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UNIQUENESS OF A LIMIT CYCLE FOR A PREDATOR-PREY SYSTEM*

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Abstract. The uniqueness of a limit cycle for a predator-prey system is proved in this paper. We assume that in the absence of predation the prey regenerates by logistic growth and the predator feeds on the prey with a saturating functional response to prey density. Specifically, we assume that Michaelis–Menten kinetics describe how feeding rates and birth rates change with increasing prey density.

1. Introduction. S. B. Hsu, S. P. Hubbell and Paul Waltman in [2] and [3] considered the following competing-predators system:

$$
\begin{aligned}
&\dot S(t)=\gamma S(t)\left(1-\frac{S(t)}{K}\right)-\left(\frac{m_1}{y_1}\right)\left(\frac{X_1(t)S(t)}{a_1+S(t)}\right)-\left(\frac{m_2}{y_2}\right)\left(\frac{X_2(t)S(t)}{a_2+S(t)}\right),\\
&\dot X_1(t)=X_1(t)\left(\frac{m_1S(t)}{a_1+S(t)}-D_1\right),\\
(1)\qquad &\dot X_2(t)=X_2(t)\left(\frac{m_2S(t)}{a_2+S(t)}-D_2\right),\\
&S(0)=S_0>0,\qquad X_i(0)=X_{i0}>0,\qquad i=1,2,
\end{aligned}
$$

where $X_i(t)$ is the population of the ith predator at time t, $S(t)$ is the population of the prey at time t, m_i is the maximum growth (birth) rate of the ith predator, D_i is the death rate of the ith predator, y_i is the yield factor of the ith predator feeding on the prey and a_i is the half-saturation constant of the ith predator, which is the prey density at which the functional response of the predator is half maximal. The parameters γ and K are the intrinsic rate of increase and the carrying capacity for the prey population, respectively. S. B. Hsu et al. analyzed solutions of this system of ordinary differential equations and found out that their behavior depends mainly on the two-dimensional system

$$
\begin{aligned}
&\dot S(t)=\gamma S(t)\left(1-\frac{S(t)}{K}\right)-\left(\frac{m}{y}\right)\left(\frac{x(t)S(t)}{a+S(t)}\right),\\
(2)\qquad &\dot x(t)=x(t)\left(\frac{mS(t)}{a+S(t)}-D_0\right),\\
&S(0)=S_0>0,\qquad x(0)=x_0>0,
\end{aligned}
$$

where γ, K, m, y, a and D_0 are positive constants.

The results they obtained for system (2) are as follows.

(a) The solutions $S(t)$, $x(t)$ of (2) are positive and bounded.

(b) Let $b=m/D_0$ and $\lambda=a/(b-1)$ if $b>1$.

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(i) If $b \leqq 1$ or $K \leqq \lambda$, then the critical point $(K, 0)$ of (2) is asymptotically stable and

$$\lim_{t\to\infty} S(t) = K, \qquad \lim_{t\to\infty} x(t) = 0.$$

(ii) If $\lambda < K \leqq a + 2\lambda$, then the critical point (λ, x^*), $x^* = (\gamma y/m)(1-\lambda/K)(a+\lambda)$, of (2) is asymptotically stable and

$$\lim_{t\to\infty} S(t) = \lambda, \qquad \lim_{t\to\infty} x(t) = x^*.$$

(iii) If $K > a + 2\lambda$, then (λ, x^*) is unstable and there exists at least one periodic orbit in the first quadrant of the S-x plane. If there is just one periodic orbit, it is stable. If the periodic orbit is not unique, then the outer one is semistable from the outside and the inner one is semistable from the inside.

S. B. Hsu et al. [3] conjectured that the limit cycle is unique and suggested that this can be a delicate question.

It is interesting mathematically to prove the uniqueness of the limit cycle for system (2). If this can be done, then we can better understand the behavior of solutions of (1). Therefore, the purpose of this paper is to show that the limit cycle of (2) is unique under the same conditions as in [2]. From now on we shall assume that $K > a + 2\lambda$.

2. Two lemmas.

LEMMA 1. *Let Γ be a nontrivial closed orbit of system* (2). *Then*

$$\Gamma \subset \{(S, x) | 0 < S < K, 0 < x\}.$$

Let L, R, H and J be the leftmost, rightmost, highest and lowest points of Γ respectively. Then

$$L \in \{(S, x) | 0 < S < \lambda, x = f(S)\},$$
$$R \in \{(S, x) | \lambda < S < K, x = f(S)\},$$
$$H \in \{(S, x) | S = \lambda, x^* < x\},$$
$$J \in \{(S, x) | S = \lambda, 0 < x < x^*\},$$

where $f(S) = \gamma(y/m)(1 - S/K)(a + S)$, the curve of which is symmetric with respect to the vertical line $S = (K-a)/2$, and $x^* = f(\lambda)$.

The proof is simple and we omit it.

LEMMA 2. *Let Γ be a nontrivial closed orbit of* (2). *Γ meets the vertical line $S = (K-a)/2$ at the points A and B with x-coordinates $x_B > x_A$.* (See Fig. 1.) *Let the mirror image of arc $\widehat{BHLJA}$ of Γ with respect to the "mirror" $S = (K-a)/2$ be $\widehat{BH'L'J'A}$. Then arc $\widehat{H'L'J'}$ intersects arc $\widehat{BRA}$ of Γ at two points $P(S_P, x_P)$ and $Q(S_Q, x_Q)$ with $x_Q > f(S_Q)$ and $x_P < f(S_P)$. Furthermore, if $P'(S_{P'}, x_{P'})$ and $Q'(S_{Q'}, x_{Q'})$ are respectively the mirror images of P and Q with respect to the mirror $S = (K-a)/2$, then*

$$0 < \frac{S_{Q'}}{\lambda - S_{Q'}} \leqq \frac{S_Q}{S_Q - \lambda} \tag{3}$$

and

$$0 < \frac{S_{P'}}{\lambda - S_{P'}} \leqq \frac{S_P}{S_P - \lambda}. \tag{4}$$

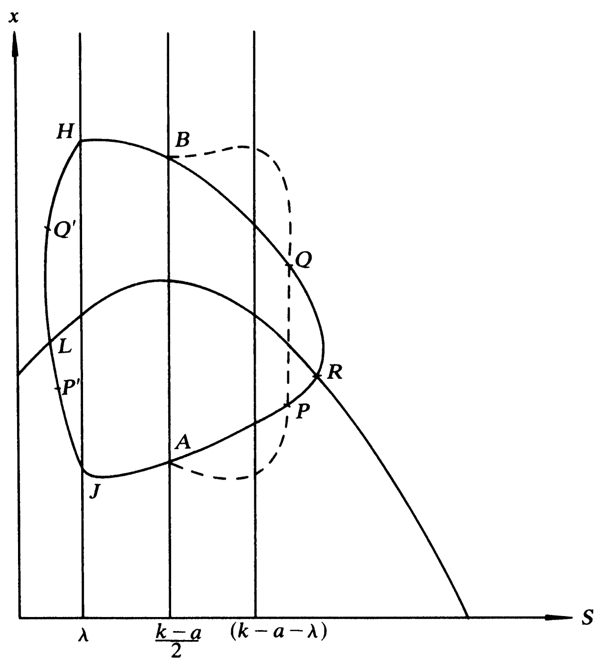

FIG. 1

Proof. Consider the function $V(S, x)$,

$$V(S,x)=\int_{\lambda}^{S}\frac{\left(\frac{m\xi}{a+\xi}-D_0\right)}{\frac{m\xi}{a+\xi}}\,d\xi+\frac{1}{y}\int_{x^*}^{x}\frac{\eta-x^*}{\eta}\,d\eta. \tag{5}$$

Then

$$\begin{aligned}\frac{dV(S(t),x(t))}{dt}&=\frac{1}{y}\left(\frac{mS}{a+S}-D_0\right)\left[\gamma\left(\frac{y}{m}\right)\left(1-\frac{S}{K}\right)(a+S)-x^*\right]\\&=\frac{1}{y}\left(\frac{mS}{a+S}-D_0\right)[f(S)-x^*].\end{aligned} \tag{6}$$

Let the period of Γ be T. We have

$$\int_0^T\frac{dV(S(t),x(t))}{dt}\,dt=0. \tag{7}$$

On the other hand,

$$\begin{aligned}\int_0^T\frac{dV}{dt}\,dt&=\frac{1}{y}\int_0^T\left(\frac{mS(t)}{a+S(t)}-D_0\right)[f(S(t))-x^*]\,dt\\&=\frac{1}{y}\oint_{\Gamma}[f(S)-x^*]\frac{dx}{x}.\end{aligned} \tag{8}$$

Now assume that arc $\widehat{H'L'J'}$ does not intersect arc $\widehat{BRA}$ of Γ.

It is easy to see that $S_{L'} > S_R$; that is, the region Ω_2 bounded by line $S=(K-a)/2$ and arc $\widehat{BRA}$ is properly contained in the region Ω_1' bounded by line $S=(K-a)/2$ and arc $\widehat{BH'L'J'A}$. From (7) and (8), we have

$$
\begin{aligned}
0 &= \int_0^T \frac{dV(S(t),x(t))}{dt}\,dt = \oint_\Gamma \frac{1}{y}\frac{[f(S)-x^*]}{x}\,dx \\
&= \frac{1}{y}\iint_{\Omega_1+\Omega_2} \frac{1}{x} f'(S)\,dS\,dx \qquad \text{(Green's theorem)} \\
&= \frac{1}{y}\iint_{\Omega_1} \frac{f'(S)}{x}\,dS\,dx + \frac{1}{y}\iint_{\Omega_2} \frac{f'(S)}{x}\,dS\,dx \qquad (9)\\
&= -\frac{1}{y}\iint_{\Omega_1'} \frac{f'(S)}{x}\,dS\,dx + \frac{1}{y}\iint_{\Omega_2} \frac{f'(S)}{x}\,dS\,dx \\
&= -\frac{1}{y}\iint_{\Omega_1'-\Omega_2} \frac{f'(S)}{x}\,dS\,dx > 0.
\end{aligned}
$$

This is a contradiction. Hence arc $\widehat{H'L'J'}$ does intersect arc $\widehat{BRA}$. Now assume that the points $Q(S_Q, x_Q)$ and $P(S_P, x_P)$ are, respectively, the "highest" and "lowest" intersection point. If $Q(S_Q, x_Q) = P(S_P, x_P)$, then arc $\widehat{H'L'J'}$ intersects arc $\widehat{BRA}$ only at a single point. In this case, the arguments leading to the conclusion that the region Ω_2 is properly contained in Ω_1' still hold. Yet this contradicts (9). Hence $Q(S_Q, x_Q) \neq P(S_P, x_P)$. Assume that $x_Q > f(S_Q)$. Let $(dx/dS)'_Q$ and $(dx/dS)_Q$ be the slopes of arcs $\widehat{BH'L'J'A}$ and $\widehat{BRA}$ at point Q respectively. It is obvious that

$$
0 > \left(\frac{dx}{dS}\right)_Q \geqq \left(\frac{dx}{dS}\right)'_Q. \qquad (10)
$$

But

$$
\begin{aligned}
\left(\frac{dx}{dS}\right)_Q &= \frac{x_Q\left(\dfrac{mS_Q}{a+S_Q} - D_0\right)}{\gamma S_Q\left(1-\dfrac{S_Q}{K}\right) - \left(\dfrac{m}{y}\right)\left(\dfrac{x_Q S_Q}{a+S_Q}\right)} \\
&= -(m-D_0)\left(\frac{y}{m}\right)\frac{x_Q(S_Q-\lambda)}{s_Q(x_Q-f(S_Q))},
\end{aligned}
$$

and

$$
\begin{aligned}
\left(\frac{dx}{dS}\right)'_Q &= -(m-D_0)\left(\frac{y}{m}\right)\frac{x_{Q'}(\lambda-S_{Q'})}{S_{Q'}(x_{Q'}-f(S_{Q'}))} \\
&= -(m-D_0)\left(\frac{y}{m}\right)\frac{x_Q(\lambda-S_{Q'})}{S_{Q'}(x_Q-f(S_Q))}.
\end{aligned}
$$

(Recall that $x_Q = x_{Q'}$, $f(S_Q) = f(S_{Q'})$.) Thus from (10) we have

$$
0 < \frac{S_{Q'}}{\lambda - S_{Q'}} \leqq \frac{S_Q}{S_Q - \lambda}. \qquad (11)
$$

Now consider the quadratic function $G(S')$,

$$G(S')=(S-\lambda)(\lambda-S')\left[\frac{S'}{\lambda-S'}-\frac{S}{S-\lambda}\right], \tag{12}$$

where $S=K-a-S'$. A straightforward calculation shows that

$$G(S')=-2S'^2+2S'(K-a)-\lambda(K-a).$$

The two positive roots of $G(S')=0$ are

$$S_\pm=\frac{K-a}{2}\pm\sqrt{\left(\frac{K-a}{2}\right)^2-\lambda\left(\frac{K-a}{2}\right)}.$$

Hence $G(S')<0$ if $S'<S_-$ or $S'>S_+$, and $G(S')>0$ if $S_-<S'<S_+$. Since $S_{Q'}<(K-a)/2<S_+$, from (11) and (12) we conclude that

$$S_{Q'}\leqq S_- \quad \text{or} \quad S_Q\geqq S_+. \tag{13}$$

The arc $\widehat{QR}$ satisfies the following differential equations:

$$\left(\frac{dx}{dS}\right)_{\widehat{QR}}=-(m-D_0)\left(\frac{y}{m}\right)\frac{x(S-\lambda)}{S(x-f(S))}, \qquad x(S_Q)=x_Q, \qquad S\geqq S_Q. \tag{14}$$

and $\widehat{QL'}$ satisfies

$$\left(\frac{dx}{dS}\right)_{\widehat{QL'}}=-(m-D_0)\left(\frac{y}{m}\right)\frac{x(\lambda-S')}{S'(x-f(S))}, \qquad x(S_Q)=x_Q, \qquad S\geqq S_Q, \tag{15}$$

where $S'=K-a-S$. Since $G(S')<0$ for $S'<S_-$, we have from (13), (14) and (15) that

$$0>\left(\frac{dx}{dS}\right)_{\widehat{QR}}>\left(\frac{dx}{dS}\right)_{\widehat{QL'}}. \tag{16}$$

for the same x and $S>S_Q$. Hence from a well-known comparison theorem we get

$$x(S)|_{\widehat{QR}}>x(S)|_{\widehat{QL'}} \quad \text{for } S_Q<S<S_{L'}. \tag{17}$$

From (17) we conclude that arc $\widehat{H'L'}$ can intersect arc $\widehat{BR}$ at most at one point.

Similarly, we obtain that

$$0<\frac{S_{P'}}{\lambda-S_{P'}}\leqq\frac{S_P}{S_P-\lambda}, \tag{18}$$

$$S_{P'}\leqq S_- \quad \text{or} \quad S_P\geqq S_+, \tag{19}$$

and arc $\widehat{J'L'}$ can intersect arc $\widehat{AR}$ at most at one point. This completes the proof of the lemma. □

3. Uniqueness of the limit cycle. Now we come to our main result.

THEOREM 1. *If $K>a+2\lambda$, then system (2) possesses a unique limit cycle which is stable.*

Proof. Let Γ be any nontrivial closed orbit of (2), and let its four extreme points be $L(S_L, f(S_L))$, $R(S_R, f(S_R))$, $H(\lambda, x_H)$ and $J(\lambda, x_J)$. Assume that Γ intersects the line $S=(K-a)/2$ at points $A((K-a)/2, x_A)$ and $B((K-a)/2, x_B)$, with $x_B > f((K-a)/2) > x_A$. From Lemma 2, the mirror image of arc $\widehat{BHLJA}$ of Γ, $\widehat{BH'L'J'A}$, intersects the arc $\widehat{BRA}$ of Γ at points $P(S_P, x_P)$ and $Q(S_Q, x_Q)$. Let the mirror images of points P and Q with respect to the line $S=(K-a)/2$ be $P'(S_{P'}, x_{P'})$ and $Q'(S_{Q'}, x_{Q'})$ respectively. It is obvious that $S_{P'} = K-a-S_P$ and $S_{Q'} = K-a-S_Q$.

Now consider

$$g(S,x)=\frac{m}{y}\frac{S(f(S)-x)}{a+S}, \qquad h(S,x)=(m-D_0)\frac{x(S-\lambda)}{a+S}. \tag{20}$$

The divergence of the vector field $(g(S,x), h(S,x))$ defined by (2) is

$$\begin{aligned}\operatorname{Div}(g,h)&=\frac{\partial g}{\partial S}+\frac{\partial h}{\partial x}\\ &=\frac{m}{y}\frac{Sf'(S)}{(a+S)}+\frac{m}{y}\frac{a(f(S)-x)}{(a+S)^2}+(m-D_0)\frac{(S-\lambda)}{a+S}.\end{aligned} \tag{21}$$

From (2) it is easy to see that

$$\oint_\Gamma \left(\frac{m}{y}\right)\frac{a}{(a+S)^2}(f(S)-x)\,dt=\oint_\Gamma \frac{a\,dS}{S(a+S)}=0, \tag{22}$$

$$\oint_\Gamma (m-D_0)\frac{S-\lambda}{a+S}\,dt=0. \tag{23}$$

Hence

$$\oint_\Gamma \operatorname{Div}(g,h)\,dt=\left(\int_{\widehat{AP}}+\int_{\widehat{PRQ}}+\int_{\widehat{QB}}+\int_{\widehat{BQ'}}+\int_{\widehat{Q'LP'}}+\int_{\widehat{P'A}}\right)\left[\frac{m}{y}\frac{Sf'(S)}{a+S}\right]dt. \tag{24}$$

Now

$$\begin{aligned}\left(\int_{\widehat{P'A}}+\int_{\widehat{AP}}\right)\left[\frac{m}{y}\frac{Sf'(S)}{a+S}\right]dt&=\int_{S_{P'}}^{S_A}\frac{f'(S)}{f(S)-x_1(S)}\,dS+\int_{S_A}^{S_P}\frac{f'(S)}{f(S)-x_2(S)}\,dS\\ &=\int_{S_A}^{S_P}\frac{f'(S)}{f(S)-x_2(S)}\,dS\\ &\quad+\int_{S_A}^{S_P}\frac{f'(K-a-S)}{f(K-a-S)-x_1(K-a-S)}\,dS\\ &=\int_{S_A}^{S_P}f'(S)\left[\frac{x_2(S)-x_1(K-a-S)}{(f(S)-x_2(S))(f(S)-x_1(K-a-S))}\right]dS.\end{aligned} \tag{25}$$

The notation in (25) is self-evident. From Lemma 2, we know that $x_2(S) > x_1(K-a-S)$ for $S_A < S < S_P$. Thus we have (recall that $f'(S)<0$ for $S_A<S<S_P$)

$$\left(\int_{\widehat{P'A}}+\int_{\widehat{AP}}\right)\left[\frac{m}{y}\frac{Sf'(S)}{a+S}\right]dt<0. \tag{26}$$

Similarly, we have

$$\left(\int_{\overline{QB}}+\int_{\overline{BQ'}}\right)\left[\frac{m}{y}\frac{Sf'(S)}{a+S}\right]dt = \int_{S_B}^{S_Q} f'(S)\left[\frac{x_3(K-a-S)-x_4(S)}{(x_4(S)-f(S))(x_3(K-a-S)-f(S))}\right]dS<0. \tag{27}$$

Let $\bar{\Omega}$ be the region bounded by arc $\widehat{Q'LP'}$ and line segment $\overline{P'Q'}$, and $\bar{\bar{\Omega}}$ be the region bounded by arc $\widehat{PRQ}$ and line segment $\overline{QP}$. We have

$$\begin{aligned}
&\int_{\widehat{Q'LP'}}\left(\frac{m}{y}\frac{Sf'(S)}{a+S}\right)dt\\
&=\left(\frac{m}{y}\right)\left(\frac{1}{m-D_0}\right)\left[\int_{\widehat{Q'LP'}}\frac{Sf'(S)}{x(S-\lambda)}dx\right]\\
&=\left(\frac{m}{y}\right)\left(\frac{1}{m-D_0}\right)\left[\left(\int_{\widehat{Q'LP'}}+\int_{\overline{P'Q'}}+\int_{\overline{Q'P'}}\right)\left(\frac{Sf'(S)}{x(S-\lambda)}\right)dx\right] \qquad (28)\\
&=\left(\frac{m}{y}\right)\left(\frac{1}{m-D_0}\right)\left[\iint_{\bar{\Omega}}\frac{-1}{x}\cdot\frac{(\gamma/K)[2(S-\lambda)^2+\lambda(K-a-2\lambda)]}{(S-\lambda)^2}dS\,dx\right.\\
&\qquad\left.+\int_{\overline{Q'P'}}\frac{Sf'(S)}{x(S-\lambda)}dx\right] \text{ (Green's theorem)}\\
&<\left(\frac{m}{y}\right)\left(\frac{1}{m-D_0}\right)\int_{x_{P'}}^{x_{Q'}}\frac{S_1(x)f'(S_1(x))}{x(\lambda-S_1(x))}dx.
\end{aligned}$$

Similarly, we have

$$\begin{aligned}
&\int_{\widehat{PRQ}}\left(\frac{m}{y}\frac{Sf'(S)}{a+S}\right)dt\\
&=\left(\frac{m}{y}\right)\left(\frac{1}{m-D_0}\right)\left[\iint_{\bar{\bar{\Omega}}}\frac{-1}{x}\cdot\frac{\gamma/K[2(S-\lambda)^2+\lambda(K-a-2\lambda)]}{(S-\lambda)^2}dS\,dx+\int_{\overline{PQ}}\frac{Sf'(S)}{x(S-\lambda)}dx\right] \qquad (29)\\
&<\left(\frac{m}{y}\right)\left(\frac{1}{m-D_0}\right)\int_{x_P}^{x_Q}\frac{S_2(x)f'(S_2(x))}{x(S_2(x)-\lambda)}dx,
\end{aligned}$$

where $S_1(x)$ and $S_2(x)$ represent the line segments $\overline{P'Q'}$ and $\overline{PQ}$ respectively. From (28), (29) and the identity $S_2(x)=K-a-S_1(x)$, we have

$$\begin{aligned}
&\left(\int_{\widehat{Q'LP'}}+\int_{\widehat{PRQ}}\right)\left[\frac{m}{y}\frac{Sf'(S)}{a+S}\right]dt\\
&<\left(\frac{m}{y}\right)\left(\frac{1}{m-D_0}\right)\left[\int_{x_{P'}}^{x_{Q'}}\frac{S_1(x)f'(S_1(x))}{x(\lambda-S_1(x))}dx-\int_{x_{P'}}^{x_{Q'}}\frac{(K-a-S_1(x))f'(S_1(x))}{x[K-a-\lambda-S_1(x)]}dx\right] \qquad (30)\\
&=\left(\frac{m}{y}\right)\left(\frac{1}{m-D_0}\right)\int_{x_{P'}}^{x_{Q'}}\frac{f'(S_1(x))}{x}\cdot\frac{G(S_1(x))}{[\lambda-S_1(x)][K-a-\lambda-S_1(x)]}dx,
\end{aligned}$$

where the polynomial G is defined in (12).

From (13) and (19) we have

$$S_1(x) \leqq \max\{S_{P'}, S_{Q'}\} \leqq S_-, \qquad x_{P'} \leqq x \leqq x_{Q'}$$

and hence

$$G(S_1(x)) \leqq 0 \quad \text{for } x_{P'} \leqq x \leqq x_{Q'}. \tag{31}$$

From (30) and (31) we finally have

$$\left(\int_{\overline{Q'LP'}} + \int_{\overline{PRQ}}\right)\left[\frac{m}{y}\,\frac{Sf'(S)}{a+S}\right] dt < 0. \tag{32}$$

From (26), (27) and (32) we get

$$\oint_{\Gamma} \operatorname{Div}(g, h)\, dt < 0. \tag{33}$$

This means that the closed orbit Γ is stable. But two adjacent periodic orbits cannot be positively stable on the sides facing each other [1, p. 397, Thm. 3.4]. Hence the uniqueness of the limit cycle of system (2) is proved. □

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