Global behaviour of n-dimensional Lotka-Volterra systems

Jean-Luc Gouzé
INRIA
BP 109
Sophia-Antipolis, 06561 Valbonne Cedex
France

Abstract. In this paper we study the behaviour of Lotka-Volterra systems; the principal tools are results from positivity and auxiliary functions that decrease along the trajectories; one typical result is that, if a decomposition of the interaction matrix into a product of a symmetric and an off-diagonal nonnegative matrix is possible, then all the trajectories either go to equilibria or cannot remain in any compact set of the interior of the positive orthant.

1 Introduction

The Lotka-Volterra models have been introduced by Volterra ([16]) in the case where several species compete for a same resource, or where some species are predators of other species, and by Lotka ([9]) in the case of symbiosis and parasitism. It is a differential non-linear system describing linear growths and quadratic interactions between variables.

The $(n-1)$-dimensional Lotka-Volterra system is usually written:

$$\dot{x}_i = x_i(b_i + \sum_{j=1}^{n-1} A_{ij} x_j) \ \ (i = 1, \ldots, n-1) \tag{1}$$

The $(n-1) \times (n-1)$ real matrix A describes the quadratic interactions, and is usually supposed to be bijective (the equilibrium will be unique if it exists). The variables x_i, standing for populations, are supposed real nonnegative.

Many results are known on these systems (see [15, 7, 8, 10, 16]). A complex (chaotic) behaviour has been shown to be possible ([1, 3]), even in three dimensions. Recently, the theory of cooperative or competitive systems (cf. [13]) has been used to study such systems ([14, 6, 7]). A known sufficient condition of global convergence to equilibrium in the whole space $\mathbf{R}_+^{n-1}$ is (cf. [4, 15]) the existence of a positive definite diagonal matrix D such that $DA + {}^tAD$ is negative definite.

We shall use here different methods: the principal tools will be results from positivity and theory of positive matrices (cf. [2]) and auxiliary functions decreasing along trajectories (cf. [11]). We can then obtain results on the global behaviour of the system, one typical result being the fact that all trajectories either have limit points at infinity or on the faces $x_i = 0$ or go towards the equilibria (there is no complex behaviour, such that periodic solutions, recurrent or chaotic behaviour, in any compact set of the interior of the positive orthant); such a behaviour will be called "regular".

Notations: For x in $\mathbf{R}^n$, we write $x > 0$ if $x_i > 0$ $(i = 1, \dots, n)$ and $x \geq 0$ if $x_i \geq 0$ $(i = 1, \dots, n)$. The closed positive orthant is $\mathbf{R}_+^n = \{x \in \mathbf{R}^n; x \geq 0\}$. We will frequently use the open positive orthant $\mathbf{P}^n = \{x \in \mathbf{R}^n; x > 0\}$. Let us denote by ${}^tu$ the transpose of u, by e^x the vector ${}^t(e^{x_1}, \dots, e^{x_n})$, and similarly for $\ln x$. If x is a vector, we denote by x^{-1} the vector of components $(1/x_i)$. $\mathbf{1}$ is the vector ${}^t(1 \dots 1)$ and diag (x) the diagonal matrix with diagonal x.

If $V \subset \mathbf{R}^n$ is open, $h : V \to \mathbf{R}^n$ 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 system

It is easy to write the above equation in a slightly more general way by introducing one new variable x_n such that $\dot{x}_n = 0$ and $x_n(0) = x_n(t) = 1$. We can write now a n-dimensional quadratic homogenous system:

$$\dot{x}_i = x_i(\sum_{j=1}^{n} B_{ij} x_j) \ \ (i = 1, \dots, n)$$

with the initial condition $x(0)$ satisfying $x_n(0) = 1$, and

$$B = \begin{pmatrix} A & b \\ 0 & 0 \end{pmatrix} \tag{2}$$

We are interested by this system for $x \geq 0$ (because x_i stands for a population); the faces $x_i = 0$ of the orthant are invariant, and so is the open positive orthant $\mathbf{P}^n$. We will study this system in $\mathbf{P}^n$, so we can make the change of variables:

$$y = \ln x$$

and obtain

$$\dot{y} = Be^y \tag{3}$$

In fact, we are going to study this last system for B a square singular $n \times n$ matrix: this system includes Lotka-Volterra system (where $y_n(0) = 0$ and B has the form (2)).

If $\ker B \cap \mathbf{P}^n = \emptyset$, then it is easy to show ([5]) that there is no equilibrium for system (3) and that all trajectories of system (3) are unbounded. The interesting case is therefore when $\ker B$ intersects the positive orthant; the system has equilibria.

Let us examine more precisely the system: if rank $B = s$, then it has $(n-s)$ linear first integrals ${}^t qy = const$, where $q \in \ker{}^t B$ and the set of equilibria is a $(n-s)$-manifold (such that $e^y \in \ker B$). So, for a given initial condition, the trajectories are constrained to stay on the linear first integrals, and the set of equilibria on these first integrals is given by the intersection of a s-dimensional vectorial space and of a $(n-s)$-manifold; we can expect that this set is "generically" of dimension zero (namely consists of a discrete set of points).

The case where $s = n-1$ ($\ker B$ is one dimensional) is important because it corresponds to the case A bijective in system (2), that is to say the usual Lotka-Volterra system. We therefore suppose that $\ker B$ is one-dimensional and intersects $\mathbf{P}^n$ with vector k. The set of equilibria is :

$$e^y = \lambda k \Leftrightarrow y = (\ln \lambda)\mathbf{1} + \ln k$$

that is a straight (affine) line L of vector $\mathbf{1}$ and containing the point $\ln k$. But ${}^t q\dot{y} = 0$ (where q is in $\ker {}^t B$) and we have one linear first-integral. The intersection of L and of the (affine) hyperplane orthogonal to $\ker^t B$ reduces to one single equilibrium if and only if ${}^t q\mathbf{1} \neq 0$.

If B has the form (2)(Lotka-Volterra systems), then ${}^t q\mathbf{1} = 1$ and there is one single equilibrium on each hyperplane depending on the initial condition; that is to say, there is one single equilibrium for Lotka-Volterra system (1).

3 Auxiliary functions

We want to find, in order to study the above system, auxiliary functions of the variables that decrease along the trajectories ([11]); it is a kind of weak version of Lyapunov functions. To construct these functions, we shall use tools from theory of positive matrices (cf. [2]), also related to probabilistic problems ([12]). We shall use the following lemma:

Lemma 1 *Let M a square off-diagonal non-negative singular matrix such that:*

$$Mk = 0 \quad {}^tM\mathbf{1} = 0$$

where k is a positive vector. Then:

$$\forall p > 0 \quad {}^t(\ln p - \ln k)Mp \leq 0$$

Proof: Let $\phi(p) = {}^t(\ln p - \ln k)Mp$. Then

$$\begin{aligned}
\phi(p) &= \sum_i \sum_j (\ln p_i - \ln k_i) m_{ij} p_j \\
&= \sum_i ((\ln p_i - \ln k_i) m_{ii} p_i + \sum_i \sum_{j \neq i} (\ln p_i - \ln k_i) m_{ij} p_j
\end{aligned}$$

and using ${}^tM\mathbf{1} = 0$

$$\begin{aligned}
\phi(p) &= \sum_i (\ln p_i - \ln k_i)(-\sum_{k \neq i} m_{ki}) p_i + \sum_i \sum_{j \neq i} (\ln p_i - \ln k_i) m_{ij} p_j \\
&= -\sum_j \sum_{i \neq j} (\ln p_j - \ln k_j) m_{ij} p_j + \sum_i \sum_{j \neq i} (\ln p_i - \ln k_i) m_{ij} p_j \\
&= \sum_i \sum_{j \neq i} (\ln \frac{p_i}{k_i} - \ln \frac{p_j}{k_j}) m_{ij} p_j
\end{aligned}$$

and we use the facts that $\ln x \leq x - 1$ (for $x > 0$) and $m_{ij} \geq 0$ to obtain

$$\begin{aligned}
\phi(p) &\leq \sum_i \sum_{j \neq i} (\frac{p_i k_j}{p_j k_i} - 1) m_{ij} p_j \\
&= \sum_i (\sum_{j \neq i} m_{ij} k_j) \frac{p_i}{k_i} - \sum_i \sum_{j \neq i} m_{ij} p_j
\end{aligned}$$

and using $Mk = 0$

$$\begin{aligned}\phi(p) &\leq -\sum_i m_{ii}p_i - \sum_i \sum_{j\neq i} m_{ij}p_j \\ &= -\sum_i (m_{ii} + (\sum_{j\neq i} m_{ji}))p_i \\ &= 0\end{aligned}$$

because of ${}^tM\mathbf{1} = 0$.

Lemma 2 *Suppose that the (non-oriented) graph of M is connected; then (for $p > 0$)*

$$\phi(p) = 0 \Leftrightarrow p \in \ker M \cap \mathbf{P}^n$$

Proof: Let us recall that the non-oriented graph of a square n-matrix M is the graph with n vertices having an edge between vertices i and j if m_{ij} or m_{ji} is non-zero. We know that $\ln x \leq x - 1$ with egality if and only if $x = 1$. Therefore we must have equality for each term of the above sum, and we deduce

$$m_{ij} \neq 0 \text{ or } m_{ji} \neq 0 \ \Rightarrow \frac{p_i}{k_i} = \frac{p_j}{k_j}$$

If the graph of M is connected, that implies that $p = \mu k$ (with $\mu > 0$). The converse is obvious.

Let us remark that, if the graph is not connected, we can consider the set of n points as the union of two or more independant subsets with connected graphs, and study each set independently.

We can now construct, under good hypotheses, an auxiliary function decreasing along the trajectories of (3):

Theorem 3.1 *Suppose that, for a given B, there exist a square off-diagonal nonnegative singular matrix M, such that ${}^tM\mathbf{1} = 0$, and a symmetric square matrix P such that:*

$$PB = M$$

Then, if

$$V(y) = \frac{1}{2}\ {}^t(y - \ln k)P(y - \ln k)$$

with $k \in \ker B \cap \mathbf{P}^n$, the function $V(y)$ decreases along the trajectories of (3) ($\overline{\dot{V}(y(t))} \leq 0$).

Moreover, if the graph of M is made of l disconnected classes, associated with matrices M_j $(j = 1, \ldots, l)$, then this derivative vanishes if and only if

$$e^y = \sum_{j=1}^{l} \lambda_j k_j$$

where k_j is a positive vector in $\ker M_j$ having the property that the components not corresponding to the vertices of the graph of M_j are zero, and the λ_j are real nonnegative.

Indeed, $\dot{\overline{V(y(t))}} = {}^t(y - \ln k)PBe^y$ and, as $PB = M$ and $Bk = 0 \Rightarrow Mk = 0$, we can apply lemma 1 with $p = e^y$. If the graph of M is not connected, according to the remark of lemma 2, we can apply this lemma to each connected class.

Remarks:

- It is clear that $\ker M$ is the direct sum of $\ker M_j$ $(j = 1, \ldots, l)$, so we conclude that the derivative vanishes if and only if $e^y \in \ker M \cap \mathbf{P}^n$.
- We can write the decomposition:

  $${}^tBP = {}^tM \quad {}^tM\mathbf{1} = 0$$

  We have $n(n+1)/2$ indeterminates in P, n^2 indeterminates in M, and $n^2 + n$ equations, and therefore more indeterminates than equations; but we impose also the sign of the off-diagonal elements of M. The above equations with sign-conditions are equivalent to :

  $${}^tB_1p_1 = m_1 \quad {}^tq_im_1 = 0 \; (i = 1, \ldots, n)$$

  where ${}^tB_1$ is a $n^2 \times n(n+1)/2$-matrix, p_1 a $n(n+1)/2$-vector and m_1 a n^2- nonnegative vector. The q_i are n^2-vectors with components equal to 0 or 1 or (-1). These equations will have at least one solution if and only if $\mathrm{im}\, {}^tB_1 \cap \mathbf{R}_+^{n^2} \neq \{0\}$, and if we can choose m_1 in this intersection such that m_1 is in addition orthogonal to the n vectors q_i. In fact, all this reduces to know (that is, to compute) if the kernel of some matrix depending on B intersects the nonnegative orthant of $\mathbf{R}^{n^2}$. This problem can be solved numerically by linear programming methods.

- It would be interesting to study more precisely the set of matrices B admitting such a decomposition; it is clear that we can restrict ourselves to the set V of the matrices B such that $\ker B \cap \mathbf{P}^n \neq \emptyset$ (if not, we know the trajectories are unbounded; cf. section 2); let $S = \{B \in V; B \text{ admits a decomposition}\}$; we want here only make some remarks:
  - If $B \in S$, then $\alpha B \in S$ for α real; in particular, $-B$ admits a decomposition, that means that the system (3) in reverse time will have the same properties.
  - If $B \in S$, then $BD \in S$ for all diagonal positive matrix D.
  - Let us suppose, moreover, that $B \in V$ is such that $\ker B$ is one-dimensional (this property is generic in V); this set V_1 is an open set on a manifold; let $S_1 = \{B \in V_1; B \text{ admits a decomposition}\}$; then we can choose a matrix $B \in S_1$ such that B_1 is of maximum feasible rank and admits a decomposition with $m_1 > 0$ (it is clear that such a matrix exists, take for example $B = M$ where M has a connected graph); then there exists a neighbourhood of B in V_1 where all matrices have the same properties. That means that S_1 has a non-empty interior relatively to V_1, and that the property of decomposition with $m_1 > 0$ is robust in V_1.
- If we suppose P is bijective, then $B = P^{-1}M$. Therefore all matrices B such that $B = QM$, where Q is bijective symmetric and M is off-diagonal nonnegative with ${}^tM\mathbf{1} = 0$ and $Mk = 0$, verify the hypotheses of the theorem.

4 Global behaviour of the system

We suppose in the following that all the hypotheses of theorem (3.1) are fulfilled: we will call these hypotheses the "PM-hypotheses".

We will also restrict the problem by supposing that P does not add equilibria, that is

$$\ker B \cap \mathbf{P}^n = \ker M \cap \mathbf{P}^n$$

Let us remark that we have always $\ker B \cap \mathbf{P}^n \subset \ker M \cap \mathbf{P}^n$, and that our hypothesis means that $\ker P$ does not intersects the set $B\mathbf{P}^n$; it is true, in particular, if P is bijective.

We can now use the auxiliary function $V(y)$ to study the global behaviour of the system (3).

Theorem 4.2 *If B satisfies the PM-hypotheses and if* $\ker B \cap \mathbf{P}^n = \ker M \cap \mathbf{P}^n$*, then all the trajectories of (3) converge towards the set of equilibria or are unbounded. The behaviour is regular.*

Indeed, as V decreases along all the trajectories, Lasalle's theorem ([11]) says that, if the positive orbit of a solution is bounded, it converges towards the set $\{y; \overline{\dot{V}(y(t))} = 0\}$, that is $e^y \in \ker M \cap \mathbf{P}^n$, namely the set of equilibria of (3) because of the supplementary hypothesis $\ker B \cap \mathbf{P}^n = \ker M \cap \mathbf{P}^n$.

Let us recall that a "regular" behaviour means that, roughly, all the trajectories are unbounded or go towards the set of equilibria; more precisely, that a trajectory converge towards an equilibrium or leaves any compact set of the interior of the positive orthant.

In fact, the trajectories are also constrained to stay on the linear first integrals (cf. section 2):

Corollary 1 *If B satisfies the PM-hypotheses and if* $\ker B \cap \mathbf{P}^n = \ker M \cap \mathbf{P}^n$*, then the trajectory of (3) initiating at y_0 converges towards the intersection of $y_0 +$*im B *and of the set of equilibria, or is unbounded. The behaviour is regular.*

Proof: Take k a positive vector of $\ker B \cap \mathbf{P}^n$, then $\ln k$ is an equilibrium. Given an initial condition $y(0)$, the trajectories stay on $y(0) + \mathrm{im}\ B$; if the intersection of the set of equilibria and $y(0)+\mathrm{im}\ B$ is non empty, then we can choose $\ln k$ in it; then $(y(t) - \ln k)$ stays in im B and we can apply Lasalle's theorem. If the intersection is empty, all the trajectories are unbounded.

We can make the description of the behaviour more precise by using the eigenvalues of P; in the following, by "P restricted to im B", we mean "the quadratic form defined on im B that takes the same values than P on im B":

Theorem 4.3 *If B satisfies the PM-hypotheses and if* $\ker B \cap \mathbf{P}^n = \ker M \cap \mathbf{P}^n$*, then, if P restricted to* im B *has positive eigenvalues, the trajectory initiating at y_0 converges towards the intersection of the set of equilibria and* $y_0 + \mathrm{im}\ B$.

If $\ln k$ *is an isolated equilibrium on* $y(0) + \mathrm{im}\ B$*, then, if P restricted to* im B *has positive eigenvalues, the equilibrium is (locally) asymptotically stable; if P restricted to* im B *has a negative eigenvalue, the equilibrium is locally unstable. The behaviour is regular.*

Proof: Suppose P restricted to im B has positive eigenvalues and take $\ln k$ in the intersection of the set of equilibria and $y_0 + \text{im } B$, then $V(y)$ is positive; the set $\{y : V(y) \leq V(y(0))\}$ is therefore compact and all trajectories are bounded. We can apply the preceeding theorem.

If moreover $\ln k$ is an isolated equilibrium on $y(0) + \text{im } B$, then $V(y)$ is a Lyapunov function, and the equilibrium is asymptotically stable.

If P restricted to im B has a negative eigenvalue, then we can choose $y(0)$ in a neighbourhood of $\ln k$ such that $V(y(0)) < 0$ and the equilibrium is unstable.
Let us remark that the jacobian matrix at the equilibrium $\ln k$ is $B(\text{diag } k)$, of rank equal to rank B, and therefore singular.

We can give a more global description in the important and simple case where $\ker B \cap \mathbf{P}^n$ is one-dimensional (the matrix A of system (1) is bijective):

Theorem 4.4 *Suppose* $\ker B \cap \mathbf{P}^n$ *is one-dimensional with vector* k, *and* $q \in \ker\ {}^tB$, *with* ${}^tq\mathbf{1} \neq 0$. *Under the PM hypotheses, and if* $\ker B \cap \mathbf{P}^n = \ker M \cap \mathbf{P}^n$, *then, given an initial condition, the trajectory converges towards the unique equilibrium on the invariant hyperplane containing the initial condition or is unbounded. Moreover, if P restricted to* im B *is positive definite, the single equilibrium is Lyapunov globally stable. If P restricted to* im B *is not positive definite, the equilibrium is unstable and some trajectories are unbounded. The behaviour is regular.*

We already know (see end of section 1) that there is a single equilibrium on the first integral containing the initial condition $y(0)$. We can then apply the preceeding theorem. Let us remark that the results are here global because of the unicity of the equilibrium and of the global nature of the auxiliary functions.

If we translate this result for system (1) with A bijective, we obtain global results in the positive orthant for stability or unstability of the unique equilibrium of Lotka-Volterra systems, where q is the vector $(0, 0, \ldots, 0, 1)$; in that case, P restricted to im B is simply the $(n-1) \times (n-1)$ matrix P_1 obtained by deleting the last row and the last line of P.

Corollary 2 *For the usual Lotka-Volterra system (1), under the hypotheses of theorem 4.4, if the submatrice P_1 is positive definite, the equilibrium is globally stable. If P_1 is not positive definite, the equilibrium is unstable, some trajectories are unbounded. The behaviour is regular.*

Remark: It is easy to describe some links between the above results and three important notions of population dynamics, that we recall very briefly (cf [8]): the notion of weak persistence ($\limsup_{t\to\infty} x_i(t) > 0$ for all i) for all orbits of the interior of system (1)), of strong persistence ($\liminf_{t\to\infty} x_i(t) > 0$ for all i) for all orbits of the interior of system (1)), and of permanence (($\liminf_{t\to\infty} x_i(t) > \delta > 0$ for all i) for all orbits of the interior of system (1)). For the system (3), it amounts to say that all the trajectories are contained in a fixed compact for permanence, and in a compact (depending on the trajectory) for strong persistence; therefore we have:

Corollary 3 *Under the hypotheses of theorem 4.4, if P restricted to* im B *is not positive definite, the equilibrium is globally unstable and the system (1) associated to (3) is neither permanent nor strongly persistent.*

5 Examples

First we are going to study analytically the decomposition (the PM hypotheses) in dimension three (it includes Lotka-Volterra models in dimension two). We will restrict ourselves to the most interesting case where $\ker B$ is one-dimensional, and $Bk = 0$, $k > 0$. We want to find a decomposition such that:

$$ {}^tBP = {}^tM \quad {}^tM\mathbf{1} = 0 $$

and M off-diagonal nonnegative. We can write down the linear system (cf. second remark of section 3). It is easy to calculate that we obtain for the 9 m_{ij} 6 equations (5 independent) given by

$$ Mk = 0 \quad {}^tM\mathbf{1} = 0 $$

and a sixth equation:

$$ b_{13}m_{12} - b_{12}m_{13} + b_{23}m_{22} - b_{22}m_{23} + b_{33}m_{32} - b_{32}m_{33} = 0 $$

If we can solve these six equations with M off-diagonal nonnegative, then we can find also a symmetric matrix P. We have nine variables, so the problem is to compute if a three-dimensional space intersects or not the nonnegative orthant in $\mathbf{R}^9$. We can remark that the first 5 equations always have a non-negative solution (${}^tM + Id$ is a stochastic matrix, see ([2])), and it remains to know if we can choose such a solution that verifies in addition the sixth equation.

Of course, solutions with the wanted signs are sometimes impossible; for example, the classical two-dimensional Lotka-Volterra system (cf. [16]), where **1** is the equilibrium, is such that the sixth equation becomes:

$$m_{12} + m_{13} - m_{22} = 0$$

and implies (because the diagonal of M is nonpositive) that $m_{11} = m_{22} = 0$, and therefore $M = 0$: the decomposition is impossible; but we know that such a system admits an infinity of periodic solutions in the first orthant.

We can also construct systems with behaviour similar to the behaviour described in the theorems, but admitting no decomposition. Take:

$$\begin{cases} \dot{x} = x(-x - y + 2) \\ \dot{y} = y(x - 2y + 1) \end{cases}$$

This system has a stable equilibrium at **1**; all trajectories go to equilibrium or leave any compact set of the interior of the orthant; but the decomposition is impossible because of the sixth equation, that implies $M = 0$.

Let us consider now the following system:

$$\begin{cases} \dot{x} = x(-x - 2y + 3) \\ \dot{y} = y(-x - y + 2) \end{cases}$$

Is it possible to apply the known sufficient condition ([15, 8]), that is to find a diagonal positive matrix D such that $DA + {}^tAD$ is negative definite? The answer is no, because in dimension two, it implies ([8][p. 200]) that $\det A > 0$. In fact, it is even impossible to find a diagonal matrix D, whatever its signs, such that $DA + {}^tAD$ is negative definite. But we can yet apply Theorem 4.4, and find a symmetric matrix P such that $PB = M$:

$$\begin{pmatrix} -3 & 5 & -2 \\ 5 & -7 & 2 \\ -2 & 2 & -1 \end{pmatrix} \begin{pmatrix} -1 & -2 & 3 \\ -1 & -1 & 2 \\ 0 & 0 & 0 \end{pmatrix} = \begin{pmatrix} -2 & 1 & 1 \\ 2 & -3 & 1 \\ 0 & 2 & -2 \end{pmatrix}$$

The matrix obtained from P by deleting the last row and the last column has one positive and one negative eigenvalue, and therefore the system, which admits $(1, 1)$ as an equilibrium, is globally unstable and neither permanent, nor strongly persistent.

We exhibit now a more elaborate example in dimension 3. Let us consider the following Lotka-Volterra model, scaled to admit $\mathbf{1}$ as the equilibrium:

$$\begin{cases} \dot{x} = x(-by + cz + b - c) \\ \dot{y} = y(-ax + by + cz + a - b - c) \\ \dot{z} = z(ax - a) \end{cases}$$

The two species x and y are in competition, the species x and z in symbiosis, and the species y is a parasite of z. The community matrix is:

$$\begin{pmatrix} 0 & -b & c \\ -a & b & c \\ a & 0 & 0 \end{pmatrix}$$

If we take now the following symmetric bijective matrix:

$$P^{-1} = \begin{pmatrix} 0 & 1 & 0 & 1 \\ 1 & 0 & 0 & 1 \\ 0 & 0 & 1 & 1 \\ 1 & 1 & 1 & 1 \end{pmatrix}$$

it is easy to verify that $B = P^{-1}M$ where M is an irreductible matrix verifying the hypotheses if:

$$c > a > b > 0$$

If these inequalities are fulfilled, we can conclude that the behaviour of the system is regular and check that the equilibrium is unstable.

6 Conclusion

The PM-decomposition enables us to build auxiliary functions and study the global behaviour of the Lotka-Volterra system; this behaviour is “regular”, in the sense that all the trajectories go to equilibria or are unbounded. It remains now to study this decomposition more deeply; we believe that the tools from the theory of positive matrices could be useful for doing that.

Acknowledgments: The author wishes to thank the anonymous referees for their remarks and constructive suggestions.

References

[1] Arnedo A., Coullet P., Peyraud J. and Tresser C., Strange attractors in Volterra equations for species in competition, J. Math. Biol. 14 (1982) 153-157

[2] A. Berman and R.J. Plemmons, Nonnegative matrices in the mathematical sciences, Academic Press, New-York (1979)

[3] M.E. Gilpin, Spiral chaos in a predator-prey model, Amer. Natur., 113 (1979), pp. 306-308.

[4] B.S. Goh, Global stability in many-species systems, Amer. Natur.,111 (1977), pp 135-143.

[5] J.L. Gouzé, Structure des modèles mathématique en biologie, in: A.Bensoussan et J.L. Lions, eds., Analysis and optimization of systems, Lecture Notes in Control and Information Sciences No. 111, Springer-Verlag, Berlin (1988)

[6] J.L. Gouzé, A criterion of global convergence to equilibrium for differential systems; application to Lotka-Volterra models, Rapport Inria No. 894, (1988)

[7] M.W. Hirsch, Systems of differential equations which are competitive or cooperative:III. Competing species, Nonlinearity, 1 (1988) pp. 51-71

[8] J. Hofbauer and K. Sigmund, The theory of evolution and dynamical systems, Cambridge University Press, (1988)

[9] Lotka A.J.,Contribution to the analysis of malaria epidemiology, (1923) in: F.M. Scudo and J.R. Ziegler, eds., The golden age of theoritical ecology: 1923-1940, Lecture notes in biomathematics No. 22, Springer-Verlag, Berlin (1978)

[10] R. Redheffer and W. Walter, Solution of the stability problem for a class of generalized Volterra prey-predator systems, J. Diff. Equ. 52 (1984) pp. 245-263.

[11] N. Rouche et J.Mahwin, Equations différentielles ordinaires, tomes 1 et 2, Masson, Paris (1973)

[12] J. Schnakenberg, Network theory of microscopic and macroscopic behavior of master equation systems, Rev. Modern Physics,48 (1976), pp. 571-585

[13] H.L. Smith, Systems of ordinary differential equations which generates an order preserving flow. A survey of results, SIAM Review, 30 (1988), pp. 87-113

[14] H.L. Smith, Competing subcommunities of mutualists and a generalized Kamke theorem, SIAM J. Appl. Math, 46(1986), pp 857-874.

[15] Y. Takeuchi, N. Adachi and H. Tokumaru, Global stability of ecosystems of the generalized Volterra type, Math. Biosci., 42 (1978), pp 119-136.

[16] V. Volterra, Variations and fluctuations in the numbers of coexisting animal species, (1927) in: F.M. Scudo and J.R. Ziegler, eds., The golden age of theoritical ecology: 1923-1940, Lecture notes in biomathematics No. 22, Springer-Verlag, Berlin (1978)