J. Math. Biology 6, 67–73 (1978)

Journal of Mathematical Biology

The Application of the Poincaré-Transform to the Lotka-Volterra Model

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Summary. In this article, we show how to apply the Poincaré-transform to the general Lotka–Volterra model and investigate the question of the global asymptotic stability of the locally stable equilibrium point. An attempt is made to estimate the domain of attraction when the critical point is not globally stable. Results for the two dimensional case, due to Goh [3], are improved.

1. Introduction

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 all perturbations of interest to the ecologist. The Lotka–Volterra model of n-species interaction is such an example. A Lotka–Volterra model can have a locally stable equilibrium without being globally stable; in fact, may not even be Lagrange-stable, i.e. there may exist an unbounded trajectory.

In this paper, we first apply the Poincaré-transform for the path at infinity to the general Lotka–Volterra model to investigate the possibility of global stability of a locally stable equilibrium. The complement of the domain of attraction of a stable, but not globally stable, equilibrium is estimated. The application of the Poincaré-transform to the Lotka–Volterra model and a criterion of Goh [2, 3] give good results in resolving the question of global stability of a two-species interaction. For a discussion of the Poincaré-transform, we refer to [1]. In the last section we discuss this result in terms of the needs of the biologist for whom local stability and a large domain of attraction may be effectively global stability.

2. The Poincaré-Transform

Consider the Lotka–Volterra model

$$\dot{N}_i = N_i\left[b_i + \sum_{j=1}^{n} a_{ij}N_j\right], \quad i = 1, \ldots, n, \tag{1}$$

0303–6812/78/0006/0067/$01.40

for an n-species system in which the species may be competitors, predators and prey, or otherwise related.

For each i, $1 \leqslant i \leqslant n$, we introduce new variables

$$u_j = \begin{cases} \dfrac{N_j}{N_i}, & j \neq i \\ & \qquad j = 1, \ldots, n, \\ \dfrac{1}{N_i}, & j = i \end{cases} \tag{2}$$

or

$$N_i = \frac{1}{u_i} \quad \text{and} \quad N_j = \frac{u_j}{u_i}, \quad j \neq i \tag{2'}$$

Under the Poincaré-transform (2) or (2′), Eq. (1) becomes

$$\dot{u}_j = (-a_{ii}) + \sum_{k=1}^{i-1} (-a_{ik})u_k + (-b_i)u_i + \sum_{k=i+1}^{n} (-a_{ik})u_k,$$

$$\dot{u}_j = \frac{u_j}{u_i}\left[(a_{ji} - a_{ii}) + \sum_{k=1}^{i-1} (a_{jk} - a_{ik})u_k + (b_j - b_i)u_i + \sum_{k=i+1}^{n} (a_{jk} - a_{ik})u_k\right]. \tag{3}$$

Let $c^+ = \max(c, 0)$ for any real number c and

$$\Omega_i = \{(N_1, \ldots, N_n)\colon N_1, \ldots, N_n > 0,$$
$$\sum_{k \neq i} (-a_{ik})^+ N_k + (-b_i)^+ < a_{ii} N_i \quad \text{and}$$
$$\sum_{k \neq i} (a_{jk} - a_{ik})^+ N_k + (b_j - b_i)^+ < (a_{ii} - a_{ji})N_i \quad \text{for each } j \neq i\}$$

Theorem 1. *If* $a_{ii} > 0$ *for some* i, $1 \leqslant i \leqslant n$ *and for such* i, $a_{ji} - a_{ii} < 0$ *for all* $j \neq i$, *then the solutions* $(N_k(t))_{k=1}^n$ *of* (1) *with initial values* $(N_{k0})_{k=1}^n$ *in* Ω_i *satisfy* $\lim_{t\to\infty} N_i(t) = \infty$.

Proof. From (2), (3) and the assumptions, the initial values $(u_{k0})_{k=1}^n$ of (3) satisfy

$$(-a_{ii}) + \sum_{i \neq k} (-a_{ik})^+ u_{k0} + (-b_i)^+ u_{i0} < 0$$

and

$$(a_{ji} - a_{ii}) + \sum_{i \neq k} (a_{jk} - a_{ik})^+ u_{k0} + (b_j - b_i)^+ u_{i0} < 0.$$

Since $u_k > 0$ for $k = 1, \ldots, n$, then the solution $u_i(t)$ of (3) decreases to zero or $N_i(t)$ approaches infinity as $t \to \infty$.

From this theorem, we note that if there is a species i which is not self-regulating and for each interaction coefficient a_{ji}, $j \neq i$, a_{ji} is less than a_{ii}, then it is impossible to achieve global stability for any equilibrium in the first octant.

Let $\Omega = \bigcup_{i=1}^{n} \Omega_i$. Every trajectory originating from Ω tends to infinity. The region Ω is contained in the complement of the domain of attraction of any locally stable equilibrium in the first octant.

3. LaSalle's Extension Theorem

We note the following definition and the theorem of LaSalle [5, 6], which will be used in Section IV. Let $(I): x' = f(x)$ be a system of differential equations. The vector-valued function $f(x)$ is continuous in x for $x \in \bar{G}$ where G is an open set in R^n. Let V be a C^1 function on R^n to R.

Definition. We say V is a Lyapunov function in G for (I) if $\dot{V} = \text{grad } V \cdot f \leqslant 0$ on G. Let $E = \{x \in \bar{G}: \dot{V}(x) = 0\}$.

Theorem. *If V is a Lyapunov function in G for (I), then each bounded solution $x(t) \subseteq G$ of (I), approaches M where M is the largest invariant set in E.*

4. Two-Species Interaction

In this section we shall apply the Poincaré-transform to improve the results of Goh in [3].

Consider the two species-interaction Lotka–Volterra model

$$\begin{aligned} \dot{N}_1 &= N_1(b_1 + a_{11}N_1 + a_{12}N_2) \\ \dot{N}_2 &= N_2(b_2 + a_{21}N_1 + a_{22}N_2) \end{aligned} \tag{4}$$

Goh gave sufficient conditions for the global stability of an equilibrium, which are:

i) the equilibrium $(\bar{N}_1, \bar{N}_2)$ is feasible, i.e. $\bar{N}_1 > 0$, $\bar{N}_2 > 0$,
ii) the equilibrium is asymptotically stable, and,
iii) both species sustain density-dependent mortalities due to the intra-specific interactions.

Conditions (i) and (ii) hold if

$$\Delta = a_{11}a_{22} - a_{12}a_{21} > 0, \tag{5}$$

$$\bar{N}_1 = \frac{b_2 a_{12} - b_1 a_{22}}{\Delta} > 0, \tag{6}$$

$$\bar{N}_2 = \frac{b_1 a_{21} - b_2 a_{11}}{\Delta} > 0,$$

$$a_{11}\bar{N}_1 + a_{22}\bar{N}_2 < 0, \tag{7}$$

while the condition (iii) means that

$$a_{11} < 0, \qquad a_{22} < 0. \tag{8}$$

In fact, under (5), (6), (7), applying the arguments in [3] and LaSalle's extension theorem, the condition (8) can be weakened to

$$a_{11} \leqslant 0, \qquad a_{22} \leqslant 0 \quad \text{with at least one being non-zero.} \tag{8'}$$

The interesting case remaining then is when $a_{11}a_{22} < 0$. For convenience in this section, we assume

$$a_{11} < 0, \qquad a_{22} > 0. \tag{9}$$

The argument for the case $a_{11} > 0$, $a_{22} < 0$ is symmetrical.

Applying the Poincaré-transform $N_1 = v/z$, $N_2 = 1/z$ or $z = 1/N_2$, $v = N_1/N_2$ to (4) yields

$$\dot{v} = \frac{v}{z}[(a_{11} - a_{21})v + (b_1 - b_2)z + (a_{12} - a_{22})], \tag{10}$$

$$\dot{z} = [(-a_{21})v + (-b_2)z + (-a_{22})],$$

while applying the Poincaré-transform $N_1 = 1/w$, $N_2 = u/w$ or $w = 1/N_1$, $u = N_2/N_1$ yields

$$\dot{u} = \frac{u}{w}[(a_{22} - a_{12})u + (b_2 - b_1)w + (a_{21} - a_{11})], \tag{11}$$

$$\dot{w} = [(-a_{12})u + (-b_1)w + (-a_{11})].$$

Theorem 2. *Let $(\bar{N}_1, \bar{N}_2)$ be the feasible, asymptotically stable equilibrium of system* (4), *i.e. let* (5), (6), (7) *hold. Assume also that* (9) *holds*

i) *If $a_{12} < a_{22}$ then there exists an unbounded trajectory,*
ii) *If*

$$a_{12} = a_{22} \quad or \tag{12}$$

$$a_{12} > a_{22} \quad and \quad b_1 \geqslant 0, \quad or \tag{13}$$

$$a_{12} > a_{22}, \qquad b_1 < 0 \quad and \quad b_2 = 0 \quad or \tag{14}$$

$$a_{12} > a_{22}, \qquad b_1 < 0, \qquad b_2 > 0 \quad and \quad a_{21} \geqslant a_{11} \tag{15}$$

then $(\bar{N}_1, \bar{N}_2)$ is globally stable.

Proof. Since $a_{22} > 0$ and $a_{12} - a_{22} < 0$. From (10) and the arguments in Theorem 1, (i) follows.

Let $\bar{z} = 1/\bar{N}_2$, $\bar{v} = \bar{N}_1/\bar{N}_2$ and $\bar{w} = 1/\bar{N}_1$, $\bar{u} = \bar{N}_2/\bar{N}_1$.

We may rewrite (10) and (11) as follows:

$$\dot{v} = \frac{1}{z}v[(a_{11} - a_{21})(v - \bar{v}) + (b_1 - b_2)(z - \bar{z})], \tag{10'}$$

$$\dot{z} = \frac{1}{z}z[(-a_{21})(v - \bar{v}) + (-b_2)(z - \bar{z})]$$

and

$$\dot{u} = \frac{1}{w}u[(a_{22} - a_{12})(u - \bar{u}) + (b_2 - b_1)(w - \bar{w})], \tag{11'}$$

$$\dot{w} = \frac{1}{w}w[(-a_{12})(u - \bar{u}) + (-b_1)(w - \bar{w})].$$

We take as a Lyapunov function V for (11),

$$V = c_1\left(u - \bar{u} - \bar{u}\ln\frac{u}{\bar{u}}\right) + c_2\left(w - \bar{w} - \bar{w}\ln\frac{w}{\bar{w}}\right)$$

for some $c_i > 0$, $i = 1, 2$. It follows that

$$\dot{V} = \frac{1}{2w}\begin{bmatrix} u - u \\ w - \bar{w} \end{bmatrix}^T (C_1A_1 + A_1^TC_1)\begin{bmatrix} u - u \\ w - \bar{w} \end{bmatrix}$$

where

$$C_1 = \begin{bmatrix} c_1 & 0 \\ 0 & c_2 \end{bmatrix}, \qquad A_1 = \begin{bmatrix} a_{22} - a_{12} & b_2 - b_1 \\ -a_{12} & -b_1 \end{bmatrix}.$$

If (12) holds, then from (5) and (7) we have $0 > a_{11} > a_{21}$, $a_{22}b_1(a_{21} - a_{11}) < 0$, and hence $b_1 > 0$.

Following the arguments in [3] and using LaSalle's extension theorem, $(\bar{u}, \bar{w})$ is globally stable with respect to the system (11) provided either (12) or (13) holds.

Consider the Lyapunov function V for (10)

$$V = c_1^*\left(v - \bar{v} - \bar{v}\ln\frac{v}{\bar{v}}\right) + c_2^*\left(z - \bar{z} - \bar{z}\ln\frac{z}{\bar{z}}\right)$$

for some $c_i^* > 0$, $i = 1, 2$. It follows that

$$\dot{V} = \frac{1}{2z}\begin{bmatrix} v - \bar{v} \\ z - \bar{z} \end{bmatrix}^T (C_2A_2 + A_2^TC_2)\begin{bmatrix} v - \bar{v} \\ z - \bar{z} \end{bmatrix}$$

where

$$C = \begin{bmatrix} c_1^* & 0 \\ 0 & c_2^* \end{bmatrix} \quad \text{and} \quad A_2 = \begin{bmatrix} a_{11} - a_{21} & b_1 - b_2 \\ -a_{21} & -b_2 \end{bmatrix}$$

If (14) holds, then from (7) we have $a_{21} > a_{11}$. Using the same arguments as above yields the global stability of $(\bar{v}, \bar{z})$ with respect to (10) provided either (14) or (15) holds.

Hence $(\bar{N}_1, \bar{N}_2)$ is globally stable provided either of (12), (13), (14), (15) holds.

Remark. We note that $b_1 < 0$ and $b_2 < 0$ implies that (0, 0) is asymptotically stable.

5. Discussion

Theorem 1 and part (i) of Theorem 2 give sufficient conditions for the existence of an unbounded trajectory of (1) and (4) respectively. If the domain of attraction of the locally stable equilibrium is large, then for any practical situation the system is still 'globally stable' in the biological sense. It is difficult to estimate the domain of attraction since the Lyapunov's function we used yielded either global stability of nothing. However, Theorem 1 does provide us an estimation of the complement of the domain of attraction. Consider the following numerical example in [3]:

$$\dot{N}_1 = N_1(5 - 2N_1 - 3N_2), \tag{16}$$

$$\dot{N}_2 = N_2(-2 + N_1 + N_2).$$

This system has a unique locally stable equilibrium (1, 1) in the first quadrant. Since $a_{12} = -3$ and $a_{22} = 1$, by part (i) of Theorem 2 there exists an unbounded trajectory. Applying Theorem 1 to (16) yields that $\Omega = \{(N_1, N_2): N_2 > 2\}$. Since Ω is a large region and is contained in the complement of the domain of attraction of the equilibrium (1, 1), we cannot treat (16) to be a 'globally stable' system.

From (5) and (9), each of (12), (13), (14) and (15) implies $a_{21} > 0$ and $a_{12} > 0$. Part (ii) of Theorem 2 can be stated as follows: The species 1, which is a self-regulating predator, can provide robust regulation of species 2, which is a non-self-regulating prey. In condition (13), $b_1 = 0$ is irrelevant in ecological contexts and $b_1 > 0$ would mean that the predator has a positive intraspecific growth coefficient. Since $b_2 = 0$ implies no intrinsic growth for the prey, the condition (14) seems artificial and is considered only for the sake of mathematical completeness. Unfortunately, we still cannot solve the case $a_{21} < a_{11} < 0$, $a_{12} > a_{22} > 0$, $b_i < 0$ and $b_2 > 0$. We note that from [1] p. 213, (4) has no limit cycle. To establish the global stability of the equilibrium is equivalent to show boundedness of the solutions.

In [4], Hasting considered the system

$$\dot{N}_1 = N_1 f(N_1, N_2),$$
$$\dot{N}_2 = N_2 g(N_1, N_2)$$

where the non-linear growth rate f and g satisfy $\partial f/\partial N_1 < 0$ and $\partial g/\partial N_2 < 0$ in the first quadrant, i.e. both species sustain density dependent mortalities at all densities. His approach which is different from ours also improves the results in [3].

For the case $n \geqslant 3$, see for example [7] and [8], the qualitative behavior of solutions of (1) is very complicated. Theorem 1 gives sufficient conditions for the existence of an unbounded trajectory. Consider the following example in [3],

$$\begin{aligned} \dot{N}_1 &= N_1[10 - 5N_1 - 3N_2 - 2N_3], \\ \dot{N}_2 &= N_2[9 - 4N_1 - 4N_2 - N_3], \\ \dot{N}_3 &= N_3[2.9 - N_1 - 2N_2 + 0.1N_3]. \end{aligned} \tag{17}$$

The equilibrium (1, 1, 1) is locally stable, but the computing result shows the trajectory from the initial value (1.0, 1.0, 1.5) tends to $(0, \infty, \infty)$. Applying Theorem 1 with $a_{33} = 0.1$, $a_{23} = -1$, $a_{13} = -2$ yields that (1, 1, 1) is not globally stable. Under our estimation,

$$\Omega = \{(N_1, N_2, N_3): N_3 > 5.5454, N_1 > 0, N_2 > 0 \text{ and } N_1 + 2N_2 \leqslant 0.1N_3\},$$

which is contained in the complement of the domain of attraction of the equilibrium (1, 1, 1), is fairly large. We may say that the system (17) is not 'globally stable' in the biological sense.

It is noted that for $n \geqslant 3$ we may apply the same technique used in part (ii) of Theorem 2 to obtain results concerning the global stability of the unique locally stable equilibrium in the feasible region.

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Received October 5, 1977/Revised December 19, 1977