sufficient and the necessary condition for the uniqueness of limit cycles for system (1.1) was very well studied by J. Sugie, but we simply prove the result again in a local sense.

This article is organized as follow. In Section 2, we investigate the existence and the stability of the equilibria $(0,0)$, $(1,0)$ and (x^*, y^*) of system (1.1). In Section 3, we show the local existence and uniqueness of limit cycles by using the Hopf bifurcation theorem in [3]. In addition, we provide a numerical simulation. The summarization of the dynamics to system (1.1) and the derivation of the Liapunov number are presented in the appendix.

2. Asymptotic behavior of system (1.1)

In this section, we study the existence and the stability of equilibria of system (1.1). System (1.1) always has equilibria, the origin $(0,0)$ and the boundary equilibrium point $(1,0)$. Moreover, system (1.1) has the unique positive critical point (x^*, y^*), where

$$x^* = -\frac{1}{a}\ln(1-D), \quad y^* = \frac{r}{D}x^*(1-x^*)$$

in the case $D < 1 - e^{-a}$.

Consider the Jacobian matrix $J(x,y)$ of system (1.1) which is given by

$$(2.1) \qquad J(x,y) = \begin{pmatrix} r - 2rx - ae^{-ax}y & -1 + e^{-ax} \\ ae^{-ax}y & 1 - D - e^{-ax} \end{pmatrix}.$$

Hereafter, denote the determinant and the trace of $J(x,y)$ by Δ and τ, respectively.

THEOREM 2.1.
  (i) $(0,0)$ *is a saddle.*
  (ii) *If* $1 - D - e^{-a} > 0$, *then* $(1,0)$ *is an saddle.*
  (iii) *If* $1 - D - e^{-a} < 0$, *then* $(1,0)$ *is a stable critical point.*

Moreover, it is a stable node when $1 - D - e^{-a} \neq -r$.

Proof. (i) From (2.1), $J(0,0) = \begin{pmatrix} r & 0 \\ 0 & -D \end{pmatrix}$, and so $(0,0)$ is a saddle point since $\Delta = -rD < 0$.

(ii) Observe that $J(1,0) = \begin{pmatrix} -r & -1 + e^{-a} \\ 0 & 1 - D - e^{-a} \end{pmatrix}$, $\Delta = -r(1 - D - e^{-a})$ and $\tau = -r + 1 - D - e^{-a}$. Since $1 - D - e^{-a} > 0$, $\Delta < 0$, and so the result follows.

(iii) In this case, we have $\Delta > 0$ and $\tau < 0$. Therefore, $(1,0)$ is a stable critical point. Furthermore, if $1 - D - e^{-a} \neq -r$, then $\tau^2 - 4\Delta = (r + 1 - D - e^{-a})^2 > 0$, and thus we see that $(1,0)$ is a stable node. $\square$

To investigate the stability of the positive equilibrium (x^*, y^*), we assume $D < 1 - e^{-a}$. Then since $1 - D - e^{-ax^*} = 0$, (2.1) yields to

$$J(x^*, y^*) = \begin{pmatrix} r - 2rx^* - a(1 - D)y^* & -D \\ a(1 - D)y^* & 0 \end{pmatrix}.$$

Here $\Delta = aD(1 - D)y^* > 0$ and $\tau = r - 2rx^* - a(1 - D)y^*$. Observe that

$$\tau = (>, <)0 \text{ if and only if } a = (>, <) - \frac{2D + (1 - D)\ln(1 - D)}{D + (1 - D)\ln(1 - D)}\ln(1 - D).$$

Therefore, it is clear that (x^*, y^*) is locally asymptotically stable(unstable) if $\tau \leq 0(\tau > 0$, respectively) since $\Delta > 0$. Moreover, if $\tau^2 - 4\Delta > 0$, then (x^*, y^*) is a stable node; if $\tau^2 - 4\Delta < 0$, then (x^*, y^*) is a stable spiral. But (x^*, y^*) may be a stable spiral, a stable node, or a degenerate stable node when $\tau^2 - 4\Delta = 0$. Consequently, we have the following theorem.

THEOREM 2.2.
(i) If $a > -\frac{2D+(1-D)\ln(1-D)}{D+(1-D)\ln(1-D)}\ln(1 - D)$, then (x^*, y^*) is unstable.
(ii) If $a \leq -\frac{2D+(1-D)\ln(1-D)}{D+(1-D)\ln(1-D)}\ln(1 - D)$, then (x^*, y^*) is locally asymptotically stable. Moreover, (x^*, y^*) is a stable node if $\tau^2 - 4\Delta > 0$ and is a stable spiral if $\tau^2 - 4\Delta < 0$.

3. Uniqueness of limit cycles

In this section, we show the local existence and uniqueness of limit cycles of system (1.1) by using the Hopf bifurcation theorem in [3]. In addition, we provide a numerical simulation.

Consider the planar analytic system:

(3.1) $\qquad \begin{cases} \frac{dx}{dt} = ex + fy + p(x, y), \\ \frac{dy}{dt} = gx + hy + q(x, y), \end{cases}$

where $\Delta := eh - fg > 0$, $\mu := e + h = 0$ and the analytic functions $p(x, y)$, $g(x, y)$ are given by the series

$$p(x,y) = \sum_{i+j\geq 2} a_{ij}x^i y^j \quad \text{and} \quad q(x,y) = \sum_{i+j\geq 2} b_{ij}x^i y^j.$$

Then the Liapunov number σ is given by the formula:

$$\begin{aligned}
\sigma &= \frac{-3\pi}{2f\Delta^{3/2}}\{[eg(a_{11}^2 + a_{11}b_{02} + a_{02}b_{11}) + ef(b_{11}^2 + a_{20}b_{11} + a_{11}b_{02}) \\
&\quad + g^2(a_{11}a_{02} + 2a_{02}b_{02}) - 2eg(b_{02}^2 - a_{20}a_{02}) - 2ef(a_{20}^2 - b_{20}b_{02}) \\
&\quad - f^2(2a_{20}b_{20} + b_{11}b_{20}) + (fg - 2e^2)(b_{11}b_{02} - a_{11}a_{20})] \\
&\quad - (e^2 + fg)[3(gb_{03} - fa_{30}) + 2e(a_{21} + b_{12}) + (ga_{12} - fb_{21})]\}.
\end{aligned}$$

The following theorem can be found in [3].

THEOREM 3.1. (The Hopf Bifurcation) *If $\sigma \neq 0$, then a Hopf bifurcation occurs at the origin of the planar analytic system (3.1) at the bifurcation value $\mu = 0$; in particular, if $\sigma < 0$, then (3.1) has a unique stable limit cycle for $\mu > 0$ and no limit cycle for $\mu \leq 0$.*

Now, we consider system (1.1) at the positive equilibrium (x^*, y^*). Translating the interior equilibrium (x^*, y^*) of system (1.1) to the origin, (1.1) can be written as

$$\begin{cases}
\frac{dx}{dt} = r(x + x^*) - r(x + x^*)^2 - (1 - e^{-a(x+x^*)})(y + y^*), \\
\frac{dy}{dt} = (y + y^*)((1 - e^{-a(x+x^*)}) - D).
\end{cases}$$

Since $e^{-ax} = \sum_{n=0}^{\infty} \frac{(-ax)^n}{n!}$, we can have the following planar analytic system:

$$(3.2) \quad \begin{cases}
\frac{dx}{dt} = (r - 2rx^* - a(1-D)y^*)x - Dy + p(x,y), \\
\frac{dy}{dt} = a(1-D)y^*x + q(x,y),
\end{cases}$$

where the analytic functions $p(x, y)$ and $q(x, y)$ are given by

$$p(x,y) = (-r + \frac{a^2}{2}(1-D)y^*)x^2 - a(1-D)xy - \frac{a^3}{6}(1-D)y^*x^3 + \frac{a^2}{2}(1-D)x^2y + \cdots,$$

$$q(x,y) = -\frac{a^2}{2}(1-D)y^*x^2 + a(1-D)xy + \frac{a^3}{6}(1-D)y^*x^3 - \frac{a^2}{2}(1-D)x^2y + \cdots.$$

In the above derivation, note that $rx^* - r(x^*)^2 - (1 - e^{-ax^*})y^* = 0$, $y^*(1 - D - e^{-ax^*}) = 0$ since (x^*, y^*) is the interior equilibrium of system

(1.1) and $e^{-a(x+x^*)} = e^{-ax^*}(1 - ax + \frac{a^2}{2}x^2 - \frac{a^3}{6}x^3 + \cdots)$. From the equation (3.2), we have

$$J(0,0) = \begin{pmatrix} r - 2rx^* - a(1-D)y^* & -D \\ a(1-D)y^* & 0 \end{pmatrix}.$$

Observe that $\Delta = aD(1-D)y^* > 0$ and $\mu = r - 2rx^* - a(1-D)y^*$. If we assume $\mu = 0$, then the Liapunov number σ is given by the formula(the detail derivation is given in the appendix):

$$(3.3) \qquad \sigma = \frac{3\pi}{2D\Delta^{3/2}}a^2 D(1-D)y^*(r - 2rD - \frac{a^2}{2}y^*(1-D)^2).$$

LEMMA 3.2. *If $\mu = 0$, then $\sigma < 0$.*

Proof. Since $\mu = r - 2rx^* - a(1-D)y^* = 0$ and $x^* = -\frac{1}{a}\ln(1-D)$, we have

$$\sigma = \frac{3\pi}{2D\Delta^{3/2}}a^2 D(1-D)y^*(r - 2rD - \frac{a}{2}r(1-D)(1-2x^*))$$

$$= \frac{3\pi}{2D\Delta^{3/2}}a^2 rD(1-D)y^*(1 - 2D - \frac{a}{2}(1-D) - (1-D)\ln(1-D)).$$

Using the fact that $a = -\frac{2D+(1-D)\ln(1-D)}{D+(1-D)\ln(1-D)}\ln(1-D) > 2$ for $0 < D < 1$ from [4],

$$\sigma < \frac{3\pi}{2D\Delta^{3/2}}a^2 rD(1-D)y^*(-D - (1-D)\ln(1-D)).$$

Let $F(D) := -D - (1-D)\ln(1-D)$, then we see that $F(D) < 0$ for $0 < D < 1$ since $F(0) = 0$ and $F'(D) = \ln(1-D) < 0$, and therefore $\sigma < 0$. $\qquad\square$

Finally, using Theorem 3.1(The Hopf Bifurcation Theorem), we have the following theorem.

THEOREM 3.3. *If*

$$a > -\frac{2D + (1-D)\ln(1-D)}{D + (1-D)\ln(1-D)}\ln(1-D),$$

then system (1.1) has a unique stable limit cycle; otherwise, system (1.1) has no limit cycle.

EXAMPLE 3.4. (Numerical simulation) *We consider the following system*

$$(3.4) \qquad \begin{cases} \frac{dx}{dt} = 0.4x(1-x) - (1-e^{-3x})y, \\ \frac{dy}{dt} = y((1-e^{-3x}) - 0.5), \\ x(0) = 1, \ y(0) = 0.5. \end{cases}$$

Comparing to system (3.3), $r = 0.3$, $a = 3$ and $D = 0.5$. It is easy to see that $1 - D - e^{-a} \cong 0.04 > 0$ and

$$a > -\frac{2D + (1 - D)\ln(1 - D)}{D + (1 - D)\ln(1 - D)} \ln(1 - D) \cong 2.95.$$

Theorem 3.3 yields that system (1.1) has a unique stable limit cycle. Figure 1 shows the dynamic behaviors of the solution $(x(t), y(t))$ which is a positive periodic solution of (3.4).
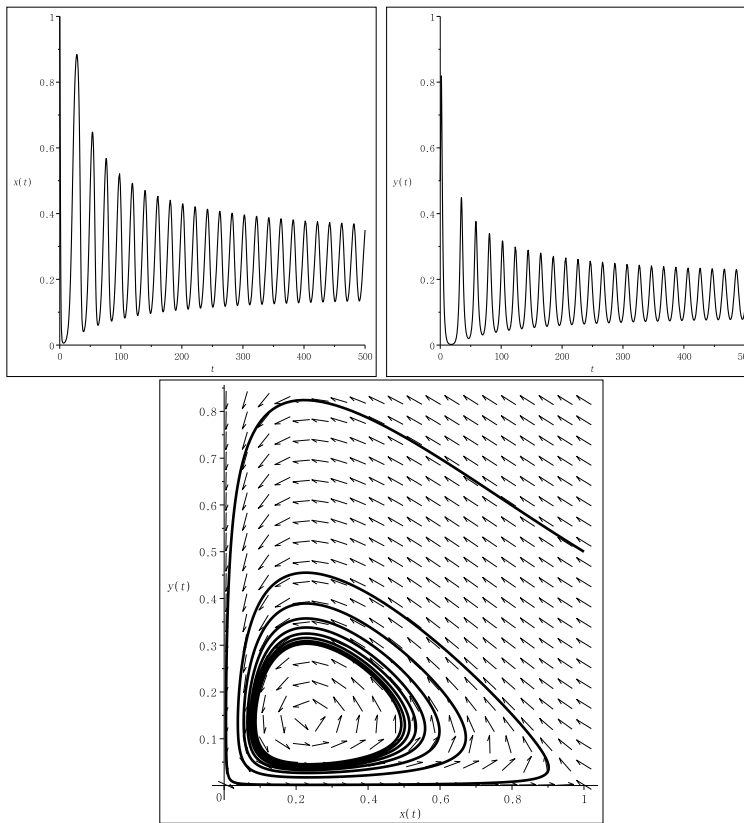

FIGURE 1. Evolution of the positive periodic solutions of system (3.1)

Appendix

In this section, we summarize the results(Theorem 2.1, 2.2 and 3.3) for system (1.1) in Table 1 and derive the equation (3.3) in detail.

I. Summarization of the dynamics for (1.1).

Conditions	$(0,0)$	$(1,0)$	(x^*, y^*)
$1 - D - e^{-a} < 0$, $1 - D - e^{-a} \neq -r$	Saddle	Stable node (Global Attractor)	Don't exist
$1 - D - e^{-a} < 0$, $1 - D - e^{-a} = -r$	Saddle	Stable (Global Attractor)	Don't exist
$1 - D - e^{-a} > 0$, $\tau \leq 0$, $\tau^2 - 4\Delta > 0$	Saddle	Saddle	Stable node (Global Attractor)
$1 - D - e^{-a} > 0$, $\tau \leq 0$, $\tau^2 - 4\Delta < 0$	Saddle	Saddle	Stable spiral (Global Attractor)
$1 - D - e^{-a} > 0$, $\tau \leq 0$, $\tau^2 - 4\Delta = 0$	Saddle	Saddle	Stable (Global Attractor)
$1 - D - e^{-a} > 0$, $\tau > 0$	Saddle	Saddle	Unique limit cycle

TABLE 1. The dynamics of (1.1).

II. Derivation of (3.3).

$$
\begin{aligned}
\sigma &= \frac{3\pi}{2D\Delta^{3/2}}\left\{-D^2[2(-r + \frac{a^2}{2}(1-D)y^*) \cdot (-\frac{a^2}{2}(1-D)y^*) \right. \\
&\quad + a(1-D) \cdot (-\frac{a^2}{2}(1-D)y^*)] \\
&\quad - aD(1-D)y^* \cdot a(1-D) \cdot (-r + \frac{a^2}{2}(1-D)y^*) \\
&\quad \left. + aD(1-D)y^* \cdot [3D \cdot (-\frac{a^3}{6}(1-D)y^*) + D \cdot (-\frac{a^2}{2}(1-D))]\right\} \\
&= \frac{3\pi}{2D\Delta^{3/2}}\left\{a^2 D^2(1-D)y^*(-r + \frac{a^2}{2}(1-D)y^*) + \frac{a^3}{2}D^2(1-D)^2 y^* \right. \\
&\quad - a^2 D(1-D)^2 y^*(-r + \frac{a^2}{2}(1-D)y^*) \\
&\quad \left. - \frac{a^4}{2}D^2(1-D)^2(y^*)^2 - \frac{a^3}{2}D^2(1-D)^2 y^*\right\} \\
&= \frac{3\pi}{2D\Delta^{3/2}}a^2 D(1-D)y^*\left\{-rD + \frac{a^2}{2}D(1-D)y^* \right. \\
&\quad \left. + r - \frac{a^2}{2}(1-D)y^* - rD + \frac{a^2}{2}D(1-D)y^* - \frac{a^2}{2}D(1-D)y^*\right\} \\
&= \frac{3\pi}{2D\Delta^{3/2}}a^2 D(1-D)y^*(r - 2rD + \frac{a^2}{2}D(1-D)y^* - \frac{a^2}{2}(1-D)y^*) \\
&= \frac{3\pi}{2D\Delta^{3/2}}a^2 D(1-D)y^*(r - 2rD - \frac{a^2}{2}y^*(1-D)^2).
\end{aligned}
$$

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