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### A CRITERION OF GLOBAL CONVERGENCE TO EQUILIBRIUM FOR DIFFERENTIAL SYSTEMS APPLICATION TO LOTKA-VOLTERRA SYSTEMS

*Programme 5*

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A CRITERION OF GLOBAL CONVERGENCE TO  
EQUILIBRIUM FOR DIFFERENTIAL SYSTEMS  
APPLICATION TO LOTKA-VOLTERRA SYSTEMS

**Abstract:** We study a rather general class of systems of ordinary differential equations in  $n$ -space that can be expressed as the difference of a quasi-monotone and a monotone increasing system. We associate to the system another cooperative system in  $2n$ -space. We obtain a sufficient condition of convergence to equilibrium, and apply it to linear and Lotka-Volterra systems.

UN CRITERE DE CONVERGENCE GLOBALE VERS  
L'EQUILIBRE POUR DES SYSTEMES  
DIFFERENTIELS  
APPLICATION AUX SYSTEMES DE LOTKA-VOLTERRA

**Résumé:** Nous étudions une classe assez générale de systèmes différentiels ordinaires de dimension  $n$  qui sont différence d'un système quasi-monotone et d'un système monotone croissant. Nous associons à ce système un autre système coopératif (quasi-monotone croissant) dans un espace de dimension  $2n$ . Nous obtenons un critère suffisant de convergence globale vers l'équilibre, et nous l'appliquons aux systèmes linéaires et de Lotka-Volterra.

# A criterion of global convergence to equilibrium for differential systems; application to Lotka-Volterra systems

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**Key words.** Global convergence, Lotka-Volterra systems, monotone flow  
**AMS(MOS) subject classification.** 34A40, 34C11, 34C35, 92A15

## 1 Introduction

The purpose of the present paper is to study the behavior, and especially the asymptotic behavior, of particular systems of ordinary differential equations that often arise in biological modelling. These systems are characterized by the fact that they can be written (in  $n$ -space):

$$\dot{x} = f(x) - g(x) \quad (1)$$

with the conditions, valid on an open set  $W \subset \mathbf{R}^n$ :

$$\frac{\partial f_i}{\partial x_j}(x) \geq 0 \text{ for } i \neq j \text{ and } \frac{\partial g_i}{\partial x_j}(x) \geq 0 \text{ (} i, j = 1, \dots, n \text{)} \quad (2)$$

The vector-function  $f$  is said to be quasi-monotone increasing and  $g$  monotone increasing (see [14]). If  $g \equiv 0$ , the system (1) is also called cooperative [2]. This last mathematical formulation has been used by Volterra and Lotka (see [13]) in connection with biological problems, and has been followed by many studies (see [5,6,7]). More recently, the study of cooperative systems has been accomplished ([2,3,4], see [10] for a review).

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To our knowledge, there are few results on the general system (1) subject to condition (2). Roughly speaking, this system is the difference of two cooperative systems, in fact of a cooperative system and a system the jacobian matrix of which is nonnegative (it is stronger than cooperative). As we shall see in section 1, many differential systems can be written in this manner.

In this paper, we show that it is sometimes possible to describe in a simple way some of the global features of (1). For instance, if (1) has a unique equilibrium, it is interesting to know if some or all solutions will converge to this point. We shall give a sufficient criterion for this. The key idea in our study of system (1) in  $\mathbf{R}^n$  is to immerse it into a cooperative system in  $\mathbf{R}^{2n}$ , where it is possible to obtain an upper and a lower bound on the solution of (1).

In section 2, we show that (1) includes many systems. In section 3, we write down the associate system in  $\mathbf{R}^{2n}$  and study some of its properties. The main results on the dynamic behavior of (1) are in section 4. In section 5, we apply these results to linear and Lotka-Volterra systems.

**Notations:** For  $x$  in  $\mathbf{R}^n$ , we write  $x > 0$  if  $x_i > 0$  ( $i = 1, \dots, n$ ) and  $x_i \geq 0$  if  $x_i \geq 0$  ( $i = 1, \dots, n$ ). If  $x \leq y$ , let  $[x, y] = \{z ; x \leq z \leq y\}$ . The closed positive orthant is  $\mathbf{R}_+^n = \{x \in \mathbf{R}^n ; x \geq 0\}$ . Let us denote by  $u^t$  the transpose of  $u$ , by  $e^x$  the vector  $(e^{x_1}, \dots, e^{x_n})$ , and similarly for  $\ln x$ .

If  $V \subset \mathbf{R}^n$  is open,  $h : V \rightarrow \mathbf{R}^n$  is  $C^1$ , and  $x \in V$ , we denote by  $Dh(x)$  the jacobian  $n \times n$  matrix  $\partial h_i / \partial x_j(x)$ .

If  $V \subset \mathbf{R}^n$  is open,  $h : V \rightarrow \mathbf{R}^n$  is  $C^1$ , and  $x_0 \in V$ , for the differential system  $\dot{x} = h(x)$  ( $\dot{x}$  is the derivative with respect to time  $t$ ), we denote by  $x(t, x_0)$  or sometimes by  $x(t)$  the (maximally defined) solution in  $V$  with initial value  $x_0$  for  $t = 0$ .

## 2 The original system

We now consider the system (1) for  $x \in W$  with conditions (2) holding in  $W$ , and we suppose that  $W$  is an open subset of  $\mathbf{R}^n$ , and  $f, g : W \rightarrow \mathbf{R}^n$  are  $C^1$ . We have therefore existence and unicity of a maximal solution of (1), and continuity with respect to the initial value. The two systems in  $\mathbf{R}^n$ :

$$\dot{x} = f(x) \tag{3}$$

and

$$\dot{x} = g(x) \tag{4}$$

are therefore two cooperative systems.

The next lemma shows that system (1) includes roughly all systems with bounded off-diagonal derivatives:

**Lemma 1** *Let  $h : W \rightarrow \mathbf{R}^n$  be  $C^1$  and such that:*

$$\left| \frac{\partial h_i}{\partial x_j}(x) \right| \leq a_{ij} \text{ for } i \neq j \text{ and } x \in W$$

*then the differential system  $\dot{x} = h(x)$  can be written in the form (1).*

For we can define:

$$g_i(x) = \sum_{j \neq i} a_{ij} x_j$$

and  $f = h + g$ . It is easy to check  $f$  and  $g$  verify condition (2).

Other examples are given in section 5.

### 3 The associate system in $\mathbf{R}^{2n}$

To the system (1), we associate a new system in  $\mathbf{R}^{2n}$ :

$$\begin{cases} \dot{y} = f(y) - g(z) \\ \dot{z} = f(z) - g(y) \end{cases} \quad (5)$$

where  $y \in \mathbf{R}^n$  and  $z \in \mathbf{R}^n$ , the initial value being  $(y_0, z_0)$ . The system is defined for  $(y, z) \in W \times W$  (one can find a similar idea, in another context, in [8]).

**Lemma 2** *If  $x^*$  is an equilibrium of system (1), then  $(x^*, x^*)$  is an equilibrium for system (5).*

For we have  $f(x^*) - g(x^*) = 0$ .

**Lemma 3** *The set  $\{(y, z); y = z\}$  is invariant under the flow defined by (5).*

For, if  $y(t) = z(t)$ , then in (5),  $\dot{y}(t) = \dot{z}(t)$ .

**Lemma 4** *If  $y_0 = z_0 = x_0$ , then the solution  $(y(t, (x_0, x_0)), z(t, (x_0, x_0)))$  of (5) is equal to  $(x(t, x_0), x(t, x_0))$ , where  $x(t, x_0)$  is the solution of (1).*

For  $y(t) = z(t)$  because of the preceding lemma, and  $y(t, x_0)$  satisfies

$$\dot{y} = f(y) - g(y)$$

with  $y_0 = x_0$ .

**Lemma 5** *By the change of variables:*

$$\begin{aligned} Y &= y \\ Z &= -z \end{aligned}$$

the system (5) is converted into the cooperative system (6).

For the new system is:

$$\begin{cases} \dot{Y} = f(Y) - g(-Z) \\ \dot{Z} = g(Y) - f(-Z) \end{cases} \quad (6)$$

The jacobian matrix of (6) is:

$$\begin{pmatrix} Df(Y) & Dg(-Z) \\ Dg(Y) & Df(-Z) \end{pmatrix}$$

Because of condition (2), the system is cooperative.

We need a basic result on cooperative systems, attributed to Kamke (see [3]):

**Theorem:** Let  $V$  an open convex set of  $\mathbf{R}^n$ ,  $h : V \rightarrow \mathbf{R}^n$  a  $C^1$  quasi-monotone increasing map. If two solutions of the differential system  $\dot{x} = h(x)$  are such that  $x_0 \leq y_0$ , then, for all  $t \geq 0$  such that the solution is defined,  $x(t) \leq y(t)$ . This result is also valid with strict inequalities.

The next theorem gives bounds on the solution of (1):

**Theorem 3.1** *Suppose  $W$  is convex. Let  $x(t, x_0)$  be a solution of (1) and  $(y(t, (y_0, z_0)), z(t, (y_0, z_0)))$  a solution of (5), and let  $z_0 \leq x_0 \leq y_0$ , then, for all  $t \geq 0$ ,  $z(t) \leq x(t) \leq y(t)$ . This result is also valid with strict inequalities.*

The inequalities  $z_0 \leq x_0 \leq y_0$  are equivalent to:

$$\begin{pmatrix} x_0 \\ -x_0 \end{pmatrix} \leq \begin{pmatrix} y_0 \\ -z_0 \end{pmatrix}$$

Because system (6) is cooperative and  $W$  is convex (in fact  $p$ -convexity suffices, see [3]), we can apply Kamke's theorem to the preceding inequality between two initial values of (6). Then we use lemma 4 to obtain:

$$\begin{pmatrix} x(t) \\ -x(t) \end{pmatrix} \leq \begin{pmatrix} y(t) \\ -z(t) \end{pmatrix}$$

which is the desired result.

**Corollary 1** *The region  $\{(y, z) ; y \geq z\}$  is positively invariant by (5).*

#### 4 Dynamical behavior

We study the dynamical behavior of (1) using theorem 3.1. We know that (5) has at least equilibrium  $(x^*, x^*)$  if  $x^*$  is an equilibrium of (1), but it may have other equilibriums  $(y^*, z^*)$ .

The next corollary of theorem 3.1 exhibits a simple situation:

**Corollary 2** *If system (5) converges to  $(x^*, x^*)$ , then system (1) converges to  $x^*$ .*

The next theorem gives a sufficient dynamical condition for this situation to prevail:

**Theorem 4.2** *Assume that  $W$  is an open convex set, and there exist  $y_0$  and  $z_0$  in  $W$  such that  $(x^*, x^*)$  is the only equilibrium  $(y^*, z^*)$  of (5) in  $[z_0, y_0] \times [z_0, y_0]$ .*

*Assume finally that there exists  $T > 0$  such that  $y(T) < y_0$  and  $z(T) > z_0$ .*

*Then, for  $z_0 \leq x_0 \leq y_0$ , the solution of (1) converges towards  $x^*$ .*

*Proof.* Let  $x_m = x(mT)$  for  $m$  integer; it is easy, using Kamke's theorem and corollary 1, to obtain the sequence of inequalities:

$$z_0 < z_1 < z_2 \dots < z_m < y_m < \dots < y_1 < y_0$$

Then the sequences  $y_m$  and  $z_m$  are strictly monotone and bounded, and converge. The solution of (6) is defined for all  $t \geq 0$ . We can then apply [3, Th. 2.2] to system (6) to conclude that  $y(t)$  and  $z(t)$  converge to  $x^*$ . By theorem 3.1, the solution  $x(t)$  of (1) converge towards the unique equilibrium  $x^*$  in



$[z_0, y_0]$ . QED.

The next theorem implies the existence of an equilibrium, because of the positive invariance of a compact region. Moreover, it gives a sufficient condition of convergence:

**Theorem 4.3** *Assume there exists  $(y_1, z_1) \in W \times W$  such that:*

$$\begin{aligned} z_1 &\leq y_1 \\ f(y_1) &\leq g(z_1) \\ f(z_1) &\geq g(y_1) \end{aligned}$$

*and that (5) is defined and has at most one equilibrium in the rectangular region  $(z_1, z_1) \leq (y, z) \leq (y_1, y_1)$ .*

*Then there exists a single equilibrium  $x^*$  of (1) in  $[z_1, y_1]$  and all the solutions  $x(t, x_0)$  of (1) such that  $z_1 \leq x_0 \leq y_1$  converge towards this point.*

*Proof.* Because of the above condition and of the cooperativeness of (6), for the system (5), the orthant  $O$  defined by  $y \leq y_1$  and  $z \geq z_1$  is positively invariant. Because of corollary 1, the region  $z \leq y$  is positively invariant. Therefore, the region  $Q$  defined by the intersection of these two regions is also positively invariant. This region is compact convex and thus there exists at least one equilibrium in it (see e.g. [9]). But by lemma 2, the edge of the preceding region  $Q$  such that  $y = z$  is also invariant by (5), and, because it is also compact convex, there exists an equilibrium  $(x^*, x^*)$  in it. It is therefore the only equilibrium in  $Q$ .

Moreover, because of the positive invariance of  $Q$ , all the orbits are bounded, and the condition implies that the vector field of (6) at  $(y_1, -z_1)$  is nonpositive. We can then apply a well known theorem (cf [3, Th. 2.5]) to obtain that all the solutions converge to  $(x^*, x^*)$ . We then apply theorem (3.1). QED.

Other links can be stressed between systems (1) and (5): let us simply mention that, if system (1) admits a linear first integral  $u$  such that  $u^t \cdot x = \text{const}$ , then, by symmetry, system (5) admits the linear first integral  $u^t \cdot (y + z) = \text{const}$ .

## 5 Applications

We first apply preceding theorem to linear systems. Given any linear system, we can always write it as:

$$\dot{x} = Fx - Gx = (F - G)(x) \quad (7)$$

where  $G$  is a nonnegative matrix and  $F$  a matrix with nonnegative off-diagonal elements. The system (6) is now:

$$\begin{cases} \dot{Y} = FY + GZ \\ \dot{Z} = GY + FZ \end{cases} \quad (8)$$

Let

$$A = \begin{pmatrix} F & G \\ G & F \end{pmatrix} \quad (9)$$

We suppose  $A$  bijective. Then  $(0, 0)$  is the unique equilibrium of (8) and  $0$  is the unique equilibrium of (7). To simplify, we take the condition of theorem (4.3) with strict inequalities. If we want to verify this condition, we must have  $z_1 < 0 < x_1$ . We want to find  $(X_1, Y_1)$  such that:

$$A \begin{pmatrix} Y_1 \\ Z_1 \end{pmatrix} < 0 \text{ and } \begin{pmatrix} Y_1 \\ Z_1 \end{pmatrix} > 0$$

But  $A$  is a matrix in  $\mathbf{R}^{2n}$  with off-diagonal nonnegative elements, and it is known (see [1]) that the last condition is equivalent to the fact  $-A$  is an M-matrix. Therefore  $A$  is stable and (8) converges.

**Theorem 5.4** *In the linear case, if  $-A$  is a bijective M-matrix, then the linear system (7) is asymptotically stable.*

To verify this criterion, we can simply check that all principal minors of  $-A$  are positive (see [1]). Remark that, because of properties of M-matrices, it implies that  $F$  is a stable matrix and has negative diagonal elements.

We now apply theorem 4.3 to Lotka-Volterra systems that we write:

$$\dot{x}_i = x_i \left( b_i + \sum_{j=1}^n c_{ij} x_j \right) \text{ for } i = 1, \dots, n \quad (10)$$

Many results are known on these systems ([11,12]). We do not assume, a priori, anything on the signs of  $c_{ij}$  or  $b_i$ . A known sufficient condition of global convergence to equilibrium in the whole space  $\mathbf{R}_+^n$  is (cf. [12]) the existence of a positive definite diagonal matrix  $D$  such that  $DC + C^t D$  is positive definite. This condition seems to be not easy to check.

We know that the interior of the closed positive orthant is invariant by (10) and take only initial values  $x_0$  in it and so, performing the change of variables  $\xi = \ln x$ , we obtain:

$$\dot{\xi} = b + Ce^{\xi} \quad (11)$$

We write  $C = F - G$  with  $F$  and  $G$  as above. We suppose (11) has at least one equilibrium  $\xi^* = \ln x^*$  ( $x^* > 0$ ). The system (6) is now:

$$\begin{pmatrix} \dot{Y} \\ \dot{Z} \end{pmatrix} = A \begin{pmatrix} U \\ V \end{pmatrix} \quad (12)$$

with

$$A = \begin{pmatrix} F & G \\ G & F \end{pmatrix} \quad \text{and} \quad \begin{cases} U = e^Y - e^{\xi^*} \\ V = e^{\xi^*} - e^{-Z} \end{cases} \quad (13)$$

One equilibrium of (12) is  $U = V = 0$  and we suppose it is unique ( $A$  is bijective). As above for linear systems, the criterion with strict inequalities of theorem 4.3 is equivalent to:

$$A \begin{pmatrix} U_1 \\ V_1 \end{pmatrix} < 0 \quad \text{and} \quad \begin{pmatrix} U_1 \\ V_1 \end{pmatrix} > 0$$

So we still find the criterion is equivalent to the fact  $-A$  is an M-matrix. But the convergence is no longer global. Suppose  $-A$  is an M-matrix, so we can find  $U_1$  and  $V_1$ . Then  $\lambda U_1$  and  $\lambda V_1$  is also a solution for all  $\lambda > 0$ . But we have:

$$V = e^{\xi^*} - e^{-Z}$$

and so we must choose  $\lambda$  such that:

$$\lambda V_1 - e^{\xi^*} < 0$$

We choose  $\lambda$  very large and obtain  $U_m, V_m$  such that one component (at least) of  $Z$  is arbitrarily large positive. Then system (11) converges for initial value  $\xi_0$  such that:

$$\ln(e^{\xi^*} - V_m) < \xi_0 < \ln(e^{\xi^*} + U_m)$$

and the original system (10) converges for:

$$x^* - V_m < x_0 < x^* + U_m$$

where  $x^* - V_m$  admits at least one component arbitrarily small.

We have therefore a theorem of global convergence:

**Theorem 5.5** *If the Lotka-Volterra system (10) admits one equilibrium, and*

$$- \begin{pmatrix} F & G \\ G & F \end{pmatrix}$$

*is a bijective M-matrix, then (10) converges to the unique equilibrium for all initial values in  $[x_{min}, x_{max}]$ , where  $x_{min}$  and  $x_{max}$  are determined as above, and where one component at least of  $x_{min}$  can be chosen to be arbitrarily small positive.*

As above, it is easy to check  $-A$  is an M-matrix by computing its principal minors.

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