

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

LII-PERNG LIOU† AND KUO-SHUNG CHENG‡

Abstract. The uniqueness of a limit cycle for a predator-prey system is proved in this paper. The method used is an improvement of the method used earlier by Cheng.

Key words. limit cycle, predator-prey system

AMS(MOS) subject classifications. primary 34D05; secondary 34C15

1. Introduction. Stability analysis for a nontrivial periodic solution of ordinary differential equations is very rare and difficult to obtain even in a two-dimensional system. One well-known example is the Lienard equation, in particular, the Van der Pol equation. See Hartman [6] and Hirsch and Smale [7] for details. For biological predator-prey systems, Hsu, Hubbell, and Waltman [8], [9] considered the following competing-predators system:

$$\begin{aligned}
 \dot{S}(t) &= rS(t) \left(1 - \frac{S(t)}{K} \right) - \left(\frac{m_1}{y_1} \right) \left(\frac{X_1(t)S(t)}{a_1 + S(t)} \right) - \left(\frac{m_2}{y_2} \right) \left(\frac{X_2(t)S(t)}{a_2 + S(t)} \right), \\
 \dot{X}_1(t) &= X_1(t) \left(\frac{m_1 S(t)}{a_1 + S(t)} - D_1 \right), \\
 \dot{X}_2(t) &= X_2(t) \left(\frac{m_2 S(t)}{a_2 + S(t)} - D_2 \right), \\
 S(0) &= S_0 > 0, \quad X_i(0) = X_{i0} > 0, \quad i = 1, 2,
 \end{aligned}
 \tag{1}$$

where $X_i(t)$ is the population of the i th predator at time t ; $S(t)$ is the population of the prey at time t ; m_i is the maximum growth rate of the i th predator; D_i is the death rate of the i th predator; y_i is the yield factor of the i th predator feeding on the prey; and a_i is the half-saturation constant of the i th predator, which is the prey density at which the functional response of the predator is half maximal. The parameters r and K are the intrinsic rate of increase and the carrying capacity for the prey population, respectively. Hsu, Hubbell, and Waltman analyzed solutions of this system and found that the behavior of solutions depends mainly on the two-dimensional system:

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

* Received by the editors January 15, 1986; accepted for publication (in revised form) May 11, 1987. This work was supported in part by the National Science Council of the Republic of China.

† Department of Applied Mathematics, National Chiao Tung University, Hsinchu, Taiwan, Republic of China.

‡ Institute of Applied Mathematics, National Tsing Hua University, Hsinchu, Taiwan 300, Republic of China.

where $r, K, m, y, a,$ and D_0 are positive constants. They analyzed system (2) and found that if $\lambda < (K - a)/2$, where $\lambda = a/(b - 1)$ and $b = m/D_0$, then the unique interior equilibrium point (λ, x^*) is unstable. They conjectured that the system (2) has a unique stable limit cycle in this case. This conjecture was answered affirmatively by Cheng in [2]. In these examples, symmetric properties are an important ingredient of the proof. The Van der Pol equations are

$$(3) \quad \begin{aligned} \dot{x} &= y - (x^3 - x), \\ \dot{y} &= -x. \end{aligned}$$

The isocline $\dot{x} = 0$, i.e., the curve $y = x^3 - x$, is symmetric with respect to the origin. This fact is important in the analysis of (3). For the system (2), the isocline $\dot{S} = 0$ is the curve

$$(4) \quad x = r(y/m)(1 - S/K)(a + S).$$

This curve is part of a parabola and hence is also symmetric with respect to the line $S = (K - a)/2$. The proof of Cheng [2] uses this symmetry property in an essential way. From the point of view of perturbation theory, there is no reason to believe that some symmetry properties are indispensable for a stable limit cycle. In this respect, if we can devise a proof that is valid for a more general “nonsymmetric” system, even if it is only a slight generalization, we will feel comfortable with it.

The purpose of this paper is to improve our method used in [2] to prove the uniqueness of a limit cycle for a more general predator-prey system without the symmetry properties of the isocline. At the end of our proof, we also close a gap in the original proof given in [2].

2. The equations and statements of the main result. We will consider the following predator-prey system:

$$(5) \quad \begin{aligned} \dot{x} &= x(f(x) - y), \\ \dot{y} &= y(g(x) - \lambda), \\ x(0) &= x_0 > 0, \quad y(0) = y_0 > 0, \quad \lambda > 0. \end{aligned}$$

Note that if $g(x) = x$ and $f(x) = (1 - x/K)(a + x)$, then the system (5) is essentially equivalent to the system (2) up to some irrelevant constants. Our general assumptions about $f(x)$ and $g(x)$ are:

- (i) $g \in C^1([0, \infty))$, $g(0) = 0$, $g'(x) > 0$ for all $x \geq 0$.
- (ii) $f \in C^2([0, \infty))$, $f(0) \geq 0$, and there exists $K > 0$ such that $f(K) = 0$ and $(x - K)f(x) < 0$ for $x \neq K$. There exists an a , $0 < a < K$, such that $f'(x) > 0$ for $0 < x < a$, $f'(a) = 0$ and $f'(x) < 0$ for $a < x$.
- (iii) $g(x^*) = \lambda$, $y^* = f(x^*)$, and $0 < x^* < a$.
- (iv) $(d/dx)(xf'(x))/(g(x) - \lambda) < 0$ for $x < x^*$ and $x > \bar{x}^*$, where $\bar{x}^* = f_2^{-1} \circ f_1(x^*)$ and $f_1 = f|_{(0,a)}$, $f_2 = f|_{(a,K)}$.

The phase plane of (5) under assumptions (i)–(iv) is roughly as shown in Fig. 1. We consider only the case $x^* < a$. In the case $a < x^* < K$, the equilibrium point (x^*, y^*) is locally asymptotically stable. We refer to Cheng, Hsu, and Lin [3] for global stability analysis.

Note that if

$$\begin{aligned} g(x) &= x, \\ f(x) &= F(x) + \varepsilon H(x), \end{aligned}$$

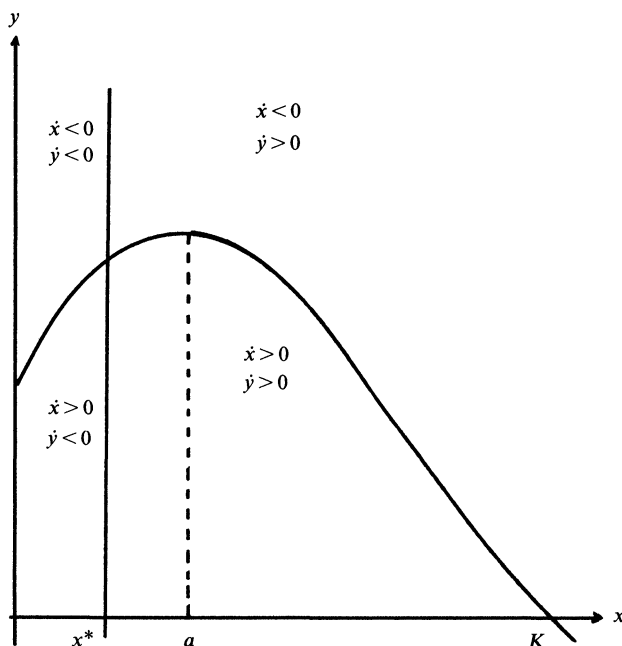


FIG. 1

then g and f satisfy assumptions (i)-(iv) if $\epsilon > 0$ is sufficiently small where

$$F(x) = (1 - x)(b + x)$$

and $H(x)$ is a C^2 function satisfying

$$H'(x) \geq 0 \quad \text{for } 0 < x < a,$$

$$H'(x) \leq 0 \quad \text{for } a < x, a = \frac{1-b}{2}.$$

In fact,

$$\frac{d}{dx} \left(\frac{xf'(x)}{x-\lambda} \right) = \frac{-1}{(x-\lambda)^2} \{ [2(x-\lambda)^2 + 2\lambda(a-\lambda)] - \epsilon [(x-\lambda)xH''(x) - \lambda H'(x)] \}.$$

Thus if $(a - \lambda)$ is reasonably large, we can allow ϵ to be reasonably large and the isocline

$$y = F(x) + \epsilon H(x)$$

can be quite unsymmetric with respect to the line $x = a$.

Our main result follows.

THEOREM 1. *Under the assumptions (i)-(iv), (5) possesses a unique limit cycle which is globally stable.*

3. Proof of Theorem 1. We need some lemmas.

LEMMA 1. *The solutions $x(t), y(t)$ of (5) are positive and bounded.*

LEMMA 2. *The unique interior equilibrium point (x^*, y^*) of (5) is a source.*

LEMMA 3. *Let Γ be a nontrivial closed orbit of (2). Then*

$$\Gamma \subset \{(x, y): 0 < x < K, 0 < y\}.$$

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

$$L \in \{(x, y): 0 < x < x^*, y = f(x)\},$$

$$R \in \{(x, y): x^* < x < K, y = f(x)\},$$

$$H \in \{(x, y): x = x^*, y > y^*\},$$

$$J \in \{(x, y): x = x^*, 0 < y < y^*\}.$$

The proof of Lemma 1 is given in Albrecht et al. [1]. Lemma 2 follows from a straightforward calculation and Lemma 3 is easy enough. Hence we omit all the proofs of these lemmas.

Before we state and prove our next lemma, we define a transformation T from $(0, a) \times (0, \infty)$ to $(a, K) \times (0, \infty)$,

$$(6) \quad \begin{aligned} T(x, y) &\equiv (T_1(x, y), T_2(x, y)) \\ &\equiv (f_2^{-1} \circ f_1(x), y), \end{aligned}$$

where f_1 and f_2 are the restriction of f on $(0, a)$ and (a, K) , respectively. From assumption (ii), it is easy to see that T is a one-to-one transformation.

Now, we can state our main lemmas.

LEMMA 4. Let Γ be a nontrivial closed orbit of (5). Γ meets the vertical line $x = a$ at points A and B with $y_B > y_A$. (See Fig. 2.) Let the image of arc \overline{BHLJA} of Γ under the transformation T be $\overline{BH'L'J'A}$. Then arc $\overline{H'L'J'}$ intersects arc \overline{BRA} of Γ at exactly two points $P = (x_1, y_1)$ and $Q = (x_2, y_2)$ with $y_1 > f(x_1)$ and $y_2 < f(x_2)$.

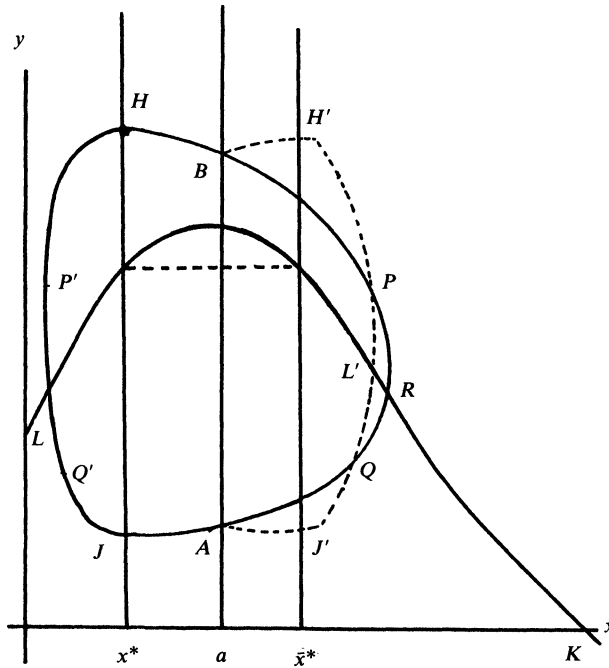


FIG. 2

Furthermore, let $P' = (x'_1, y'_1) = T^{-1}(P)$ and $Q' = (x'_2, y'_2) = T^{-1}(Q)$. Then

$$(7) \quad 0 > \frac{x'_1 f'_1(x'_1)}{g(x'_1) - \lambda} \cong \frac{x_1 f'_2(x_1)}{g(x_1) - \lambda},$$

$$(8) \quad 0 > \frac{x'_2 f'_1(x'_2)}{g(x'_2) - \lambda} \cong \frac{x_2 f'_2(x_2)}{g(x_2) - \lambda}.$$

Proof. Consider the function

$$(9) \quad V(x, y) = \int_{x^*}^x \frac{g(\xi) - \lambda}{\xi} d\xi.$$

Then

$$(10) \quad \frac{dV(x(t), y(t))}{dt} = [g(x(t)) - \lambda][f(x(t)) - y(t)].$$

Let the period of Γ be τ . We have

$$(11) \quad \int_0^\tau \frac{dV(x(t), y(t))}{dt} dt = 0.$$

On the other hand, we have

$$(12) \quad \begin{aligned} \int_0^\tau \frac{dV(x(t), y(t))}{dt} dt &= \int_0^\tau [g(x(t)) - \lambda][f(x(t)) - y(t)] dt \\ &= \oint_{\Gamma} (f(x) - y) \frac{dy}{y}. \end{aligned}$$

Let Ω_1 be the interior of the domain bounded by arc \widehat{BHLJA} and line $x = a$ and Ω_2 be the interior of the domain bounded by arc \widehat{BRA} and the line $x = a$. Also, let $\Omega = \Omega_1 \cup \Omega_2$ and $\Omega'_1 = T(\Omega_1)$. From the definition of T it is easy to see arc $\widehat{BH'}$ lies above Γ and arc $\widehat{J'A}$ lies below Γ . Hence either

$$(13) \quad \widehat{BH'LJ'A} \cap \Omega_2 = \emptyset \text{ (empty)} \quad \text{and} \quad \Omega_2 \subset \Omega'_1$$

or

$$S \equiv \widehat{BH'LJ'A} \cap \Omega_2 \neq \emptyset.$$

We now show that the assumption $\Omega_2 \subset \Omega'_1$ leads to a contradiction. From (11) and (12), we have

$$(14) \quad \begin{aligned} 0 &= \int_0^\tau \frac{dV(x(t), y(t))}{dt} dt \\ &= \oint_{\Gamma} \frac{1}{y} [f(x) - y] dy \\ &= \iint_{\Omega} \frac{f'(x)}{y} dx dy \quad \text{(Green's theorem)} \\ &= \iint_{\Omega_1} \frac{f'(x)}{y} dx dy + \iint_{\Omega_2} \frac{f'(x)}{y} dx dy \\ &= \iint_{\Omega_1} \frac{f'_1(x)}{y} dx dy + \iint_{\Omega_2} \frac{f'_2(x)}{y} dx dy. \end{aligned}$$

Now let $T: \Omega_1 \rightarrow \Omega'_1$ be the transformation defined in (6). Let

$$T(x, y) = (u, v).$$

Then

$$\begin{aligned} u &= f_2^{-1} \circ f_1(x), \\ v &= y. \end{aligned}$$

Hence $(x, y) = T^{-1}(u, v)$ and

$$(15) \quad \begin{aligned} x &= f_1^{-1} \circ f_2(u), \\ y &= v. \end{aligned}$$

The Jacobian of T^{-1} is

$$(16) \quad \begin{aligned} \frac{\partial(x, y)}{\partial(u, v)} &= \begin{vmatrix} (f_1^{-1})'(f_2(u)) \cdot f_2'(u) & 0 \\ 0 & 1 \end{vmatrix} \\ &= (f_1^{-1})'(f_2(u)) \cdot f_2'(u). \end{aligned}$$

But since $f_2'(u) < 0$ and $(f_1^{-1})'(f_2(u)) > 0$, we have

$$(17) \quad \left| \frac{\partial(x, y)}{\partial(u, v)} \right| = -(f_1^{-1})'(f_2(u)) \cdot f_2'(u).$$

Hence, we have from (17)

$$(18) \quad \begin{aligned} \iint_{\Omega_1} \frac{f_1'(x)}{y} dx dy &= \iint_{\Omega'_1} \frac{f_1'(f_1^{-1} \circ f_2(u))}{v} \cdot [-(f_1^{-1})'(f_2(u)) \cdot f_2'(u)] du dv \\ &= - \iint_{\Omega'_1} \frac{f_1'(f_1^{-1} \circ f_2(u)) \cdot (f_1^{-1})'(f_2(u)) \cdot f_2'(u)}{v} du dv. \end{aligned}$$

But

$$(19) \quad \begin{aligned} f_1'(f_1^{-1} \circ f_2(u)) \cdot (f_1^{-1})'(f_2(u)) &= \frac{d}{dz} (f_1 \circ f_1^{-1}(z)) \Big|_{z=f_2(u)} \\ &= 1. \end{aligned}$$

From (18) and (19), we obtain

$$(20) \quad \begin{aligned} \iint_{\Omega_1} \frac{f_1'(x)}{y} dx dy &= - \iint_{\Omega'_1} \frac{f_2'(u)}{v} du dv \\ &= - \iint_{\Omega'_1} \frac{f_2'(x)}{y} dx dy \quad (\text{identify } u = x, v = y). \end{aligned}$$

Combining (13), (14), and (20), finally we have

$$(21) \quad \begin{aligned} 0 &= \int_0^\tau \frac{dV(x(t), y(t))}{dt} dt \\ &= \iint_{\Omega_1} \frac{f_1'(x)}{y} dx dy + \iint_{\Omega_2} \frac{f_2'(x)}{y} dx dy \\ &= - \iint_{\Omega'_1} \frac{f_2'(x)}{y} dx dy + \iint_{\Omega_2} \frac{f_2'(x)}{y} dx dy \\ &= - \iint_{\Omega_1 - \Omega_2} \frac{f_2'(x)}{y} dx dy \\ &> 0 \quad (\text{recall that } f_2'(x) < 0). \end{aligned}$$

This is a contradiction. Hence $S = \overline{BH'L'J'A} \cap \Omega_2 \neq \emptyset$.

Let \bar{S} denote the closure of S and let $P = (x_1, y_1)$ and $Q = (x_2, y_2)$ be the “highest” and “lowest” points of \bar{S} , respectively. Then, P is the highest point and Q is the lowest point where arc $\overline{BH'L'J'A}$ enters the region Ω_2 from the outside of Ω_2 . It is easy to see that $y_1 > y_2$. First we assume that $y_1 > f(x_1)$. Let $(dy/dx)'_P$ and $(dy/dx)_P$ be the slopes of arcs $\overline{BH'L'J'A}$ and \overline{BRA} at point P , respectively. Since arc $\overline{BH'L'J'A}$ enters Ω_2 from the outside of Ω_2 at point P , we have

$$(22) \quad 0 > \left(\frac{dy}{dx}\right)'_P \cong \left(\frac{dy}{dx}\right)'_P.$$

But we have

$$(23) \quad \begin{aligned} \left(\frac{dy}{dx}\right)'_P &= \frac{y_1(g(x_1) - \lambda)}{x_1(f(x_1) - y_1)} \\ &= \frac{y_1(g(x_1) - \lambda)}{x_1(f_2(x_1) - y_1)}, \end{aligned}$$

and

$$(24) \quad \begin{aligned} \left(\frac{dy}{dx}\right)'_P &= \left(\frac{dv}{du}\right)_{(u,v)=(x_1,y_1)} \\ &= \left(\frac{dy}{d(f_2^{-1} \circ f_1(x))}\right)_{(x,y)=(x'_1,y'_1)=T^{-1}(x_1,y_1)} \\ &= \frac{y'_1(g(x'_1) - \lambda)}{(f_2^{-1})'(f_1(x'_1)) \cdot f'_1(x'_1) \cdot x'_1 \cdot (f_1(x'_1) - y'_1)}. \end{aligned}$$

Since

$$(25) \quad f_1(x'_1) = f_1(f_1^{-1} \circ f_2(x_1)) = f_2(x_1),$$

$$(26) \quad y'_1 = y_1,$$

and

$$(27) \quad \begin{aligned} (f_2^{-1})'(f_1(x'_1)) \cdot f'_2(f_2^{-1} \circ f_1(x'_1)) &= (f_2^{-1})'(f_1(x'_1)) \cdot f'_2(x_1) \\ &= 1. \end{aligned}$$

We have from (24), (25), (26), and (27)

$$(28) \quad \left(\frac{dy}{dx}\right)'_P = \frac{y'_1(g(x'_1) - \lambda)}{x'_1(f_2(x_1) - y_1) \cdot (1/f'_2(x_1)) \cdot f'_1(x'_1)}.$$

Thus from (22), (23), and (29) we obtain

$$(29) \quad 0 > \frac{y_1(g(x_1) - \lambda)}{x_1(f_2(x_1) - y_1)} \cong \frac{y_1(g(x'_1) - \lambda)}{x'_1 \cdot f'_1(x'_1) \cdot (f_2(x_1) - y_1) \cdot (1/f'_2(x_1))}.$$

Finally we get

$$(30) \quad 0 > \frac{x'_1 f'_1(x'_1)}{g(x'_1) - \lambda} \cong \frac{x_1 f'_2(x_1)}{g(x_1) - \lambda}.$$

Now the arc \widehat{PR} satisfies the following differential equations:

$$(31) \quad \left(\frac{dy}{dx}\right)_{\widehat{PR}} = \frac{y(g(x) - \lambda)}{x(f_2(x) - y)}$$

and the arc \widehat{PL} satisfies

$$(32) \quad \begin{aligned} \left(\frac{dy}{dx}\right)_{\widehat{PL}} &= \left(\frac{dv}{du}\right)_{(u,v)=(x,y)} \\ &= \frac{y'(g(x') - \lambda)}{(f_2^{-1})'(f_1(x')) \cdot f_1'(x') \cdot x' \cdot (f_1(x') - y')} \\ &= \frac{y(g(x') - \lambda)}{x'(f_2(x) - y) \cdot (1/f_2'(x)) \cdot f_1'(x')} \end{aligned}$$

as in (24)–(28).

From (31) and (32) we have

$$(33) \quad \left(\frac{dy}{dx}\right)_{\widehat{PR}} = \frac{g(x) - \lambda}{xf_2'(x)} \cdot \frac{yf_2'(x)}{f_2(x) - y},$$

$$(34) \quad \left(\frac{dy}{dx}\right)_{\widehat{PL}} = \frac{g(x') - \lambda}{x'f_1'(x')} \cdot \frac{yf_2'(x)}{f_2(x) - y}.$$

From the assumption (iv) and (30), we have

$$(35) \quad \frac{g(x') - \lambda}{x'f_1'(x')} < \frac{g(x_1') - \lambda}{x_1'f_1'(x_1')} \cong \frac{g(x_1) - \lambda}{x_1f_2'(x_1)} < \frac{g(x) - \lambda}{xf_2'(x)}$$

for all $x_1 < x$ (hence $x' < x_1'$).

Hence we have

$$0 > \frac{g(x) - \lambda}{xf_2'(x)} \cdot \frac{yf_2'(x)}{f_2(x) - y} > \frac{g(x') - \lambda}{x'f_1'(x')} \cdot \frac{yf_2'(x)}{f_2(x) - y}$$

for all $x_1 < x$.

From a well-known comparison theorem we get

$$(36) \quad y(x)_{\widehat{PR}} > y(x)_{\widehat{PL}} \quad \text{for } x_1 < x < x_{L'},$$

where $x_{L'}$ is the x -coordinate of L' .

This proves that if $y_1 > f(x_1)$, then the arc $\widehat{BH'L'}$ intersects the arc \widehat{BR} only at the point P .

Now assume that $y_2 < f(x_2)$. Let $(dy/dx)'_Q$ and $(dy/dx)_Q$ be the slopes of arcs $\widehat{BH'L'J'A}$ and \widehat{BRA} at the point $Q = (x_2, y_2)$, respectively. Then since $y_2 < f(x_2)$, it is obvious that

$$(37) \quad 0 < \left(\frac{dy}{dx}\right)'_Q \cong \left(\frac{dy}{dx}\right)_Q.$$

By arguments similar to those in (23)–(28), we have

$$(38) \quad \begin{aligned} \left(\frac{dy}{dx}\right)_Q &= \frac{y_2(g(x_2) - \lambda)}{x_2(f_2(x_2) - y_2)} \\ &= \frac{g(x_2) - \lambda}{x_2f_2'(x_2)} \cdot \frac{y_2f_2'(x_2)}{f_2(x_2) - y_2}, \end{aligned}$$

$$(39) \quad \left(\frac{dy}{dx}\right)'_Q = \frac{g(x_2') - \lambda}{x_2'f_1'(x_2')} \cdot \frac{y_2f_2'(x_2)}{f_2(x_2) - y_2}.$$

Hence from (37), (38), and (39) we obtain

$$(40) \quad 0 > \frac{x'_2 f'_1(x'_2)}{g(x'_2) - \lambda} \cong \frac{x_2 f'_2(x_2)}{g(x_2) - \lambda}.$$

By arguments similar to those in (31)–(36), we can prove that if $y_2 < f(x_2)$, then the arc $\widehat{L'J'A}$ intersects the arc \widehat{RA} only at the point Q . From the above conclusion, P cannot be one of the intersection points of arcs $\widehat{L'J'A}$ and \widehat{RA} . Hence we conclude that

$$(41) \quad y_1 > f(x_1), \quad y_2 < f(x_2)$$

and P and Q are the only intersection points of arcs $\widehat{BH'L'J'A}$ and \widehat{BRA} . Hence (30) and (40) hold. This completes the proof of the lemma. \square

LEMMA 5. Let Γ be a nontrivial closed orbit of (5) as described in Lemma 4. Define

$$h(x, y) = x(f(x) - y), \quad k(x, y) = y(g(x) - \lambda).$$

Then

$$(42) \quad \oint_{\Gamma} \text{Div}(h, k) dt \equiv \oint_{\Gamma} \left(\frac{\partial h(x, y)}{\partial x} + \frac{\partial k(x, y)}{\partial y} \right) dt < 0.$$

Proof. From the definitions of h and k , we have

$$(43) \quad \frac{\partial h(x, y)}{\partial x} + \frac{\partial k(x, y)}{\partial y} = (f(x) - y) + (g(x) - \lambda) + xf'(x).$$

But since Γ is a closed orbit, we have

$$\oint_{\Gamma} [f(x) - y] dt = \oint_{\Gamma} \frac{\dot{x}}{x} dt = 0$$

and

$$\oint_{\Gamma} [g(x) - \lambda] dt = \oint_{\Gamma} \frac{\dot{y}}{y} dt = 0.$$

Thus

$$(44) \quad \oint_{\Gamma} \text{Div}(h, k) dt = \oint_{\Gamma} xf'(x) dt.$$

We divide the integration along Γ into integration along several arcs, that is, we let

$$(45) \quad \oint_{\Gamma} = \int_{\widehat{AQ}} + \int_{\widehat{QRP}} + \int_{\widehat{PB}} + \int_{\widehat{BP}} + \int_{\widehat{P'LQ'}} + \int_{\widehat{Q'A}}.$$

Consider the integration along $\widehat{Q'A}$ first. The arc $\widehat{Q'A}$ of Γ can be parametrized by $(x, y_1(x))$, where $x'_2 \cong x \cong a$. Hence

$$(46) \quad \begin{aligned} \int_{\widehat{Q'A}} x(t)f'(x(t)) dt &= \int_{x'_2}^a \frac{f'(x)}{x_2 f(x) - y_1(x)} dx \\ &= \int_{x'_2}^a \frac{f'_1(x)}{f_1(x) - y_1(x)} dx. \end{aligned}$$

Now let

$$u = f_2^{-1} \circ f_1(x), \quad x \in [x'_2, a]$$

or

$$x = f_1^{-1} \circ f_2(u), \quad u \in [a, x_2].$$

Then

$$\begin{aligned}
 \int_{x_2}^a \frac{f_1'(x)}{f_1(x) - y_1(x)} dx &= \int_{x_2}^a \frac{f_1'(f_1^{-1} \circ f_2(u)) \cdot (f_1^{-1})'(f_2(u)) \cdot f_2'(u)}{f_1(f_1^{-1} \circ f_2(u)) - y_1(f_1^{-1} \circ f_2(u))} du \\
 (47) \qquad &= \int_{x_2}^a \frac{f_2'(u)}{f_2(u) - y_1(f_1^{-1} \circ f_2(u))} du \\
 &= - \int_a^{x_2} \frac{f_2'(x)}{f_2(x) - y_1(f_1^{-1} \circ f_2(x))} dx.
 \end{aligned}$$

We parametrize the arc \overline{AQ} of Γ by $(x, y_2(x))$, where $x \in [a, x_2]$. Then

$$\begin{aligned}
 \int_{\overline{AQ}} x(t)f'(x(t)) dt &= \int_a^{x_2} \frac{f'(x)}{f(x) - y_2(x)} dx \\
 (48) \qquad &= \int_a^{x_2} \frac{f_2'(x)}{f_2(x) - y_2(x)} dx.
 \end{aligned}$$

Combining (47) and (48), we obtain

$$\begin{aligned}
 &\left(\int_{\overline{Q'A}} + \int_{\overline{AQ}} \right) (x(t)f'(x(t))) dt \\
 &= \int_a^{x_2} \frac{f_2'(x)[y_2(x) - y_1(f_1^{-1} \circ f_2(x))]}{[f_2(x) - y_2(x)][f_2(x) - y_1(f_1^{-1} \circ f_2(x))]} dx.
 \end{aligned}$$

But for $x \in (a, x_2)$, we have

$$\begin{aligned}
 f_2'(x) &< 0, & y_2(x) - y_1(f_1^{-1} \circ f_2(x)) &> 0, \\
 f_2(x) - y_2(x) &> 0, & f_2(x) - y_1(f_1^{-1} \circ f_2(x)) &> 0.
 \end{aligned}$$

Hence

$$(49) \qquad \left(\int_{\overline{Q'A}} + \int_{\overline{AQ}} \right) (x(t)f'(x(t))) dt < 0.$$

Next we parametrize arc $\overline{BP'}$ of Γ by $(x, y_3(x))$ and arc \overline{PB} by $(x, y_4(x))$. Then

$$\begin{aligned}
 \int_{\overline{BP'}} (x(t)f'(x(t))) dt &= \int_a^{x_1} \frac{f'(x)}{f(x) - y_3(x)} dx \\
 (50) \qquad &= \int_a^{x_1} \frac{f_1'(x)}{f_1(x) - y_3(x)} dx.
 \end{aligned}$$

Let $x = f_1^{-1} \circ f_2(u)$ or $u = f_2^{-1} \circ f_1(x)$. Then from (50)

$$\begin{aligned}
 &\int_{\overline{BP'}} (x(t)f'(x(t))) dt \\
 (51) \qquad &= \int_a^{x_1} \frac{f_1'(f_1^{-1} \circ f_2(u)) \cdot (f_1^{-1})'(f_2(u))f_2'(u)}{f_1(f_1^{-1} \circ f_2(u)) - y_3(f_1^{-1} \circ f_2(u))} du \\
 &= \int_a^{x_1} \frac{f_2'(u)}{f_2(u) - y_3(f_1^{-1} \circ f_2(u))} du \\
 &= \int_a^{x_1} \frac{f_2'(x)}{f_2(x) - y_3(f_1^{-1} \circ f_2(x))} dx.
 \end{aligned}$$

Now from the parametrization of arc \overline{PB} , we have

$$(52) \quad \int_{\overline{PB}} (x(t)f'(x(t))) dt = \int_{x_1}^a \frac{f'(x)}{f(x) - y_4(x)} dx$$

$$= - \int_a^{x_1} \frac{f_2'(x)}{f_2(x) - y_4(x)} dx.$$

Combining (51) and (52) we obtain

$$(53) \quad \left(\int_{\overline{PB}} + \int_{\overline{BP'}} \right) (x(t)f'(x(t))) dt$$

$$= \int_a^{x_1} \frac{f_2'(x)[y_3(f_1^{-1} \circ f_2(x)) - y_4(x)]}{[f_2(x) - y_4(x)][f_2(x) - y_3(f_1^{-1} \circ f_2(x))]} dx$$

$$< 0.$$

Now let us assume that $x'_1 \geq x'_2$, i.e., $x_2 \geq x_1$. (The case $x'_1 < x'_2$ can be treated in the same manner.) Let

$$L_1 = \{(x, y) : x = x'_1, y'_2 \leq y \leq y'_1\},$$

$$L_2 = \{(x, y) : y = y'_2, x'_2 \leq x \leq x'_1\}.$$

We parametrize the arc $\overline{P'LQ'}$ by $(h_1(y), y)$ and let the domain bounded by the arc $\overline{P'LQ'}$, L_2 and L_1 be denoted by D_1 . Then we have

$$(54) \quad \int_{\overline{P'LQ'}} (x(t)f'(x(t))) dt$$

$$= \int_{\overline{P'LQ'}} \frac{xf'(x)}{y[g(x) - \lambda]} \Big|_{x=h_1(y)} dy$$

$$= \left(\int_{\overline{P'LQ'}} + \int_{L_2} + \int_{L_1} \right) \left(\frac{xf'(x)}{y[g(x) - \lambda]} \right) dy$$

$$- \left(\int_{L_2} + \int_{L_1} \right) \left(\frac{xf'(x)}{y[g(x) - \lambda]} \right) dy$$

$$= \iint_{D_1} \frac{1}{y} \frac{d}{dx} \left(\frac{xf'(x)}{g(x) - \lambda} \right) dx dy - \int_{y'_2}^{y'_1} \frac{x'_1 f'_1(x'_1)}{y[g(x'_1) - \lambda]} dy$$

$$< - \int_{y'_2}^{y'_1} \frac{x'_1 f'_1(x'_1)}{y[g(x'_1) - \lambda]} dy \quad (\text{by assumption (iv)}).$$

Now we can consider the integration along the arc \overline{QRP} . Let $L'_1 = TL_1$, $L'_2 = TL_2$ and let D_2 be the domain bounded by the arc \overline{QRP} of Γ , L'_1 , and L'_2 . Then

$$(55) \quad \int_{\overline{QRP}} xf'(x) dt = \left(\int_{\overline{QRP}} + \int_{-L'_1} + \int_{-L'_2} \right) \frac{xf'(x)}{y[g(x) - \lambda]} dy$$

$$- \left(\int_{-L'_1} + \int_{-L'_2} \right) \frac{xf'(x)}{y[g(x) - \lambda]} dy$$

$$= \iint_{D_2} \frac{1}{y} \frac{d}{dx} \left(\frac{xf'(x)}{g(x) - \lambda} \right) dx dy + \int_{y_2}^{y_1} \frac{x_1 f'_2(x_1)}{y[g(x_1) - \lambda]} dy$$

$$< \int_{y_2}^{y_1} \frac{x_1 f'_2(x_1)}{y[g(x_1) - \lambda]} dy.$$

Combining (54) and (55), we have

$$(56) \quad \left(\int_{\overline{P'Q'}} + \int_{\overline{QR}} \right) (xf'(x)) dt < \int_{y_2}^{y_1} \left[\frac{x_1 f'_2(x_1)}{g(x_1) - \lambda} - \frac{x'_1 f'_1(x'_1)}{g(x'_1) - \lambda} \right] \frac{dy}{y} < 0 \quad (\text{by (7)}).$$

Combining (49), (53), and (56), we have

$$(57) \quad \oint_{\Gamma} \text{Div}(h, k) dt = \oint_{\Gamma} xf'(x) dt < 0.$$

This completes the proof of this lemma. \square

Now we are in a position to prove Theorem 1.

Proof of Theorem 1. From Lemma 1, the solutions are positive and bounded. From Lemma 2, the equilibrium point (x^*, y^*) is a source. Hence there exists a closed orbit. But from Lemmas 3, 4, and 5, each closed orbit must be stable. But two adjacent periodic orbits cannot be positively stable on the sides facing each other (Coddington and Levinson [4, Thm. 3.4, p. 397]). Hence the closed orbit is a unique limit cycle. It is easy to see that this limit cycle is also globally stable, that is, nonequilibrium solutions will tend to this cycle eventually. This completes the proof of Theorem 1. \square

Remark. In the proof of Lemma 5, we introduce the line segments L_1 and L_2 . In the original proof of Cheng [2], we use the line segment $\overline{P'Q'}$ instead. Haderler pointed out to us that $\overline{P'Q'}$ may intersect the orbit Γ [5]. This is the gap (in [2]) mentioned in the Introduction.

Acknowledgments. K.-S. Cheng thanks K. P. Haderler for pointing out the gap referred to in the above remark. Both authors express thanks to Paul Waltman and Sze-Bi Hsu for their constant interest in this problem and their kind encouragement.

REFERENCES

- [1] F. ALBRECHT, H. GATZKE, A. HADDAD, AND N. WAX, *The dynamics of two interacting populations*, J. Math. Anal. Appl., 46 (1974), pp. 658-670.
- [2] K. S. CHENG, *Uniqueness of a limit cycle for a predator-prey system*, SIAM J. Math. Anal., 12 (1981), pp. 541-548.
- [3] K. S. CHENG, S. B. HSU, AND S. S. LIN, *Some results on global stability of a predator-prey system*, J. Math. Biol., 12 (1981), pp. 115-126.
- [4] E. A. CODDINGTON AND N. LEVINSON, *Theory of Ordinary Differential Equations*, McGraw-Hill, New York, 1955.
- [5] K. P. HADELER, Private communication.
- [6] P. HARTMAN, *Ordinary Differential Equations*, John Wiley, New York, 1964.
- [7] M. W. HIRSCH AND S. SMALE, *Differential Equations, Dynamical Systems, and Linear Algebra*, Academic Press, New York, 1973.
- [8] S. B. HSU, S. P. HUBBELL, AND P. WALTMAN, *Competing predators*, SIAM J. Appl. Math., 35 (1978), pp. 617-625.
- [9] ———, *A contribution to the theory of competing predators*, Ecological Monographs, 48 (1978), pp. 337-349.