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The Lotka–Volterra canonical format

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Abstract

Most of the dynamical systems used in models of mathematical biology can be related to the simplest known model: the Lotka–Volterra (LV) system. Brenig (1988) showed that no matter the degree of nonlinearity of the considered model is often possible to relate it to a LV by a suitable coordinate transformation plus an embedding (Brenig, L., 1988. Complete factorization and analytic solutions of generalized Lotka–Volterra equations. Phys. Lett. A 133, 378–382). The LV system has then a status of canonical format. In this paper, we show how analytical properties of the original system can be studied from the dynamics of its associated LV. Our methodology is exemplified through the analysis of the stability of the interior fixed points and determination of conserved quantities.

Keywords: Lotka–Volterra; Population dynamics; Stability; First integrals

1. Introduction

One of the first models introduced in the literature concerning problems of population dynamics was the Lotka–Volterra (LV) format in the beginning of the last century (Volterra, 1931). The properties of this system of equations were considered in many papers and was one of the most studied set of differential equations (see for example, May and Leonard (1975), Rhedeffer and Walter (1984), Hofbauer and Sigmund (1988), Blanco (1993), Takeuchi (1995), Raychaudhuri et al. (1996), Wu et al. (1996), Moreira and Yuquen (1997), Svirizhev (2000), Huang and Yuangang (2001), Zhang (2003)). In the second half of the past century, as a theoretical framework devoted to nonlinear systems became available, as well as computational tools, generalizations of the LV model appeared in the literature in the attempt to leave the models closer to reality.

The ecology of populations deals basically with the growth and interaction between species. The detailed description of all these interactions, even for the simplest case of a predator and a prey, is a rather difficult matter. Concerning the stability of the ecosystems, as a general rule, more complex the system, more

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stable it is, although this is not the kind of behavior presented by the mathematical set of equations. Indeed, chaotic behavior is the general rule instead of stability.

In the LV system, the complex problem of interactions between species is simplified to three basic ones: competition, mutual cooperation (symbiosis) and predator–prey. Unilateral relations, i.e., amensalism and commensalism, are also present in the LV model. Competition is an universal aspect, the basis of natural selection. Individuals in a single species fight among themselves for the available resources and the more the fitness the greater the chance of a single individual to propagate its genes to further generations. Even symbiosis can be seen as an agreement between two individuals (or two species) in the competition of both against the others.

The generalizations in the LV system are often a tentative to leave the models closer to reality, for example, LV models are not in accordance with mass conservation, which is a shortcoming of LV equations. Other nonlinear terms are included, which has as result a much more difficult set of ordinary differential equations to handle.

Most of the ecological models can be related to the simplest system, namely the LV one, as showed by Brenig (1988) (see also Hernández-Bermejo and Fairén (1997)). Nonlinear models, which take into account other forms of interaction, terms for dispersion, etc. are found to be equivalent, up to a coordinate transformation plus an embedding, to a system of LV type. This elevates the LV system to a category of *canonical* format.

The LV model was one of the most studied differential equation system and a huge number of papers and books are devoted to it. One of the consequences of the results presented in this paper is that a series of analytical properties of general nonlinear systems can be analyzed with the same theoretical tools developed for the LV model, particularly the determination of conserved quantities and of Lyapunov functions (Figueiredo et al., 1998, 2000). The structure of the paper is the following: in Section 2, we present the Lotka–Volterra canonical format and show how it is applicable in models of population dynamics. In Section 3, we discuss how to study the stability problem of fixed points through the determination of a Lyapunov function using the canonical format. In Section 4, we show how to obtain conserved quantities and close the paper with some concluding remarks in Section 5.

2. The Lotka–Volterra canonical format

The LV system has the following generic form:

$$\dot{U}_i = \lambda_i U_i + U_i \sum_{j=1}^{m} M_{ij} U_j; \quad U_i \in \Re;\ i = 1, \ldots, m, \tag{1}$$

where M denotes a square $m \times m$ matrix and U_i the population density of species i. A generalized LV system is defined in the following way:

$$\dot{x}_i = l_i x_i + x_i \sum_{j=1}^{m} A_{ij} \prod_{k=1}^{n} x_k^{B_{jk}}; \quad x_i \in \Re;\ i = 1, \ldots, n, \tag{2}$$

where A and B are real, constant rectangular matrices. The number m is related to the number of monomials in the vector field of Eq. (2) (we extend here the denomination for monomials to include real exponents). We assume without loss of generality $m \geq n$ in Eq. (2). In the case $m < n$, the system in Eq. (2) can be reduced by a suitable transformation of variables into a decoupled system of m equations [8]. We also assume that the rank of B is maximal, i.e. it is equal to n. This represents no restriction at all for the present approach. Indeed if the rank is less than n then the system can be decoupled into a new system with a new exponent B' whose rank is maximal (Hernández-Bermejo et al., 1998).

Let us introduce $m - n$ extra variables $x_{n+1}, x_{n+2}, \cdots, x_{n+m}$ such that:

$$\dot{x}_k = 0; \quad k = n+1, \ldots, n+m, \tag{3}$$

and obtain the extended system:

$$\dot{x}_i = \tilde{l}_i x_i + x_i \sum_{j=1}^{m} \tilde{A}_{ij} \prod_{k=1}^{m} x_k^{\tilde{B}_{jk}}; \quad i = 1, \ldots, m, \tag{4}$$

where

$$\tilde{A} = \begin{bmatrix} A_{11} & A_{12} & \cdots & A_{1m} \\ A_{21} & A_{22} & \cdots & A_{2m} \\ \cdots & \cdots & \cdots & \cdots \\ A_{n1} & A_{n2} & \cdots & A_{nm} \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 \end{bmatrix} \tag{5}$$

and

$$\tilde{B} = \begin{bmatrix} B_{11} & B_{12} & \cdots & B_{1n} & b_{1,n+1} & \cdots & b_{1,m} \\ B_{21} & B_{22} & \cdots & B_{2n} & b_{2,n+1} & \cdots & b_{2,m} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ B_{m1} & B_{m2} & \cdots & B_{mn} & b_{m,n+1} & \cdots & b_{m,m} \end{bmatrix}. \tag{6}$$

The parameters b_{jk} are arbitrary up to the restriction that $\tilde{B}$ is invertible. To ensure the equivalence between (2) and (4) the following initial conditions are imposed:

$$x_k(t=0) = 1; \quad k = n+1, \ldots, m. \tag{7}$$

Let us now define the new variable U through:

$$x_i = \prod_{\beta=1}^{m} U_\beta^{D_{i\beta}}. \tag{8}$$

with D invertible. The inverse of the above transformation is given by:

$$U_\alpha = \prod_{i=1}^{m} x_i^{D^{-1}_{\alpha i}}. \tag{9}$$

Performing the dynamics of U we obtain:

$$\dot{U}_\alpha = U_\alpha \left(l'_\alpha + \sum_{k=1}^{m} A'_{\alpha k} \prod_{\beta=1}^{m} U_\beta^{B'_{k\beta}} \right), \tag{10}$$

where $D^{-1}\tilde{l} = l'$, $D^{-1}\tilde{A} = A'$ e $\tilde{B}D = B'$. The Eq. (10) has the same analytical form (4), and therefore, this class of equations is form invariant for transformations of type (8). In particular, Eq. (4) is embedded into a LV type equation by choosing $D = \tilde{B}^{-1}$:

$$\dot{U}_\alpha = (\tilde{B}\tilde{l})_\alpha U_\alpha + U_\alpha \sum_{\beta=1}^{m} (\tilde{B}\tilde{A})_{\alpha\beta} U_\beta; \qquad \alpha = 1, \ldots, m. \tag{11}$$

Now let us define the characteristic matrix $M \equiv BA = \tilde{B}\tilde{A}$ and $\lambda \equiv Bl = \tilde{B}\tilde{l}$, which identifies (11) as a LV system of type (1). Therefore, every system of type (2) can be cast into a LV by a suitable embedding defined by Eqs. (4) and (7), and the coordinate transformation in Eq. (8). Using (7) and Eq. (8) we have:

$$\prod_{\beta=1}^{m} U_\beta^{\tilde{B}^{-1}_{\alpha\beta}} = 1; \quad \alpha = n+1, \ldots, m, \tag{12}$$

which defines a subspace of the m-dimensional LV space where lies the original dynamics of Eq. (2). So the LV Eq. (11), with $M = BA$ and $\lambda = Bl$, restricted to the hypersurface defined by (12) are equivalent to the system (2).

Model (2) is unique in the sense that it encompasses a great variety of nonlinear equations. To analyze its analytical properties one can generalize results developed to the study of the simpler LV system, which is an advantage of our model. Let us exemplify this approach with some examples.

2.1. Some models in population dynamics

We begin with a model proposed in Freedman and Takeuchi (1989) for the dynamics of two species such that one of them can migrate among n regions. This is normally called a metapopulation in the literature. Let us consider the simplest case of a predator and a prey, the prey being able to migrate but not the predator. A simple example would be of a bird (the prey) living in n regions separated by rivers and mountains, the birds being able to fly from a region to other. For the predators, these are natural barriers which they cannot surpass.

The population of the prey in the region i will be denoted by $x_i(t)$, with $i = 1, \ldots, n$ representing the n regions where is possible to find individuals of this species. The following dynamics is assumed for $x_i(t)$:

$$\dot{x}_i = x_i g_i(x_i) - y p_i(x_i) + \epsilon \sum_{j=1}^{n} \Pi_{ji} \alpha_j h_j(x_j); \qquad i = 1, \ldots, n, \tag{13}$$

where y represents the predator population. For each one of the terms in (13) we have the following interpretation:

- $g_i(x_i)$ is the growth rate of preys in the absence of the predators y, when restricted to the i-th region. Taking into account the limitation of the available resources, this will be a decreasing function of x_i:

$$g_i(0) > 0, \qquad \frac{\mathrm{d}g_i(x_i)}{\mathrm{d}x_i} < 0; \quad i = 1, \ldots, n.$$

- $p_i(x_i)$ is the response of the predator to the prey in region i. Since a growth in the prey population is benefic to the predators we have:

$$p_i(0) = 0, \qquad \frac{\mathrm{d}p_i(x_i)}{\mathrm{d}x_i} > 0; \quad i = 1, \ldots, n.$$

- $h_i(x_i)$ is an impulse for migration. The usual assumption is to take this impulse as a function of the prey population.

$$h_i(0) = 0, \qquad \frac{\mathrm{d}h_i(x_i)}{\mathrm{d}x_i} \geq 0; \quad i = 1, \ldots, n.$$

- α_i represents the inverse of the barrier "height", which forbids migration. If $\alpha_i = 0$, then it is impossible to leave region i.
- Π_{ji} is the probability that a given member of the population, leaving region j, reaches region i.

For the dynamics of y (the predator population) the model is represented by the equation:

$$\dot{y} = y\left(-s(y) + \sum_{i=1}^{n} c_i p_i(x_i)\right). \tag{14}$$

Here $s(y)$ represents the mortality rate of the predator in the absence of the prey, which is an increasing function of y:

$$s(0) = 0, \qquad \frac{\mathrm{d}s(y)}{\mathrm{d}y} \geq 0.$$

Possible forms for the functions g_i, h_i, p_i and s are given by:

$$\begin{aligned}
&g_i(x_i) = G_{i0}x_i^{G_i} + g_i^*, \qquad G_{i0}G_i < 0; \;\; i = 1, \ldots, n,\\
&p_i(x_i) = P_{i0}x_i^{P_i}, \qquad P_{i0}P_i > 0; \;\; i = 1, \ldots, n,\\
&h_i(x_i) = H_{i0}x_i^{H_i}, \qquad H_{i0}H_i > 0; \;\; i = 1, \ldots, n,\\
&s(y) = S_0 y^S, \qquad S_0 S > 0.
\end{aligned} \tag{15}$$

It is worth noting that $p_i(x_i)$ would be more realistic with a saturation curve. Nevertheless (15) is sufficient to illustrate our methodology. With the above assumptions, Eqs. (13) and (14) can be written as:

$$\begin{aligned}
\dot{x}_i &= x_i\Bigg(g_i^* + G_{i0}x_i^{G_i} - P_{i0}x_i^{P_i-1}y\\
&\quad + \epsilon\sum_{j=1}^{n}\Pi_{ji}\alpha_j x_j^{H_j}x_i^{-1}H_{j0}\Bigg); \quad i = 1, \ldots, n,\\
\dot{y} &= y\left(-S_0 y^S + \sum_{i=1}^{n} c_i x_i^{P_i} P_{i0}\right),
\end{aligned} \tag{16}$$

which can be rewritten as a LV by defining:

$$B = \begin{bmatrix} B_1 \\ B_2 \\ B_3 \\ B_4 \end{bmatrix},$$

where each B_i is a matrix. Explicitly we have:

$$B_1 = \begin{bmatrix} G_1 & 0 & \ldots & 0 & 0 \\ 0 & G_2 & \ldots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \ldots & G_n & 0 \end{bmatrix},$$

$$B_2 = \begin{bmatrix} P_1 - 1 & 0 & \ldots & 1 \\ 0 & P_2 - 1 & \ldots & 1 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & \ldots & P_n - 1 & 1 \end{bmatrix},$$

$$B_3 = \begin{bmatrix} B_3^1 \\ B_3^2 \\ \vdots \\ B_3^n \end{bmatrix},$$

where each B_n^j is given by:

$$B_3^1 = \begin{bmatrix} H_1 - 1 & 0 & \dots & 0 & 0 \\ -1 & H_2 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ -1 & 0 & \dots & H_n & 0 \end{bmatrix},$$

$$B_3^2 = \begin{bmatrix} H_1 & -1 & 0 & \dots & 0 \\ 0 & H_2 - 1 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & -1 & & \dots H_n & 0 \end{bmatrix},$$

$$B_3^n = \begin{bmatrix} H_1 & 0 & \dots & -1 & 0 \\ 0 & H_2 & \dots & -1 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & H_n - 1 & 0 \end{bmatrix}.$$

And finally we also have:

$$B_4 = \begin{bmatrix} 0 & 0 & \dots & S \\ P_1 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & \dots & P_n & 0 \end{bmatrix}.$$

The matrix A is of the form:

$$A = \begin{bmatrix} A_1 & A_2 & A_3 & 0 \\ 0 & 0 & 0 & A_4 \end{bmatrix},$$

where 0 is a null matrix and each A_i is given by:

$$A_1 = \begin{bmatrix} G_{10} & 0 & \dots & 0 \\ 0 & G_{20} & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & G_{n0} \end{bmatrix},$$

$$A_2 = \begin{bmatrix} -P_{10} & 0 & \dots & 0 \\ 0 & -P_{20} & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & -P_{n0} \end{bmatrix},$$

$$A_3 = \begin{bmatrix} K_1 & 0 & \dots & 0 \\ 0 & K_2 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & K_n \end{bmatrix},$$

where $K_i = [k_{1i}, k_{2i}, \dots, k_{ni}]$ and $k_{ji} = \Pi_{ji}\alpha_j H_{j0}$.

$$A_4 = \begin{bmatrix} -S_0 & 0 & \dots & 0 \\ 0 & -c_1 P_{10} & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & \dots & -c_n P_{n0} & 0 \end{bmatrix}.$$

The LV system associated to (16) is characterized by $M = BA$. Of course there is a price for the gain in simplicity, the original system has dimension n and is highly nonlinear. The LV system has only quadratic nonlinearities, however, the dimension is higher than n. As we shall see in next section, if one is interested in analyzing the analytical properties of the system, results developed originally for the LV system can be readily extended to encompass this model as well as every methodology built for LV systems.

As another example we take the Gause ecological model, which deals with a predator–prey interaction (Gause, 1938). Let x and y denote a prey and its predator. In the absence of predators, the x population grows till a maximum $K > 0$. The presence of the predators have as effect on x a decrease in the population governed by cx^{α_1}, $c > 0, \alpha_1 > 0$. Therefore:

$$\dot{x} = xg(x) - cyx^{\alpha_1}, \tag{17}$$

where $g(x) > 0$ for $x < K$, $g(x) < 0$ for $x > K$ e $g(K) = 0$. In LaSalle and Lefshets (1961) the following functional form for $g(x)$ is assumed:

$$g(x) = r(1 - \frac{x}{K}), \qquad r > 0.$$

For the predators we consider a constant mortality rate $d > 0$ in the absence of prey and a growth rate $bx^{\alpha_2},\ b > 0,\ \alpha_2 > 0$. Therefore:

$$\dot{y} = y(-d + bx^{\alpha_2}) \tag{18}$$

The system given by the Eqs. (17) and (18) is dubbed Gause ecological model:

$$\dot{x} = xr\left(1 - \frac{x}{K}\right) - cyx^{\alpha_1}, \qquad \dot{y} = y(-d + bx^{\alpha_2}). \tag{19}$$

This system can be recasted in the LV format defining:

$$B = \begin{bmatrix} 1 & 0 \\ \alpha_1 - 1 & 1 \\ \alpha_2 & 0 \end{bmatrix}, \tag{20}$$

$$A = \begin{bmatrix} -r/K & -c & 0 \\ 0 & 0 & b \end{bmatrix}, \tag{21}$$

$$l = \begin{bmatrix} r \\ -d \end{bmatrix}, \tag{22}$$

and the characteristic matrix $M = BA$ is given by:

$$M = \begin{bmatrix} -r/K & -c & 0 \\ r(1-\alpha_1)/K & (1-\alpha_1)c & b \\ -\alpha_2 r/K & -\alpha_2 c & 0 \end{bmatrix}, \tag{23}$$

The above procedure can be applied to all models presented in Blanco (1993), Takeuchi (1995), Raychaudhuri et al. (1996), Wu et al. (1996), Moreira and Yuquen (1997), Svirizhev (2000), Huang and Yuangang (2001), Zhang (2003).

3. Stability problem in generalized Lotka–Volterra systems

In this section, we present some results concerning the stability of LV systems and how they can be extended to general LV systems of form (2). We stress that every other analytical property of (2) can be considered from the dynamics of the associated system. Therefore, the problem of stability here considered must be taken as an example of our methodology. We follow the approach due to Rhedeffer and Walter (1984), although the first study of the problem dates back to Volterra himself. The theorems stated here were first proved in Figueiredo et al. (2000). In a LV system given by (1), the fixed points in the positive orthant are the solutions of:

$$\lambda_i + \sum_{j=1}^{m} M_{ij} q_j = 0; \quad i = 1, \ldots, m,\ q_i > 0. \tag{24}$$

Many authors have faced the problem of the stability of (1) since the pioneer work of V. Volterra (see Takeuchi, 1995 and references therein). In Rhedeffer and Walter (1984) the concept of admissible matrix was introduced to deal with the problem of stability and asymptotic behavior of LV systems. A $m \times m$ matrix M is said admissible if there are constants $a_i > 0,\ i = 1, \ldots, m$, such that:

$$\sum_{i,j=1}^{m} a_i M_{ij} w_i w_j \leq 0; \quad w \in \Re^m. \tag{25}$$

This condition implies $M_{ii} \leq 0$, and can hold even in the case of a singular matrix.

The following theorems were proved in Figueiredo et al. (2000):

Theorem 1. If the matrix $M = BA$ is admissible and system (2) has a fixed point x^* in the interior of the positive orthant $\Re^n_+$, then there exists a Lyapunov function V valid in $\Re^n_+$.

The Lyapunov function is given by:

$$V = \sum_{i=1}^{m} a_i \left(U_i - q_i \ln \frac{U_i}{q_i} - q_i\right); \tag{26}$$

where

$$q_i = \prod_{k=1}^{m} (x_k^*)^{B_{jk}} > 0. \tag{27}$$

and U_i is obtained with the help of (9).

Theorem 2. If the matrix $M = BA$ is admissible and the initial condition is in the positive orthant, then the corresponding solution is bounded and componentwise bounded away from zero, i.e., if $(x_1(0), \ldots, x_n(0)) \in \Re^n_+$ then:

$$\exists\, \epsilon_i, \delta_i \in \Re \mid 0 < \epsilon_i < x_i(t) < \delta_i; \quad i = 1, \ldots, n,\ \forall\, t.$$

Theorem 2 ensures that the solutions are away from the coordinate planes $x_i = 0$ and bounded.

As for the LV equations, the restriction to the positive orthant is not necessary. In fact, if system (2) is defined in other orthants, the above results are still valid provided the initial condition and the fixed point are in the same orthant.

The conditions on the statements of Theorems 1 and 2 can be somewhat relaxed as follows. Let us suppose once again that the functions U_i in Eq. (9) are ordered in such a way that the first lines of B are linearly independent. This ensures the inversibility of the transformation. Then, the condition $a_i > 0$ in Eq. (25) can be replaced by $a_i \geq 0$ for $i = n+1, \ldots, m$ and $a_i > 0$ for $i = 1, \ldots, n$. The proof follows as for Theorems 1 and 2.

Our approach can be extended by considering the transformation of the time variable:

$$\mathrm{d}t = \prod_{k=1}^{n} x_k^{\Omega_k} \mathrm{d}t', \tag{28}$$

for $\Omega_k \in \Re$. The original system in Eq. (2) is thus rewritten as:

$$\frac{\mathrm{d}x_i}{\mathrm{d}t'} = x_i \sum_{j=1}^{m+1} A'_{ij} \prod_{k=1}^{n} x_k^{B'_{jk}}; \quad i = 1, \ldots, n, \tag{29}$$

where

$$A'_{ij} = A_{ij}; \quad i = 1, \ldots, n; \; j = 1, \ldots, m,$$

$$A'_{i,m+1} = l_i; \quad i = 1, \ldots, n,$$

and

$$B'_{ij} = B_{ij} + \Omega_j; \quad i = 1, \ldots, m; \quad j = 1, \ldots, n;$$

$$B'_{m+1,j} = \Omega_j; \quad j = 1, \ldots, n.$$

Note that there are no linear terms in Eq. (29), except for the particular case where B' has at least one zero line. Therefore, the above results can be applied using the transformed matrix $M' = B'A'$. Considering the Ω_k in Eq. (28) as free parameters gives much more freedom to satisfy the conditions on Theorems 1 and 2. In Section 3.2, we apply such reparametrizations in the systems presented in Section 2.1, in order to illustrate our approach.

3.1. Conditions on an admissible matrix

The necessary and sufficient conditions for the admissibility of M can be obtained in a systematic way as shown in Figueiredo et al. (2000). The basis of the method is to consider the simpler inequality:

$$\alpha y^2 + \beta y + \gamma \leq 0; \quad \forall y. \tag{30}$$

The necessary and sufficient conditions for Eq. (30) to be satisfied are:

$$\alpha < 0 \quad \text{and} \quad \beta^2 - 4\alpha\gamma \leq 0, \tag{31}$$

or

$$\alpha = \beta = 0 \quad \text{and} \quad \gamma \leq 0. \tag{32}$$

Eq. (25) is a quadratic inequality on the w_i's and we group different terms according to their order in one of the variables, say w_1:

$$\begin{aligned}\sum_{i,j=1}^{m} a_i M_{ij} w_i w_j &= a_1 M_{11} w_1^2 + \beta(w_2, \ldots, w_m) w_1 \\ &\quad + \gamma(w_2, \ldots, w_m) \leq 0.\end{aligned} \tag{33}$$

Eq. (33) is a quadratic algebraic inequation in w_1, and therefore, one of the following sets of conditions must hold: from (31):

$$\begin{aligned}&a_1 M_{11} < 0 \quad \text{and} \\ &\beta(w_2, \ldots, w_m)^2 - 4a_1\gamma(w_2, \ldots, w_m) \leq 0,\end{aligned} \tag{34}$$

or, from (32):

$$\begin{aligned}&a_1 M_{11} = 0 \Rightarrow M_{11} = 0; \quad \text{and} \\ &\beta(w_2, \ldots, w_m) = 0 \quad \text{and} \quad \gamma(w_2, \ldots, w_m) \leq 0.\end{aligned} \tag{35}$$

The conditions in Eqs. (34) and (35) are independent of w_1 and quadratic in $w_2, \ldots, w_m$. The procedure can be iterated for these inequalities, now in the variables $w_2, \ldots, w_m$. At each step, one set of conditions split in two, corresponding to the different possibilities to satisfy Eq. (30). Therefore, for a m-dimensional matrix M we obtain 2^{m-1} independent sets of conditions, each set yielding different solutions for the parameters and the numbers a_i's such that M is admissible. These conditions can be analyzed using a computer algebra system. The case, such that the free parameters in the system are numerically specified, can be dealt efficiently using an algorithm developed in Gléria et al. (2003).

3.2. Examples

3.2.1. Prey dispersion with no predators

Let us consider the dynamics of dispersion of a prey among two regions, in the absence of predators. From (13)we obtain:

$$\begin{aligned}\dot{x}_1 &= x_1(g_1^* + \epsilon\Pi_{11}\alpha_1 H_{10} + G_{10}x_1^{G1} + \epsilon\Pi_{21}\alpha_2 H_{20}x_1^{-1}x_2),\\ \dot{x}_2 &= x_2(g_2^* + \epsilon\Pi_{22}\alpha_2 H_{20} + G_{20}x_2^{G2} + \epsilon\Pi_{12}\alpha_1 H_{10}x_2^{-1}x_1),\end{aligned} \tag{36}$$

where we assumed $H_1 = H_2 = 1$. For this system we have:

$$B = \begin{bmatrix} G_1 & 0 \\ -1 & 1 \\ 0 & G_2 \\ 1 & -1 \end{bmatrix}, \tag{37}$$

$$A = \begin{bmatrix} G_{10} & k_2 & 0 & 0 \\ 0 & 0 & G_{20} & k_4 \end{bmatrix}, \tag{38}$$

where:

$$k_1 \equiv \epsilon\Pi_{11}\alpha_1 H_{10},$$

$$k_2 \equiv \epsilon\Pi_{21}\alpha_2 H_{20},$$

$$k_3 \equiv \epsilon\Pi_{22}\alpha_2 H_{20},$$

$$k_4 \equiv \epsilon\Pi_{12}\alpha_1 H_{10}.$$

The matrix $M = BA$ is:

$$M = \begin{bmatrix} G_1G_{10} & G_1k_2 & 0 & 0 \\ -G_{10} & -k_2 & G_{20} & k_4 \\ 0 & 0 & G_2G_{20} & G_2k_4 \\ G_{10} & k_2 & -G_{20} & -k_4 \end{bmatrix}, \tag{39}$$

Using our methodology it is possible to show that (39) cannot be admissible whatever the parameter values. Nevertheless, there is still the possibility to perform a reparametrization in the time variable of the form $\mathrm{d}t = U_1^{-1}\,\mathrm{d}t'$, which introduces a modification in the original system such that the new characteristic matrix M' is given by:

$$M' = \begin{bmatrix} -G_1(g_1^* + k_1) & -G_1k_2 & 0 & 0 \\ (g_1^* + k_1)(-1 - G - 1) + g_2^* + k_3 & k_2(-1 - G_1) & G_{20} & k_4 \\ G_2(g_2^* + k_3) - G_1(g_1^* + k_1) & -G_1k_2 & G_2G_{20} & G_2k_4 \\ (g_1^* + k_1)(1 - G_1) - g_2^* - K_3 & K_2(1 - G_1) & -G_{20} & -k_4 \end{bmatrix}. \tag{40}$$

The conditions for the admissibility of (40) are shown in Tables 1 and 2 . Under these conditions the following Lyapunov function is obtained for system (36):

$$V = \sum_{i=1}^{4} a_i\left(V_i - q_i \ln\frac{V_i}{q_i} - q_i\right),$$

where $V_1 = x_1^{-G_1}$, $V_2 = x_2/x_1^{1+G_1}$, $V_3 = x_2^{G_2}/x_1^{G_1}$ and $V_4 = x_1^{1-G_1}/x_2$, $q_1 = 1/q_1^*$, $q_i = q_i^*/q_1$, $i \neq 1$ and

$$q_1^* = q_1^*,$$

$$q_2^* = -\frac{g_1^* + k_1 + G_{10}q_1^*}{k_2},$$

$$q_3^* = q_3^*,$$

$$q_4^* = -\frac{g_2^* + k_3 + G_{20}q_3^*}{k_4}.$$

Different transformations of the time variable lead to different conditions. The results are obtained simi-

Table 1
Set 1 of conditions for the LV system with dispersion in Eq. (36)

Conditions 1	$a_1 = 1$
	$G_1(g_1^* + k_1) < 0$
	$a_2 = \dfrac{k_2 G_1 \left((g_1^* + k_1)(1 + G_1) + g_2^* + k_3 \pm 2\sqrt{(g_2^* + k_3)(g_1^* + k_1)(1 + G_1)}\right)}{(g_1^* + k_1)(G_1 - 1) - (g_2^* - k_3)^2}$
	$a_3 = \dfrac{-4G_1 G_2 G_{20}(g_1^* + k_1)}{(g_1^* + k_1)(G_1 - 1) - (g_2^* - k_3)^2},$
	$a_4 = -a_2 2G_1 k_4(g_1^* + k_1)/((-{g_2^*}^2 + 2(-k_3 + g_1^* + k_1)g_2^* + (G_1^2 - 1){g_1^*}^2 + 2(k_3 - k_1 + G_1^2 k_1)g_1^* - (k_1 + k_3)^2$ $+ G_1^2 k_1^2)a_2 + G_1 k_2 g_2^* + G_1 k_2 g_1^*(1 - G_1) + G_1 k_2(-G_1 k_1 + k_1 + k_3))$
	$[2\left((g_1^* + k_1)(G_1 - 1) + g_2^* + k_3\right)\left(G_1(g_1^* + k_1) - G_2(k_3 + g_2^*)\right)a_2 - 2G_1 k_2\left(G_1(g_1^* + k_1) + G_2(k_3 + g_2^*)\right)]a_3$ $+ 4G_1 G_{20}(g_1^* + k_1)a_2 = 0$
	$[2((g_1^* + k_1)(G_1 - 1) + g_2^* + k_3)(G_1(g_1^* + k_1) - G_2(g_2^* + k_3))a_4 + 4G_1 G_2 k_4(g_1^* + k_1)]a_3 - 4a_4 G_1 G_{20}(k_1 + g_1^*) = 0$
	$a_4 \leq \dfrac{G_1 k_4(g_1^* + k_1)}{(G_1 - 1)(g_1^* + k_1) + g_2^* + k_3}$

larly and will not be presented here for economy of space.

3.2.2. Gause system

The matrix M associated with the Gause system (19) is not admissible. In order to obtain sufficient conditions for the stability of (19), we define $\mathrm{d}t = U_2^{-1}\mathrm{d}t'$. The new matrix M' associated to (19) will be given by:

$$M' = \begin{bmatrix} r(1-\alpha_1) + d & (\alpha_1 - 1)r/K & -b \\ r(2-\alpha_1) + d & (\alpha_1 - 2)r/K & -b \\ r + r(\alpha_2 - \alpha_1) + d & (\alpha_1 - \alpha_2 - 1)r/K & -b \end{bmatrix}. \tag{41}$$

Admissibility conditions for (41) are given in Table 3. The corresponding Lyapunov function is:

$$V = \sum_{i=1}^{3} a_i \left(V_i - q_i \ln \frac{V_i}{q_i} - q_i \right), \tag{42}$$

with $V_1 = 1/x$, $V_3 = x^{\alpha_1 - 2}y$, $V_3 = y^{\alpha_2}/x$, $q_2 = 1/q_2^*$ e $q_i = q_i^*/q_2$, $i \neq 2$ and

$$q_1^* = \frac{K(r - cq_2^*)}{r},$$

$$q_2^* = q_2^*,$$

$$q_3^* = \frac{d}{b}.$$

Fig. 1 shows level curves for a special case of this Lyapunov function. The solution always stays inside the closed curve defined by the initial condition. The asymptotic limit of the dynamics corresponds to the region of the model state space such that $\dot{V} = 0$. If a limit cycle also exists, it lies on one (hyper) surface of constant V, and coincides with the curve for a two-dimensional system.

Table 2
Set 2 of conditions for the LV system with dispersion in Eq. (36)

Conditions 2	$a_1 = 1$
	$G_1(g_1^* + k_1) < 0$
	$a_2 = \dfrac{k_2 G_1 \left((g_1^* + k_1)(1 + G_1) + g_2^* + k_3 \pm 2\sqrt{(g_2^* + k_3)(g_1^* + k_1)(1 + G_1)}\right)}{(g_1^* + k_1)(G_1 - 1) - (g_2^* - k_3)^2}$
	$a_3 = 4a_2 G_1 G_{20}(k_1 + g_1^*)/([2((g_1^* + k_1)(G_1 - 1) + g_2^* + k_3)(G_1(g_1^* + k_1) - G_2(k_3 + g_2^*))a_2$ $- 2G_1 k_2\big(G_1(g_1^* + k_1) + G_2(k_3 + g_2^*)\big)])a_2 + 4G_1 G_{20}(g_1^* + k_1)a_2$
	$a_4 = -a_2 2G_1 k_4(g_1^* + k_1)/((-{g_2^*}^2 + 2(-k_3 + g_1^* + k_1)g_2^* + (G_1^2 - 1){g_1^*}^2 + 2(k_3 - k_1 + G_1^2 k_1)g_1^* - (k_1 + k_3)^2 + G_1^2 k_1^2)a_2$ $+ G_1 k_2 g_2^* + G_1 k_2 g_1^*(1 - G_1) + G_1 k_2(-G_1 k_1 + k_1 + k_3))$
	$(G_1^2(k_1 + g_1^*)^2 - 2G_2 G_1(g_2^* g_1^* + k_2 g_1^* + k_3 k_1 + g_2^* k_1) + G_2^2(g_2^* + k_3)^2)a_3^2 + 4G_1 G_{20}(g_1^* + k_1)a_3 < 0$
	$G_1^5 G_2^5 G_{20}^2[a_3 a_4^2(G_1((G_1 - 2)(g_1^* + k_1) + g_2^* + k_3) + k_1 - k_3 - g_2^*) - 2G_1 a_3 a_4 k_4][(g_1^* + k_1)(a_3^2 a_4 k_4(G_2 - 2) + a_3 a_4^2 G_{20})]$ $\times [k_4 a_3^2 a_4(-k_3 - g_2^*)(1 + G_1)][a_3^2 a_4 k_4(k_3 + g_2^* + k_1 + g_1^*)] \times [G_{20}(a_3 a_4^2(g_2^* + k_3 - k_1 - g_1^*)) - a_4^2 G_{20}^2 - a_3^2 G_2 k_4^2] \geq 0$

Table 3
Conditions for the Gause system Eq. (19)

Conditions 1	$a_1 = 1$
	$r(1-\alpha_1) + d < 0$
	$a_2 = r\dfrac{\alpha_1(3r + d - r\alpha_1) - 3d - 2r \pm 2\sqrt{-d(-2+\alpha_1)(r - r\alpha_1 + d)}}{K(2r - \alpha_1 r + d)^2}$
	$a_3 = -b(r - r\alpha_1 + a_2(dK - \alpha_1 rK))/a_2 rK(2r - r\alpha_1 + d)(d - \alpha_1 r + r + \alpha_2 r) \times (r(1 + \alpha_2 - \alpha_1\alpha_2 + \alpha_1^2 - 2\alpha_1) + d(1 + 2\alpha_2 - \alpha_1))$
	$\dfrac{b(r(-1+\alpha_2+\alpha_1)) - d - 2\sqrt{-\alpha_2 r(r - r\alpha_1 + d)}}{(d + r(1 - \alpha_1 + \alpha_2))^2} \leq a_3 \leq \dfrac{b(r(-1+\alpha_2+\alpha_1)) - d + 2\sqrt{-\alpha_2 r(r - r\alpha_1 + d)}}{(d + r(1 - \alpha_1 + \alpha_2))^2}$
Conditions 2	$a_1 = 1$
	$r(1-\alpha_1) + d = 0$
	$a_2 = \dfrac{1-\alpha_1}{K}$
	$a_3 = \dfrac{b}{\alpha_2 r}$
	$2\alpha_1^2 + \alpha_2^2 - 4 \leq 0$

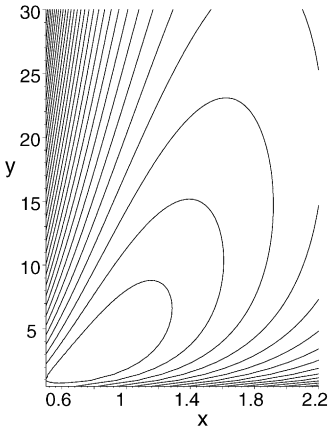

Fig. 1. Typical level curves for the Lyapunov function in Eq. (42). The values of the parameters are $b = 1$, $c = 1$, $d = 1$, $\alpha_1 = 3/2$, $\alpha_2 = 1/2$ and $d = 1$.

Other examples of application arising from biology and chemistry of the numerical algorithm are presented in Gléria et al. (2003).

4. Invariant surfaces and conserved quantities

Let us consider a system of the form (2). The first term of its right-hand can be absorbed by the second term by a convenient redefinition of matrix B. In this way we consider a nonlinear system of the form

$$\dot{x}_i = x_i \sum_{j=1}^{m} A_{ij} \prod_{k=1}^{n} x_k^{B_{jk}}; \qquad x_i \in \Re^n,\ i = 1, \ldots, n. \tag{43}$$

Then using (9) with $D = B$ yields

$$\dot{U}_i = U_i \sum_{j=1}^{m} M_{ij} U_j; \qquad U_i \in \Re^m,\ i = 1, \ldots, m, \tag{44}$$

with $M = BA$. An invariant surface in the space of $\{x_1, \ldots, x_n\}$ is preserved by the time evolution, i.e., if an initial condition lies on the manifold, the corresponding solution stays on it for all time. As we shall see below, this notion is closely related to the conserved quantities (invariants) of system (1). A function $I(x_1, \ldots, x_n)$ is an invariant if $\dot{I} = 0$ at every point.

We define a quasi-polynomial (QP) function as a generalization of the polynomial to allow any real exponent (in the positive orthant). Once our original dynamical system is cast in the LV format some important results can be used to obtain quasi-polynomial invariants (QPIs) for the system. First, let us define a semi-invariant as a polynomial function $f(U)$ that satisfies:

$$\dot{f} = \sum_{j=1}^{m} \dot{U}_i \frac{\partial f}{\partial U_j} = \lambda f, \tag{45}$$

where λ is a polynomial function called eigenvalue of f.

For the Lotka–Volterra form, the following properties were proved in Figueiredo et al. (1998):

(1) λ is a linear function, i.e.,

$$\lambda = \sum_{j=1}^{m} \lambda_j U_j. \tag{46}$$

(2) Any polynomial semi-invariant f can be decomposed as:

$$f = \sum_p f^{(p)}, \tag{47}$$

where $f^{(n)}$ is a homogeneous polynomial of degree p. Furthermore, each $f^{(n)}$ is also a semi-invariant with the same eigenvalue as f.

(3) If a polynomial semi-invariant f with eigenvalue λ can be factorized as:

$$f = \prod_i f_{(i)}\,, \tag{48}$$

where the $f_{(i)}$'s are polynomial, then each $f_{(i)}$ is also a semi-invariant with eigenvalue $\lambda_{(i)}$ such that:

$$\lambda = \sum_i \lambda_{(i)}. \tag{49}$$

(4) An invariant can be obtained from a semi-invariant by multiplying by a monomial $y^\theta \equiv {y_1}^{\theta_1}{y_2}^{\theta_2}\ldots{y_m}^{\theta_m}$:

$$I = y^\theta f\,; \tag{50}$$

i.e., $\dot{I} = 0$, if and only if:

$$\sum_{i=1} \theta_i M_{ij} + \lambda_j = 0\,. \tag{51}$$

(5) Any QPI can be decomposed as:

$$I = \sum_p y^{\theta(p)} f^{(p)}\,; \tag{52}$$

where $y^{\theta(p)} f^{(p)}$ is an invariant.

Therefore, the key result is that any QP invariant can be obtained from the knowledge of polynomial semi-invariants, which can be algorithmically determined as exposed above. Also, each polynomial semi-invariant f defines the invariant surface $f = 0$.

4.1. Example - the Gause system

For the Gause system (19), the monomials in Eq. (43) are $U_1 = x$, $U_2 = x^{\alpha_2}$, $U_3 = x^{\alpha_1 - 1}y$ and $U_4 = 1$. The characteristic matrix is

$$M = \begin{bmatrix} -r/K & 0 & -c & r \\ -\alpha_2 r/K & 0 & -\alpha_2 c & \alpha_2 r \\ (1-\alpha_1)r/K & b & (1-\alpha_1)c & (\alpha_1 - 1)r - d \\ 0 & 0 & 0 & 0 \end{bmatrix}. \tag{53}$$

All polynomial semi-invariants up to degree 2 and the corresponding QP invariants are given in Table 4. The only non-trivial invariant (up to this order) is obtained for the parameter values $r = 0$ and $\alpha_2 = 2(\alpha_1 - 1)$ and is given by:

$$\begin{aligned} I = {} & -2\,x^{1-\alpha_1} cyd + 2\,x^{1-\alpha_1} cy\alpha_1\, d - 2\,x^{-1+\alpha_1} cby \\ & + 2\,x^{-1+\alpha_1} cby\alpha_1 + x^{2\,\alpha_1 - 2} b^2 + c^2 y^2 \\ & - 2\,c^2 y^2 \alpha_1 + c^2 y^2 {\alpha_1}^2 + x^{2-2\,\alpha_1} d^2. \end{aligned} \tag{54}$$

Fig. 2 shows two typical cases for the contour levels of the invariant I, which show the structure for the solutions of the Gause system for this case.

For economy of space we do not show results for higher order calculations, but they can be obtained similarly.

Table 4
Polynomial semi-invariants up to degree 2 for the Gause system. The trivial case $c = 0$ is not considered

Conditions	Semi-invariant	Eigenvalue
$\alpha_2 = 1, r = 0, \alpha_1 = 3/2$	$4d^2 + 4x^2b^2 + xc^2y^2 + 4x^{3/2}cyb + 4\sqrt{x}cdy$	$-\sqrt{x}cy$
$\alpha_2 = 2, r = 0, \alpha_1 = 2$	$d^2 + x^4b^2 + x^2c^2y^2 + 2x^3cyb + 2xcdy$	$-2xcy$
$r = d, \alpha_2 = \alpha_1 - 2$	$x^{-1+\alpha_1}b - x^{-2+\alpha_1}bK + x^{-1+\alpha_1}cKy$	$-\dfrac{dx(\alpha_1 - 1)}{K} - x^{-1+\alpha_1}cy$ $+x^{-1+\alpha_1}cy\alpha_1 + 2d - d\alpha_1$
$\alpha_2 = 1, d = 0, \alpha_1 = 1$	$-x(-bKx - xr - cyK + rK + bK^2)$	$r - \dfrac{2xr}{K} - cy$
$\alpha_1 = 2, \alpha_2 = 0$	$bx - rK + Kd + xr - dx - bK + cKxy$	$-x(\dfrac{r}{K} + cy)$
$r = 0, \alpha_2 = 2\,\alpha_1 - 2$	$d^2 + x^{-4+4\alpha_1}b^2 + x^{-2+2\alpha_1}c^2y^2 - 2x^{-2+2\alpha_1}c^2y^2\alpha_1 +$ $x^{-2+2\alpha_1}c^2y^2{\alpha_1}^2$ $-2x^{-3+3\alpha_1}cyb + 2\,x^{-3+3\alpha_1}cyb\alpha_1 - 2x^{-1+\alpha_1}cdy + 2x^{-1+\alpha_1}cdy\alpha_1$	$-2x^{\alpha_1 - 1} \times cy(\alpha_1 - 1)$

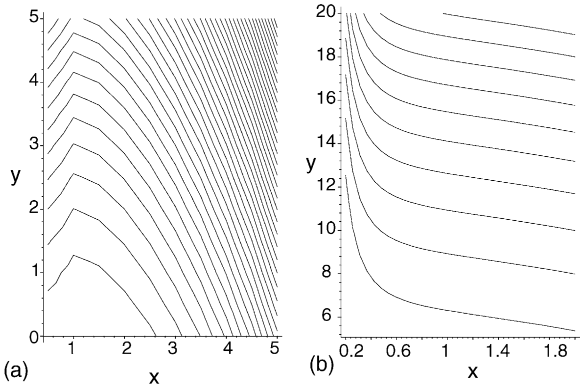

Fig. 2. Typical contour plots for the invariant I in Eq. (54). The values of the parameters are $b = 1$, $c = 2$, $d = 1$, $\alpha_1 = 3$, $\alpha_2 = 1/2$ and (a) $d = 1$ and (b) $d = -1$.

5. Concluding remarks

We presented the Lotka–Volterra canonical format and showed how it leads to a method to obtain relevant information on the dynamics of ecological models through the determination of invariants and Lyapunov functions, which constrains the solutions in the phase space of the system. The present approach is systematic and is implemented in the computer algebra system MAPLE, and therefore, allows a systematic study of more complex systems. Our method for the determination of Lyapunov functions generalizes known results in the literature.

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