Generalized Predator–Prey Oscillations in Ecological and Economic Equilibrium

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ABSTRACT The standard predator–prey model is generalized beyond the Volterra linear-log form. Conservative oscillations are deduced and also conversion to a variational Hamiltonian form. Generalization to more than two species is also castable into Hamiltonian form, with small vibrations around equilibrium being of undamped sinusoidal type by virtue of associated characteristic exponents all being pure imaginaries. However, introduction into ecological equilibrium of a recognition of limited space and inorganic matter destroys the autonomous periodicity of the motions and makes inapplicable the elegant formalism of classical statistical mechanics. Introduction of simple diminishing returns leads to damped motions that are kept cyclically alive by shocks of the weather and other exogenous stochastic elements. Introduction of increasing returns solely in an interval near equilibrium leads to autonomous self-exciting oscillations near a stable limit cycle; under stochastic forcing functions, a long-run ergodic state becomes predictable.

TWO-SPECIES MODELS Conservative periodic motions are a characteristic feature of the well-known predator–prey model of Lotka (ref. 1) and Volterra (ref. 2)

\[ \dot{X}_1 = X_1(a_1 - a_{12}X_2) \]
\[ \dot{X}_2 = -X_2(a_2 - a_{21}X_1) \]

(1)

where \( X_2 \) is the predator species (tigers, foxes, capitalists), \( X_1 \) the prey species (deer, rabbits, laborers), and \( \dot{X}_1 \) denotes \( dX_1/dt \). The numbers of “interactions” that give rise to a decrease in prey and increase in predator are assumed proportional to the products \( X_1X_2 \).

This is the special case of the more general model

\[ \dot{Y}_1 = F_{12}(Y_2), \quad F_{12}(Y_2^{*}) = 0 \]
\[ \dot{Y}_2 = -F_{21}(Y_1), \quad F_{21}(Y_1) > 0 \]

(2)

got by letting \( Y_1 = \log X_1, F_{12}(Y_1) = a_1 - a_2 \exp Y_2 \).

System (2) is a special case of the trivially more general model

\[ \dot{Z}_1 = g_1(Z_1)f_{12}(Z_2) \]
\[ \dot{Z}_2 = -g_2(Z_2)f_{21}(Z_1) \]

(3)

where \( Z_1 = \int_{\gamma}^{\delta} g_1(u)^{-1}du \) a monotone increasing and reversible function of \( Z_2 \), implying \( Z_1 = G_1(Y_1), F_{12}(Y_1) = f_{12}(G_1(Y_1)) \).

It is usually convenient to reduce (3) to standard form (2), but occasionally there are advantages to the alternative form

\[ \dot{W}_1 = W_2 \]
\[ \dot{W}_2 = -g_2(W_2)f_{21}(W_1) \]

(4)

where \( W_2 = F_{12}(Y_2), Y_2 = F_{12}^{-1}(W_2) = \psi(W_2) \),

\[ g_2(W_2)^{-1} = \psi'(W_2) \]

Under various regularity conditions, differentiating the first equation with respect to time and utilizing its original form to eliminate all dependence on \( Y_2 \) will lead to a second-order differential equation in a single variable

\[ \dot{Y}_1 = -f_1(Y_1)f_{12}(Y_1) \]

(5)

where \( f_1(Y_1) = f_{12}'(F_{12}^{-1}[Y_1]) > 0 \). In (5), one cannot necessarily be free to select \( Y_1 \) arbitrarily in the interval \((-\infty, \infty)\), as can be seen from a case like that in which \( F_{12}(Y_2) = \arctan Y_2 \), and \( Y_1 \) is confined to the range \((-\pi, \pi)\). (Of course (4) is essentially a variant of (5), but with \( Y_2 = W_2 \) being the autonomous variable instead of \( Y_1 \).)

Eqs. (1)–(5) are all seen to be qualitatively unchanged if time is reversed, as in the transformations \( T = -t, dX_i/dT = -X_i \) provided the roles of the species are reversed. That is, if you run a movie film of the struggle backwards in time, it will appear, so to speak, that rabbits are the predators feasting on the tigers. This time reversibility is consistent with the first law of thermodynamics, as applied to frictionless mechanical systems, but is quite inconsistent with a macroscopic second law of thermodynamics in which some entropy steadily increases as time’s arrow flows irreversibly forward. As will be seen in the final two sections, introducing limited land and inorganic environmental elements, with the implied action of diminishing returns (or in the final section, varying returns), will give the system a one-directional asymmetry in time that is incompatible with conservative periodicity.

CONSERVATIVE OSCILLATIONS

Integrals of motion for the L-V model of (1) can be derived by elementary integration. But even for the general model (2), where no solution in terms of elementary functions can be found, simple quadratures yield integrals of motions that are closed, periodic
orbits around the unique stationary state \( Y^* = (Y_1^*, Y_2^*) \), defined as the root of the simultaneous equations

\[
F_{1n}(Y_1^*) = 0, \quad F_{2n}(Y_1^*) = 0.
\]

To derive integrals of motions, multiply the first equation by \( F_{1n}(Y_1) \), the second by \( F_{2n}(Y_2) \), and add, to get

\[
F_{1n}(Y_1) Y_1 + F_{2n}(Y_2) Y_2 = 0 = \frac{d}{dt} \{ H_1(Y_1) + H_2(Y_2) \},
\]

(6)

where \( H(Y) = \sum H_i(Y_i) \) is a convex Hamiltonian function with \( H_i'(Y_i) = F_{jn}(Y_j) \), and which reaches its minimum at \( H(Y^*) \), where \( H_i'(Y_i^*) = 0, H_i''(Y_i^*) = F_{kj}'(Y_k^*) > 0 \).

Let \( \theta \) be the period of a complete cycle of \([Y_i(\theta)]\). Since \( Y_i(t + \theta) = Y_i(t) \),

\[
0 = \int_{t}^{t + \theta} \dot{Y}_i(u) du = \frac{1}{\theta} \int_{t}^{t + \theta} F_{lj}(u) du
\]

(7)

\[
\lim_{T \to \infty} \frac{1}{T} \int_{t}^{t + T} F_{lj}(u) du = 0.
\]

When, as in the case of (1), \( F_{lj} \) is proportional to the linear expression \( X_i - X_j \), this yields immediately Volterra’s law of conservation of the means of species. Such an interpretation will not hold for the general case, although for small-enough vibrations we will have

\[
\lim_{T \to \infty} \frac{1}{T} \int_{t}^{t + T} Y_i(u) du = Y_i^*(1 + \epsilon),
\]

where \( \epsilon \) will go to zero as the initial distance from equilibrium

\[
\Sigma \left| Y_i(0) - Y_i^* \right| \to 0.
\]

CONVERSION TO A MINIMUM PROBLEM

Eqs. (2) can now be rewritten in Hamilton’s canonical form

\[
\begin{align*}
\dot{Y}_1 &= \partial H / \partial Y_2 = H_2'(Y_2) \\
\dot{Y}_2 &= -\partial H / \partial Y_1 = -H_1'(Y_1).
\end{align*}
\]

(2')

Even if Andronov and Chaikin (ref. 3) had not shown that Eq. (1)’s motions possess a Poincaré integral invariant of the form \( \int \int (dX_1/X_1)(dX_2/X_2) \), the canonical form of (2') would alert one to the possibility of relating these struggle-for-life equations to a minimizing variation problem, as I have already shown (ref. 4).

We have merely to invert the first equation of (2') to get

\[
Y_2 = T''(\dot{Y}_1), \quad T'' = (H_1')^{-1} > 0,
\]

where \( T(Y_1) \) is kind of a kinetic-energy function, in terms of which \( Y_2 \) can be defined as a Newton–Hamilton momentum.

In terms of these transformed variables, (2') becomes

\[
\frac{d}{dt} T'(\dot{Y}_1) - H_1'(Y_1) = 0,
\]

(8)

which is essentially of form (5), and can be seen to be the Euler extremal condition for the maximization of

\[
I = \int_{t_0}^{t_1} [T(\dot{Y}_1) - H_1(Y_1)] dt,
\]

(8')

That the solution represents a true minimum of \( I \) and not merely a stationary value is assured by the fact that the strict convexity of \( T(Y_1) \) implies strong Legendre and Weierstrass conditions that suffice for a strong minimum provided that \( \mid t_1 - t_0 \mid \) is sufficiently small. However, when the time interval becomes larger than a half period of oscillation, the existence of a Jacobi conjugate point will destroy the minimum character of the struggle-for-life motion.

A classic theorem of Poincaré requires that the characteristic roots associated with a stationary point of Hamiltonian variational system come in opposite-signed pairs. For the present case of closed contours of motion, those roots must be pure imaginaries, so that small vibrations around the equilibrium state will perform the sinusoidal oscillations of simple harmonic motion.

MULTI-SPECIES PREDATOR-PREY MODEL

The case of \( n \geq 2 \) predators \((Y_1, \ldots, Y_n)\) interacting with preys \((y_1, \ldots, y_n)\) to produce conservative fluctuations around an equilibrium \((y^*, Y^*)\) can be analyzed by exact analogy to the previous general procedures. We consider

\[
\begin{align*}
\dot{y}_i &= \partial H_1(y_1, \ldots, y_n)/\partial Y_1 = -\partial H_1(Y, y_2) / \partial y_i + \\
\dot{Y}_i &= -\partial H_1(y_1, \ldots, y_n) / \partial y_i = -\partial H_1(Y, y_2) / \partial y_i \quad (i = 1, 2, \ldots, n),
\end{align*}
\]

(9)

with the immediate integral of motion

\[
\sum_{j=1}^{n} \left[ \partial H_{1j}(y_1, \ldots, y_n)/\partial y_j \right] \dot{y}_j + \sum_{j=1}^{n} \left[ \partial H_{1j}(Y, y_2)/\partial Y_j \right] \dot{Y}_j = \sum_{j=1}^{n} \left[ \partial H_{2j}(y_1, \ldots, y_n)/\partial y_j \right] \dot{y}_j - \sum_{j=1}^{n} \left[ \partial H_{1j}(Y, y_2)/\partial Y_j \right] \dot{Y}_j = 0 = \frac{d}{dt} [H_1(y_1, \ldots, y_n) + H_{11}(y_1, \ldots, y_n)].
\]

(10)

If \( H = H_1 + H_{11} \) is a strongly convex function, the first set of equations of (9) can be uniquely inverted to
Figs. 1, 2, and 3 show, respectively, the contours of motion for the conservative razor's-edge case, the case recognizing simple diminishing returns, and the case where returns are increasing at intermediate scales near the equilibrium.

give

\[ Y_i = \frac{\partial T(y_1, \ldots, y_n)}{\partial \dot{y}_i} \quad (i = 1, \ldots, n), \quad (11) \]

where \( T \) is a convex “kinetic energy function” and \( Y_i \) are “generalized momenta”.

The motions of (10) can now be recognized as the Euler variational condition for minimization of the integral

\[ I = \int_0^t [T(y_1, \ldots, y_n) + H_{ii}(y_1, \ldots, y_n)] dt \]

\[ \delta \int_0^t [T - H_{ii}] dt = 0 \]

\[ \frac{d}{dt} \frac{\partial T(y_1, \ldots, y_n)}{\partial \dot{y}_i} - \frac{\partial H_{ii}(y_1, \ldots, y_n)}{\partial y_i} = 0. \quad (12) \]

From classical mechanics, it is straightforward to deduce that the conservative motions approach, in the neighborhood of the equilibrium point \((y^*, y^*) = (y^*, 0)\), defined by the saddlepoint of \( T - H_{ii} \),

\[ T(0) - H_{ii}(y^*) \leq T(0) - H_{ii}(y^*) \leq T(\dot{y}) - H_{ii}(y^*) \]

superimposed sinusoidal motions of the form

\[ y_i - y_i^* \approx \sum_{j=1}^{n} C_{ij} \sin(\omega_j t + \gamma_j). \]

Eqs. (9) are both more and less general than Volterra's many-species case

\[ \dot{N}_i/N_i = a_i + \sum_{j=1}^{m} a_{ij} N_j \quad (i = 1, \ldots, m) \]

\[ a_{ij} = -a_{ji} \]

For \( m = 2n \) and \( a_{ij} \equiv 0 \), when both \( i \) and \( j \) are greater than \( n \) or are less than \( n + 1 \), Volterra's system becomes a special case of (9), but not otherwise. On the other hand, Volterra's system generally lacks the independence of \( H_i \) of \( y_i \), and the independence of \( H_{ii} \) of \( Y_i \). A formulation that includes all cases is

\[ \dot{y}_i = +\frac{\partial H}{\partial Y_i}, \quad (i = 1, \ldots, n) \]

where \( H(Y_1, \ldots, Y_n, y_1, \ldots, y_n) \) is strictly convex, say, with a positive definite Hessian matrix of second partial derivatives, so that \( H(Y^*, y^*) \) is a true minimum, with closed contours on which the motions around equilibrium must lie. If \( H \) has a minimum, the Lagrangian \( L(y_1, \ldots, y_n, y_1, \ldots, y_n) = L(y, y) \) enjoys a saddlepoint, \( L(0,y) \leq L(0,y^*) \leq L(y,y^*) \), and the characteristic exponents of the extremal motions must be pure imaginaries as in the \( H_i + H_{ii} \) sinusoidal case.

**DISSIPATIVE DIMINISHING RETURNS**

The pretty formalisms above should not blind us to the fact that the Lotka-Volterra struggle for existence has forgotten all about the limitation of land and inorganic elements in the environment. Ecological equilibrium without the law of diminishing returns is like Hamlet without the Prince. Conservative motions are always a razor's-edge state: if the first law of thermodynamics, the law of conservation of energy, were not a brute fact of nature, one would have to consider its invention infinitely improbable. Although the molecules in foxes and rabbits satisfy energy laws, the macrocosmic variables denoting population numbers do not.

Thus, as I have shown (ref. 5), adding into the right-hand-side parenthesis of (1)'s first equation a small perturbing term \(-\alpha X_i \), to reflect the fact that the prey would ultimately encounter diminishing returns, will destroy the periodicity of the motions in phase space.
STABLE LIMIT CYCLE

If autonomous periodicity in the struggle for existence is insisted upon, I found it more plausible to introduce into the parentheses of (1) a nonlinear term \( \epsilon f(X_1) \), with the property that \( f \) is increasing in the neighborhood of the \( X^* \) equilibrium point but reverses its direction at small and large scales for \( X_1 \). This will imply an auto-relaxation limit cycle of the Rayleigh-van der Pol type (refs. 3–5). Such a stable periodic motion will be of unique amplitude, independently of initial conditions. Moreover, a small change in any of the coefficients of the system will not destroy the periodicity as it would for a vulnerable, razor's-edge conservative system.

Figs. 1, 2, and 3 show, respectively, the contours of motion for the conservative razor's-edge case, the case recognizing simple diminishing returns, and the case where returns are increasing at intermediate scales near the equilibrium. Only in the first case will the elegant methods of classical statistical mechanics apply.

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2. Volterra, V., Légons sur la théorie mathématique de la lutte pour la vie (Gauthier-Villars, Paris, 1931); Acta biotheoretica, III (1937), reproduced in Volterra, V., Opera Matemática, V, 414, gives an alternative variational principle to that given here.