J. Math. Biol. (1988) 26: 65–71

Journal of
Mathematical
Biology

Global stability of a predator–prey system*

Lii-Perng Liou and Kuo-Shung Cheng

Department of Applied Mathematics, National Chiao Tung University, Hsinchu, Taiwan 300, Republic of China

Abstract. In this paper we derive a result to ensure the global stability of a predator–prey system. The method used is quite general and may have applications to other situations.

Key words: Global stability — Predator–prey system

1. Introduction

It is quite an interesting mathematical problem to estimate the basin of an asymptotic equilibrium of a dynamical system. For a predator–prey system, usually the biologists believe that a unique, "positive", locally asymptotically stable equilibrium is globally stable. Thus Goh [6] constructs a Lyapunov function to prove global stability of the classical Lotka–Volterra system. Hsu, Hubbel and Waltman [9] employ the Dulac criterion (Bendixson's negative criterion) to prove global stability for a specific predator–prey model. In a subsequent paper, Hsu [8] constructs a Lyapunov function to ensure the global stability of a general predator–prey system which was discussed by many authors (Freedman [4], Gaus, Smaragdova and Witt [5], May [11], Oaten and Murdoch [12], and Rosenzweig and MacArthur [15], for example). Recently, Cheng, Hsu and Lin [3] give some results which cover most of the models proposed in the ecological literature. One of the methods they use is the comparison of two similar systems. We like to note that either constructing a Lyapunov function, or using the Dulac criterion is not an easy job.

In this paper, we employ a general comparison method to prove the global stability of a class of predator–prey systems. The method is quite effective and useful. In fact, Liou and Cheng [10] prove a uniqueness theorem of a limit cycle for a predator–prey system by using a similar comparison method.

For other discussions of a predator–prey system, we refer to Albrecht, Gatzke, Haddad and Wax [1], Cheng [2], Hastings [7], Rosenzweig [14, 16] and Maynard Smith [17].

We would like to thank the referee for his useful suggestions.

* Works were partially supported by the National Science Council of the Republic of China

2. The model and global stability

As in Cheng et al. [3], we consider the following basic model for the predator–prey system

$$dx/dt = xg(x) - yh(x), \tag{2.1}$$

$$dy/dt = y(mh(x) - d), \tag{2.2}$$

$$x(0) > 0, \qquad y(0) > 0,$$

where x represents the prey population (or density), y represents the predator population (or density), $g(x)$ is the specific growth rate which governs the growth of the prey in the absence of predators, $h(x)$ is the predator response function which has been much discussed in the literature, m is the efficiency rate of the predator in predating the prey and d is the death rate of the predator.

The general assumptions on $g(x)$ and $h(x)$ are:

(a) $g \in C^1([0, \infty), R)$, $g(0) > 0$ and there exists $K > 0$ such that $g(K) = 0$ and $(x - K)g(x) < 0$ for $x \neq K$.

(b) $h \in C^1([0, \infty), R)$, $h(0) = 0$ and $h'(x) > 0$ for all $x > 0$.

Some of the specific forms of $g(x)$ and $h(x)$ frequently used are (see Freedman [4], May [11], Oaten and Murdoch [12], Real [13] and Rosenzweig [14]):

$$g(x)\colon r\left(1 - \frac{x}{K}\right); \frac{r(K-x)}{K+ax}; r\left[1 - \left(\frac{x}{K}\right)^b\right], \qquad 1 > b > 0, \tag{2.3}$$

$$h(x)\colon \frac{bx^n}{a + x^n}, n \geq 1; \qquad ax^b, 1 \geq b > 0; \qquad a(1 - e^{-bx}), a > 0. \tag{2.4}$$

We assume that there is a locally stable equilibrium:

(c) There exists (x^*, y^*) such that $mh(x^*) - d = 0$ and $x^*g(x^*) - y^*h(x^*) = 0$ with $0 < x^* < K$, $y^* > 0$,

$$f'(x) < 0 \quad \text{for all } x^* \leq x \leq K, \tag{2.5}$$

where $f(x) = xg(x)/h(x)$.

Now since $f'(x) < 0$ for $x^* \leq x \leq K$, the inverse function of f exists. Let G be the inverse function of f in the range $x^* \leq x \leq K$. Then

$$f\colon [x^*, K] \to [0, y^*] \tag{2.6}$$

$$G\colon [0, y^*] \to [x^*, K] \tag{2.7}$$

and

$$f(G(y)) = y \quad \text{and} \quad G(f(x)) = x. \tag{2.8}$$

Let Q be the solution of the initial value problem

$$\begin{aligned} \frac{dQ(y)}{dy} &= \frac{m - d/h(G(y))}{m - d/h(Q(y))} G'(y) \\ Q(y^*) = x^*, &\qquad Q(y) \in (0, x^*) \quad \text{for } y \in [0, y^*). \end{aligned} \tag{2.9}$$

It is easily seen that Q is uniquely determined and satisfies $0 < Q(y) < x^*$ for $0 \leq y < y^*$ and $Q'(y) > 0$ for $0 \leq y < y^*$. From the assumption (b) of h, we can easily see that $Q(0) \geq 0$. Let $\tilde{K} = Q(0)$. Now let F be the inverse function of Q, that is, F and Q satisfy

$$Q:[0, y^*] \to [\tilde{K}, x^*], \tag{2.10}$$

$$F:[\tilde{K}, x^*] \to [0, y^*], \tag{2.11}$$

$$F(Q(y)) = y \quad \text{and} \quad Q(F(x)) = x. \tag{2.12}$$

Our last assumption is

(d) Assume that $f(x) \geq F(x)$ for all $x \in [\tilde{K}, x^*]$.

Now we can state our main result.

Theorem 1. *Under the assumptions* (a)-(d), (x^*, y^*) *is globally asymptotically stable for system* (2.1), (2.2) *in the interior of the first quadrant.*

To prove Theorem 1, we introduce an auxiliary system

$$dx/dt = x\tilde{g}(x) - yh(x), \tag{2.14}$$

$$dy/dt = y(mh(x) - d), \tag{2.15}$$

where the constants m and d and the function h are the same as in system (2.1), (2.2), and $\tilde{g}(x)$ is defined by

$$\tilde{g}(x) = \begin{cases} g(x) & \text{if } x \in [x^*, K], \\ F(x)h(x)/x & \text{if } x \in [\tilde{K}, x^*]. \end{cases} \tag{2.16}$$

We have the following lemma which follows directly from the proof in [1].

Lemma 1. *Solutions of system* (2.1), (2.2) *are positive and bounded.*

For system (2.14), (2.15), we have

Lemma 2. *For system* (2.14), (2.15) *under the assumptions* (a)-(d), *every trajectory* γ *starting at* $p_0 = (x^*, y_0)$ *with* $0 < y_0 < y^*$ *is a closed orbit contained in the strip* $\{(x, y): \tilde{K} \leq x \leq K, 0 < y < \infty\}$.

Proof. Let $\gamma = (x(t), y(t))$ be the trajectory which starts at $p_0 = (x^*, y_0)$ with $0 < y_0 < y^*$. Choose $t_1 < t_2$ such that $y(t) < f(x(t))$ for all $0 \leq t < t_1$, $y(t_1) = f(x(t_1))$, $y(t) > f(x(t))$ for all $t_1 < t \leq t_2$ and $x(t_2) = x^*$. Let $p_1 = (x(t_1), y(t_1)) = (x_1, y_1)$ and $p_2 = (x(t_2), y(t_2)) = (x_2, y_2) = (x^*, y_2)$. We let the trajectory of γ between p_0 and p_1 be denoted by γ_1 and that between p_1 and p_2 be denoted by γ_2.

Now define the transformation T

$$T:[x^*, K] \times (0, \infty) \to [\tilde{K}, x^*] \times (0, \infty)$$

by

$$\begin{aligned} T(x, y) &= (T_1(x, y), T_2(x, y)) \\ &= (Q \circ f(x), y). \end{aligned} \tag{2.17}$$

The trajectory γ_1 satisfies

$$\frac{dy}{dx} = \frac{y\left[m - \dfrac{d}{h(x)}\right]}{(f(x) - y)}, \qquad y(x^*) = y_0, \quad x \in [x^*, x_1). \tag{2.18}$$

Let $\tilde{\gamma}_1 = T\gamma_1$. Then $\tilde{\gamma}_1$ satisfies

$$\frac{d\tilde{y}}{d\tilde{x}} = \frac{dy}{d(Q\circ f(x))} = \frac{1}{Q'(f(x))f'(x)}\frac{dy}{dx}$$

$$= \frac{1}{Q'(f(x))f'(x)} \cdot \frac{y\left[m - \dfrac{d}{h(x)}\right]}{(f(x)-y)}. \tag{2.19}$$

Now let $f(x) = z$, then $Q(z) = \tilde{x}$ and $z = F(\tilde{x})$.

From (2.9), we have

$$Q'(f(x)) = Q'(z) = \frac{m - \dfrac{d}{h(G(z))}}{m - \dfrac{d}{h(Q(z))}} G'(z). \tag{2.20}$$

From (2.8), we have

$$G'(f(x))f'(x) = 1. \tag{2.21}$$

Using (2.19), (2.20) and (2.21), we have

$$\frac{d\tilde{y}}{d\tilde{x}} = \frac{1}{\left(m - \dfrac{d}{h(G(z))}\right) \Big/ \left(m - \dfrac{d}{h(Q(z))}\right) G'(z)f'(x)} \cdot \frac{\tilde{y}\left[m - \dfrac{d}{h(G(z))}\right]}{(F(\tilde{x})-\tilde{y})}$$

$$= \frac{\tilde{y}\left[m - \dfrac{d}{h(\tilde{x})}\right]}{(F(\tilde{x})-\tilde{y})}. \tag{2.22}$$

Hence γ_1 coincides with the trajectory $\gamma = (x(t), y(t))$ with $t < 0$. Similarly, we can prove that $\tilde{\gamma}_2 = T\gamma_2$ coincides with the trajectory $\gamma = (x(t), y(t))$ for $t \geq t_2$. This proves that γ is a closed orbit. In fact, $\gamma = \gamma_1 U \gamma_2 U T\gamma_2 U T\gamma_1$. The lemma is proved. Q.E.D.

Lemma 3. *If we represent the systems* (2.1), (2.2) *and* (2.14), (2.15) *in the same phase plane* (*see Fig.* 1), *let*

$$C_1 = \{(x, y) \mid y = f(x), 0 \leq x \leq x^*\},$$

$$C_2 = \{(x, y) \mid y = F(x), \tilde{K} \leq x \leq x^*\}$$

and consider trajectories Γ_1 and Γ_2 for systems (2.1) *and* (2.14), *respectively,*

$$\Gamma_1 = p_1p_2p_3p_4p_5, \qquad \Gamma_2 = q_1q_2q_3q_4q_1,$$

where p_1, q_1 and p_5 belong to C_1, p_2 and q_2 belong to C_2, and $p_3 = q_3 = (x^*, y_3)$ with $y_3 < y^*$ and $p_4 = q_4 = (x^*, y_4)$ with $y_4 > y^*$, then we have $x_{p_1} < x_{q_1} < x_{p_5}$, where x_{p_i} and x_{q_i} are the x-coordinates of points p_i and q_i respectively.

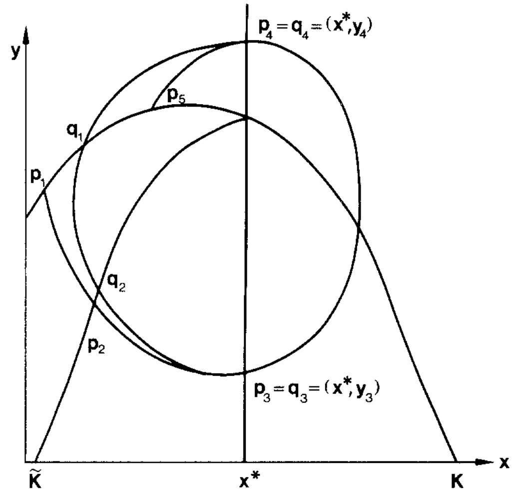

Fig. 1. Phase plane of (2.1), (2.2), (2.14) and (2.15)

Proof. Consider the arcs $\widehat{p_4p_5}$ and $\widehat{q_4q_1}$. Arc $\widehat{p_4p_5}$ satisfies

$$\frac{dy}{dx}=\frac{y\left[m-\dfrac{d}{h(x)}\right]}{f(x)-y}, \qquad y(x^*)=y_4. \tag{2.23}$$

Arc $\widehat{q_4q_1}$ satisfies

$$\frac{dy}{dx}=\frac{y\left[m-\dfrac{d}{h(x)}\right]}{F(x)-y}, \qquad y(x^*)=y_4. \tag{2.24}$$

Since we have $f(x)\geqslant F(x)$ for all $x\in[\tilde{K}, x^*]$ and $f(x)>F(x)$ at least in a small neighborhood of x^*, we obtain that

$$x_{q_1}<x_{p_5}.$$

Similarly we can prove that

$$x_{p_1}<x_{q_1}.$$

This completes the proof. Q.E.D.

Now we are in a position to prove Theorem 1.

Proof of Theorem 1. From Lemma 1, solutions of (2.1), (2.2) are positive and bounded. From Lemma 3, $x_{p_1}<x_{p_5}$ for all trajectories Γ_1, and hence there is no periodic solution. Furthermore (x^*, y^*) of (2.1), (2.2) is locally asymptotically stable. Thus (x^*, y^*) of (2.1), (2.2) is globally stable. This completes the proof of Theorem 1. Q.E.D.

We shall use the above general theorem to derive some specific theorems which include the theorem obtained by Cheng et al. in [3].

Let the assumptions (e) and (f) be

(e) $f(2x^*-x) \leqslant f(x)$ for all x satisfying

$$\max\{0, 2x^*-K\} \leqslant x \leqslant x^*.$$

(f) $d/h(x)-m > m-d/h(2x^*-x)$ for all x satisfying

$$x^* \leqslant x < \min\{2x^*, K\}.$$

Theorem 2. *Under the assumptions* (a), (b), (c), (e) *and* (*f*), (x^*, y^*) *is globally asymptotically stable for system* (2.1), (2.2) *in the interior of the first quadrant.*

Proof. Let $H(x)=f(2x^*-x)$ for $\max\{0, 2x^*-K\} \leqslant x \leqslant x^*$. Then the inverse function V of H has derivative

$$V'(y)=\frac{1}{H'(x)}=\frac{1}{-f'(2x^*-x)}=-G'(y). \tag{2.25}$$

From assumption (f), we have

$$V'(y)=-G'(y) \geqslant \frac{m-\dfrac{d}{h(G(y))}}{m-\dfrac{d}{h(V(y))}} G'(y). \tag{2.26}$$

From (2.26) and (2.9), we have

$$V(y) \leqslant Q(y) \quad \text{and hence} \quad H(x) \geqslant F(x). \tag{2.27}$$

From assumption (e) and (2.27), we have

$$f(x) \geqslant H(x) \geqslant F(x).$$

This means that assumption (d) is satisfied. From Theorem 1, we prove this theorem. Q.E.D.

We define now

$$H(x)=\min\{f(x), f(2x^*-x)\}, \max\{0, 2x^*-K)\} \leqslant x \leqslant x^*. \tag{2.28}$$

Let the assumption (g) be

(g) Assume that the H defined in (2.28) satisfies $H'(x)>0$ for all x except at a set of finite points and that

$$\left(m-\frac{d}{h(x)}\right)\cdot\frac{1}{f'(x)} \geqslant \left(m-\frac{d}{h(V\circ f(x))}\right)\cdot\frac{1}{H'(V\circ f(x))}$$

for all $x^* \leqslant x \leqslant K$, where V is the inverse function of H.

Now we have

Theorem 3. *Under the assumptions* (a), (b), (c) and (g), (x^*, y^*) *is globally asymptotically stable for system* (2.1), (2.2) *in the interior of the first quadrant.*

Proof. Assumption (g) means that

$$V'(y)=\frac{1}{H'(V(y))}\geqslant\frac{m-\dfrac{d}{h(G(y))}}{m-\dfrac{d}{h(V(y))}}G'(y).$$

Hence as in the proof of Theorem 2, we have

$$f(x)\geqslant H(x)\geqslant F(x),\qquad \max\{0,2x^*-K\}\leqslant x\leqslant x^*.$$

Hence assumption (d) is satisfied. This completes the proof. Q.E.D.

3. Discussion

Assumptions (e), (f) and (g) are more easy to check than assumption (d). But using computer, it is relatively easy to check assumption (d). Computer simulations indicate that almost all combinations from (2.3) and (2.4) satisfy the assumption (d).

References

1. Albrecht, F., Gatzke, H., Haddad, A., Wax, N.: The dynamics of two interacting populations. J. Math. Anal. Appl. **46**, 658-670 (1974)
2. Cheng, K. S.: Uniqueness of a limit cycle for a predator-prey system, SIAM J. Math. Anal. **12**, 541-548 (1981)
3. Cheng, K. S., Hsu, S. B., Lin, S. S.: Some results on global stability of a predator-prey system. J. Math. Biol. **12**, 115-126 (1981)
4. Freedman, H. I.: Graphical stability, enrichment, and pest control by a natural enemy. Math. Biosci. **31**, 207-225 (1976)
5. Gaus, G. F., Smaragdova, N. P., With, A. A.: Further studies of interaction between predators and prey. J. Anim. Ecol. **5**, 1-18 (1936)
6. Goh, B. S.: Global stability in many species systems. Am. Natur. **111**, 135-143 (1977)
7. Hastings, A.: Global stability of two species system. J. Math. Biol. **5**, 399-403 (1978)
8. Hsu, S. B.: On global stability of a predator-prey system. Math. Biosci. **39**, 1-10 (1978)
9. Hsu, S. B., Hubbel, S. P., Waltman, P.: Competing predators. SIAM Applied Math. **35**, 617-625 (1978)
10. Liou, L. P., Cheng, K. S.: On the uniqueness of a limit cycle for a predator-prey system. Preprint
11. May, R. M.: Stability and complexity in model ecosystems. Princeton: Princeton University Press 1974
12. Oaten, A., Murdoch, W. W.: Functional response and stability in predator-prey system. Am. Natur. **109**, 289-298 (1975)
13. Real, L. A.: The kinetics of functional response. Am. Natur. **111**, 289-300 (1977)
14. Rosenzweig, M. L.: Why the prey curve has a hump. Am. Natur. **103**, 81-87 (1969)
15. Rosenzweig, M. L., MacArthur, R. H. Graphical representation and stability conditions of predator-prey interaction. Am. Natur. **97**, 209-223 (1963)
16. Rosenzweig, M. L.: Paradox of enrichment: Destabilization of exploitation ecocystem in ecological time. Science **171**, 385-387 (1971)
17. Maynard Smith, J.: Models in ecology. Cambridge: Cambridge University Press 1974

Received April 30, 1986/Revised October 26, 1987