Journal of Mathematical Analysis and Applications **256,** 242–256 (2001)
doi:10.1006/jmaa.2000.7318, available online at http://www.idealibrary.com on IDEAL®

Local Stability and Lyapunov Functionals for n-Dimensional Quasipolynomial Conservative Systems

Benito Hernández-Bermejo[1] and Víctor Fairén

Departamento de Física Matemática y Fluidos, Universidad Nacional de Educación a Distancia, Senda del Rey S/N, 28040, Madrid, Spain

Submitted by H. L. Smith

Received March 24, 2000

We present a method for determining the local stability of equilibrium points of conservative generalizations of the Lotka–Volterra equations. These generalizations incorporate both an arbitrary number of species—including odd-dimensional systems—and nonlinearities of arbitrarily high order in the interspecific interaction terms. The method combines a reformulation of the equations in terms of a Poisson structure and the construction of their Lyapunov functionals via the energy-Casimir method. These Lyapunov functionals are a generalization of those traditionally known for Lotka–Volterra systems. Examples are given. © 2001 Academic Press

Key Words: Lyapunov functionals; stability; Lotka–Volterra equations; Hamiltonian systems.

1. INTRODUCTION

Consider the following Lotka–Volterra system [26, 41]

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

which is assumed to have a unique equilibrium point, $\mathbf{x}_0 \in \text{int}\{\mathbb{R}^n_+\}$. One of the most relevant results about its stability is well summarized in a theorem originally enunciated by Kerner [17], and later generalized by many different authors [5, 6, 8, 16, 21, 24, 27, 35, 37–40] (see also [14, 25, 36] for detailed reviews of the subject). The result makes use of the

[1] To whom correspondence should be addressed. E-mail: bhernand@apphys.uned.es.

0022-247X/01 $35.00

well-known Lyapunov functional

$$V(\mathbf{x}) = \sum_{i=1}^{n} d_i \left(x_i - x_{0i} - x_{0i} \ln \frac{x_i}{x_{0i}} \right). \tag{2}$$

The time derivative of (2) along the trajectories of (1) is

$$\dot{V}(\mathbf{x}) = \tfrac{1}{2}(\mathbf{x} - \mathbf{x}_0)^T (D \cdot A + A^T \cdot D)(\mathbf{x} - \mathbf{x}_0), \tag{3}$$

where $D = \mathrm{diag}(d_1, \ldots, d_n)$. Thus, it can be stated that if there exists a positive definite diagonal matrix D such that $D \cdot A + A^T \cdot D$ is negative definite, $\mathbf{x}_0$ is Lyapunov asymptotically stable. Moreover if, instead, $D \cdot A + A^T \cdot D$ is negative semi-definite, then $\mathbf{x}_0$ is Lyapunov semi-stable and every solution of (1) in $\mathrm{int}\{\mathbb{R}_+^n\}$ tends to the maximal invariant set M contained in the set (see [22, 23, 28] and references therein)

$$E = \left\{ \mathbf{x} \in \mathrm{int}\{\mathbb{R}_+^n\} / (\mathbf{x} - \mathbf{x}_0)^T (D \cdot A + A^T \cdot D)(\mathbf{x} - \mathbf{x}_0) = 0 \right\}. \tag{4}$$

Every one of the two previous alternatives encompasses the already classical community models, respectively: The so-called Lotka–Volterra dissipative and conservative systems [25]. In particular, Lotka–Volterra conservativeness implies that (2) is a constant of motion, thus making conservative systems formally amenable to analysis by standard theoretical mechanics methods [3, 19, 20] and statistical mechanics considerations [4, 17, 18]. On this respect, the Hamiltonization of classical Lotka–Volterra conservative systems [19, 20] proceeds by defining the canonical variables, z_i, as linear transforms of new dependent variables $y_i = \ln(x_i / x_{0i})$. If the Hamiltonian, H, is simply identified with the functional in (2) appropriately rewritten in the canonical variables, z_i, the conservative Lotka–Volterra equations adopt the familiar symplectic form

$$\dot{\mathbf{z}} = S \cdot \nabla H(\mathbf{z}), \tag{5}$$

where S is the classical symplectic matrix [7].

Unfortunately, this constructive procedure cannot be carried out beyond the class of even-dimensional classical conservative Lotka–Volterra systems. This made the Hamiltonian description of rather limited use until Nutku [30] and Plank [33] suggested reconsidering it under the light of the more general Poisson structure representation (see [31] for an overview; see also references therein). Poisson systems constitute a natural extension of classical Hamiltonian dynamical systems, but have the advantage of embracing odd-dimensional flows as well. In the Poisson context, no prior transformation on the variables is necessary, and the conservative Lotka–

Volterra equations can be put into Poisson form in terms of the original variables

$$\dot{\mathbf{x}} = \mathcal{J} \cdot \nabla H(\mathbf{x}), \tag{6}$$

where the elements of the structure matrix $\mathcal{J}$ are defined as $J_{ij} = K_{ij} x_i x_j$, K being a skew-symmetric matrix, and H is the classical Volterra's constant of motion (2).

In fact, form (6) happens to be suitable for embracing a higher number of families of conservative systems than those of type (1), as stated in the following result (see [12]):

THEOREM 1 [12]. *Let us consider a differential system defined in the positive orthant, of the form*

$$\dot{x}_i = x_i \left(\lambda_i + \sum_{j=1}^{m} A_{ij} \prod_{k=1}^{n} x_k^{B_{jk}} \right), \qquad i = 1, \ldots, n, \; m \geq n \tag{7}$$

such that $\mathrm{rank}(B) = n$ *and*

$$\lambda = K \cdot L, \qquad A = K \cdot B^T \cdot D, \tag{8}$$

with K, L, *and* D *matrices of real entries, where* K *is* $n \times n$ *and skew-symmetric;* L *is* $n \times 1$; *and* D *is* $m \times m$, *diagonal and of maximal rank. Then the system has a constant of motion of the form*

$$H = \sum_{i=1}^{m} D_{ii} \prod_{k=1}^{n} x_k^{B_{ik}} + \sum_{j=1}^{n} L_j \ln x_j . \tag{9}$$

Moreover, the system is Poisson with Hamiltonian H *and a structure matrix* $\mathcal{J}$ *with entries* $J_{ij} = K_{ij} x_i x_j$.

Note that systems (7) appear when we combine a quadratic structure matrix (first identified by Plank [33]) together with Hamiltonian (9), which is a generalization of Volterra's constant of motion (2). Important dynamical features of certain particular cases of such systems have recently deserved detailed attention in the literature [34]. In what follows, we shall denote systems described by Theorem 1 as quasipolynomial of Poisson form, or QPP in brief. QPP systems (7) include the conservative Lotka–Volterra equations as a particular case when $m = n$, B is the identity matrix, the dimension is even, and A is invertible. In such a case, the Hamiltonian (9) also reduces to Volterra's first integral, as it can be easily verified.

The purpose of the present article is to investigate under which conditions the equilibrium points of the QPP systems are stable and compare the resulting generalization with what is known for conservative Lotka–Volterra models (1). In particular, we shall also carry out a generalization of the corresponding Lyapunov functionals (2). In this way, we shall complete a treatment that simultaneously embraces arbitrary-dimensional systems and also arbitrary nonlinearities in the flow.

The construction of suitable Lyapunov functionals for the QPP systems involved will be possible thanks to their Poisson structure, which allows the use of the energy-Casimir method (see [15] and references therein) in which the stability analysis of a given fixed point $\mathbf{x}_0$ proceeds by defining an *ansatz* for the Lyapunov functional, which takes the form

$$H_C(\mathbf{x}) = H + F(C_1, \ldots, C_k), \tag{10}$$

where $F(z_1, \ldots, z_k)$ is a C^2 real function to be determined and $\{C_1, \ldots, C_k\}$ is a complete set of independent Casimir invariants. The method amounts to the search of one suitable F, by imposing two conditions on H_C: (i) H_C must have a critical point at $\mathbf{x}_0$; and (ii) the second derivative of H_C at $\mathbf{x}_0$ must be either positive or negative definite. Once one suitable F has been found, stability of $\mathbf{x}_0$ follows automatically, and the method provides us with a Lyapunov functional for this point.

The structure of the article is as follows: Section 2 is devoted to the establishment of the main stability theorem. Different consequences of the result are considered in the examples of Section 3.

2. STABILITY OF QPP SYSTEMS

Let us start by recalling the following definition, valid for normed spaces (see [15]):

DEFINITION 1 [15]. A given steady state $\mathbf{x}_0$ of a dynamical system is said to be locally stable if for every $\varepsilon > 0$ there exists a $\delta > 0$ such that if $\|\mathbf{x}(0) - \mathbf{x}_0\| < \delta$, then $\|\mathbf{x}(t) - \mathbf{x}_0\| < \varepsilon$ for every $t > 0$.

In what follows, stability shall denote local stability. We give now our main result:

THEOREM 2. *Consider a QPP system with either $m = n$ and $|B| > 0$, or with $m > n$. If matrix D is positive or negative definite, then:*

(i) *Every fixed point belonging to the interior of the positive orthant is stable.*

(ii) *For every fixed point belonging to the interior of the positive orthant there is a Lyapunov functional of the form*

$$H_C = H + \sum_{i=1}^{n} N_k \ln x_k, \qquad N \in \ker(K), \tag{11}$$

where H is the Hamiltonian (9).

Proof. The proof rests strongly on the quasimonomial formalism. The unfamiliar reader is referred to the basic references on the subject [1, 2, 10–13, 32].

The strategy of the proof consists in reducing the problem to the Lotka–Volterra representative and analyzing there the stability of the fixed points. The resulting criteria and Lyapunov functionals are then mapped back into the original system.

For the sake of clarity, we omit in what follows the proofs of the auxiliary lemmas, which can be found in the Appendix.

Proof of the First Statement of Theorem 2. We begin by examining the behaviour of stability properties under embeddings. Consider an arbitrary quasipolynomial system with $m > n$,

$$\dot{x}_i = x_i \left(\lambda_i + \sum_{j=1}^{m} A_{ij} \prod_{k=1}^{n} x_k^{B_{jk}} \right), \qquad i = 1, \ldots, n. \tag{12}$$

Let $\tilde{A}$, $\tilde{B}$, and $\tilde{\lambda}$ be the matrices of the expanded system which are defined in the following way,

$$\tilde{A} = \begin{pmatrix} A_{n\times m} \\ O_{(m-n)\times m} \end{pmatrix}, \qquad \tilde{B} = \left(B_{m\times n} \,|\, B'_{m\times(m-n)} \right), \qquad \tilde{\lambda} = \begin{pmatrix} \lambda_{n\times 1} \\ O_{(m-n)\times 1} \end{pmatrix}, \tag{13}$$

where we have explicitly indicated by means of indexes the sizes of the submatrices for the sake of clarity, O denotes a null matrix, B' is a matrix of arbitrary entries chosen in such a way that $|\tilde{B}| > 0$, and $x_i = 1$ for $i = n+1, \ldots, m$.

LEMMA 1. *Let* $\mathbf{x}_0 = (x_{01}, \ldots, x_{0n})$, *with* $x_{0i} > 0$ *for* $i = 1, \ldots, n$, *be a phase-space point of* (12), *and let* $\tilde{\mathbf{x}}_0 = (x_{01}, \ldots, x_{0m})$, *with* $x_{0i} = 1$ *for* $i = n+1, \ldots, m$, *be the corresponding phase-space point of the expanded system. Then*:

(i) $\mathbf{x}_0$ *is a fixed point of* (12) *if and only if* $\tilde{\mathbf{x}}_0$ *is a fixed point of the expanded system.*

(ii) *If* $\mathbf{x}_0$ *and* $\tilde{\mathbf{x}}_0$ *are fixed points, then* $\mathbf{x}_0$ *is stable if and only if* $\tilde{\mathbf{x}}_0$ *is stable.*

We can now examine the effect of quasimonomial transformations (QMTs from now on) of the form

$$x_i = \prod_{k=1}^{n} y_k^{\Gamma_{ik}}, \qquad i = 1, \dots, n, |\Gamma| > 0. \tag{14}$$

LEMMA 2. *Given a quasipolynomial system of the form* (12) *with* $m \geq n$, *and a stable fixed point* $\mathbf{x}_0$ *belonging to the positive orthant*, *the image of* $\mathbf{x}_0$ *under an arbitrary QMT of the form* (14) *is also stable*.

In particular, Lemma 2 applies to the expanded QP system (13). Let us choose a QMT such that Γ in (14) is given by $\tilde{B}^{-1}$ in (13). The result is a new QP system with characteristic matrices,

$$\tilde{A}' = \tilde{B} \cdot \tilde{A}, \qquad \tilde{B}' = I, \qquad \tilde{\lambda}' = \tilde{B} \cdot \tilde{\lambda} \tag{15}$$

and thus a Lotka–Volterra system ($\tilde{B}'$ is the identity matrix). The inverse transformation, leading from (15) to (13), is also a QMT, thus validating Lemma 2 for (15).

Alternatively, in the case $m = n$ no embedding is to be performed and Lemma 2 is applied directly to the original flow setting $\Gamma = B^{-1}$.

In either case ($m > n$ or $m = n$) we have reduced the stability problem to that corresponding to the Lotka–Volterra representative: If we establish stability for the corresponding fixed point of the Lotka–Volterra system, the steady state of the original flow will automatically be stable. Note that these considerations hold irrespectively of the fact that now the Lotka–Volterra representative may have an infinity of fixed points, even if this is not the case for the original flow.

Let us then consider an arbitrary m-dimensional QPP system of Lotka–Volterra form. Since the tildes and primes appearing in (15) will not be necessary in what follows, we drop them for the sake of clarity. We then have $A = K \cdot D$, $\lambda = K \cdot L$ and, according to [12], $\text{rank}(A) = \text{rank}(K) \equiv r \leq m$. Steady states are given in parametric form by

$$\mathbf{x}_0(N) = -D^{-1} \cdot (L - N), \qquad N \in \ker(K). \tag{16}$$

We can now turn to the characterization of stability of steady-states by means of the energy-Casimir method. The $(m - r)$ independent Casimir functions are of the form

$$C^{(N)} = \sum_{j=1}^{m} N_j \ln x_j, \qquad N \in \ker(K) \tag{17}$$

and we can accordingly take the following convenient form for the energy-Casimir functional,

$$H_C \equiv \sum_{j=1}^{m} \left(D_{jj} x_j + (L_j + N_j) \ln x_j \right), \tag{18}$$

where $N \in \ker(K)$ is to be determined. Let us concentrate on a particular steady state $\mathbf{x}_0^* = -D^{-1} \cdot (L - N_0)$. We can state:

LEMMA 3. *If the entries of* $(L - N_0)$ *are either all positive or all negative, then* $\mathbf{x}_0^*$ *is stable.*

Now notice that

$$L - N_0 = -D \cdot \mathbf{x}_0^*. \tag{19}$$

Since we consider only steady states belonging to the positive orthant, Lemma 3 can be equivalently formulated in terms of positiveness or negativeness of matrix D. Since D is invariant under QMTs and embeddings [12], the same result is valid for the original QPP system and the first part of Theorem 2 is demonstrated.

Proof of the Second Statement of Theorem 2. The energy-Casimir functional (18) is mapped into a functional of the form (11) for the original QPP system [12]. We need to prove, however, that (11) is also an energy-Casimir functional. This is done in the following two lemmas:

LEMMA 4. *Every QMT of the form* (14) *maps an energy-Casimir functional into an energy-Casimir functional.*

And finally:

LEMMA 5. *The property of being an energy-Casimir functional is preserved in the process of decoupling the* $(m - n)$ *variables of the embedding.*

This completes the proof of Theorem 2.

Remark 1. The stable character of the steady state is independent of important features of the system, such as the degree of nonlinearity or the number of fixed points present in the positive orthant. This implies that there are certain degrees of freedom available in the Hamiltonian which can be varied without destroying the stability of motion. This has relevant consequences that we shall illustrate in the next section.

Remark 2. The criterion in Theorem 2 can be verified straightforwardly by simple inspection of the Hamiltonian. In particular, a precise knowledge of the coordinates of the fixed point(s) is not required.

Remark 3. In the specific case of conservative Lotka–Volterra equations, we have from (8) that B is the identity matrix and then $A = K \cdot D$. Therefore, if the hypothesis of Theorem 2 is verified then there exists a diagonal positive definite matrix $\overline{D}$, which is the absolute value of D, such that $\overline{D} \cdot A + A^T \cdot \overline{D} = 0$ due to the skew-symmetry of K. Accordingly, the classical stability criterion for conservative Lotka–Volterra systems is implied by Theorem 2 and now appears as a particular case.

3. EXAMPLES

EXAMPLE 1. We first consider Volterra's predator-prey equations [41]

$$\begin{aligned} \dot{x}_1 &= x_1(a - bx_2) \\ \dot{x}_2 &= x_2(-d + cx_1). \end{aligned} \tag{20}$$

Here a, b, c, and d are positive constants. This system is QPP with

$$K = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix}, \qquad D = \begin{pmatrix} -c & 0 \\ 0 & -b \end{pmatrix}, \qquad L = \begin{pmatrix} d \\ a \end{pmatrix}. \tag{21}$$

The Hamiltonian is

$$H(x_1, x_2) = -cx_1 - bx_2 + d \ln x_1 + a \ln x_2. \tag{22}$$

It is well known that there is a unique fixed point in the positive orthant, which is stable. We can immediately verify this from the point of view of Theorem 2, since D in (21) is negative definite. Therefore the steady state is stable. Moreover, (22) is a Lyapunov functional for it, since flow (20) is symplectic.

EXAMPLE 2. Taking the system of Example 1 as starting point, let us now consider the following generalization of the Hamiltonian,

$$H(x_1, x_2) = -cx_1^{\alpha}x_2^{\beta} - bx_1^{\gamma}x_2^{\delta} + d \ln x_1 + a \ln x_2. \tag{23}$$

Now the equations become

$$\begin{aligned} \dot{x}_1 &= x_1\left(a - \beta c x_1^{\alpha} x_2^{\beta} - \delta b x_1^{\gamma} x_2^{\delta}\right) \\ \dot{x}_2 &= x_2\left(-d + \alpha c x_1^{\alpha} x_2^{\beta} + \gamma b x_1^{\gamma} x_2^{\delta}\right). \end{aligned} \tag{24}$$

Let us assume that α, β, γ, and δ are all positive. Since in Volterra's model α and δ are greater than β and γ, we shall also extend this requirement here and consider

$$|B| = \alpha\delta - \beta\gamma > 0. \tag{25}$$

Within these assumptions, which are not very restrictive, it is not difficult to prove that there exists a unique fixed point inside the positive orthant if and only if

$$\frac{\delta}{\gamma} > \frac{a}{d} > \frac{\beta}{\alpha}. \tag{26}$$

We have that matrix D retains the same form as in (21). Therefore, according to Theorem 2 the point is stable, Hamiltonian (23) is also a Lyapunov functional of the generalized system (given that (24) is a symplectic flow), and (26) remains as the only condition both for the positiveness of the fixed point and for its stability.

It is clear that the generalized Hamiltonian (23) must incorporate dynamical features not present in Volterra's model. To see this, we first put (24) into classical Hamiltonian form by means of transformation $y_i = \ln x_i$, for $i = 1, 2$ (see [12] for the general reduction algorithm of QPP systems into the Darboux canonical form). After that, we perform a phase-space translation with the new axes centered in the steady state: $y_i = y_i^0 + \varepsilon_i$, $i = 1, 2$. Finally, we consider the case of small oscillations around the steady state and neglect terms of order ε^3. The resulting system has the Hamiltonian

$$H(\varepsilon_1, \varepsilon_2) = \mu_1 \varepsilon_1^2 + \mu_2 \varepsilon_2^2 + 2\mu\varepsilon_1\varepsilon_2, \tag{27}$$

where μ_1, μ_2, and μ are negative constants.

We shall first consider a particular case of (24)

$$\begin{aligned} \dot{x}_1 &= x_1\left(a - (1 + \delta^*) b x_2^{1+\delta^*}\right) \\ \dot{x}_2 &= x_2\left(-d + (1 + \alpha^*) c x_1^{1+\alpha^*}\right), \end{aligned} \tag{28}$$

where α^* and δ^* are greater than -1. It is a simple task to demonstrate that for (28), $\mu = 0$ in (27), and then the trajectories are ellipses aligned with the coordinate axes, similarly to what occurs in Volterra's case. However, the frequency of the oscillations is now generalized to

$$\omega = \sqrt{(1 + \alpha^*)(1 + \delta^*) a d}\,. \tag{29}$$

If α^* and δ^* remain small, ω is of the order of Volterra's frequency $\omega_0 = \sqrt{ad}$. In the most general case, ω can take any positive value, and is not restricted to any particular range.

There are some additional features not present in Volterra's model which are due to the off-diagonal terms in matrix B. These are related to the phase shift between the oscillations of the predator and the prey. To see this, let us turn back to the general Hamiltonian (27) for the case of small oscillations. It is well known that there exists a canonical transformation, which is a rotation of angle ϕ of the axes, such that in the new variables the Hamiltonian is

$$H(\xi_1, \xi_2) = \lambda_1 \xi_1^2 + \lambda_2 \xi_2^2, \tag{30}$$

where λ_1 and λ_2 are the eigenvalues of the ellipse. The solution for (ξ_1, ξ_2) is straightforward. Then, if we transform back into the variables $(\varepsilon_1, \varepsilon_2)$, a simple calculation shows that the phase shift between the predator and the prey is just

$$\Phi(\rho, \phi) = \frac{\pi}{2} + \arctan(\rho \tan \phi) - \arctan(\rho^{-1} \tan \phi), \tag{31}$$

where $\rho = \sqrt{\lambda_1/\lambda_2}$. Thus, we now have phase shifts which may be different to $\pi/2$, which is the classical Volterra value ($\phi = 0$). Notice that, in the neighbourhood of $\phi = 0$ we have

$$\Phi(\rho, \phi) = \frac{\pi}{2} + \left(\rho - \frac{1}{\rho}\right)\phi + o(\phi^3). \tag{32}$$

Therefore, if the eigenvalues do not have exactly the same magnitude (which is a reasonable assumption) these models can reproduce, in particular, a whole range of phase shifts centered around $\pi/2$. This is consistent with observed time series in predator-prey systems (see, for example, [9, pp. 60, 92; 29, p. 67]) in which the average phase shifts may differ from $\pi/2$.

We can then conclude that generalization (23) accounts for additional features observed in real systems, while retaining the advantages and the basic framework provided by a Hamiltonian formulation.

EXAMPLE 3. We shall start again with the Lotka–Volterra equations (20). Let us now consider the addition to the Hamiltonian (22) of two extra nonlinear terms,

$$H(x_1, x_2) = -cx_1 - bx_2 + \sigma_1 x_1^{\alpha} + \sigma_2 x_2^{\beta} + d \ln x_1 + a \ln x_2 \tag{33}$$

with both α and β positive and different from 1. Notice that matrix D is

$$D = \begin{pmatrix} -c & 0 & 0 & 0 \\ 0 & -b & 0 & 0 \\ 0 & 0 & \sigma_1 & 0 \\ 0 & 0 & 0 & \sigma_2 \end{pmatrix}. \tag{34}$$

The resulting generalized equations are

$$\begin{aligned} \dot{x}_1 &= x_1\left(a - bx_2 + \beta\sigma_2 x_2^{\beta}\right) \\ \dot{x}_2 &= x_2\left(-d + cx_1 - \alpha\sigma_1 x_1^{\alpha}\right). \end{aligned} \tag{35}$$

Before considering the existence of steady states, note from the form of H and D and from Theorem 2 that every fixed point of the positive orthant is stable if $\sigma_1 < 0$ and $\sigma_2 < 0$, independently of the values of α and β. Let us assume that this is the case. It is then simple to prove that there exists a unique point in the interior of the positive orthant which verifies the fixed point conditions

$$\begin{aligned} cx_1 - \alpha\sigma_1 x_1^{\alpha} &= d \\ bx_2 - \beta\sigma_2 x_2^{\beta} &= a. \end{aligned} \tag{36}$$

Therefore there is a unique steady state inside the positive orthant, it is stable, and H is a Lyapunov functional for it. The analytic determination of the coordinates of the point may be a nontrivial problem, since α and β are real constants in general. However, it is now possible to establish stability even without knowing the exact position of the point, but only by demonstrating its existence.

EXAMPLE 4. We shall finally look upon the following system, characterized by Nutku [30],

$$\begin{aligned} \dot{x}_1 &= x_1(\rho + cx_2 + x_3) \\ \dot{x}_2 &= x_2(\mu + x_1 + ax_3) \\ \dot{x}_3 &= x_3(\nu + bx_1 + x_2). \end{aligned} \tag{37}$$

As Nutku has pointed out, this is a Poisson system if

$$abc = -1, \qquad \nu = \mu b - \rho ab. \tag{38}$$

In fact, if conditions (38) hold the system is QPP with Hamiltonian

$$H = abx_1 + x_2 - ax_3 + \nu \ln x_2 - \mu \ln x_3. \tag{39}$$

The associated QPP matrices are

$$K = \begin{pmatrix} 0 & c & bc \\ -c & 0 & -1 \\ -bc & 1 & 0 \end{pmatrix}, \qquad D = \begin{pmatrix} ab & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & -a \end{pmatrix}, \qquad L = \begin{pmatrix} 0 \\ \nu \\ -\mu \end{pmatrix}. \tag{40}$$

System (37), being odd-dimensional, falls out of the scope of the traditional Hamiltonian domain. However, the previous results hold in this context as well. If we apply Theorem 2 to this case, from D in (40) together with (38) we immediately obtain that the fixed points of the positive orthant are stable if $a < 0$, $b < 0$, and $c < 0$. Notice that system (37) has an infinite number of fixed points, so stability is simultaneously demonstrated for all those belonging to $\mathrm{int}\{\mathbb{R}_+^3\}$.

Notice also that the flow is not symplectic, and we have one independent Casimir invariant

$$C = ab \ln x_1 - b \ln x_2 + \ln x_3 = \text{constant}. \tag{41}$$

Thus, according to (11) the Lyapunov functional of every positive steady state will be of the form

$$\begin{aligned} H_C = H + \kappa C = abx_1 + x_2 - ax_3 + \kappa ab \ln x_1 + (\nu - \kappa b) \ln x_2 \\ + (\kappa - \mu) \ln x_3, \qquad \kappa \in \mathbb{R}. \end{aligned} \tag{42}$$

Obviously, the Lyapunov functional (i.e., the appropriate value of the parameter κ) will be different for every fixed point and can be determined without difficulty by following the constructive procedure given in the proof of Theorem 2. We do not elaborate further on this issue for the sake of conciseness.

Finally, notice that the flow can be easily generalized to account for higher order nonlinearities while preserving stability, by means of the same techniques employed in Examples 2 and 3. Such techniques are completely general.

APPENDIX

Proof of Lemma 1. For (i), we have

$$\begin{aligned} &\sum_{j=1}^{m} \tilde{A}_{ij} \prod_{k=1}^{m} (x_{0k})^{\tilde{B}_{jk}} + \tilde{\lambda}_i = 0, \qquad \forall i = 1, \ldots, m \Rightarrow \\ &\sum_{j=1}^{m} A_{ij} \prod_{k=1}^{n} (x_{0k})^{B_{jk}} + \lambda_i = 0, \qquad \forall i. \end{aligned} \tag{43}$$

The converse follows after noting that the sense of these implications can be reversed.

The proof of (ii) is a consequence of the fact that the removal or addition of variables of constant value 1 does not affect the stable character of the point. QED

Proof of Lemma 2. It is a consequence of the fact that QMTs (14) are orientation-preserving diffeomorphisms and therefore relate topologically orbital equivalent systems. QED

Proof of Lemma 3. The gradient of the energy-Casimir functional vanishes identically at $\mathbf{x}_0^*$ if we set $N = -N_0$ in H_C. For the second part of the criterion, we note that the Hessian of H_C at $\mathbf{x}_0^*$ is diagonal due to the simple form of H in the case of Lotka–Volterra equations and takes the value

$$\text{Hess}\left(H_C \,|_{\mathbf{x}_0^*}\right) = \text{diag}\left(\frac{(N_0 - L)_1}{(x_{01}^*)^2}, \dots, \frac{(N_0 - L)_m}{(x_{0m}^*)^2} \right). \tag{44}$$

QED

Proof of Lemma 4. It is a simple consequence of the chain rule for C^2 functions of m real arguments. QED

Proof of Lemma 5. Clearly, if the gradient of H_C vanishes at $\tilde{\mathbf{x}}_0$, the gradient of the n-dimensional restriction of H_C will also vanish at $\mathbf{x}_0$. Similarly, the Hessian of the restriction of H_C will be a $n \times n$ minor of the Hessian of H_C, corresponding to the first n rows and columns. Consequently, the Hessian of the restriction will also be definite. QED

REFERENCES

1. L. Brenig, Complete factorisation and analytic solutions of generalized Lotka–Volterra equations, *Phys. Lett. A* **133** (1988), 378–382.
2. L. Brenig and A. Goriely, Universal canonical forms for time-continuous dynamical systems, *Phys. Rev. A* **40** (1989), 4119–4122.
3. A. Gasull, A. Guillamon, C. Li, and Z. Zhang, Study of perturbed Lotka–Volterra systems via Abelian integrals, *J. Math. Anal. Appl.* **198** (1996), 703–728.
4. N. S. Goel, S. C. Maitra, and E. W. Montroll, On the Volterra and other nonlinear models of interacting populations, *Rev. Mod. Phys.* **43** (1971), 231–276.
5. B. S. Goh, Global stability in many-species systems, *Amer. Naturalist* **111** (1977), 135–143.
6. B. S. Goh, Sector stability of a complex ecosystem model, *Math. Biosci.* **40** (1978), 157–166.
7. H. Goldstein, “Classical Mechanics,” 2nd ed., Addison–Wesley, Reading, MA, 1962.

8. G. W. Harrison, Global stability of food chains, *Amer. Naturalist* **114** (1979), 455–457.
9. M. P. Hassell, "The Dynamics of Arthropod Predator-Prey Systems," Princeton Univ. Press, Princeton, NJ, 1978.
10. B. Hernández-Bermejo and V. Fairén, Nonpolynomial vector fields under the Lotka–Volterra normal form, *Phys. Lett. A* **206** (1995), 31–37.
11. B. Hernández-Bermejo and V. Fairén, Lotka–Volterra representation of general nonlinear systems, *Math. Biosci.* **140** (1997), 1–32.
12. B. Hernández-Bermejo and V. Fairén, Hamiltonian structure and Darboux theorem for families of generalized Lotka–Volterra systems, *J. Math. Phys.* **39** (1998), 6162–6174.
13. B. Hernández-Bermejo, V. Fairén, and L. Brenig, Algebraic recasting of nonlinear systems of ODEs into universal formats, *J. Phys. A* **31** (1998), 2415–2430.
14. J. Hofbauer and K. Sigmund, "The Theory of Evolution and Dynamical Systems," Cambridge Univ. Press, Cambridge, UK, 1988.
15. D. D. Holm, J. E. Marsden, T. Ratiu, and A. Weinstein, Nonlinear stability of fluid and plasma equilibria, *Phys. Rep.* **123** (1985), 1–116.
16. S. B. Hsu, The application of the Poincaré-transform to the Lotka–Volterra model, *J. Math. Biol.* **6** (1978), 67–73.
17. E. H. Kerner, A statistical mechanics of interacting species, *Bull. Math. Biophys.* **19** (1957), 121–146.
18. E. H. Kerner, "Gibbs Ensemble: Biological Ensemble," Gordon & Breach, New York, 1972.
19. E. H. Kerner, Note on Hamiltonian format of Lotka–Volterra dynamics, *Phys. Lett. A* **151** (1990), 401–402.
20. E. H. Kerner, Comment on Hamiltonian structures for the n-dimensional Lotka–Volterra equations, *J. Math. Phys.* **38** (1997), 1218–1223.
21. N. Krikorian, The Volterra model for three-species predator-prey systems: Boundedness and stability, *J. Math. Biol.* **7** (1979), 117–132.
22. J. P. LaSalle, Some extensions of Liapunov's second method, *IRE Trans. Circuit Theory* **7** (1960), 520–527.
23. J. P. LaSalle, Stability theory for ordinary differential equations, *J. Differential Equations* **4** (1968), 57–65.
24. X.-Z. Li, C.-L. Tang, and X.-H. Ji, The criteria for globally stable equilibrium in n-dimensional Lotka–Volterra systems, *J. Math. Anal. Appl.* **240** (1999), 600–606.
25. D. O. Logofet, "Matrices and Graphs: Stability Problems in Mathematical Ecology," CRC Press, Boca Raton, FL, 1993.
26. A. J. Lotka, "Elements of Mathematical Biology," Dover, New York, 1956.
27. Z.-Y. Lu and Y. Takeuchi, Global stability conditions for three-dimensional Lotka–Volterra systems, *Appl. Math. Lett.* **7** (1994), 67–71.
28. Z. Lu and Y. Takeuchi, Global dynamic behavior for Lotka–Volterra systems with a reducible interaction matrix, *J. Math. Anal. Appl.* **193** (1995), 559–572.
29. J. D. Murray, "Mathematical Biology," 2nd ed., Springer-Verlag, Berlin, 1993.
30. Y. Nutku, Hamiltonian structure of the Lotka–Volterra equations, *Phys. Lett. A* **145** (1990), 27–28.
31. P. J. Olver, "Applications of Lie Groups to Differential Equations," 2nd ed., Springer-Verlag, New York, 1993.
32. M. Peschel and W. Mende, "The Predator-Prey Model: Do We Live in a Volterra World?" Springer-Verlag, Vienna, 1986.
33. M. Plank, Hamiltonian structures for the n-dimensional Lotka–Volterra equations, *J. Math. Phys.* **36** (1995), 3520–3534.
34. M. Plank, On the dynamics of Lotka–Volterra equations having an invariant hyperplane, *SIAM J. Appl. Math.* **59** (1999), 1540–1551.

35. R. Redheffer, A new class of Volterra differential equations for which the solutions are globally asymptotically stable, *J. Differential Equations* **82** (1989), 251–268.
36. Y. Takeuchi, "Global Dynamical Properties of Lotka–Volterra Systems," World Scientific, Singapore, 1996.
37. Y. Takeuchi and N. Adachi, The existence of globally stable equilibria of ecosystems of the generalized Volterra type, *J. Math. Biol.* **10** (1980), 401–415.
38. Y. Takeuchi and N. Adachi, Stable equilibrium of systems of generalized Volterra type, *J. Math. Anal. Appl.* **88** (1982), 157–169.
39. Y. Takeuchi, N. Adachi, and H. Tokumaru, The stability of generalized Volterra equations, *J. Math. Anal. Appl.* **62** (1978), 453–473.
40. Y. Takeuchi, N. Adachi, and H. Tokumaru, Global stability of ecosystems of the generalized Volterra type, *Math. Biosci.* **42** (1978), 119–136.
41. V. Volterra, "Leçons sur la Théorie Mathématique de la Lutte pour la Vie," Gauthier–Villars, Paris, 1931.