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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.

Comportement global des systèmes de Lotka-Volterra en dimension n

Résumé : Nous étudions les systèmes de Lotka-Volterra en dimension n; nous utilisond des résultats de positivité et des fonctions auxiliaires décroissant le long des trajectoires. Un des résultats est que s'il existe une décomposition de la matrice d'interaction en un produit d'une matrice symmétrique et une matrice positive en dehors de la diagonale, alors toutes les trajectoires vont vers l'ensemble des équilibres ou ne peuvent rester dans aucun compact dans l'intérieur de l'orthant positif.

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1 Introduction

The Lotka-Volterra models have been introduced by Volterra ([14]) in the case where several species compete for a same resource, or where some species are predators of other species, and by Lotka ([7]) 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:

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

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 non-negative.

Many results are known on these systems (see [13,6,8,14]). A complex (chaotic) behaviour has been shown to be possible ([1]). Recently, the theory of cooperative or competitive systems (cf. [11]) has been used to study such systems ([12,5,6]). A known sufficient condition of global convergence to equilibrium in the whole space $\mathbf{R}_+^{n-1}$ is (cf. [3,13]) the existence of a positive definite diagonal matrix D such that $DA + {}^tAD$ is positive 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. [9]). 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 periodic solutions, recurrent or chaotic behaviour, in any compact set of the interior of the positive orthant).

Notations: For x in $\mathbf{R}^n$, we write $x > 0$ if $x_i > 0$ $(i = 1,\ldots,n)$ and $x \geq 0$ if $x_i \geq 0$ $(i = 1,\ldots,n)$. 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 ${}^t(e^{x_1},\ldots,e^{x_n})$, and similarly for $\ln x$. The Kronecker product between two vectors $x \otimes y$ is the vector with components (x_iy_i). If x is a vector, we denote by x^{-1} the vector of components $(1/x_i)$. $\mathbf{1}$ is the vector ${}^t(1 \ldots 1)$ 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:

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

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 ([4]) 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 :

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

that is a straight (affine) line L of vector 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 ${}^t q 1 \neq 0$.

If B has the form (2)(Lotka-Volterra systems), then ${}^t q 1 = 1$ 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 ([9]); 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 ([10]). We shall use the following lemma:

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

$$Mk = 0 \quad {}^t M 1 = 0$$

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

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

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and using $^tM1 = 0$

$$\phi(p) = \sum_i (\ln p_i - \ln k_i)(-\sum_{k \neq i} m_{ki})p_i + \sum_i \sum_{j \neq i}(\ln p_i - \ln k_i)m_{ij}p_j$$

$$= -\sum_j \sum_{i \neq j}(\ln p_j - \ln k_j)m_{ij}p_j + \sum_i \sum_{j \neq i}(\ln p_i - \ln k_i)m_{ij}p_j$$

$$= \sum_i \sum_{j \neq i}(\ln \frac{p_i}{k_i} - \ln \frac{p_j}{k_j})m_{ij}p_j$$

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

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

$$= \sum_i (\sum_{j \neq i} m_{ij}k_j)\frac{p_i}{k_i} - \sum_i \sum_{j \neq i} m_{ij}p_j$$

and using $Mk = 0$

$$\phi(p) \leq -\sum_i m_{ii}p_i - \sum_i \sum_{j \neq i} m_{ij}p_j$$

$$= -\sum_i (m_{ii} + (\sum_{j \neq i} m_{ji}))p_i$$

$$= 0$$

because of $^tM1 = 0$.

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 $\mu > 0$). For the converse, it is enough to note that, if an off-diagonal nonnegative

singular matrix M has a connected graph, then its kernel is reduced to a positive vector ([2]).

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 $^tM1 = 0$, 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) $\overline{(V(y(t)))} \le 0$).

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, $\overline{V(y(t))} = {}^t(y - \ln k)PBe^y$ 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 $e^y \in \ker M \cap \mathbf{P}^n$.

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- We can write the decomposition:

$$^{t}BP = {}^{t}M \quad {}^{t}M1 = 0$$

We have $n(n+1)/2$ indeterminates in P, n^2 indeterminate 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 :

$$^{t}B_1 p_1 = m_1 \quad {}^{t}q_i m_1 = 0 \ (i = 1, \ldots, n)$$

where ${}^{t}B_1$ 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 im ${}^{t}B_1 \cap \mathbf{R}_+^{n^2} \neq \{0\}$, 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

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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 ${}^tM\mathbf{1} = 0$, 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 $\ker B \cap \mathbf{P}^n \subset \ker M \cap \mathbf{P}^n$, and that our hypothesis means that $\ker P$ does not intersects (except at 0) 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) go towards the set of equilibria or are unbounded.*

Indeed, as V decreases along all the trajectories, Lasalle's theorem ([9]) says that, if the positive orbit of a solution is bounded, it goes towards the set $\{y; \overline{\dot{V}(y(t))} = 0\}$, that is $\ker M \cap \mathbf{P}^n$, namely the set of equilibria of (3) because of the supplementary hypothesis $\ker B \cap \mathbf{P}^n = \ker M \cap \mathbf{P}^n$.

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 all the trajectories of (3) go towards the intersection of* im B *and of the set of equilibria, or are unbounded.*

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 $y(0) +$ im B; if the

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intersection of the set of equilibria and $y(0)$+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:

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, all trajectories go towards the intersection (assumed to be non empty) of the set of equilibria and* im B.

If ln k *is an isolated equilibrium on* $y(0)$ + 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.*

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

If moreover ln k is an isolated equilibrium on $y(0)$ + 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 detailed 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 ${}^tq1 \ne 0$. Under the PM hypotheses, and if* ker $B \cap$ $\mathbf{P}^n$ = ker $M \cap \mathbf{P}^n$, *all the trajectories go towards the unique equilibrium on the invariant hyperplane (given an initial condition) or are unbounded. Moreover, if P is positive definite or if P has all his eigenvalues positive except μ with $Pq = \mu q$, the single equilibrium is Lyapunov globally stable. If P has a negative eigenvalue not associated with eigenvector q, the equilibrium is unstable and some trajectories are unbounded.*

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We already know (see end of section 1) that there is a single equilibrium on the first integral containing the initial condition $y(0)$. If $Pq = \mu q$, then P restricted to im B is positive definite (because q is in the orthogonal of im B), and we can apply the preceeding theorem. Let us remark that the results are here global, because of the unicity of the equilibrium.

If we traduce 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.

5 Examples

It is easy to construct many examples by using the third and fourth remarks of section 3. We are going here to study the decomposition (the PM hypotheses) in dimension three (it includes Lotka-Volterra models in dimension two). We will restrict ourselves to the case where ker B is one-dimensional, and $Bk = 0$, $k > 0$. We want to find a decomposition such that:

$$^tBP = {}^tM \quad {}^tM1 = 0$$

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

$$Mk = 0 \quad {}^tM1 = 0$$

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 nonnegative 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. [14]), where 1 is the equilibrium, is such that the sixth equation becomes:

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

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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 $M = 0$.

6 Conclusion

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

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