Hamiltonian Dynamics of the Lotka-Volterra Equations

Rui Loja Fernandes *
Waldyr Muniz Oliva
Departamento de Matemática
Instituto Superior Técnico
1096 Lisboa Codex, Portugal

In this paper we discuss several aspects of the Hamiltonian structure of the Lotka-Volterra equations. In particular we show that the dynamics on the attractor are hamiltonian.

Introduction

In his famous book "Leçons sur la Théorie Mathématique de la Lutte pour la Vie" ([6]) Volterra introduced the system of differential equations

$$\dot{x}_j = \varepsilon_j x_j + \frac{1}{\beta_j} \sum_{k=1}^{n} a_{jk} x_j x_k \qquad (j = 1, \dots, n) \tag{1}$$

as a model for the competition of n biological species. In this model, x_j represents the number of individuals of species j (so Volterra assumes $x_j > 0$), the a_{jk}'s are the interaction coefficients, the ε_j's and the β_j's(> 0) are parameters that depend on the environment. For example, $\varepsilon_j > 0$ means that species j is able to increase with food from the environment, while $\varepsilon_j < 0$ means that it cannot survive when left alone in the environment. One can also have $\varepsilon_j = 0$ which means that the population stays constant if the specie does not interact. Notice that by performing the change of variables $x_j \mapsto x_j/\beta_j$ we can assume that the $\beta_j = 1$.

The following type of qualitative behavior can be expected (and can probably be justified in biological grounds). At first, the species evolve with varying interaction to reach some final stage. In this final stage, some species will attain some constant value population, while a few others continue to evolve without ever reaching a steady population. It is therefore natural that the dynamics in the final stage will be conservative. In fact, in this paper we will show the following result holds (some of the terms used will be explained later):

Theorem 0.1. *Consider system (1) restricted to the flow invariant set $\mathbb{R}^n_+ \equiv \{(x_1, \dots, x_n) \in \mathbb{R}^n : x_j > 0, j = 1, \dots, n\}$, and assume that the system has a singular point in $\mathbb{R}^n_+$. If the matrix (a_{jk}) is stably dissipative then the system has an attractor and the dynamics on the attractor are hamiltonian.*

The word "hamiltonian" is to be interpreted in a convenient way to be explained in the first two sections. The hypothesis "stably dissipative" was introduced by Redheffer et al. ([3, 4, 5]) under the name "stable admissible", who used it to demonstrate the existence of an attractor

*Supported in part by JNICT grant PBIC/C/MAT/2140/95.

(see section 3). We prefer the former name in honor to Volterra (see [6], chp. III). We shall proof theorem 0.1 in section 4.

This paper is an account of some of the results presented at the conference. A more detailed account, including a description of the possible dynamics on the attractor, the Painlevé analysis of system (1), a discussion of integrability and further analysis of the Poisson geometry associated with the system, will be published alsewhere.

1 Volterra's hamiltonian formulation

Let us recall that in the case were the interaction matrix is skew-symmetric ($a_{jk} = -a_{kj}$) Volterra was able to introduce a hamiltonian structure for system (1) by enlarging the system. One introduces new variables Q_j (called by Volterra *quantity of life*) by the formula:

$$Q_j = \int_0^t x_j(\tau)d\tau \qquad (j = 1, \ldots, n) \tag{2}$$

and rewrites system (1) as a second order o.d.e.:

$$\ddot{Q}_j = \varepsilon_j \dot{Q}_j + \sum_{k=1}^{n} a_{jk}\dot{Q}_j\dot{Q}_k \qquad (j = 1, \ldots, n). \tag{3}$$

Then the function $H = \sum_{j=1}^{n}(\varepsilon_j Q_j - \dot{Q}_j)$ is a first integral of the system because, on account of skew-symmetry,

$$\begin{aligned} \dot{H} &= \sum_{j=1}^{n}(\varepsilon_j \dot{Q}_j - \ddot{Q}_j), \\ &= \sum_{j,k=1}^{n} a_{jk}\dot{Q}_j\dot{Q}_k = 0. \end{aligned}$$

Now, if we introduce another set of variables P_j by the formula

$$P_j = \log \dot{Q}_j - \frac{1}{2}\sum_{k=1}^{n} a_{jk}Q_k \qquad (j = 1, \ldots, n) \tag{4}$$

(which are well defined when we restrict the original system to $\mathbb{R}^n_+$), then in the coordinates (Q_j, P_j) the function H is expressed as

$$H = \sum_{j=1}^{n} \varepsilon_j Q_j - \sum_{j=1}^{n} e^{(P_j + \frac{1}{2}\sum_{k=1}^{n} a_{jk}Q_k)} \tag{5}$$

and a simple computation shows that system (3) can be rewritten in hamiltonian form:

$$\left\{ \begin{aligned} \dot{P}_j &= \frac{\partial H}{\partial Q_j} \\ \dot{Q}_j &= -\frac{\partial H}{\partial P_j} \end{aligned} \right. \qquad (j = 1, \ldots, n). \tag{6}$$

We remark that this system has n, time-dependent (if $\varepsilon_j \neq 0$), first integrals given by the formulas

$$I_j(Q_j, P_j, t) = P_j - \frac{1}{2}\sum_{k=1}^{n} a_{jk}Q_k - \varepsilon_j t \qquad (j = 1, \dots, n). \tag{7}$$

In fact, one checks easily that

$$\dot{I}_j = \frac{\partial I_j}{\partial t} + \{I_j, H\} = 0,$$

where $\{\ ,\ \}$ is the classical Poisson bracket associated with the symplectic structure $\omega = \sum_{j=1}^{n} dQ_j \wedge dP_j$:

$$\{f_1, f_2\} = \sum_{j=1}^{n}\left(\frac{\partial f_1}{\partial P_j}\frac{\partial f_2}{\partial Q_j} - \frac{\partial f_2}{\partial P_j}\frac{\partial f_1}{\partial Q_j}\right) \tag{8}$$

Moreover, one finds

$$\{I_j, I_k\} = a_{jk}. \tag{9}$$

2 A new hamiltonian formulation

The modern approach to hamiltonian systems is based on the following definition of a Poisson bracket (see for example [1]).

Definition 2.1. A **Poisson bracket** on a smooth manifold M is a bilinear operation $\{\ ,\ \} : C^\infty(M) \times C^\infty(M) \to C^\infty(M)$ on the space of smooth functions satisfying the following properties:

i) $\{f_1, f_2\} = -\{f_2, f_1\}$ (skew-symmetry);

ii) $\{f_1 f_2, f\} = f_1\{f_2, f\} + \{f_1, f\}f_2$ (Leibnitz's identity);

iii) $\{f_1, \{f_2, f_3\}\} + \{f_2, \{f_3, f_1\}\} + \{f_3, \{f_1, f_2\}\} = 0$ (Jacobi's identity);

A hamiltonian system on a Poisson manifold M is defined by a choice of a function $h \in C^\infty(M)$, namely, the defining equations for the flow are

$$\dot{x} = X_h(x), \tag{10}$$

where the hamiltonian vector field X_h is the vector field on M defined by

$$X_h(f) = \{f, h\}, \qquad \forall f \in C^\infty(M).$$

With this extended concept of hamiltonian system it is possible, in the case where the matrix (a_{jk}) is skew-symmetric (and under the additional assumption (12)), to give a hamiltonian formulation for system (1), without extending the number of variables in the system.

One introduces on $\mathbb{R}^n$ the Poisson bracket

$$\{f_1, f_2\} = \sum_{j<k} a_{jk}x_j x_k\left(\frac{\partial f_1}{\partial x_j}\frac{\partial f_2}{\partial x_k} - \frac{\partial f_2}{\partial x_j}\frac{\partial f_1}{\partial x_k}\right) \tag{11}$$

which one easily verifies satisfies the conditions of definition 2.1. Then, if there is an equilibrium $(q_1, \ldots, q_n)$ for system (1) satisfying

$$\varepsilon_j + \sum_{k=1}^{n} a_{jk} q_k = 0, \qquad j = 1, \ldots, n \tag{12}$$

and we let

$$h = \sum_{j=1}^{n} (x_j - q_j \log x_j), \tag{13}$$

we see that system (1) can be written in the form

$$\dot{x}_j = \{x_j, h\}$$

and therefore is hamiltonian.

Although this may seem an artificial construction, in fact the quadratic bracket (5) and the classical Poisson bracket (4) are related in a natural way by a geometric type of "reduction":

Theorem 2.2. *The map $\Psi : (Q_i, P_i) \mapsto x_j$ defined by*

$$x_j = e^{\left(P_j + \frac{1}{2}\sum_{k=1}^{n} a_{jk} Q_k\right)} \qquad \forall (Q, P) \in \mathbb{R}^{2n}$$

is a Poisson map from $\mathbb{R}^{2n}$ with the canonical Poisson bracket (8) to $\mathbb{R}^n$ with bracket (11). If $(q_1, \ldots, q_n)$ is a solution of (12), this map reduces the enlarged system (6) to the Volterra system (1).

Remarks.

(i) *In general, even in the skew-symmetric case, one cannot get way without some assumption of the type of (12) and so it is not possible to give a hamiltonian formulation without introducing new variables (if, for example, $(a_{ij}) = 0$ and $\varepsilon_j > 0$ then the origin is a source and the system cannot be hamiltonian).*

(ii) *If the $\varepsilon_j = 0$ $(j = 1, \ldots, n)$, then system (1) is always hamiltonian. If one considers the action on $\mathbb{R}^{2n}$ of the group of symmetries generated by the integrals (7) then it can be shown, using the commutation relations (9) that the reduction given in theorem 2.2 is in fact a symmetry reduction.*

(iii) *In [2] the hamiltonian structure (11) is also introduced, along with other hamiltonian formulations valid for particular classes of interaction matrices. However, there is no reference to its relation to the Volterra hamiltonian formulation.*

3 The non skew-symmetric case

Even in the case where (a_{jk}) is not skew-symmetric it is sometimes possible to introduce a hamiltonian formulation. For this we need the following definition

Definition 3.1. A matrix A is called **skew-symmetrizable** if there exists an invertible diagonal matrix D such that AD is skew-symmetric.

Suppose the interaction matrix associated with system (1) is skew-symmetrizable through some diagonal matrix $D = diag(d_1, \ldots, d_n)$. Then the change of variables

$$\tilde{N}_j = \frac{1}{d_j} x_j \qquad (j = 1, \ldots, n)$$

transforms the system into the equivalent system

$$\dot{\tilde{N}}_j = \varepsilon_j \tilde{N}_j + \sum_{k=1}^{n} d_k a_{jk} \tilde{N}_j \tilde{N}_k, \qquad (j = 1, \ldots, n) \tag{14}$$

which has a skew-symmetric interaction matrix. Therefore, this system can be turn into a hamiltonian system either if it has a singular point satisfying (12) or by Volterra's extension procedure.

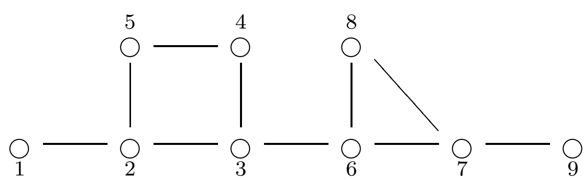
The following proposition gives a necessary and sufficient condition for a matrix to be skew-symmetrizable.

Proposition 3.2. *A matrix (a_{jk}) is skew-symmetrizable if, and only if, $a_{ii} = 0$ and it satisfies*

$$a_{i_1 i_2} a_{i_2 i_3} \cdots a_{i_s i_1} = (-1)^s a_{i_s i_{s-1}} \cdots a_{i_2 i_1} a_{i_1 i_s} \tag{15}$$

for every finite sequence of integers $(i_1, \ldots, i_s)$, with $i_r \in \{1, \ldots, n\}$ for $r = 1, \ldots, s$.

Condition (15) is better understood in terms of the graph $G(A)$ associated with the matrix (or the system). With each species j we associate a vertex ○ labeled with the letter j and we draw an edge connecting vertex j to vertex k whenever $a_{jk} \neq 0$ or $a_{kj} \neq 0$.



Graph $G(A)$ associated with a matrix $A = (a_{jk})$.

Then the exact meaning of condition (15) is the following. The matrix associated with the system is skew-symmetrizable if, and only if, for each cycle in the diagram with a even (resp. odd) number of vertices we obtain the product (resp. minus the product) of the coefficients when we go around the cycle in opposite directions. Hence, for example, a matrix with the diagram above is skew-symmetrizable if, and only if, $a_{ii} = 0$ and

$$\begin{aligned} a_{jk} \neq 0 &\implies a_{kj} \neq 0, \\ a_{67}a_{78}a_{86} &= -a_{68}a_{87}a_{76}, \\ a_{23}a_{34}a_{45}a_{52} &= a_{25}a_{54}a_{43}a_{32}. \end{aligned} \tag{16}$$

Recall that a graph K is a *forest* if $K = K_1 \bigcup \cdots \bigcup K_r$ (disjoint) where each K_i is a tree.In this case, we obtain

Corollary 3.3. *If the matrix associated with the system satisfies* $a_{ii} = 0$*,*

(17) $$a_{jk} \neq 0 \Longrightarrow a_{kj} \neq 0$$

and the graph is a forest, then the system has a direct hamiltonian formulation.

Remark. *If we do not allow the sign change in condition (15) then we obtain a necessary and sufficient condition for the matrix to be symmetrizable. In this case, the system is gradient with respect to the pseudo-metric* $ds^2 = \sum_{jk}(d_j a_{jk} x_j x_k) dx_j dx_k$*.*

4 Asymptotic stability and hamiltonian dynamics

In a series of papers [3, 4, 5] Redheffer *et al.* have studied the asymptotic stability of a class of Volterra systems. They consider the system

(18) $$\begin{cases} \dot{x}_j = \varepsilon_j x_j + \sum_{k=1}^n a_{jk} x_j x_k \\ \varepsilon_j + \sum_{k=1}^n a_{jk} q_k = 0 \end{cases} \qquad (j = 1, \ldots, n)$$

restricted to $\mathbb{R}^n_+$, under the assumption that the system (or the matrix (a_{jk})) is *stably dissipative*, a concept we now recall.

Definition 4.1. A matrix A is said to be **dissipative** if there exists a positive diagonal matrix D such that $AD \leq 0$. By a **perturbation** of A one means a matrix $\tilde{A}$ such that $\tilde{a}_{jk} = 0 \Leftrightarrow a_{jk} = 0$. Finally, a matrix A is called **stably dissipative** if every sufficiently small perturbation $\tilde{A}$ is dissipative:

$$\exists \delta > 0 \ : \max_{jk} |a_{jk} - \tilde{a}_{jk}| < \delta \Longrightarrow \tilde{A} \text{ is dissipative.}$$

Redheffer *et al.* use the name *stably admissible*. Since what they call *admissible* is called by Volterra *dissipative* ([6],chp. III), we prefer the term *stably dissipative*. For conditions for a matrix to be stably dissipative see [3].

Let us start then with a Volterra system (18) with $A = (a_{ij})$ stably dissipative. If $D = diag(d_1, \ldots, d_n)$ is a positive matrix such that $AD \leq 0$, we perform the change of coordinates $x_j \mapsto d_j x_j$ so we can assume that $A \leq 0$. It can be shown that one can also choose the matrix D so that the following condition holds

(19) $$\sum_{j,k=1}^n a_{jk} w_i w_j = 0 \Longrightarrow a_{jj} w_j = 0, (j = 1, \ldots, n).$$

Then we have a Liapunov function given by

(20) $$V = \sum_{j=1}^n (x_j - q_j \log x_j) \, .$$

In fact, we find that

$$\dot{V} = \sum_{j,k=1}^n a_{jk}(x_j - q_j)(x_k - q_k) \leq 0$$

which implies, by La Salle's theorem, that the solutions exist for all $t \geq 0$ and that the set $\dot{V} = 0$ is an attractor. Therefore one would like to understand the set $\dot{V} = 0$.

Notice that by (19) and (20) solutions on the set $\dot{V} = 0$ satisfy

$$\begin{cases} \dot{x}_j = x_j \sum_{k=1}^{n} a_{jk}(x_k - q_k), \\ \\ a_{jj}(x_j - q_j) = 0 \qquad (j = 1, \ldots, n). \end{cases} \tag{21}$$

Therefore, one has either $a_{jj} = 0$ or $a_{jj} < 0$, and in the later case we have $x_j = q_j$ on the attractor. Hence it will be convenient to modify slightly the notion of graph associated with the system as follows. One now draws a black dot $\bullet$ at vertex j if either $a_{jj} < 0$ or $a_{jj} = 0$ and somehow we have shown that $x_j = q_j$ on the attractor. Otherwise, one draws an open circle $\bigcirc$ at vertex j. It is also convenient to put a $\oplus$ at vertex j if one can show that x_j is constant on $\dot{V} = 0$. Then, using (21) the following propagation rules are deduced:

(a) If there is a $\bullet$ or $\oplus$ at vertex j and $\bullet$ at all neighbors of j except one vertex l, then we can put a $\bullet$ at vertex l;

(b) If there is a $\bullet$ or $\oplus$ at vertex j, and a $\bullet$ or $\oplus$ at all neighbors of j except one vertex l, then we can put a $\oplus$ at vertex l;

(c) If there is $\bigcirc$ at vertex j, and $\bullet$ or $\oplus$ at all neighbors of j, then we can put $\oplus$ at vertex j;

One calls the *reduced graph* $R(A)$ of the system, the graph obtained by repeated use of the rules of reduction (a), (b) and (c).

A graph $G(A)$ and it's reduced form $R(A)$.

For more details on these rules and on the reduced graph see ([4]). Here we shall only need the following fact which follows from the results in [5].

Proposition 4.2. *Let K denote the subgraph of the reduced graph formed by vertices with $\bigcirc$ or $\bigoplus$ and connections between them. Then K is a forest.*

We are now in condition to prove:

Theorem 4.3. *Consider system (1) restricted to the flow invariant set $\mathbb{R}^n_+ \equiv \{(x_1, \ldots, x_n) \in \mathbb{R}^n : x_j > 0, j = 1, \ldots, n\}$, and assume that the system has a singular point in $\mathbb{R}^n_+$. If the matrix (a_{jk}) is stably dissipative then the system has an attractor and the dynamics on the attractor are hamiltonian.*

Proof. Consider the system restricted to $\{\dot{V}\} = 0$. We split the variables x_j into two groups labeled by sets J_o and $J_\bullet$. In the first group $\{x_j\}_{j \in J_o}$ we have all the x_j's corresponding to vertices with open circles $\bigcirc$ or $\bigoplus$ in $R(A)$, while the second group $\{x_j\}_{j \in J_\bullet}$ we have all the

x_j's corresponding to vertices with black circles $\bullet$ in $R(A)$. For $j \in J_\bullet$ we have $x_j = q_j$, hence the restricted system satisfies

$$(22) \qquad \begin{cases} \dot{x}_j = (\varepsilon_j + \sum_{k \in B} a_{jk} q_k) x_j + \sum_{k \in A} a_{jk} x_j x_k & \text{if } j \in J_o \\ x_j = q_j & \text{if } j \in J_\bullet \end{cases}$$

Therefore if we define $\tilde{\varepsilon}_j = \varepsilon_j + \sum_{k \in J_\bullet} a_{jk} q_k$, $\tilde{a}_{jk} = a_{jk}$ $(j, k \in J_o)$, we obtain a new Volterra type system:

$$(23) \qquad \dot{x}_j = \tilde{\varepsilon}_j x_j + \sum_{k \in A} \tilde{a}_{jk} x_j x_k \qquad (j \in J_o)$$

where the graph associated with the matrix $(\tilde{a}_{jk})_{j,k \in J_o}$ is precisely the subgraph K of the reduced graph $R(A)$ formed by vertices with $\circ$ or $\bigoplus$ and connections between them. Also, the $(q_j)_{j \in J_o}$ form a solution of the system

$$\tilde{\varepsilon}_j + \sum_{k \in A} \tilde{a}_{jk} q_k = 0 \qquad (j \in J_o).$$

By proposition 4.2 and corollary 3.3, the system (23) is hamiltonian. □

References

[1] P. J. Olver, *Applications of Lie Groups to Differential Equations.* GTM vol. 107, Springer-Verlag, New-York, 1986.

[2] M. Plank, Hamilton structure for n-dimensional Lotka-Volterra equations. *J. Math. Phys.* **36** (1995), 3520–3534.

[3] R. Redheffer, Volterra multipliers I. *SIAM J. Discrete Math.* **6** (1985), 592–611.

[4] R. Redheffer, W. Walter, Solution of the stability problem for a class of generalized Volterra prey-predator systems. *J. Diff. Eqs.* **52** (1984), 245–263.

[5] R. Redheffer, Z. Zhiming, Global asymptotic stability for a class of many-variable Volterra prey-predator systems. *J. Nonlinear Math. Appl.* **5** (1981), 1309–1329.

[6] V. Volterra, *Leçons sur la Théorie Mathématique de la Lutte pour la Vie.* Gauthier-Villars et Cie., Paris, 1931.