Dynamical behaviour of Lotka-Volterra systems

Jean-Luc Gouzé
INRIA projet COMORE
BP 93
06902 Sophia-Antipolis Cedex
France
gouze@sophia.inria.fr

Keywords: Dynamical systems, population dynamics, Lotka-Volterra systems, global behaviour, growth control.

Abstract

We consider the $(n-1)$-dimensional Lotka-Volterra system (arising in biological modelling of species interactions), and associate with it a family of n-dimensional systems having the same phase portrait. We obtain some results on global behaviour and convergence towards the equilibrium in the case where the LV system is "nearly symmetric" or "nearly cooperative" (that is, there exists a member of the equivalence class that is symmetric or cooperative). We apply these results to stabilize the system by controlling the total or individual growth rates of the species.

1 Introduction

The $(n-1)$-dimensional Lotka-Volterra (LV) system describes the interaction between $(n-1)$ species of ecological systems and 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 positive equilibrium will be unique if it exists). The vector b describes the individual growth rates of each species. The variables x_i, standing for populations, are supposed real non-negative.

Many results are known on these systems (see Volterra (1927), Takeuchi et al. (1978), Redheffer and Walter (1984), Hirsch (1988), Hofbauer and Sigmund (1988), Gouzé (1993), Takeuchi (1996)). A complex (chaotic) behaviour has been shown to be possible (Gilpin (1979), Arneodo et al. (1982)), even in three dimensions. A well known sufficient condition for global convergence to equilibrium in the whole space $\mathbf{R}_+^{n-1}$ is (cf. Goh (1977), Takeuchi et al. (1978)) the existence of a positive definite diagonal matrix D such that $DA + {}^tAD$ is negative definite. A few results concerning the control of such systems exist also (see Goh et al. 1974, Gouzé 1994).

We will give here some more tools to study this system and obtain indications on its global behaviour. We begin by associating with the system (1) a new n-dimensional system. A preliminar version of this study was given in (Gouzé 1992).

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 $\ln x$. $\mathbf{1}$ is the vector ${}^t(1 \ldots 1)$ and $\mathrm{diag}\,(x)$ the diagonal matrix with diagonal x.

2 The associated family of systems

We make the usual hypotheses that A is bijective and that there exists a single positive equilibrium x^*. We can scale the system by the following change of variables

$$x_i' = x_i / x_i^*\ \ (i = 1, \ldots, n)$$

and the new equilibrium is now the vector $\mathbf{1}$. We keep the same notation for (1). We transform the system by introducing an additional 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 homogeneous system:

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

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 in this system for $x \geq 0$ (because x_i stands for a population or a population density); the faces

$x_i = 0$ of the orthant are invariant, and so is the open positive orthant $\mathbf{P}^n$. We study this system in $\mathbf{P}^n$, so we can make the change of variables:

$$y = \ln x$$

and obtain

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

Moreover, we know that $B\mathbf{1} = 0$ because $A\mathbf{1} + b = 0$. We consider any bounded open subset O of $\mathbf{R}^n$.

Now, let $k \in \mathbf{R}^n$ such that ${}^t k\mathbf{1} = 1$. We define the linear transformation:

$$z = y - ({}^t ky)\mathbf{1}$$

and we obtain after some calculations

$$\dot{z} = (B - \mathbf{1}({}^t kB))e^z e^{(({}^t ky)\mathbf{1})} = (B - \mathbf{1}({}^t kB))e^z e^{({}^t ky)}$$

and, for y in O, we can scale the time in this equation to suppress the last term (which is positive) and to obtain a differential equation having the same phase portrait as (3):

$$\dot{z} = (B - \mathbf{1}({}^t kB))e^z \tag{4}$$

This system has the linear first integral ${}^t kz = 0$. The family indexed by k contains n LV systems obtained by taking k equal to each of the vectors of the canonical basis.

Proposition 1 *The LV system (1) can be associated with a family, indexed by $k \in \mathbf{R}^n$, $\sum k_i = 1$, of n-dimensional differential systems having the same phase portrait on any open bounded domain of the positive orthant. This family contains the original system and $(n-1)$ other LV systems.*

Example: Let us take a simple example in $\mathbf{R}^2$:

$$\begin{cases} \dot{x} = x(x + 3y - 4) \\ \dot{y} = y(2x + y - 3) \end{cases}$$

This LV system is associated with a system (3) with

$$B = \begin{pmatrix} 1 & 3 & -4 \\ 2 & 1 & -3 \\ 0 & 0 & 0 \end{pmatrix}$$

and to a family indexed by k, $k_1 + k_2 + k_3 = 1$:

$$\dot{z} = (B - \mathbf{1}(k_1 + 2k_2, 3k_1 + k_2, -4k_1 - 3k_2))e^z$$

This family contains two other LV systems having the same phase portrait on any bounded open domain:

$$\begin{cases} \dot{x}_1 = x_1(-x_1 - y_1 + 2) \\ \dot{y}_1 = y_1(-2x_1 + 3y_1 - 1) \end{cases} \quad \begin{cases} \dot{x}_2 = x_2(4x_2 - 3y_2 - 1) \\ \dot{y}_2 = y_2(x_2 - 2y_2 + 1) \end{cases}$$

These systems are all equivalent, and we can obtain results on the behaviour of one LV system by studying the others. For instance, the system (x_2, y_2) is a predator-prey system; a priori, the orbits could rotate around the positive equilibrium ; but this system has the same phase portrait as the system (x, y) that is cooperative (see Smith (1988)); such a behaviour is therefore excluded.

Remark. It is easy to see that the transformation indexed by k sends some points of the phase space of x (system (1)) to infinity. In particular, the $(n-1)$ LV systems having the same phase portrait as (1) are nothing but the Poincaré transforms (see Andronov et al. (1973)) of the system. This transform can be used to study the behaviour at infinity in the phase space, and to investigate the behavior of the LV systems (for an application see Hsu (1978)).

If we take again the above example, we see that in fact:

$$x_1 = x/y \ ; \ y_1 = 1/y \ ; \ x_2 = 1/x \ ; \ y_2 = y/x$$

that is to say the two Poincaré transforms of the system.

The system (x_1, y_1) admits the equilibrium (on the axes) $x_1 = 2, \ y_1 = 0$ and it is easy to verify that it is locally asymptotically stable; we can deduce that, for the original LV system, there exist unbounded orbits going to infinity along the direction $(2, 1)$. A more detailed study shows that all the unbounded orbits have this property; moreover, the positive equilibrium is unstable. We therefore deduce that, for large values of the variables, the variable x increases (and goes to infinity) two times faster than y. As this example suggests, it is quite easy to study the equilibria on the axes and their local stability for the n equivalent LV systems, and this gives indications on the behaviour at infinity of the original system.

3 Nearly symmetric system

Now we make more detailed hypotheses on some property of one particular member of the family. Our first hypothesis concerns symmetry.

If the matrix B of the system (3) is symmetric, we can say more on its global behaviour. Consider the function:

$$V(y) = \frac{1}{2} \, {}^t e^y B \, e^y.$$

Along the trajectories the time derivative of V is

$$\dot{\overline{V(y(t))}} = \, {}^t(Be^y)\mathrm{diag}\,(e^y)(Be^y) \geq 0$$

The function increases along the trajectories and we can apply Lasalle's theorem (see Rouche and Mahwin (1973)): either the orbit is unbounded or converges towards the set of points y such that $Be^y = 0$, that is to say the equilibrium of the system. Because all the systems (4) have the same phase portrait, these results are valid if one element of the family is symmetric.

If it is the case, because $B\mathbf{1} = 0$, then ${}^t\mathbf{1}(B - \mathbf{1}({}^t kB)) = 0$ and therefore the vector must be such that $k = \mathbf{1}/n$.

Theorem 1 *If for $k = \mathbf{1}/n$, the matrix $(B - \mathbf{1}({}^t kB))$ is symmetric, then the orbits of the original LV system (1) either are unbounded or converge towards the equilibrium.*

If this matrix is semi-definite negative (as a quadratic form), the equilibrium is globally asymptotically stable.

If this matrix is not semi-definite negative, the equilibrium is unstable and there exist unbounded orbits.

If the matrix is semi-definite negative, the function $V(y)$ is in fact a Liapunov function. If the matrix is not semi-definite negative, if we take the initial condition y_0 in the neighborhood of the equilibrium such that $V(y_0) > 0$, then this orbit will be unbounded.

Example. The three-dimensional LV system:

$$\begin{cases} \dot{x} = x(4x - y + 2z - 5) \\ \dot{y} = y(4x - 4y) \\ \dot{z} = z(4x - 3y + 2z - 3) \end{cases}$$

is associated (by $k = (1/4, 1/4, 1/4, 1/4)$) to the symmetric system

$$\dot{z} = Ce^z \quad C = \begin{pmatrix} 1 & 1 & 1 & -3 \\ 1 & -2 & -1 & 2 \\ 1 & -1 & 1 & -1 \\ -3 & 2 & -1 & 2 \end{pmatrix}$$

the eigenvalues are $0, -4, 3 + \sqrt{5}, 3 - \sqrt{5}$; we deduce that the LV system has an unstable equilibrium with unbounded orbits that go to infinity.

4 Nearly cooperative system

Our second hypothesis concerns cooperativity. A differential system is called cooperative if the Jacobian matrix has non-negative off-diagonal elements; many results are known on these systems (cf. Smith (1988)). In our case, the system (3) will be cooperative if and only if the matrix B has non-negative off-diagonal elements. Because of the Perron-Frobenius theorem (applied to $(B + \alpha\, Id)$, α positive large enough), there exists $q \geq 0$ such that ${}^t qB = 0$ (Berman and Plemmons (1979)). The main results of convergence for cooperative systems are applicable when the system is strictly cooperative, that is, in our case, when the matrix B is irreducible (i.e., its directed graph is connected). In fact, B is irreducible if and only if q is strictly positive; in that case, the global convergence towards the equilibrium is known (Mierczynski (1987), Arino et al. (1988)) and we can even exhibit a simple Liapunov function (Gouzé (1993)).

Proposition 2 *If B is irreducible and cooperative with ${}^t Bq = 0$, then the function $V(y) = \frac{1}{2}\, {}^t y \text{ diag } (q) y$ is a Liapunov function, and the equilibrium is globally stable.*

Indeed, $\dot{\overline{V(y(t))}} = {}^t y \text{ diag } (q) Be^y$ and $M = \text{diag } (q) B$ is an off-diagonal non-negative matrix such that $M\mathbf{1} = {}^t M\mathbf{1} = 0$. We deduce (Gouzé (1993)) that $\dot{\overline{V(y(t))}} \leq 0$ and cancels only when $Be^y = 0$, that is , at the equilibrium. Moreover, q is positive, and so $V(y)$ is Liapunov.

Clearly, if there is an element of the family (4) indexed by k that is cooperative, we will be able to deduce the global convergence of the equilibrium.

To construct the matrix $(B - \mathbf{1}({}^t kB))$, we subtract from each line of B the vector ${}^t Bk = h$; since h belongs to the range of ${}^t B$, $\mathbf{1}^t h = 0$. Moreover, $B_{ij} - h_j$ must be non-negative for $i \neq j$. It will be possible to obtain these signs if the sum of the minima of the off-diagonal elements on each column is non-negative. If this last sum is positive, let us choose for h the vector of components

$$\min_{i, i \neq j} B_{ij} - \epsilon_j$$

where ϵ_j is positive small enough; the resulting matrix $(B - \mathbf{1}({}^t kB))$ will be off-diagonal positive, and clearly irreducible. If the sum is zero, the resulting matrix will have zeros, and its irreducibility must be checked.

Therefore we have following proposition:

Theorem 2 *If the LV system (1) is such that*

$$\sum_{j=1}^{n} \min_{i \neq j}(A_{ij}, 0) + \min_i b_i > 0$$

then the positive equilibrium is globally asymptotically stable.

If the LV system (1) is such that

$$\sum_{j=1}^{n} \min_{i \neq j}(A_{ij}, 0) + \min_i b_i = 0$$

and if the resulting matrix is irreducible, then the positive equilibrium is globally asymptotically stable.

We can remark that the given conditions imply that $b > 0$; from a biological point of view, it is a very reasonable hypothesis on the growth of one isolated species.

Let us consider for instance the three-dimensional LV system:

$$\begin{cases} \dot{x} = x(-3x - y + 2z + 2) \\ \dot{y} = y(x - 3y + 2) \\ \dot{z} = z(-\frac{1}{2}x + 2y - \frac{9}{2}z + 3) \end{cases}$$

The vector of the minimum on the columns of the B_{ij} is $(-1/2, -1, 0, 2)$ and the sum of its components is $1/2$. The positive equilibrium $\mathbf{1}$ of this system is therefore globally stable in the whole positive orthant.

It can be interpreted from a biological point of view in the following way: for each species, let us consider the greatest negative interaction with the other species. If the (absolute value of the) sum of these interactions is smaller than the smallest isolated growth rate, the system is globally stable.

Remark. A similar result exists when an element of the family is competitive (cooperative in reverse time); in such a case, if

$$\sum_{j=1}^{n} \max_{i \neq j}(A_{ij}, 0) + \max_i b_i < 0$$

then the system is globally unstable (i.e. globally stable in reverse time).

5 Control of Lotka-Volterra systems: total growth

It is easy to use the above results to obtain simple conclusions concerning a rudimentary control of LV systems: we will suppose that a control is allowed on the total growth rate of a variable x_k, i.e. the control applies to $\dot{x}_k/x_k$; we suppose also that the scalar control u is positive, that means that we are able to regulate the total growth rate of one individual species, but not to change the sign.

The controlled system is therefore:

$$\begin{aligned} \dot{x}_i &= x_i\,(\sum_{j=1}^{n-1} A_{ij}x_j + b_i) \;\; (i = 1,\ldots,n-1; i \neq k) \\ \dot{x}_k &= ux_k\,(\sum_{j=1}^{n-1} A_{kj}x_j + b_k) \end{aligned}$$

The following is an easy corollary of Theorem (2), and is better explained with an example. Let us remark that the positive equilibrium still exists (and is equal to $\mathbf{1}$) for any $u > 0$ if it exists for $u = 1$ (no control), as it is supposed.

Corollary 1 *In some cases, it is possible to adjust the positive constant control u, such that the controlled LV system is globally asymptotically stable towards the positive equilibrium.*

Let us consider for example the system:

$$\begin{cases} \dot{x} = x(-3x - y + 2z + 2) \\ \dot{y} = uy(x/2 - 3/2y + 1) \\ \dot{z} = z(-\frac{1}{2}x + 2y - \frac{9}{2}z + 3) \end{cases}$$

For $u = 1$ this system does not meet the criterion, but for $u = 2$ we have the same system as above in section (4), and again the global stability.

Of course, we could obtain many variations of this result for multiple positive controls $u_k; k = 1 \ldots m$.

6 Control of Lotka-Volterra systems: individual growth

In a similar way, it is easy to obtain some results concerning the stabilization of Lotka-Volterra systems when a control on the individual growth rate is allowed. We will consider here the simple case when one control is allowed on the growth rate b_k of x_k; we wish also that the equilibrium remains at the same value $\mathbf{1}$. A possibility is to take the control (d is a vector in $\mathbf{R}^n$):

$$u = {}^t d(x - \mathbf{1})$$

Let us remark that this control does not stay positive as above; there exists also other possibilities (cf. Gouzé 1992). The controlled system is now:

$$\begin{aligned} \dot{x}_i &= x_i\,(\sum_{j=1}^{n-1} A_{ij}x_j + b_i) \;\; (i = 1,\ldots,n-1; i \neq k) \\ \dot{x}_k &= x_k\,(\sum_{j=1}^{n-1} A_{kj}x_j + b_k + {}^t d(x - \mathbf{1})) \end{aligned}$$

As above, it is sometimes possible to apply our theorem 2 to obtain results of stabilization. We give only an example.

Corollary 2 *In some cases, it is possible to choose the vector d such that, with the control u, the controlled LV system is globally asymptotically stable towards the positive equilibrium.*

We take the same example:

$$\begin{cases} \dot{x} = x(-3x - y + 2z + 2) \\ \dot{y} = y(x/2 - 3/2y + 1 + d_2(y - 1)) \\ \dot{z} = z(-\frac{1}{2}x + 2y - \frac{9}{2}z + 3) \end{cases}$$

For $d_2 = 0$ (no control), the system does not meet the criterion. For $d_2 = -1$, the equation in y becomes

$$\dot{y} = y(x/2 - 5/2y + 2)$$

and is globally stable by theorem (2). Many variations are possible.

References

A.A. Andronov, E. Leontovitch, I. Gordon, A. Maier (1973) Qualitative theory of second order systems. Wiley

O. Arino, F. Bouvard, et N. Hassani, (1988) Un résultat sur le comportement asymptotique des solutions de systèmes dynamiques monotones, C. R. Acad. Sci., Paris, Ser. I 307, No.7, pp. 311-315

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

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

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

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

B.S. Goh, G. Leitmann and T. Vincent, (1994) Optimal control of a prey-predator system, Math. Biosciences 19, pp. 263-286.

J.L. Gouzé, (1988) A criterion of global convergence to equilibrium for differential systems; application to Lotka-Volterra models, Rapport Inria 894

J.L. Gouzé, (1992) Behaviour at infinity of Lotka-Volterra systems, 3rd International conference on mathematical population dynamics, O. Arino and M. Kimmel editors, Pau, mai 1992.

J.L. Gouzé, (1993) Global behaviour of Lotka-Volterra systems, Math. Biosc., 113, pp. 231-243

J.L. Gouzé, (1993) Global stabilization of n-dimensional population models by a positive control, Proceedings of the 33rd IEEE Conf. on Decision and Control, Orlando, USA, pp. 1335-1336.

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

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

S.B. Hsu, (1978) The application of the Poincaré-transform to the Lotka-Volterra model. J. Math. Biol. 6, pp. 67-73

J. Mierczynski, (1987) Strictly cooperative system with a first integral, Siam Math. Anal. 18, 3, pp. 642-646

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

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

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

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

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

Y. Takeuchi, (1996) Global dynamical properties of Lotka-Volterra systems, World Scientific

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