

LIMIT CYCLES IN A PREY-PREDATOR SYSTEM

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Abstract—We consider a generalised Gause-type prey-predator system, where both the prey and the predator species have independent specific growth rate. We proved that the system has limit cycles globally.

1. INTRODUCTION

We consider a generalised Gause-type model of two interacting species which are in prey-predator relationship and where both species have independent specific growth rate in the absence of other, by the following set of autonomous differential equations:

$$\dot{x} = xg(x) - yp(x) \quad (1.1a)$$

$$\dot{y} = yG(x, y) \quad (1.1b)$$

$$x(0) = x_0 > 0, \quad y(0) = y_0 > 0 \quad \text{and} \quad \cdot \equiv \frac{d}{dt}.$$

Here, $x(t)$ and $y(t)$ denote the biomass of the prey species x and the predator species y respectively at time t . The specific growth rate of the prey species x is $g(x)$, and $p(x)$ is the rate at which the species x are consumed by the predator y . $G(0, y)$ is the specific growth rate of the predator y in the absence of the prey species x . It is considered in (1.1b) that the predator species has an alternative resource so that in the absence of prey, it can survive. Thus, this prey-predator model is quite different from the usual prey-predator model (see [1–3]). Such prey-predator model (1.1) can be obtained as a subsystem of a generalised model of three-species cyclic loops [4,5]. Three-species cyclic loops are found in some aquatic ecosystems [6]. Cyclic loops can occur in ecological communities [7] and also in bio-geo-chemical food webs [8].

We consider the following assumptions:

(H1)

- (a) g, p and G are continuously differentiable functions.
- (b) $g(0) = \alpha > 0$. There exists a unique $k > 0$ such that $g(k) = 0$. $g'(x) < 0$ for $x \geq 0$.
- (c) $G(x, 0) = \alpha_1 > 0$, $\frac{\partial G(x, y)}{\partial y} < 0$, $x, y \geq 0$. This implies that the predator population growth rate is density dependent and slows down as the population increases. Since species x and y are in prey-predator relation,

$$\frac{\partial G(x, y)}{\partial x} > 0 \text{ holds.}$$

- (d) There exists a $L(x)$ such that $G(x, L(x)) = 0$ where $L : R_+ \rightarrow R_+$ and $L'(x) \geq 0$. This implies the existence of a monotonically increasing density dependent carrying capacity for the predator and also we assume

$$\lim_{x \rightarrow \infty} L(x) = \bar{L} < +\infty.$$

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- (e) $p(0) = 0 \cdot p'(x) > 0$ for $x \geq 0$.
 $\lim_{x \rightarrow \infty} p(x) = p_\infty$ where $0 < p_\infty < +\infty$.
 $\lim_{x \rightarrow 0^+} p(x)/x = p'(0) = \beta > 0$.

This means that the predator functional response $p(x)$ is zero when x is sufficiently small and it is the increasing function of x , but approaches asymptotically to a finite positive value when x is large enough. The specific loss rate $p(x)/x$ is a non-zero quantity when x is sufficiently small.

(H2) All the feasible equilibria are hyperbolic.

2. DISSIPATIVITY OF THE SYSTEM (1.1)

The system (1.1) describing the evolution of $X(t) = (x(t), y(t))$, is said to be dissipative if all the trajectories of (1.1) are uniformly asymptotically bounded for $t \geq 0$. In other words, there exists a constant M such that

$$\limsup_{t \rightarrow \infty} \|X(t)\| \leq M$$

For our system (1.1) the result regarding dissipativity is given in the following lemma.

LEMMA 2.1. *All solutions of (1.1) that initiate in R_+^2 are uniformly asymptotically bounded for some $\bar{x}, \bar{y} > 0$ to be specified later and they are ultimately in the region $B \subseteq R_+^2$, where*

$$B = \{(x, y) : 0 \leq x \leq \bar{x}; \quad 0 \leq y \leq \bar{y}\}.$$

PROOF. By (H1b) $g'(x) < 0 \Rightarrow x \leq xg(x) \Rightarrow x(t) \leq \max(k, x_0) = \bar{x}$ (say).

Again, $\partial G(x, y)/\partial y < 0 \Rightarrow$ if $y_0 < \bar{L}$, $y(t) \leq L(x) + \epsilon \leq \bar{L} + \epsilon$ for any $\epsilon > 0$. If $y_0 \geq \bar{L}$ then $y(t) \leq \max(\bar{L} + \epsilon, y_0) = \bar{y}$ (say) (see [9]).

2.1. Equilibria and Their Stability

By (H1), the trivial equilibrium $E_0(0, 0)$ and the two axial equilibria $E_1(k, 0)$, $E_2(0, L(0))$, always exist.

The interior positive equilibrium of the system (1.1) is the intersection of the two isoclines $\dot{x} = \dot{y} = 0$ in the positive quadrant of the xy plane.

From (1.1a), the prey isocline: $\dot{x} = 0$ is equivalent to

$$y = \frac{xg(x)}{p(x)} = F(x) \text{ say} \tag{2.1a}$$

and from (1.1b), the predator isocline: $\dot{y} = 0$ gives $G(x, y) = 0$. This is equivalent to the curve

$$y = L(x). \tag{2.1b}$$

The predator isocline (2.1b) meets the y -axis at $(0, L(0))$ and it is a monotonically increasing function. The prey isocline $F(x)$ intersects the x -axis at E_1 and the y -axis at $(0, \alpha/\beta)$. For mathematical convenience we impose the following assumption on $F(x)$.

(H3) The prey isocline $F(x)$ possesses a unique global maximum at $x_M \geq 0$ satisfying

$$\begin{aligned} \frac{dF}{dx} &> 0 \quad \text{for } 0 \leq x < x_M \\ &< 0 \quad \text{for } x_M < x \leq k. \end{aligned}$$

Together with (H1)–(H3), we get the following result which ensured the existence of the interior positive equilibrium of the system (1.1).

PROPOSITION 2.2. *Let (H1)–(H3) hold. Further let $L(0) < \alpha/\beta$ hold. Then there is a positive equilibrium $E(\hat{x}, \hat{y})$ in the interior of B .*

PROOF. By Lemma (2.1), the system (1.1) is dissipative. The variational matrix $V(x, y)$ of the system (1.1) is

$$V(x, y) = \begin{bmatrix} p(x)F'(x) & -p(x) \\ yG_x(x, y) & -yG_y(x, y) \end{bmatrix} \quad (2.2)$$

From (2.2), it follows that E_0 is a repeller along both the x - and y -directions. E_1 is locally stable along the x -direction but unstable along the y -direction. E_2 is locally unstable along the x -direction since $L(0) < \alpha/\beta$. So there exists an equilibrium E in the interior of the positive xy plane. This follows from an application of the Poincare-Bendixson theorem.

Now if the condition $L(0) < \alpha/\beta$ is satisfied there may be more than one equilibria in the interior of B and hence, we further assume.

(H4) If $L(0) < \alpha/\beta$, then the positive equilibrium E is unique in the interior of B .

Moreover, the equilibrium E in the interior of B may lie on the increasing part of $F(x)$ or may lie on the decreasing part of $F(x)$.

REMARK 2.3. If $L(0) \geq \alpha/\beta$, then there does not exist or exists multiple interior equilibria (see [5]) in the positive xy plane. We shall not consider this case in this paper.

PROPOSITION 2.4. Let (H1)–(H4) and $L(0) < \alpha/\beta$ hold. In addition,

- (a) let E lie on the decreasing part of $F(x)$, then E is a sink, and
- (b) let E lie on the increasing part of $F(x)$, then E is a sink provided $\bar{A} < -G_y(\hat{x}, \hat{y}) < \bar{B}$ and E is a source if $-G_y(\hat{x}, \hat{y}) < \bar{A}$, where

$$\bar{A} = \frac{p(\hat{x})F'(\hat{x})}{\hat{y}} \text{ and } \bar{B} = \frac{G_x(\hat{x}, \hat{y})}{F'(\hat{x})} \quad (2.3)$$

PROOF. The characteristic equation for $E(\hat{x}, \hat{y})$ is obtained from (2.2):

$$\mu^2 + p_1\mu + q_1 = 0 \quad (2.4)$$

where

$$p_1 = -(p(\hat{x})F'(\hat{x}) + \hat{y}G_y(\hat{x}, \hat{y})) \quad (2.5a)$$

and

$$q_1 = \hat{y}p(\hat{x}) \{G_y(\hat{x}, \hat{y})F'(\hat{x}) + G_x(\hat{x}, \hat{y})\} \quad (2.5b)$$

- (a) From (2.5), it is clear that if E lies on the decreasing part of $F(x)$, that is, $F'(x) < 0$, then $p_1 > 0$ and $q_1 > 0$. This implies that E is a sink. This completes the proof of part (a).
- (b) Let E lie on the increasing part of $F(x)$. We shall prove first that E cannot be a saddle point. E must be either a sink or a source. It follows from the Index Theorem [3] that the sum of the indices of all the saturated regular equilibria of a dissipative two-dimensional system is $(-1)^2 = +1$. By Lemma (2.1), the system (1.1) is dissipative. In the positive xy plane, the axial equilibria E_1, E_2 are non-saturated and the only saturated fixed point is E . So the index of E must be $(+1)$. Then E must be a sink with two-dimensional (local) stable manifolds or a source with two dimensional (local) unstable manifolds. Let E be a saddle point, then its index is (-1) which contradicts the Index Theorem [3]. Hence, E can never be a saddle point. E can only be either a sink or a source.

From (2.5),

$$\begin{aligned} p_1 > 0 &\Rightarrow -G_y(\hat{x}, \hat{y}) > \bar{A} \quad \text{and} \\ q_1 > 0 &\Rightarrow -G_y(\hat{x}, \hat{y}) < \bar{B} \end{aligned}$$

Thus, whenever E lies on the increasing part of $F(x)$, E is a sink provided $\bar{A} < -G_y < \bar{B}$ and E is a source if $-G_y < \bar{A}$.

2.2. The Existence of Limit Cycles

Next, we investigate the existence of limit cycles globally. For this purpose, we consider that the equilibrium E lies on the increasing part of $F(x)$ and $-G_y(\hat{x}, \hat{y}) < \bar{A}$, that is, the equilibrium E is a source. Then by boundedness of solutions, there is an attracting limit cycle around E . This follows from our last result.

THEOREM 2.6. *Let (H1)–(H4) and $L(o) < \alpha/\beta$ hold. Further, let E lie on the increasing part of $F(x)$ and $-G_y(\hat{x}, \hat{y}) < \bar{A}$. Then there exists a limit cycle enclosing E , which is globally stable from the outside.*

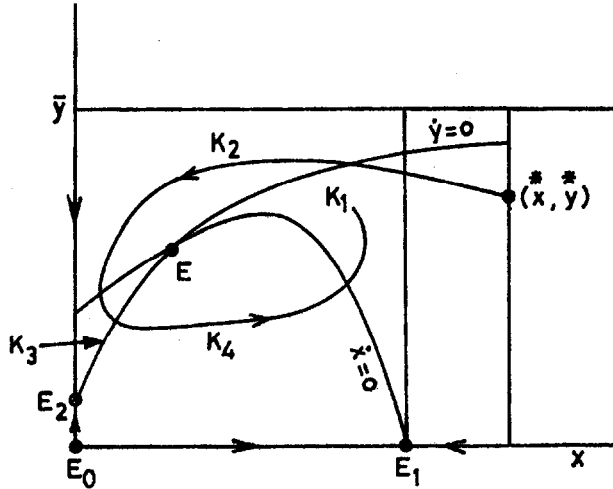


Figure 1. Illustrating the proof of Theorem 2.6.

PROOF. Let R be the rectangle with $0 < x < k$ and $0 < y < \bar{y}$. The closure \bar{R} of R is divided by the isoclines $\dot{x} = \dot{y} = 0$ into four compact regions k_1, k_2, k_3 and k_4 (see Figure 1). Let \bar{R}^* be the compact rectangle: $0 \leq x \leq \max(k, x^*)$ and $0 \leq y \leq \max(\bar{y}, y^*)$ for arbitrary fixed $x^*, y^* > 0$ and $(x^*, y^*) \notin R$. Also let γ^+ be the positive semiorbit of (1.1) with initial value (x^*, y^*) and $\omega(\gamma^+)$ be its omega limit set. Since \bar{R}^* is positively invariant, $\gamma^+ \in \text{Int}\bar{R}^*$ (interior of \bar{R}^*) and $\omega(\gamma^+) \subseteq \bar{R}^*$. Again, while γ^+ is contained in a compact region where \dot{x} and \dot{y} of (1.1) do not change sign, γ^+ tends to a limit as $t \rightarrow \infty$ and this limit is an equilibrium. But we get the following:

- (1) As the equilibrium E_1 is locally unstable along the direction into the interior of positive xy plane, γ^+ cannot tend to E_1 for $t \rightarrow \infty$. Rather γ^+ reaches k_1 (or k_2 if (x^*, y^*) lies above the $\dot{y} = 0$ isocline).
- (2) Entering region k_1 , after a finite time, as stated earlier γ^+ cannot approach to E_1 . E is a source. So γ^+ cannot also converge E . γ^+ must leave k_1 and enter k_2 .
- (3) From k_2 , after finite times, γ^+ moves to k_3 . In region k_3 , convergence of γ^+ to E_2 is not possible, as E_2 is locally unstable along its orthogonal direction. So after some times on γ^+ leaves k_3 and moves to k_4 .
- (4) In k_4 , E_0 is a repeller. So γ^+ cannot converge E_0 or E_1 . γ^+ must enter k_1 .

Following the same process described in (1)–(4), for $t \rightarrow \infty$. γ^+ spirals inwards R . (γ^+ cannot leave R , as R is positively invariant). Further, γ^+ starts outside of R and γ^+ cannot intersect itself. Hence γ^+ is not a closed trajectory.

From (1)–(4) it is also clear that $E_0, E_1, E_2, E \notin \omega(\gamma^+)$. By Poincare-Bendixson theorem, $\omega(\gamma^+)$ is a closed orbit and since $\gamma^+ \neq \omega(\gamma^+)$, $\omega(\gamma^+)$ is a limit cycle. Again by Poincare-Bendixson theorem, any closed orbit of (1.1) enclosing E must be in a positively invariant rectangle R . Thus, any closed orbit in $R \neq \omega(\gamma^+)$ must be encircled by $\omega(\gamma^+)$. Hence, $\omega(\gamma^+)$ is the ω -limit set for each initial value (x^*, y^*) lying outside domain of $\omega(\gamma^+)$.

REFERENCES

1. H.I. Freedman, *Deterministic Mathematical Models in Population Ecology*, Marcel Dekker, New York, (1980).
2. M. Farkas and H.I. Freedman, Stability conditions of two predator one prey systems, *Acta Appl. Math.* **14**, 3–10 (1989).
3. J. Hofbauer and K. Sigmund, *Dynamical Systems and Theory of Evolution*, Cambridge University Press, Cambridge, (1988).
4. A.B. Roy and F. Solimano, Global stability and oscillations in classical Lotka-Volterra loop, *J. Math. Biol.* **24**, 603–617 (1987).
5. A. Sikder, Persistence and oscillations of models of three or more interacting species, Ph.D. Thesis, Department of Mathematics, Jadavpur University, India, (1991).
6. L.R. Lawlor, A comment on randomly constructed model ecosystems, *Am. Nat.* **112**, 445–447 (1978).
7. G.C. Gallopín, Structural properties of food web, In *Systems Analysis and Simulation in Ecology*, Volume 2, (Edited by B.C. Patten), Academic Press, New York, (1972).
8. R.H. Wittaker, *Communities and Ecosystems*, MacMillan, New York, (1970).
9. B. Rai, H.L. Freedman and J.F. Addicott, Analysis of three species models of mutualism in predator-prey and competitive systems, *Math. Biosci.* **65**, 13–50 (1983).