

On Global Stability of a Predator-Prey System

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ABSTRACT

A two-dimensional model for predator-prey interaction is proposed. Two criteria for global stability of the locally stable equilibrium are presented. These make the graphical method of Rosenzweig and MacArthur more significant.

1. INTRODUCTION

The main purpose of this paper is to establish global stability of the locally stable equilibrium of a predator-prey model discussed in [2]. In that paper, Freedman proved the graphical stability criteria of Rosenzweig and MacArthur [11] and discussed the graphical criterion for stability first suggested by Gause, Smaragdova, and Witt [3] for systems without carrying capacity, and rediscovered for such systems by Oaten and Murdoch [9]. When the equilibrium is unstable, the behavior of the solutions is quite clear by the Poincaré-Bendixson theorem. When the equilibrium is locally stable, it seems, however, that no rigorous analysis for global stability of this model has yet appeared in the literature, although such a criterion has been given by Goh [4] for Lotka-Volterra systems.

In Sec. 2, we state the model and its functional properties, which are more general than those given in [2].

In Sec. 3, we will look at the global stability of the equilibrium which lies in the interior of first quadrant. The result of Theorem 3.2 is quite general, though it only partially satisfies the special model discussed in [5]. In Theorem 3.3, we add a biologically significant restriction to the prey isocline and apply Dulac criterion to the model. Theorem 3.3 generalizes the results in [5] and also provides those results which the technique in Theorem 3.2 fails to obtain.

Section 4 is the discussion section, and we defer the proofs to the appendix.

2. THE MODEL

The basic model that we shall consider is

$$\frac{dx}{dt} = xg(x) - yp(x), \quad (2.1a)$$

$$\frac{dy}{dt} = y[-q(x) + cp(x)], \quad (2.1b)$$

where x represents the prey population (or density) and y represents the predator population (or density). The assumptions on $g(x)$, $q(x)$, and $p(x)$ are given below.

The specific growth rate, $g(x)$, governs the growth of the prey in the absence of predators. Several forms of $g(x)$ have been catalogued in [9] or [10]. For examples, $g(x) = \gamma[1 - (x/K)]$, $g(x) = \gamma(K - x)/(K + \epsilon x)$ or $g(x) = \gamma[1 - (x/K)^c]$, $1 \geq c > 0$.

We assume that

$$g(0) > 0, \quad (2.2).$$

and that

there exists $K > 0$ such that

$$g(K) = 0 \quad \text{and} \quad (x - K)g(x) < 0 \quad \text{for } x \neq K. \quad (2.3)$$

The predator response function, $p(x)$, has been much discussed in the literature. Several typical forms can be found in [9] or [10]. In some models $p(x)$ is assumed unbounded, for instance, $p(x) = kx$ in the Lotka-Volterra model. There are many models in which $p(x)$ is assumed bounded above, for example, $p(x) = kx/(a + x)$, $p(x) = kx^c$, $1 \geq c > 0$, or $p(x) = k(1 - e^{-cx})$. In general, we assume

$$p(0) = 0, \quad p'(x) > 0, \quad x \geq 0 \quad \left(' = \frac{d}{dx} \right). \quad (2.4)$$

The death rate $q(x)$, which depends on the prey population, is assumed to satisfy

$$q(0) > 0; \quad q'(x) \leq 0, \quad x \geq 0; \quad \lim_{x \rightarrow \infty} q(x) = q_\infty > 0. \quad (2.5)$$

For the density-independent case for example in [2], $q(x) \equiv s$, while for the density-dependent case, for example [7],

$$q(x) = \frac{ex + f}{rx + s}, \quad \text{where} \quad \frac{f}{s} > \frac{e}{r}.$$

We will write down conditions for there to exist an equilibrium interior to the first quadrant, i.e., a "positive" equilibrium.

From (2.1b) we will need to solve

$$-q(x) + cp(x) = 0. \quad (2.6)$$

From (2.4) and (2.5), let $x^* > 0$ be the unique point such that

$$cp(x^*) = q(x^*). \quad (2.7)$$

Substituting into (2.1a) we get for the y -value of the equilibrium,

$$y^* = \frac{x^*g(x^*)}{p(x^*)}. \quad (2.8)$$

In order to guarantee y^* positive it is necessary to assume

$$x^* < K. \quad (2.9)$$

Then (x^*, y^*) is the required equilibrium.

3. GLOBAL STABILITY

Following in the same way as in [2], we compute the variational matrix evaluated at (x^*, y^*) . The stability conditions are

$$H(x^*) \begin{cases} < 0 & \rightarrow \text{asymptotic stability} \\ > 0 & \rightarrow \text{instability} \end{cases} \quad (3.1)$$

where

$$H(x^*) = x^*g'(x^*) + g(x^*) - \frac{x^*g(x^*)p'(x^*)}{p(x^*)}. \quad (3.2)$$

Rewrite (3.2) as

$$H(x^*) = x^*g(x^*) \frac{d}{dx} \ln \left[\frac{xg(x)}{p(x)} \right]_{x=x^*}. \quad (3.3)$$

Hence the stability conditions can be stated graphically as follows: if the prey isocline $y = xg(x)/p(x)$ is decreasing (increasing) at x^* , then (x^*, y^*) is asymptotically stable (unstable). That is precisely the stability criterion of Rosenzweig and MacArthur [14], which states that (x^*, y^*) is unstable if the isoclines intersect to the left of a local maximum of the prey isocline, and stable if they intersect to the right.

The question we are mainly interested in is: Under which conditions on the shape of the prey isocline will local stability of (x^*, y^*) imply global stability of (x^*, y^*) .

In this section we state the principal results of the paper. The proofs are deferred to the appendix. The first lemma is a statement that the system (2.1) is as “well behaved” as one intuitively from the biological problem.

LEMMA

The solutions of (2.1) are positive and bounded, and furthermore, there exists $T \geq 0$ such that $x(t) < K$ for $t \geq T$.

The next two theorems are our main results. We have some restrictions on the shape of the prey isocline.

THEOREM 3.2

If $[xg(x)/p(x) - y^](x - x^*) \leq 0$, then (x^*, y^*) is globally stable in the 1st quadrant.*

The assumptions on $p(x)$ and $g(x)$ [even that $g(x)$ is decreasing] provide little information about the shape of the isocline $y = xg(x)/p(x)$. From Theorem 3.2, we know that as long as the portion of the prey curve $y = xg(x)/p(x)$, $0 \leq x \leq x^*$ lies above the line $y = y^*$ and that the portion of the prey curve $y = xg(x)/p(x)$, $x^* \leq x \leq K$ lies below $y = y^*$, then (x^*, y^*) is globally stable. We also note that in this case we require only that (x^*, y^*) be stable.

Unfortunately, Theorem 3.2 cannot cover all the cases in the literature. Consider the following example in [5], with $g(x) = \gamma[1 - (x/K)]$, $p(x) = kx/(a+x)$, $c = m/k$, and $q(x) \equiv D$,

$$\begin{aligned} x' &= \gamma x \left(1 - \frac{x}{K}\right) - \frac{kxy}{a+x}, \\ y' &= \left(\frac{mx}{a+x} - D\right)y. \end{aligned} \tag{3.4}$$

The author showed that if $m > D$, $x^* = a/[(m/D) - 1] < K$ and $y^* = (\gamma/k)(1 - x^*/K)(a + x^*)$, then (x^*, y^*) is the unique “positive equilibrium” and (x^*, y^*) is asymptotically stable if $x^* < K < a + 2x^*$. Furthermore the author used the Dulac criterion to show that local stability in fact implies global stability. However, if we apply Theorem 3.2 we only obtain partial results, i.e., if $x^* < K \leq a + x^*$, then (x^*, y^*) is globally stable.

We may consider the prey isocline $y = (\gamma/k)[1 - (x/K)](a + x)$, which is concave downward, and we make the following additional assumption (also see [11], [13]): The prey isocline $y = [xg(x)/p(x)]$ belongs to $C^2[0, K]$ and is concave downward, i.e.,

$$\frac{d^2}{dx^2} \left(\frac{xg(x)}{p(x)} \right) < 0, \quad 0 \leq x \leq K. \tag{3.5}$$

We have the following theorem, which generalizes a result in [5].

THEOREM 3.3

Assume the equilibrium (x^*, y^*) of (2.1) is stable, i.e., $H(x^*) \leq 0$, and let (3.5) hold. Then (x^*, y^*) is globally stable.

4. DISCUSSION:

It is a well-known fact that the local stability of an equilibrium point in a system of ordinary differential equations does not necessarily imply its global stability. However, the usual methods used in the analysis of stability of equilibrium points in population models establishes only local stability. The restriction to sufficiently small perturbations of the initial conditions frequently rules out the perturbations of interest to the ecologist.

The system (2.1) contains a general class of predator-prey models. In Theorem 3.2 we construct a Lyapunov function which is similar to those Goh constructed in [4] for the Lotka-Volterra model. The result of Theorem 3.2 looks special but it can be applied to some models—for instance, the Lotka-Volterra model,

$$\begin{aligned}\frac{dx}{dt} &= \gamma x \left(1 - \frac{x}{K}\right) - kxy, \\ \frac{dy}{dt} &= y(mx - D).\end{aligned}$$

Theorem 3.3 is an improvement of the graphical criterion of Rosenzweig and MacArthur [14], which has been proved analytically in the form of this model (see [2]). The criterion may be stated as follows: (x^*, y^*) is unstable if the prey isocline $y = xg(x)/p(x)$ is increasing at x^* and stable if it is decreasing at x^* . From [11] and [13], it is reasonable to assume that the prey isocline is concave downward. Under this assumption and by Theorem 3.2, it follows that the local stability of (x^*, y^*) in (2.1) implies global stability. A typical example for Theorem 3.3 is

$$\begin{aligned}\frac{dx}{dt} &= \gamma x \left(1 - \frac{x}{K}\right) - \frac{kxy}{a+x}, \\ \frac{dy}{dt} &= y \left(\frac{mx}{a+x} - D\right).\end{aligned}$$

Kolmogorov [6] considers what in some sense is the most general growth model:

$$\begin{aligned}\frac{dx}{dt} &= xf(x, y), \\ \frac{dy}{dt} &= yg(x, y),\end{aligned}\tag{4.1}$$

where f and g satisfy (i) $\partial f/\partial y < 0$, (ii) $x \partial f/\partial x + y \partial g/\partial y < 0$, (iii) $\partial g/\partial y < 0$,

(iv) $x \partial g / \partial x + y \partial g / \partial y \geq 0$, (v) $f(0,0) > 0$, (vi) $f(0,A) = 0$ with $A > 0$, (vii) $f(B,0) = 0$ with $B > 0$, (viii) $g(C,0) = 0$ with $C > 0$, and (ix) $B > C$. Under these conditions he claims the system (4.1) possesses either a stable critical point or a stable limit cycle. For the biological meaning of (i)–(ix), we refer to [9].

The system (2.1) can be reduced to the form (4.1) with $f(x,y) = g(x) - [p(x)/x]y$ and $g(x,y) = cp(x) - q(x)$. It satisfies (i)–(ii) and (iv)–(ix) with $A = p'(0)/g(0)$, $B = K$, and $C = x^*$. The difference between (2.1) and (4.1) is that the growth of predators just depends on the population of prey, i.e., there is no interspecific competition in predator species.

When (x^*, y^*) is unstable, it is easy to verify that (x^*, y^*) is an unstable spiral or node. From Lemma 3.1 and the Poincaré-Bendixson theorem, the system (2.1) has a periodic solution surrounding (x^*, y^*) which is stable from the outside and which lies in the strip $\{(x,y) : 0 < x < K, y > 0\}$.

Hence we have the following conclusion: Let the hypothesis of Theorem 3.2 or Theorem 3.3 hold. Then at least one of the following is valid: (i) (x^*, y^*) is a global attractor, or (ii) the system (2.1) has a periodic solution surrounding (x^*, y^*) which is stable from the outside and which lies in the strip $\{(x,y) : 0 < x < K, y > 0\}$.

5. APPENDIX

PROOF OF LEMMA 3.1

Since $x(0), y(0)$ are positive, from (2.1) it follows that $x(t), y(t)$ are positive for all $t \geq 0$.

If $x(0) < K$ then $x(t) < K$ for all $t \geq 0$. Otherwise, there exists $t_1 > 0$ such that

$$x(t_1) = K \quad \text{and} \quad \frac{dx}{dt}(t_1) \geq 0.$$

By (2.1a), (2.2), (2.3), and (2.4), it follows that

$$c \frac{dx}{dt}(t_1) = -y(t_1)p(x(t_1)) < 0.$$

This is the desired contradiction.

If $x(0) \geq K$, then from (2.1a), (2.2), and (2.3), either $x(t)$ decreases to some constant $X \geq K$ or there exists $t_2 > 0$ such that $x(t_2) < K$. Using the same argument as the case $x(0) < K$ yields that $x(t) < K$ for $t \geq t_2$. Hence $x(t) \leq \max(K, x(0))$ for all $t \geq 0$.

Multiplying (2.1a) by c and adding (2.1b) yields

$$c \frac{dx}{dt}(t) + \frac{dy}{dt}(t) = cx(t)g(x(t)) - y(t)q(x(t)),$$

or

$$c \frac{dx}{dt}(t) + \frac{dy}{dt}(t) \leq cx(t)g(x(t)) - y(t)q_\infty.$$

Let $\eta = \max(cxg(x) + cq_\infty x)$. Then

$$\frac{d}{dt} [cx(t) + y(t)] \leq \eta - q_\infty [cx(t) + y(t)],$$

or

$$cx(t) + y(t) \leq Ae^{-q_\infty t} + \frac{\eta}{q_\infty},$$

where $A = cx(0) + y(0) - \eta/q_\infty$. Hence $y(t)$ is also bounded.

In order to show that there exists $T \geq 0$ such that $x(t) < K$ for $t \geq T$, it suffices to show that it is impossible to have $\lim x(t) = X \geq K$. Since $K > x^*$, if $\lim x(t) = X \geq K$, then by (2.1b), (2.4), (2.5), and (2.7) we have that $y(t)$ becomes unbounded as $t \rightarrow \infty$. This is a contradiction.

PROOF OF THEOREM 3.2

From (2.4) we construct a Lyapunov function

$$V = \int_{x^*}^x \frac{cp(\xi) - q(\xi)}{p(\xi)} d\xi + y - y^* - y^* \ln\left(\frac{y}{y^*}\right)$$

on $G = \{(x, y) : x > 0, y > 0\}$. Then the time derivative of V computed along solution of (2.1) is

$$V' = (cp(x) - q(x)) \left(\frac{xg(x)}{p(x)} - y^* \right) \leq 0 \quad \text{on } G.$$

Let $E = \{(x, y) \in \bar{G} : V(x, y) = 0\}$. Then $E = \{(x, y) : xg(x)/p(x) = y^*, y \geq 0\}$, and the largest invariant set M in E is $\{(x^*, y^*)\}$. Hence Theorem 3.2 follows directly from Lemma 3.1 and Lasalle's extension theorem [7].

PROOF OF THEOREM 3.3

From Lemma 3.1 and the Poincaré-Bendixson theorem it suffices to show that there is no limit cycle in the region $D = \{(x, y) : x > 0, y > 0\}$. The absence of a limit cycle will follow from a theorem of Dulac (see [1]).

Let

$$\begin{aligned} f_1(x, y) &= xg(x) - yp(x), \\ f_2(x, y) &= y[cp(x) - q(x)], \end{aligned}$$

and

$$h(x,y) = [p(x)]^\alpha y^\delta, \quad x > 0, \quad y > 0,$$

where $\alpha, \delta \in R$ will be selected below. The Dulac theorem states that there will be no limit cycle if the expression $\partial(f_1 h)/\partial x + \partial(f_2 h)/\partial y$ does not change sign in D . The expression can be computed to be

$$\begin{aligned} \Delta &= \frac{\partial(f_1 h)}{\partial x} + \frac{\partial(f_2 h)}{\partial y} \\ &= -y^{\delta+1} [p(x)]^\alpha p'(x)(1+\alpha) \\ &\quad + [p(x)]^{\alpha-1} y^\delta \{ \alpha p'(x) x g(x) \\ &\quad + x g'(x) p(x) + g(x) p(x) + \beta p(x) [c p(x) - q(x)] \}, \end{aligned}$$

where $\beta = \delta + 1 > 0$.

Let $\alpha = -1$. Then

$$\Delta = (p(x))^{-2} y^\delta F(x), \quad (3.6)$$

where

$$F(x) = p(x) [g(x) + x g'(x)] - p'(x) x g(x) + \beta p(x) [c p(x) - q(x)]. \quad (3.7)$$

We may rewrite $F(x)$ as follows:

$$F(x) = p^2(x) \left[\frac{xg(x)}{p(x)} \right]' + \beta p(x) [c p(x) - q(x)]. \quad (3.8)$$

Then

$$\begin{aligned} F'(x) &= 2p(x)p'(x) \left[\frac{xg(x)}{p(x)} \right]' + p^2(x) \left[\frac{xg(x)}{p(x)} \right]'' + 2\beta c p(x)p'(x) \\ &\quad - \beta p'(x)q(x) - \beta p(x)q'(x). \end{aligned} \quad (3.9)$$

Since $F(0) = 0$ and $F'(0) = -\beta q(0)p'(0) < 0$, there exist $\delta_1 > 0$ such that $F(x) < 0$ for $0 < x < \delta_1$. Let

$$0 < \beta < \min \left\{ \frac{-g'(K)K}{cp(K) - q(K)}, \frac{-\min_{\delta < x < K} \left[\frac{xg(x)}{p(x)} \right]''}{\max_{\delta < x < K} \frac{q(x)p'(x) - q'(x)p(x)}{p^2(x)}} \right\}. \quad (3.10)$$

Then from (3.2), (3.7), and (3.10), it follows that $F(x^*) \leq 0$, and

$$F(K) = Kp(K)g'(K) + \beta p(K)[cp(K) - q(K)] < 0.$$

We claim that

$$F(x) \leq 0 \quad \text{for } \delta \leq x \leq K. \quad (3.11)$$

If not, there exists x_1 , $\delta < x_1 < K$, such that

$$F(x_1) = p^2(x_1) \left[\frac{xg(x)}{p(x)} \right]'_{x=x_1} + \beta p(x_1)[cp(x_1) - q(x_1)] = 0 \quad (3.12)$$

and

$$\begin{aligned} F'(x_1) &= 2p(x_1)p'(x_1) \left[\frac{xg(x)}{p(x)} \right]_{x=x_1} + p^2(x_1) \left[\frac{xg(x)}{p(x)} \right]''_{x=x_1} \\ &\quad + 2\beta cp(x_1)p'(x_1) - \beta q(x_1)p'(x_1) - \beta q'(x_1)p(x_1) > 0 \end{aligned}$$

But from (3.12)

$$\begin{aligned} F'(x_1) &= 2p'(x_1) \{ -\beta [cp(x_1) - q(x_1)] \} + p^2(x_1) \left[\frac{xg(x)}{p(x)} \right]''_{x=x_1} \\ &\quad + 2\beta cp(x_1)p'(x_1) - \beta [q(x_1)p'(x_1) + q'(x_1)p(x_1)] \\ &= \beta [p'(x_1)q(x_1) - q'(x_1)p(x_1)] + p^2(x_1) \left[\frac{xg(x)}{p(x)} \right]''_{x=x_1} \\ &\leq \beta [p'(x_1)q(x_1) - q'(x_1)p(x_1)] + p^2(x_1) \min_{\delta < x < K} \left[\frac{xg(x)}{p(x)} \right]'' \\ &= p^2(x_1) \left[\beta \frac{p'(x_1)q(x_1) - q'(x_1)p(x_1)}{p^2(x_1)} + \min_{\delta < x < K} \left[\frac{xg(x)}{p(x)} \right]'' \right] \\ &\leq p^2(x_1) \left\{ \beta \max_{\delta < x < K} \frac{p'(x)q(x) - q'(x)p(x)}{p^2(x)} + \min_{\delta < x < K} \left[\frac{xg(x)}{p(x)} \right]'' \right\} \\ &< 0. \end{aligned}$$

Hence (3.11) holds. By Lemma 3.1, (3.6), and the Dulac criterion, Theorem 3.3 follows.

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