Comment on Hamiltonian structures for the $n$-dimensional Lotka–Volterra equations

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Plank’s recent discussion in this Journal of Hamiltonian structure of Lotka–Volterra dynamics is shown to have roots going back many years. This is briefly sketched together with an infrastructure of the Lie–Koenigs theorem and Gibbs ensemble theory. © 1997 American Institute of Physics.

I. INTRODUCTION

In a recent paper in this Journal, 1 Manfred Plank reports on Hamiltonian formulations of several forms of Lotka–Volterra dynamics, expressing that the idea of casting certain of their conservation laws into the role of Hamiltonian is new. But this idea is, in fact, quite old, having been brought forward and implemented by the present author thirty years ago, 2 and extensively applied statistically mechanically; the earlier work will here be briefly reinstated.

The emphasis in the present note is on the Lie–Koenigs theorem, which addresses the Hamiltonization of virtually arbitrary ordinary differential systems. In this context the original Volterra system stands as a prime illustrative example. By contrast, Plank confines his discussion to a set of two-dimensional examples, including Volterra–Lotka’s, and generalizes this limited set upwards to $n$-dimensions. A key skew-symmetric matrix enters the Lie–Koenigs theorem and also (in specialized forms) in Plank’s examples. Whereas a fundamental differential identity in this matrix falls out simply and directly in the Lie–Koenigs discussion, it is set out by Plank in his Definition 2.1 purely formally as a so-called Jacobi identity, whose meaning and origin are obscure. Finally, the far-reaching implications of Hamiltonized Volterra dynamics in Gibbs ensemble theory, absent in Plank’s work, are sketched here.

II. VOLterra DYNAMICS

Following early independent formulations by Lotka and by Volterra for the case of two interacting biospecies, Volterra in his 1931 Paris lectures 3 developed the dynamics for any number of species with populations $N_i(t)$ in predator–prey pairs

$$\frac{dN_i}{dt} = \varepsilon_i N_i + \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} N_j N_j \quad (i=1,2,\ldots,m), \sim$$

where Greek indices are summed over; and where $\varepsilon_i$ is an autoinCREASE or -decrease parameter, and $\beta_i$ is Volterra’s “equivalent number” parameter (much like mean effective biomass of the individuals in the $i$th species); and where $\alpha_{ij}$ is the interaction strength of species $i$ with species $j$. To enforce that when $i$ is predatory on $j$ the binary interaction leads to increase of $i$ and decrease of $j$, Volterra took $\alpha_{ij}$ to be skew-symmetric, e.g., $\alpha_{ij}>0$ and $\alpha_{ji}=-\alpha_{ij}<0$ [this is sufficient for predator/prey reciprocity, but is not necessary—for example, $\text{sign}$ skew symmetry, $\text{sgn}(\alpha_{ij}) = -\text{sgn}(\alpha_{ji})$ is less stringent and more realistic but harder to deal with]. A simple example is a microecology studied by Gause, 4 consisting of predatory paramecia feeding upon prey yeast supported by an unlimited sugar supply (absent any interaction the predators die out exponentially, while the prey grow exponentially on the sugar background; with interaction an oscillatory regime ensues).
Stationary population levels \( N_i = q_i \), making all \( \dot{N}_i = 0 \) occur for
\[ \varepsilon \beta_i + \alpha_{ij} q_j = 0 \]
and it is presumed that \( \alpha \) is nonsingular (hence only even total speciation \( m \)) and all \( q_i > 0 \). Thereupon, going to new variables \( v_i = \log (N_i/q_i) \), Eq. (1) becomes
\[ \dot{v}_i = \gamma_{i\lambda} \tau_{i\lambda} (e^{v_{i\lambda}} - 1) = \gamma_{i\lambda} \frac{\partial G}{\partial v_{i\lambda}} \] (2)
with
\[ G = \tau_a (e^{v_a} - v_a) \]
and with
\[ \gamma_{ij} = \frac{\alpha_{ij}}{\beta_i \beta_j} = -\gamma_{ji}, \quad \tau_i = q_i \beta_i. \]

III. HAMILTONIANS

At once it is visible that Eq. (2) is already a Hamiltonian dynamics in the two-species case
\[ v_1 = Q, \quad v_2 = P, \]
\[ H = \gamma \tau_1 (e^Q - Q) + \gamma \tau_2 (e^P - P), \]
\[ \dot{Q} = \frac{\partial H}{\partial P}, \quad \dot{P} = -\frac{\partial H}{\partial Q}, \]
where \( \gamma_{12} = -\gamma_{21} = \gamma \).

Very simply, the rudimentary Volterra–Lotka model speaks to the elemental situation where, say, a starting configuration of abundant prey (e.g., yeast) and sparse predators (e.g., paramecia) leads to the latter feeding strongly on the former, resulting in the prey population falling to low levels and the predators rising to high;—but then the numerous predators have not enough sustenance from the thin prey, and so decline while the prey are free to increase, returning presently to the initial state of prey abundance and predator sparseness. This completes the notably nonlinear Volterra–Lotka cycle, which in \( Q, P \) space is represented by the loop \( H = \text{const} \), consisting of small excursions of \( Q \) and \( P \) in the positive quadrant (where \( H \) is dominated by \( e^Q \) and \( e^P \)), but large excursions in the negative quadrant (where \( H \) is dominated by \( -Q \) and \( -P \)). This lopsided loop quiets down to a little ellipse when \( H \) is small, with \( e^Q = 1 + Q + \frac{1}{2} Q^2 \), and \( e^P = 1 + P + \frac{1}{2} P^2 \), and the motion becomes simple harmonic.

In the general case, make a linear transformation \( w_i = T_{ia} v_a \), to bring
\[ \dot{w}_i = T_{ia} \gamma_{ak} \frac{\partial H}{\partial W_k} = \beta_{ia} \frac{\partial H}{\partial W_a} \]
\[ H(w) = G(v(w)). \] (3)
Using the well-known theorem\(^5\) on reduction of a skew-symmetric matrix to canonical form by orthogonal transformation, one can obtain by structuring \( T \) correctly the symplectic form
\[ \beta = T \gamma T = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix} + \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix} + \cdots \]
where $\oplus$ denotes direct sum. That is, relabelling $w_1, w_2$ as $Q_1, P_1$ and $w_3, w_4$ as $Q_2, P_2$, etc.,

$$P_i = -\frac{\partial H}{\partial Q_i}, \quad \dot{Q}_i = \frac{\partial H}{\partial P_i},$$

producing finally the familiar Hamiltonian format.

As is clear from Eq. (2), Liouville’s theorem holds in $v$-space

$$\text{div } V = \frac{\partial v^\mu}{\partial v^\mu} = \gamma^\mu_{\nu\lambda} \frac{\partial^2 G}{\partial v^\nu \partial v^\lambda} = 0,$$

telling of incompressible fluid flow (or volume conservation) in that space as in $Q, P$ space. This is of capital importance in going to Gibbs ensembles (see below).

### IV. LIE–KOENIGS PERSPECTIVE

The covering theorem for results like those of Volterra’s model is the Lie–Koenigs theorem,\(^6\) stating that any dynamics $\dot{x}_i = X_i(x)$ may be brought to Hamiltonian form.

A simple instrument for its demonstration is the variational principle

$$\delta \int [U_a(x) \dot{x}_a - U_0] dt = 0,$$

whose Euler–Lagrange equations

$$\frac{dU_k}{dt} = \frac{\partial U_a}{\partial x_k} \dot{x}_a - \frac{\partial U_0}{\partial x_k} (k = 1, 2, \ldots, m)$$

are, first, to be made to embrace the prescribed differential system $\dot{x}_i = X_i$. Taking $dU_k/dt = (\partial U_k/\partial x_a) \dot{x}_a$ we obtain

$$\left( \frac{\partial U_k}{\partial x_a} - \frac{\partial U_a}{\partial x_k} \right) \dot{x}_a = -\frac{\partial U_0}{\partial x_k},$$

or

$$\Gamma_{ka} \dot{x}_a = \frac{\partial U_0}{\partial x_k},$$

where

$$\Gamma_{kj} = \frac{\partial U_j}{\partial x_k} - \frac{\partial U_k}{\partial x_j},$$

is a key skew-symmetric matrix, which is taken to be nonsingular,—this requires that its order $m$ be even, but that is no problem since to $\dot{x}_i = X_i(i = 1, 2, \ldots, m)$ there can always be appended an additional equation $\dot{x}_{m+1} = X_{m+1}$ to make any initially odd system into an even one. The fundamental matrix $\Gamma$ clearly satisfies

$$\frac{\partial \Gamma_{kj}}{\partial x_i} + \frac{\partial \Gamma_{ik}}{\partial x_j} + \frac{\partial \Gamma_{ji}}{\partial x_k} = 0.$$
as a moment’s calculation shows. For prescribed $X_i$, the partial-differential system for the $U_i$ is

$$\left( \frac{\partial U_k}{\partial x_a} - \frac{\partial U_a}{\partial x_k} \right) X_a = - \frac{\partial U_0}{\partial x_k}.$$ 

If $U_0$ is built as $U_0 X_a + W_0$, then

$$X_a \frac{\partial U_k}{\partial x_a} = - U_a \frac{\partial X_a}{\partial x_k} - \frac{\partial W_0}{\partial x_k}.$$ 

This is recognizably a system of Cauchy–Kowalewski type, for which a local existence theorem is classically settled. The remainder of the proof of Hamiltonization of $\dot{x}_i = X_i$ consists in noting that (replacing $m$ by $2n$)

$$\sum_{i=1}^{2n} U_\alpha dx_\alpha$$

is reducible, by solution of a successions of Pfaff’s problems\(^7\) to

$$\sum_{i=1}^{n} P_\gamma(x) dQ_\gamma(x)$$

to within an exact differential. This brings Eq. (4) to

$$\delta \int (P_\gamma Q_\gamma - H) dt = 0,$$

$$H(Q,P) = U_0(x(Q,P)),$$

so that $\dot{x}_i = X_i$ is now rendered into final Hamiltonian form. It is to be noted that explicit Hamiltonian form can often be dropped in favor of the “effectively Hamiltonian” format of Eq. (5) which may be restated\(^8\)

$$\dot{x}_i = \gamma_i^a \frac{\partial U_0}{\partial x_a},$$

$$(\gamma = \Gamma^{-1}).$$

This format is invariant to arbitrary transformations of the coordinate $x_i$, as the variational principle Eq. (4) clearly tells. Thus a considerable advance over the canonical transformations of Hamiltonian theory. Poisson brackets may be represented as

$$(A,B) = \frac{\partial A(x)}{\partial x_\alpha} \gamma_{\alpha\beta} \frac{\partial B(x)}{\partial x_\beta},$$

while the identity, Eq. (6), written in terms of the $\gamma$ matrix is

$$\gamma_{ia} \frac{\partial \gamma_{jk}}{\partial x_a} + \gamma_{ja} \frac{\partial \gamma_{ki}}{\partial x_a} + \gamma_{ka} \frac{\partial \gamma_{ij}}{\partial x_a} = 0.$$ 

The latter result hides the simplicity of the original Eq. (6), and without the insight behind Eq. (6) appears rather mysterious as an a priori characteristic of the $\gamma$ matrix.
It is also easily shown that $|\det \Gamma|^{1/2}$ is a Jacobi last-multiplier of the starting system $\dot{x}_i = X_i$, hence that the weighted volume

$$|\det \Gamma|^{1/2} dx_1 \cdot dx_2 \cdots dx_m = |\det \Gamma|^{1/2} dx$$

is conserved (note that $\det \Gamma$ is a perfect square). This constitutes Liouville's theorem in $x$ space.

### V. GIBBS ENSEMBLES

The traditional setting of Hamiltonian dynamics for classical ensemble theory is easily extended to cover the much broader "effectively Hamiltonian" scheme above. First we have the extended Liouville theorem of Eq. (7), and second we have the conservation law

$$\frac{dU_0}{dt} = x_\beta \frac{\partial U_0}{\partial x_\beta} - \gamma_{\alpha\beta} \frac{\partial U_0}{\partial x_\alpha} \frac{\partial U_0}{\partial x_\beta} = 0$$

owing to the skew-symmetry of $\gamma$. Consequently, the extended canonical distribution function in $x$ space is

$$\rho \: dx \sim |\det \Gamma|^{1/2} \exp \left( - \frac{U_0}{\Theta} \right) dx$$

for a system under "heat bath" conditions at temperature $\Theta$.

A simple but telling example here is the Volterra system above, where $\gamma$ and $\Gamma$ are constant matrices and the canonical distribution in $v$-space is simply

$$\rho \: dv \sim \exp \left( - \frac{G}{\Theta} \right) dv, \quad G = \sum \tau_a \left( e^{v_a} - v_a \right).$$

Now owing to the structure of conserved $G$ as a sum-function, this is

$$\rho \: dv \sim \Pi_i \exp - \frac{\tau_i}{\Theta} \left( e^{v_i} - v_i \right) dv_i$$

so the separability of $G$ provides a private distribution in each $v_k$ individually

$$\rho_k \: dv_k \sim \exp - \frac{\tau_k}{\Theta} \left( e^{v_k} - v_k \right) dv_k$$

in a striking parallel with the Maxwell–Boltzmann distribution. Thus notwithstanding that the interspecies interaction strengths, $\alpha_{ij}$ may be arbitrarily strong, the separability of $G$ ensures the ensemble behavior as a sort of ideal (ecological) gas, with each component split off from the rest, and the calculation of ensemble averages greatly facilitated. The transition to strictly Hamiltonian form, Eq. (3), quite clearly ruins this simplicity and is definitely to be avoided: a nice case of the superiority of the effective-Hamiltonian scheme over the strictly Hamiltonian one.

Reverting directly to population levels \(n_k = N_k / q_k\), the distribution law Eq. (8) is

$$\rho_k \: dn_k \sim n_k^{\lambda_k - 1} e^{-\lambda_k v_k} \: dn_k, \quad (\lambda_k = \tau_k / \Theta),$$
namely, a gamma distribution, and the meaning of $\Theta$ is revealed (in two ways) by the simple canonical averages

$$\overline{(n_k-1)^2} = \frac{\Theta}{r_k} = (n_k-1) \log n_k,$$

while $\overline{n_k} = 1$. For very low temperatures, $\Theta \ll \tau_k$, the $\rho_k$ is strongly peaked at $n_k = 1$, and the population $N_k$ just ripples gently around $q_k$. At very high temperatures $\Theta \gg \tau_k$, the $\rho_k$ is dominated by very low values of $n_k$. Here, the population $n_k$ spends long intervals of time at very low levels, occasionally and briefly rocketing to high levels (holding thus to $N_k = q_k$). This behavior of “surge-and-crash” of a population is well observed in the field. Thus the whole system divides roughly into species which are rippling lightly about their mean values, and a second group surging-and-crashing about them.

For the considerable variety of ensemble averages that may be explicitly calculated, the reader is referred to the original works. Suffice it to say that the single statistical parameter $\lambda_k$ appears to be adequate to appreciable ranges of data. The case of odd-speciation (odd $m$) admits the important possibility that one species dies out asymptotically, in a “passage to parity” that was recognized by Volterra. The gradual grinding out of this one species, who typically will be a close competitor of a neighboring, slightly advantaged species, can be elaborated in detail, and then models the so-called “competitive exclusion principle” understood since Darwin to be a mainspring of evolution.

3 V. Volterra, Lecons sur la Theorie Mathematique de la Lutte pour la Vie (Gauthier-Villars, Paris, 1931).
4 G. F. Gause, The Struggle for Existence (Williams & Wilkins, Baltimore, 1934).
8 This is also called a “coordinate free” Hamiltonian scheme, P. J. Olver, Applications of Lie Groups to Differential Equations (Springer, Berlin, 1986).