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Uniqueness of limit cycle in the predator-prey system

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Contents

1. Basic facts on predator-prey systems

The predator-prey model was originally developed by Lotka (1925) and Volterra (1931) from observations of the various fish populations in the upper Adriatic in the 1920's. It describes the nature of population fluctuations. The model is

$$\begin{aligned} x' &= x(a - cy), \\ y' &= y(dx - b), \end{aligned} \tag{1}$$

where x is the prey density, y is predator density and a, b, c, d are positive constants. Without predators the prey population grows at the Malthusian rate ax which is decreased by cx as a result of encounters with predators. Similarly, without preys as food predators decrease at rate $-by$, but the appearence of preys helps slow down this decrease by dx. It is easy to see that there are two critical points of system (1) $(0, 0)$ and $(\frac{b}{d}, \frac{a}{c})$. Simple analysis, which can be omited here, shows that the first critical point $(0, 0)$ is a saddle point and the second critical point $(\frac{b}{d}, \frac{a}{c})$ is a centre with neutral stability.

The existence and the uniqueness of the limit cycle are two important problems closely connected with two-dimensional predator-prey models, which are generalizations of system (1). This question has been completely solved for the well-known system

$$\begin{aligned} x' &= rx\left(1 - \frac{x}{k}\right) - \frac{m}{\alpha}\left(\frac{yx}{a + x}\right), \\ y' &= y\left(\frac{mx}{a + x} - D_0\right), \end{aligned} \tag{2}$$

where x is the prey density, y the predator density, and r, k, m, α, a, D_0 are positive constants. The coefficient D_0 is the relative death-rate of the predator, m is the maximal relative increase of the predator and a is the Michaelis – Menten constant. It represents the amount of prey necessary for the reproduction rate $p/2$ of the predator. We have $\alpha < 1$, since the whole biomass of the prey is not transformed to the biomass of the predator and the constant k is the carrying capacity of the prey population. In the absence of the predator, the prey population develops according to the logistic equation.

Hsu, Hubbell and Waltman showed [7] that if there exists an asymptotically stable positive equilibrium, then it is also globally stable. For the same model Cheng [1] proved that if such an equilibrium is unstable, then it possesses a unique globally asymptotically stable limit cycle. His proof was extended by Conway and Smoller [3] to systems for which the prey isocline is symmetric with respect to its maximum. Moreover, the existence of a system with at least two limit cycles is proved in [3].

In this dissertation thesis we consider the predator-prey system

$$\begin{aligned} x' &= xg(x) - yp(x), \\ y' &= y[q(x) - \gamma], \\ & (x(0) \geq 0, \;\; y(0) \geq 0), \end{aligned} \tag{3}$$

which is a a special case of the model introduced by Gause ([5]). The function $g(x)$ represents the relative increase of the prey in terms of its density. For low densities the number of offspring is greater than the number who have died, and so $g(x)$ is positive. As the density increases, living conditions deteriorate and the death-rate is greater than birth-rate and hence $g(x)$ is negative. The function $cp(x) - \gamma$ gives the total increase of the predator population. This is negative for low values of prey densities, i.e., the prey population is insufficient to sustain the predator. The function $p(x)$, called trophic function of the predator or functional response, expresses the number of consumed prey by a predator in a unit of time as a function of the density of the prey population [12].

In chapter 2 we extend Cheng's proof of uniqueness of the limit cycle for system (3) under the assumption $q(x) = cp(x)$. This extension cannot be done without several additional assumptions. Keeping the original assumption of symmetry of the prey isocline with respect to its maximum, which was implicitly contained in the Cheng's paper, we have to assume two further conditions. First, a condition concerning $p(x)$ is natural since in system (3) but not in (2) $p(x)$ is an arbitrary function. The latter condition was found by Kuang and Freedman [10]. They investigated a predator - prey system of the Gause type. By transforming to a generalized Lienard system they derived sufficient conditions for the uniqueness of limit cycle, which can be applied to system (3). But since this system has certain symmetric properties, we can considerably contract the interval in which this condition must be satisfied. In this chapter we also show that extension of Cheng's proof due to Conway and Smoller [3] contains a serious gap.

In chapter 3 we generalized the condition ensuering the uniqueness of limit cycle due to Liou and Cheng [11]. They further developed a method of reflection from [1]. Our generalization extends a class of predator-prey systems for which the uniqueness of limit cycle is ensured.

We study system (3) under the following assumptions:

(i) There exists a number $k > 0$ such that
$g(x) > 0$ for $0 \leq x < k$; $\quad g(k) = 0$; $\quad g(x) < 0$ for $x > k$.

(ii) $p(0) = 0$; $\quad p'(x) > 0$ for $x > 0$; $\quad p'_+(0) > 0$.

$$q(0) = 0; \quad q'(x) > 0 \text{ for } x > 0; \quad q'_+(0) > 0.$$

(iii) There is a unique point (x^*, y^*) with $0 < x^* < k,\ \ y^* > 0$ such that $q(x^*) - \gamma = 0$, $x^* g(x^*) - y^* p(x^*) = 0$.

(iv) The prey isocline $h(x) := \frac{xg(x)}{p(x)}$ is an unimodal function and there exists m, $0 < m < k$, such that $h'(x) > 0$ for $x \in (0, m)$, $h'(x) = 0$ for $x = m$ and $h'(x) < 0$ for $m < x$.

(v) The functions $g(x)$, $p(x)$, $q(x)$ are as smooth as required.

The conditions (i) - (iii) are natural in the biological context mentioned above. The last two conditions are necessary for mathematical calculations.

Under these assumptions system (3) has three equilibria $\mathbf{0} = (0, 0)$, $\mathbf{K} = (k, 0)$, and $\mathbf{E}^* = (x^*, y^*)$. Simple analysis of the Jacobian of system (3), which has the form

$$\mathbf{J} = \begin{bmatrix} g(x) + xg'(x) - yp(x) & -p(x) \\ yq'(x) & q(x) - \gamma \end{bmatrix},$$

yields that points $(0, 0)$ and $(k, 0)$ are saddle points. Next since Jacobian $\mathbf{J}$ at point (x^*, y^*) is

$$\mathbf{J} = \begin{bmatrix} p(x^*)h'(x^*) & -p(x^*) \\ y^* q'(x^*) & 0 \end{bmatrix}$$

the eigenvalues are given by

$$\frac{1}{2}\left(p(x^*)h'(x^*) \pm \sqrt{[p(x^*)h'(x^*)]^2 - 4p(x^*)y^* q'(x^*)} \right).$$

Hence (x^*, y^*) is stable if $h'(x^*) < 0$, and (x^*, y^*) is unstable if $h'(x^*) > 0$. If $h'(x^*) = 0$ point (x^*, y^*) is a center.

It is known that the existence and stability of a limit cycle is related to the existence of a positively invariant set of system (3) and to the existence and stability of positive equilibrium. If the equilibrium is asymptotically stable, then there may exist limit cycles, the innermost of which must be unstable from the inside, and the outermost of which must be stable from the outside. If limit cycles do not exist in this case, the equilibrium is globally asymptotically stable. Conditions for the last situation are given e.g. by Cheng, Hsu, and Lin [2].

From the existence of a positively invariant set of system (3) and from unstability of the critical point (x^*, y^*) follows that there is at least one periodic orbit surrouding point (x^*, y^*) (Poincaré-Bendinxon theorem). It is posible to prove that such invarint set can be found as a trapezoid

0KAB (see Fig. 1). Moreover, the orbit passing through every point in the positive quadrant enters trapezoid **0K**AB in finite time. Proofs of the existence of limit cycles are given e.g. in [4]

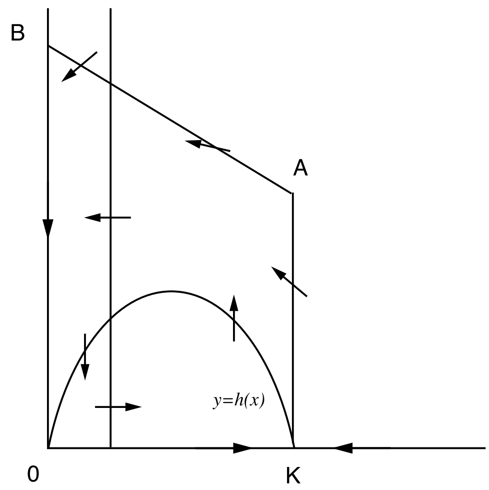

Fig. 1

It is well-known fact that for analysis of the global stability of the positve equilibrium as well as for analysis concerning the uniquness of the limit cycle Lyapunov function may be useful. Its suitable form was found by Harrison [6] in 1979. He proved that function

$$V(x,y) = \int_{x^*}^{x} \frac{q(\xi) - q(x^*)}{p(\xi)} d\xi + \int_{y^*}^{y} \frac{\eta - y^*}{\eta} d\eta$$

is Lyapunov function of system (3). We use his result in proofs of our results in both following chapters.

2. The known conditions of the uniqueness of the limit cycle for system (3)

As we mentioned above Cheng [1] in 1981 proved the uniqueness of the limit cycle for predator-prey system. In the next years several criteria for the uniqueness of the limit cycle was found. Kuang and Freedman [10] and Huang and Merrill [8] transformed a class of predator prey models of Gause type to a generalized Lienard system, where the results of uniqueness of the limit cycle are available. Their main result, rewritten for system (3) is the following theorem.

THEOREM 1.1

Suppose in system (3)
(i) $h'(x^*) > 0$,
(ii) $\frac{d}{dx}\left(\frac{p(x)h'(x)}{q(x)-\gamma}\right) \leq 0$,
in $0 \leq x < x^*$ *and* $x^* < x \leq k$. *Then system (3) has exactly one limit cycle which is globally asymptotically stable with respect to the set* $\mathbf{R}_+^2 \setminus E^*$.

Liou and Cheng [11] further developed a method of reflection from [1] to extend the class of predator prey models for which the uniqueness of limit cycle is ensured. They studied system (3) under te condition $p(x) = x$. It is interesting to compare their main result with theorem 1.3.

THEOREM 1.2

Suppose in system (3)
(i) $h'(x^*) > 0$
(ii) $\frac{d}{dx}\left(\frac{xh'(x)}{q(x)-\gamma}\right) \leq 0$,
in $0 \leq x < x^*$ *and* $\bar{x}^* < x \leq k$, *where* $\bar{x}^* = h_2^{-1} \circ h_1(x^*)$ *and* $h_1 = h|_{(0,m)}, h_2 = h|_{(m,k)}$. *Then system (3) has exactly one limit cycle which is globally asymptotically stable with respect to the set* $\mathbf{R}_+^2 \setminus E^*$.

Recently the generalization of the result from Theorem 1.1 appeared in Tzy-Wei Hwang's paper [9]. His result, again rewritten for system (3), is

THEOREM 1.3

Suppose in system (3)
(i) $h'(x^*) > 0$,
(ii) there exist $\alpha, \beta \geq 0$ *such that* $\frac{d}{dx}\left(\frac{p(x)h'(x)}{(q(x)-\gamma)(\alpha+\beta h(x))}\right) \leq 0$,
in $0 \leq x < x^*$ *and* $x^* < x \leq k$. *Then system (3) possesses exactly one limit cycle which is globally asymptotically stable with respect to the set* $\mathbf{R}_+^2 \setminus E^*$.

3. The new results

Our main result in chapter 2 gives further contraction of the interval where condition (ii) from theorems 1.1 and 1.2 must be satisfied. Through this chapter we assume that the prey isocline $h(x)$ is symmetric function with respect to its maximum and consider the case $q(x) = cp(x)$. Under these assumptions the following theorem holds.

THEOREM (3.1 chapter 2)

Let for system (3) the following assumptions be satisfied.
(i) $h(x^*) > 0$,
(ii) $p(x')(cp(x) - \gamma) + p(x)(cp(x') - \gamma) \leq 0$ *for* $x' \in [0, x_Q]$, *where* $x' = 2m - x$,
(iii) $\frac{d}{dx}\left(\frac{p(x)h'(x)}{cp(x)-\gamma}\right) \leq 0$, *for* $x \in (2m - x^*, k]$.
Then system (3) possesses a unique limit cycle which is globally asymptotically stable in the positive quadrant.

In chapter 3 we derive the condition ensuring the uniqueness of the limit cycle. We generalize the result from theorem 1.2 by introducing the function $W(x)$, which was motivated by Tzy-Wei Hvang's paper. The result is

THEOREM (2.1 chapter 3)

Let for the system (1) the following assumptions be satisfied:
(i) $x^\star < m$,
(ii) $\frac{d}{dx}\left(\frac{p(x)h'(x)}{(q(x)-\gamma)(W(x))}\right) \leq 0$ *for* $x \in (0, x^*) \cup (\bar{x}^*, k)$,
where $W(x)$ *is a smooth positive funcion such that*
$W(x) = W(\bar{x})$ *for* $x \in (0, x^*) \cup (\bar{x}^*, k)$,
$W'(x)$ *is negative for* $x \in [0, x^*)$ *and positive for* $x \in (\bar{x}^*, k]$,
the equality $W(x) = -\frac{(q(x)-\gamma)}{p(x)h'(x)}$ *holds in no subinterval of intervals* $(0, x^*)$, $(\bar{x}^*, k)$.
Then system (1) possesses a unique limit cycle which is globally asymptotically stable in the positive quadrant.

4. Presentation and publications

The main results of the dissertation were reported at the Seminar on Dynamical Systems in Opava (Mathematical Institute of the Silesian University, 1997 - 2000), Seminar on Differential Equations and Integration Theory in Prague (Mathematical Institute of the Czech Academy of Sciences, 2000),and on Sixth Colloquium on the Qualitative Theory of Differential Equations in Szeged (1999). They are published in the paper

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