STABILITY ANALYSIS OF PREDATOR-PREY MODELS VIA LIAPUNOV METHOD

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Abstract

As it is well known from the classical applications in the electrical and mechanical sciences, energy is a suitable Liapunov function: thus, by analogy, all energy functions proposed in ecology are potential Liapunov functions. In this paper, a generalized Lotka-Volterra model is considered and the stability properties of its non-trivial equilibrium are studied by means of an energy function, first proposed by Volterra in the context of conservative ecosystems. The advantage of this Liapunov function with respect to the one that can be induced through linearization is also illustrated.

1. Introduction

As is well-known, one of the most classical problems in mathematical ecology is the stability analysis of equilibria and, in particular, the determination of the region of attraction associated to any asymptotically stable equilibrium point. It is also known that the best way of obtaining an approximation of such regions is La Salle's extension of Liapunov method[1], [2].

Nevertheless, this approach has not been very popular among ecologists, the main reason being that Liapunov functions (i.e. functions that satisfy the conditions of Liapunov method) are in general difficult to devise.

The aim of this paper is to show how the energy function first proposed by Volterra and more recently by Kerner [3] turns out to be quite often a Liapunov function even for non-conservative ecosystems. In order to avoid complexity in notation and proofs, the only case that is dealt with in the following is the one of second order (pre -

dator-prey) systems, but the authors strongly conjecture that the results presented in this paper could be easily generalized to more complex ecological models.

2. The Volterra Function

Consider the simple Lotka-Volterra model

$$\frac{dx}{dt} = x\,(a-by) \qquad (1.a)$$

$$\frac{dy}{dt} = y\,(-c+dx) \qquad (1.b)$$

where x and y are prey and predator populations and (a,b,c,d) are strictly positive constants. This system has a non-trivial equilibrium (x,y) given by (x,y) = (c/d, a/b) which is simply stable in the sense of Liapunov. Moreover, any initial state in the positive quadrant gives rise to a periodic motion.

This can easily be proved by means of the energy function proposed by Volterra

$$V = (x/\bar{x} - \log(x/\bar{x})) + p(y/\bar{y} - \log(y/\bar{y})) - (1+p) \qquad (2)$$

where

$$p = b\bar{y}/d\bar{x}$$

since this function is constant along any trajectory and its contour lines are closed lines in the positive quadrant.

In other words, the Volterra function (2) is a Liapunov function because it is positive definite and its derivative dV/dt is negative semidefinite (identically zero).

In the following, the Volterra function will be used in relation with non-conservative ecosystems of the form :

$$\frac{dx}{dt} = x(a - by + f(x,y))$$
$$\frac{dy}{dt} = y(-c + dx + g(x,y)) \qquad (3)$$

where f and g are continuously differentiable functions. Moreover, we assume that there exists a non-trivial equilibrium $(\bar{x},\bar{y}) > 0$ and that the positive quadrant is an invariant set for system (3) so that it can be identified from now on with the state set of the system.

3. The Volterra Function as a Liapunov Function

Consider the generalized Lotka-Volterra model (3) and the Volterra function V given by eq. (2). Then, the derivative of the Volterra function along trajectories is given by

$$\frac{dV}{dt} = \frac{\partial V}{\partial x} \cdot \frac{dx}{dt} + \frac{\partial V}{\partial y}\frac{dy}{dt} = \left(\frac{x}{\bar{x}} - 1\right)(a - by + f(x,y))$$

$$+ \frac{b\bar{y}}{d\bar{x}}\left(\frac{y}{\bar{y}} - 1\right)(-c + dx + g(x,y))$$

In order to study $\frac{dV}{dt}$ in a neighborhood of the equilibrium $(\bar{x},\bar{y})$, it is possible to expand this function in Taylor's series up to the second order terms, i.e.

$$\frac{dV}{dt} \simeq \left.\frac{dV}{dt}\right|_{\bar{x},\bar{y}} + \left.\frac{d}{dx}\left(\frac{dV}{dt}\right)\right|_{\bar{x},\bar{y}} \delta x + \left.\frac{d}{dy}\left(\frac{dV}{dt}\right)\right|_{\bar{x},\bar{y}} \delta y$$

$$+ \frac{1}{2}\left.\frac{d^2}{dx^2}\left(\frac{dV}{dt}\right)\right|_{\bar{x},\bar{y}} (\delta x)^2 + \frac{1}{2}\left.\frac{d^2}{dy^2}\left(\frac{dV}{dt}\right)\right|_{\bar{x},\bar{y}} (\delta y)^2$$

$$+ \left.\frac{d^2}{dxdy}\left(\frac{dV}{dt}\right)\right|_{\bar{x},\bar{y}} \delta x \delta y \qquad (4)$$

Since

$$\left.\frac{dV}{dt}\right|_{\bar{x},\bar{y}} = \left.\frac{d}{dx}\left(\frac{dV}{dt}\right)\right|_{\bar{x},\bar{y}} = \left.\frac{d}{dy}\left(\frac{dV}{dt}\right)\right|_{\bar{x},\bar{y}} = 0$$

$$\left.\frac{d^2}{dx^2}\left(\frac{dV}{dt}\right)\right|_{\bar{x},\bar{y}} = \frac{2\bar{f}_x}{\bar{x}}$$

$$\left.\frac{d^2}{dy^2}\left(\frac{dV}{dt}\right)\right|_{\bar{x},\bar{y}} = \frac{2b\bar{g}_y}{d\bar{x}}$$

$$\left.\frac{d^2}{dxdy}\left(\frac{dV}{dt}\right)\right|_{\bar{x},\bar{y}} = \frac{\bar{f}_y}{\bar{x}} + \frac{b\bar{g}_x}{d\bar{x}}$$

where $\bar{f}_x, \bar{f}_y, \bar{g}_x, \bar{g}_y$ are the partial derivatives of f and g evaluated at $(\bar{x},\bar{y})$, eq. (4) becomes:

$$\frac{dV}{dt} \simeq \frac{1}{2}\,[\delta x\ \delta y] \begin{bmatrix} \frac{2\bar{f}_x}{\bar{x}} & \frac{\bar{f}_y}{2\bar{x}} + \frac{b\bar{g}_x}{2d\bar{x}} \\ \frac{\bar{f}_y}{2\bar{x}} + \frac{b\bar{g}_x}{2d\bar{x}} & \frac{2b\bar{g}_y}{d\bar{x}} \end{bmatrix} [\delta x\ \delta y]^T \qquad (5)$$

Therefore the second order approximation of $\frac{dV}{dt}$ turns out to be a homogeneous quadratic form; by studying the negative or positive definiteness of such a form, it is possible to derive sufficient conditions for the Volterra function to be a Liapunov function. More precisely, by applying the well-known Sylvester conditions and performing easy computations, it results

$$\left.\begin{array}{l} \bar{f}_x < 0 \\ (b\bar{g}_x + d\bar{f}_y)^2 < 4bd\bar{f}_x\bar{g}_y \end{array}\right\} \Rightarrow \frac{dV}{dt} \text{ negative definite} \qquad (6)$$

$$\left.\begin{array}{l} \bar{f}_x > 0 \\ (b\bar{g}_x + d\bar{f}_y)^2 < 4bd\bar{f}_x\bar{g}_y \end{array}\right\} \Rightarrow \frac{dV}{dt} \text{ positive definite} \qquad (7)$$

Notice that these conditions are only sufficient for Liapunov methods to be applicable; thus, even if these conditions are not satisfied, it is possible that the Volterra function turns out to be a Liapunov function (see Ex. 2).

As far as the study of stability properties in the large is concerned, the Volterra function is definitely advantageous with respect to quadratic forms. This is apparent in the case of global stability; in fact, global stability can be inferred by means of Volterra function, whose contour lines in the state set are closed, while this is never possible by means of a positive definite quadratic form since the contour lines are not closed (see Ex. 1 and 2).

4. Examples

This section is devoted to clarify by means of some examples what has been previously exposed.

Example 1

The first example is a simple symmetric competition model between two species described by the following equations (see May [4]):

$$\frac{dx}{dt} = x(k_1 - x - \alpha y)$$

$$\frac{dy}{dt} = y(k_2 - y - \alpha x)$$

where k_1, k_2 and α are positive parameters.

Provided that

$$\begin{cases} \alpha k_2 > k_1 \\ \alpha k_1 > k_2 \end{cases} \quad \text{or} \quad \begin{cases} \alpha k_2 < k_1 \\ \alpha k_1 < k_2 \end{cases}$$

a non-trivial equilibrium $(\bar{x},\bar{y})$ exists and is given by

$$(\bar{x},\bar{y}) = \left(\frac{\alpha k_2 - k_1}{\alpha^2 - 1} , \frac{\alpha k_1 - k_2}{\alpha^2 - 1} \right)$$

Thus, the matrix F of the linearized system is given by

$$F = \begin{bmatrix} -\bar{x} & -\alpha\bar{x} \\ -\alpha\bar{y} & -\bar{y} \end{bmatrix}$$

and its eigenvalues have negative real parts, provided that its trace is strictly negative and its determinant is strictly positive. These conditions are obviously satisfied if $\alpha < 1$. On the other hand, also the sufficient conditions given by eq. (6) work well. In fact

$$\bar{f}_x = - 1 < 0$$

and

$$(b\bar{g}_x + d\bar{f}_y)^2 = \alpha^2(1+\alpha)^2 < 4bd\bar{f}_x\bar{g}_x = 4\alpha$$

provided that $\alpha < 1$.

However, the Volterra function guarantees the global stability of the equilibrium. This can be easily understood when taking into account that there is no error in the Taylor's expansion (4), because the functions f and g are linear. Thus, $\frac{dV}{dt}$ is negative definite in the state set and global stability follows from La Salle's conditions.

Example 2

Consider the well-known modification obtained from the classical Lotka-Volterra model, when assuming, in the absence of predation, a logistic growth for the prey :

$$\frac{dx}{dt} = x(a - by - kx) \qquad\qquad k > 0$$

$$\frac{dy}{dt} = y\,(-c + dx)$$

If $ad > kc$ a non-trivial equilibrium

$$(\bar{x},\bar{y}) = \left(\frac{c}{d}, \frac{a}{b} - \frac{kc}{bd}\right)$$

exists and linearization around it yields

$$F = \begin{bmatrix} -\frac{kc}{d} & -\frac{bc}{d} \\ \frac{da - kc}{b} & 0 \end{bmatrix}$$

which has eigenvalues with negative real parts. On the other hand , it turns out that

$$\bar{f}_x = -k$$

$$4bd\bar{f}_x\bar{g}_y = (b\bar{g}_x + d\bar{f}_y)^2 = 0$$

Therefore eq. (6) is not satisfied. Nevertheless, by means of a direct computation, it results

$$\frac{dV}{dt} = - \frac{k}{b\bar{x}\bar{y}} (x - \bar{x})^2$$

i.e. $\frac{dV}{dt}$ is negative semidefinite. Since the locus $\frac{dV}{dt} = 0$ is not a trajectory of the system (easy to check), Krasowskyi conditions are met with and asymptotic stability can be inferred. Moreover, since $\frac{dV}{dt}$ is negative semidefinite in the whole state set, global stability can be straight forwardly deduced.

6. Concluding Remarks

The energy function proposed by Volterra has been used in this paper to analyze the asymptotic behaviour of non-conservative ecosystems of the predator-prey type. The main result is that the Volterra function turns out to be a well-defined Liapunov function for a large class of systems and therefore allows the discussion of the local and global stability properties of such systems. The Volterra function seems to be definitively advantageous with respect to the Liapunov functions that can be obtained through linearization particularly in the case of global stability.

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