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LETTER TO THE EDITOR

Existence of more limit cycles in general predator–prey models

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Abstract. Determining the number of limit cycles for a system is normally very difficult. In this letter, we present some sufficient conditions which guarantee that the general predator-prey model of Huang has at least three limit cycles around the equilibrium point. Our approach can be generalised to discuss the existence of $2n+1$ limit cycles in the model.

To determine how many limit cycles a system has is not an easy problem. Most of the work reported on this topic has been the following (Zhang 1985).

1. Finding the least upper bound of the number of limit cycles in the system concerned.
2. Constructing examples to show that exactly n limit cycles can exist for the system.
3. Providing some sufficient conditions that guarantee there are at least n limit cycles in the system.
4. Finding conditions that guarantee n and only n limit cycles exist in the system.

Recently we proposed a general predator-prey model (Huang 1988a) and discussed the local and global stability, existence, non-existence and uniqueness of limit cycles of the model (Huang 1988b, Huang and Merrill 1988). In this letter, we provide some sufficient conditions that guarantee that the system has at least three limit cycles.

We consider the following model:

$$\begin{aligned} dx/dt &= \phi(x)(F(x) - \pi(y)) \\ dy/dt &= \rho(y)\psi(x) \end{aligned} \tag{1}$$

where x is the prey density, y is the predator density, $\phi(x)$, $\psi(x)$ are the predator response functions, $\pi(y)$, $\rho(y)$ are the predator density functions, $\phi(x)F(x)/x$ is the 'relative' or 'per capita' growth function which governs the growth of the prey in the absence of predators, $\phi(x)\pi(y)/x$ is the death rate of the prey due to the predator, $\rho(y)\psi(0)/y$ is the death rate of predator in the absence of prey.

Our fundamental assumptions are as follows.

(H_1) $\phi, F, \psi, \pi, \rho \in C^1[0,\infty)$, $\phi(0) = \pi(0) = \rho(0) = 0$, $F \in C^1(0,\infty)$; $\phi' > 0$ for $x \geq 0$, $\pi' > 0, \rho' > 0$ for $y \geq 0$; there exists $x^* > 0$ such that $\psi(x^*) = 0, \psi'(x^*) > 0$ and $(x - x^*)\psi(x) > 0$ for $x \neq x^*$; there exist positive constants m_1 and m_2 such that

(H_1^*) $\qquad \phi(x) \leq m_1 + m_2 x \qquad$ for $x \geq 0$.

(H_2) The curve $\pi(y) - F(x) = 0$ is defined for all $x > 0$.

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(H_3) $F(0)\in(0,\infty)$, there exists a $k>x^*$ such that $F(k)=0$, $F'(k)<0$, $F(x)>0$ for $0<x<k$, and for any $\bar{k}>k$, $F'(\bar{k})\neq 0$ if $F(\bar{k})=0$. Moreover, there exists a $k^*<\infty$ such that $F(k^*)=0$ and $F(x)\neq 0$, for any $x>k^*$.
(H_4) There exist positive numbers M and ε such that $\pi(y)\geq M\rho(y)$ for $y\geq\varepsilon$ and such that there exists a number y_1 with

$$\rho(y_1)>(F(x)/M)+\varepsilon \text{ for all } x\in[x^*, k].$$

It has been shown that very many predator-prey models satisfy these assumptions. It is also possible to have $F(0)=\infty$ in (H_3) in most of this discussion. In that case $(0, 0)$ is no longer an equilibrium point. Moreover, we can easily extend ϕ, ψ, π and ρ to the whole real axis and consider, if necessary, $\phi, \psi, \pi, \rho\in C^1(-\infty, +\infty)$.

For the global analysis we need to assume that:
(H_5) there exists a k^* such that $F(x)<0$ for $x>k^*$.

All our discussion is in the interior of the first quadrant $\Omega=\{(x, y): x>0, y>0\}$. Clearly, for system (2.1) there is only one equilibrium point (x^*, y^*) in Ω.

Our uniqueness theorem of limit cycles is as follows.

Theorem 1 (Huang 1988a, Huang and Merril 1988). If, in addition to assumptions (H_1)-(H_4), we let

(i) $F'(x^*)>0$,

(ii) $-F'(x)\phi(x)/\psi(x)$ is non-decreasing for $0<x<x^*$ and $x^*<x<k$,

then the system (2.1) has a unique limit cycle around (x^*, y^*). The limit cycle is stable and globally asymptotically stable in Ω if (H_5) holds; otherwise it is locally asymptotically stable.

Consider the following auxiliary system:

$$\begin{aligned} &\mathrm{d}x/\mathrm{d}t=\phi(x)(F_i(x)-\pi(y))\\ &\mathrm{d}y/\mathrm{d}t=\rho(y)\psi(x)\\ &x(0)=x_0>0 \qquad y(0)=y_0>0 \qquad i=1,2. \end{aligned} \tag{2}$$

Suppose that (x^*, y^*) is the only equilibrium point in Ω of system (2). That is, $\psi(x^*)=0$ and $\pi(y^*)=F_1(x^*)=F_2(x^*)$. Let $P_0=(x^*, y_0)$ with $y_0<y^*$ and Γ_i be the orbit of system (2) starting at P_0. Also, suppose that A_i, Q_i, B_i are the first points (in time spent) of Γ_i intersecting with the rays $x=x^*, y>y^*$, $y=y^*, x<x^*$ and $x=x^*, y<y^*$, respectively (as shown in figure 1). Denote (x_P, y_P) as the coordinates of the point P. Then we have the following.

Lemma 1. If

$$\begin{aligned} &F_1(x)\leq F_2(x) \qquad \text{if } x\in[0, x^*]\\ &F_1(x)\geq F_2(x) \qquad \text{if } x\in[x^*, k] \end{aligned} \tag{3}$$

with strict inequality for some x in $[0, x^*]$ and $[x^*, k]$, respectively, then

(i) $y_{A_1}>y_{A_2}$,

(ii) $y_{B_1}<y_{B_2}$,

(iii) $x_{Q_1}<x_{Q_2}$ and

(iv) $\pi(y_{B_i})\leq F_i(x_{Q_i})$ if $F_i'(x)\geq 0$ for $0\leq x\leq x^*$, $i=1,2$.

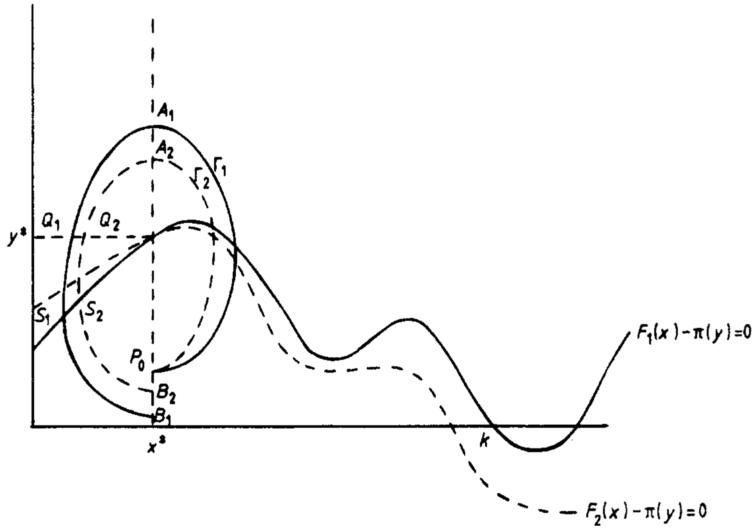

Figure 1. Full curves are for system (2), broken curves for system (3).

Proof. Let the vector $\overline{V_i}$ be defined as

$$\overline{V_i}=(\phi(x)(F_i(x)-\pi(y)),\ \rho(y)\psi(x),\ 0) \qquad i=1,2.$$

Consider the cross product of $\overline{V_1}$ and $\overline{V_2}$:

$$\overline{V_1}\times\overline{V_2}=(0,0,\ \phi(x)\rho(y)\psi(x)(F_1(x)-F_2(x))). \tag{4}$$

By (3),

$$\phi(x)\rho(y)\psi(x)(F_1(x)-F_2(x))\geqslant 0$$

for $0\leqslant x\leqslant x^*$. Hence the flow of (2) is always directed outside with respect to the flow of (3). Therefore (i)–(iii) hold.

Suppose Γ_i intersects with the prey isocline $\pi(y)-F_i(x)=0 (0\leqslant x\leqslant x^*)$ at S_i. Then, since

$$\begin{aligned}
&\mathrm{d}y/\mathrm{d}t<0 && \text{if } 0<x<x^*\\
&\mathrm{d}x/\mathrm{d}t<0 && \text{if } 0<x<x^* \text{ and } F_i(x)-\pi(y)<0\\
&\mathrm{d}x/\mathrm{d}t=0 && \text{if } F_i(x)-\pi(y)=0\\
&\mathrm{d}x/\mathrm{d}t>0 && \text{if } 0<x<x^* \text{ and } F_i(x)-\pi(y)>0
\end{aligned} \tag{5}$$

we have

$$x_{S_i}\leqslant x_{Q_i} \qquad i=1,2.$$

If $F_i'(x)\geqslant 0$ for $x\in[0,x^*]$, then

$$\pi(y_{B_i})\leqslant\pi(y_{S_i})=F_i(x_{S_i})\leqslant F_i(x_{Q_i}).$$

Thus (iv) is verified and the proof of lemma 1 is completed.

Now, following the arguments of the existence theorems of Huang (1988b) and Huang and Merrill (1988), there exists $\delta>0$ such that

$$y_0-y_{B_1}(y_0)<0 \qquad \text{for all} \qquad y_0\in(0,\delta). \tag{6}$$

Here B_1 is the intersection of the orbit $\Gamma_1(x^*, y_0)$ and the line segment $x = x^*, 0 < y < y^*$; $y_{B_1}(y_0)$, the y coordinate of B_1, is a continuous function of y_0.

We now fix δ and find an $x_1 \in (x^*, k)$ such that $F(x) > 0$ for $x \in [x^*, x_1]$ and all the orbits starting at (x^*, y_0) with $y_0 \in (\delta/2, y^*)$ will be contained in the region $\{(x, y) \mid y > 0, 0 < x < x_1\}$. Moreover, by the boundedness of solutions with the initial values $x(0) = x^*$, $y(0) = y_0 \in (\delta/2, y^*)$ (see, Huang 1988b, for example), we can assume, if a limit cycle in system (1) exists, it must be inside a circle. Assume it is inside the circle

$$(x - x^*)^2 + (y - y^*)^2 = r_0 \qquad r_0 \in (0, y^*). \tag{7}$$

Let

$$\alpha_1 = \min_{x \in [x^*, x_1]} \{\pi^{-1}(F(x))\} \qquad \alpha_2 = y^* = \pi^{-1}(F(x^*)).$$

Suppose $F'(x^*) > 0$. There exists $x_2 \in [x^*, x_1]$ such that

$$F(x_2) = F(x^*) \text{ and } F(x) \geq F(x^*) \text{ for all } x \in [x^*, x_2].$$

Moreover, since $F(k) = 0$, there exist $x_3 \in [x_2, x_1]$ and $x_4 \in [x_1, k)$ such that

$$F(x_3) = F(x_4) = \pi(\alpha_1).$$

Define $F_i(x)$ $(i = 1, 2)$ as

$$F_1(x) = F(x)$$

$$F_2(x) = \begin{cases} \alpha_2 & 0 \leq x \leq x_2 \\ F(x) & x_2 < x \leq x_3 \\ \alpha_1 & x_3 < x \leq x_4 \\ F(x) & x_4 < x \leq k. \end{cases} \tag{8}$$

Clearly, $F_i(x)$ is continuous and satisfies Lipschitz's condition.

Now, consider the system

$$\begin{aligned} dx/dt &= \phi(x)(F_i(x) - \pi(y)) \\ dy/dt &= \rho(y)\psi(x) \end{aligned} \tag{9}$$

and denote its orbit starting at (x^*, y_0) as $\Gamma_i(x^*, y_0)$, $i = 1, 2$. We can prove the following.

Theorem 2. In addition to (H_1)–(H_4), suppose system (1) satisfies

(i) $F'(x) \geq 0$ for $0 \leq x \leq x^*$ and $F'(x^*) > 0$,

(ii) there exists $\bar{y} \in (0, y^* - r_0)$ such that

$$\pi(\bar{y}) > F(x_{Q_2}(\bar{y}))$$

where Q_2 is the intersection of $\Gamma_2(x^*, \bar{y})$ and the line segment $y = y^*, 0 < x < x^*$.

The system (1) has at least three limit cycles around (x^*, y^*).

Proof. Define a function of y_0 as

$$g(y_0) = y_0 - y_{B_1}(y_0) \tag{10}$$

where B_1 is the intersection of $\Gamma_1(x^*, y_0)$ and the line segment $x = x^*, 0 < y < y^*$.

Since $F'(x^*) > 0$, (x^*, y^*) is unstable, and, if $y_0 < y^*$ and y_0 is sufficiently close to y^*,

$$g(y_0) > 0. \tag{11}$$

Also, since system (1) satisfies the existence conditions of limit cycles (Huang 1988b, Huang and Merrill 1988), there is at least one stable limit cycle around (x^*, y^*). Thus, we can find a $y_1 \in (y^* - r_0, y^*)$ such that

$$g(y_1) = 0. \tag{12}$$

The stability of the above limit cycle implies that there exists $\delta > 0$ such that

$$g(y_0) < 0 \qquad \text{for} \qquad y_0 \in (y_1 - \delta, y_1). \tag{13}$$

Now, by lemma 1 and (ii),

$$\begin{aligned}\pi(y_{B_1}(\bar{y})) &\leqslant F_1(x_{S_1}(\bar{y}))\\ &\leqslant F_1(x_{Q_1}(\bar{y}))\\ &\leqslant F_2(x_{Q_2}(\bar{y}))\\ &< \pi(\bar{y}).\end{aligned}$$

Thus,

$$g(\bar{y}) > 0. \tag{14}$$

Since $g(y_0)$ is continuous with respect to y_0, there exist

$$y_2 \in (\bar{y}, y_1) \qquad \text{and} \qquad y_3 \in (0, \bar{y})$$

such that

$$g(y_2) = g(y_3) = g(y_1) = 0.$$

Clearly each orbit starting at (x^*, y_i) $(i = 1, 2, 3)$ is a limit cycle of system 1. We thus complete the proof of theorem 2.

We would like to make the following remarks on our discussion and the related problems.

1. The condition (ii) in theorem 2 is not difficult to check since, by the uniqueness of solutions, we can solve the separable equation

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{\rho(y)\psi(x)}{\phi(x)(\alpha_2 - \pi(y))}$$

$$x(0) = x^* \qquad y(0) = \bar{y}$$

in $0 \leqslant x \leqslant x^*$ and then determine $x_{Q_2}(\bar{y})$.

2. A similar argument will result in the existence of $2n + 1$ limit cycles in system (1).

3. The study of model (1) is similar to that of Kuang (1988). But we would like to mention that Kuang's model is only a special case of our model with $F(0) < \infty$ and $F(x) < 0$ for all $x > k$. Also, the assumptions (H_1^*), (H_2) and (H_4) (or something similar) are necessarily required by Kuang. Without these assumptions most of his results can be shown to be incorrect. As an easy example, Kuang claimed (1988, p 57) that every trajectory of the system

$$\mathrm{d}x/\mathrm{d}t = p(x)(\beta - \xi(y)) \qquad x(0) = x_0 > 0$$

$$\mathrm{d}y/\mathrm{d}t = \eta(y)(r - q(x)) \qquad y(0) = y_0 > 0$$

with constant $\beta > 0$, is a closed orbit. But if we let

$$\xi(y) = y \qquad \eta(y) = y(y+1) \qquad p(x) = q(x) = q(x) = x \qquad \text{and} \qquad \beta = x_0 = y_0 = r = 1$$

then the above system satisfies all the hypotheses of Kuang (1988), but no periodic solutions exist.

In fact, in most of the arguments of Kuang, $\xi(y)$ and $\eta(y)$ are automatically considered as y. For instance, according to the definition that the prey isocline is the curve along which the rate of prey growth is instantaneously zero (Freedman 1980), that of Kuang's model should be $\xi(y) = xg(x)/p(x)$. But it was employed as $y = xg(x)/p(x)$ (see, for example, Kuang 1988, p 60).

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