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PREFACE

In this paper, the authors summarize recent results obtained by applying the Lotka-Volterra approach to problems in nonlinear systems analysis. This approach was developed at the Mathematics and Cybernetics Division of the GDR Academy of Sciences (Berlin); various applications have been investigated in collaboration with the System and Decision Sciences Program at IIASA.

This paper should also be seen as a contribution to the debate on future directions of research at IIASA, in particular possible research into the evolution of macrosystems.

ANDRZEJ WIERZBICKI
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M. Peschel, W. Mende and M. Grauer

INTRODUCTION

This paper summarizes recent results obtained by applying the Lotka-Volterra approach to problems in nonlinear systems theory.

Ref. 1 introduces a general structure design principle by which it is possible to obtain a unified description of a large class of systems normally described by ordinary differential equations in terms of the Lotka-Volterra equations:

$$Fx_i = \sum G_{ij}x_j + \sum H_{is}y_s \quad .$$

Ref. 2 proposes a group of equivalence transformations for the Lotka-Volterra equations once these equations have been embedded in the huge class of multinomial differential equations. One particularly important member of these equivalence classes is the Riccati representation of a nonlinear system:

$$\dot{u}_i = K_i \Pi u_r^{k_{ir}} \quad .$$

This Riccati representation has important properties which can help to simplify qualitative analysis. To a good approximation,

the behavior of nonlinear systems can be locally represented by Riccati models. It can be shown [3] that the Volterra approach may also be used to advantage in the study of linear systems.

Shift cones, which exist for a huge class of Volterra systems, are discussed and the importance of some of their qualitative properties noted (see [4]).

The strength of the Volterra approach in applied systems analysis may be demonstrated by a number of interesting examples, one of which involves the use of the approach for modeling the dynamics of growth. Some systems descriptions of growth functions are discussed [5] and the Volterra approach is then applied to the resulting equations [6]. An outline of the general Lotka-Volterra approach is given in a previous IIASA paper [7].

1. CHAINS AND CYCLES

We often find that the highly complicated external appearance of complex systems (ecological, economic, astrophysical, etc.) conceals quite a simple basic structure or skeleton composed of chains and cycles linked together with a relatively small number of feedbacks or other connections.

Growth and structure are the main characteristics of evolutionary systems. Dynamic interaction usually leads to actions controlling the growth rates, which from a functional point of view means that rate coupling is the most important type of interaction in complex systems.

A very broad but simple model of a chain structure is given by the following equations:

$$Fx_i = K_i x_{i+1} - L_i x_{i-1} - a_i x_i \quad , \quad F = d\ell n/dt \ , \ i = 0,1,2,\ldots,$$

where

K_i reflects the influence of the next level up on the growth of x_i

L_i represents the loss of x_i connected with the next level down

a_i reflects the wastage on level i

If the loss terms can be neglected we obtain what is called an exponential chain with

$$Fx_i = K_i x_{i+1} \quad , \qquad i = 0,1,\ldots \quad .$$

We can try to use such an exponential chain to generate any given signal $x_0(t)$. In this case the state variables $x_i(t)$ should be normalized such that $x_i(0) = 1$. The coefficients K_i can then be uniquely determined by

$$K_i = Fx_i\Big|_{t=0} = F^{i+1}x_0\Big|_{t=0} \quad .$$

This is an expansion very similar to the Taylor expansion of a given function $x_0(t)$. (Recall that the Taylor expansion involves the approximation of $x_0(t)$ by a linear chain

$$\dot{x}_i = K_i + x_{i+1} \quad , \qquad i = 0,1,2,\ldots,$$

normalized such that $x_i(0) = 0$.)

Both chain constructions are special cases of a more general construction based on an arbitrary differentiable and monotonic function $\phi(u)$ and the following chain:

$$\frac{d\phi(x_i)}{dt} = \phi^{-1}(\phi(K_i) + \phi(x_{i+1})) \quad .$$

Again we have the normalization condition

$$\phi(x_i(0)) = 0 \quad .$$

In this case the coefficients K_i can be computed from

$$K_i = F^{i+1}x_0(t)\Big|_{t=0} \quad , \qquad F = d\phi(\cdot)/dt \quad .$$

Another chain construction can also be useful when trying to approximate systems behavior by a local chain model. This one is based on the generalized difference quotient:

$$\frac{\phi(x_i(t))-\phi(x_i(t_0))}{\psi(t)-\psi(t_0)} = \phi^{-1}(\phi(K_i)+\phi(x_{i+1}(t))) \quad .$$

For $\phi(u) = u$ and $\psi(u) = u$ this expression is equivalent to a Taylor series expansion about the reference time t_0. The normalization condition for these chains is:

$$\phi(x_i(t_0)) = 0 \quad , \quad i = 1,2,\ldots, \quad .$$

Note that this does not necessarily hold for $i = 0$. The corresponding parameters can then be computed using

$$K_i = \frac{d\phi(x_i(t_0))/dt}{d\psi(t_0)/dt} \quad .$$

In this case it is difficult to obtain an estimate of K_i based directly on $x_0(t)$; it is only possible to derive the following iterative procedure for $L_i(t) = d\phi(x_i(t))/dt$:

$$L_{i+1}(t) = \frac{d}{dt}\,\phi\left(\int_{t_0}^{t} L_i(u)\,du/[\psi(t)-\psi(t_0)]\right) \quad .$$

We shall now return to the concept of the <u>exponential chain</u>, and describe some of its most important properties and some (as yet) unsolved problems.

Assuming that $K_i = K$ for all i, the exponential chain

$$Fx_i = Kx_{i+1}$$

converges to $x_0(t)$ as the length of the chain increases, where

$$x_0(t) = x_0(0)/(1-Ktx_0(0)) \quad .$$

For simplicity we assume that $x_i(0) = 1$ for $i = 0,1,\ldots$. The signal $x_0(t)$ is a solution of the following autocatalytic differential equation:

$$\dot{x}_0 = Kx_0 \quad .$$

This equation can be represented by the cyclic structure shown in Figure 1 which is a hypercycle of the simplest form (see [8]).

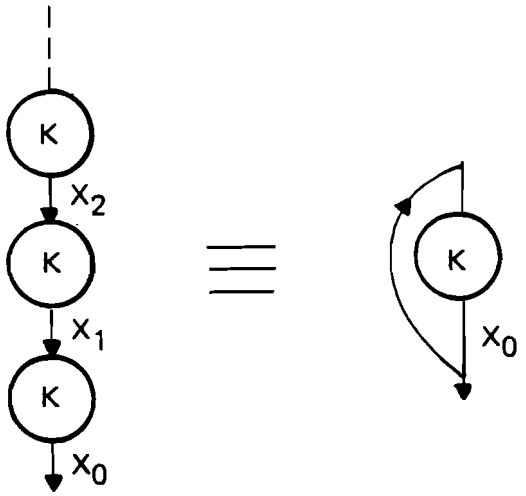

Figure 1. A hypercycle of the simplest form.

A hypercycle of order n is produced by a finite chain with feedback after n elements and is represented by the equations

$$\dot{x}_i = K_i x_{i+1} \quad , \qquad i = 0,1,\ldots,n \quad .$$

This hypercycle corresponds to an exponential chain with periodic coefficients

$$K_0, K_1, \ldots, K_{n-1} \quad .$$

We can consider our finite chain to be built up by repeating this sequence m times, and this leads to our first unsolved problem. Does the signal $x_0(t)$ always converge to the corresponding hypercycle solution as $m \to \infty$?

Eigen and Schuster considered in detail the hypercycle with homogeneous flow ϕ on every level represented by the equations

$$Fx_i = K_i x_{i+1} - \phi \quad , \qquad \phi = \sum x_k K_k x_{k+1} \quad .$$

In this case the normalization condition $\sum x_i = 1$ is obviously satisfied, which means that the interesting behavior of the system is concentrated completely on this simplex. This hypercycle behavior can be transformed in such a way that we have

$$Fy_i = K_i y_{i+1}/y \quad , \qquad y = \sum y_i$$

where the relation between the new state variables y_i and the old ones x_i is given by $x_i = y_i/y$.

It was shown by Schuster, Sigmund, Hofbauer and Wolff [9] that for $n \leq 3$ the hypercycle can have only foci, but for $n \geq 4$ limit cycles can occur.

We shall now consider the behavior of a complex hypercycle, i.e., a complex exponential chain. In this case we allow $x_i(t)$ to take complex values and substitute into the chain equations the Gaussian representation

$$x_i(t) = R_i(t) \exp\left(j\theta_i(t)\right) \quad .$$

On separating real and imaginary parts we obtain the following real equations:

$$FR_i = K_i R_{i+1} \cos\theta_{i+1} \quad , \qquad \dot{\theta}_i = K_i R_{i+1} \sin\theta_{i+1}$$

which lead to

$$F\left(\frac{\dot{\theta}_{i-1}}{K_{i-1}\sin\theta_i}\right) = \frac{\dot{\theta}_i \cos\theta_{i+1}}{\sin\theta_{i+1}}$$

$$R_i = \frac{1}{K_{i-1}} \frac{\dot{\theta}_{i-1}}{\sin\theta_i} \quad .$$

These relations can be used to help clarify the dynamics of the complex hypercycle.

The analysis of an exponential chain in which the K_i are independent stochastic variables (do not depend on time t) is also of great interest.

Consider the following case:

$$Fx_i = Kx_{i+1} \quad , \quad x_{n+1} \equiv 1 \quad , \quad i = 0,1,\ldots,n \quad ,$$

where K is a stochastic variable with probability density $\phi(K)$. We would like to show that the probability density $\phi(x_{0,n}(t))$ (where $x_{0,n}(t)$ is the lowest signal of a chain of length n) converges to $\phi(x_0(t))$ as $n \to \infty$, with

$$x_0(t) = 1/(1-Kt) \quad .$$

This is still an open question, but if proven would be of great importance because it would mean that a chain with nearly equal coefficients K_i, with differences caused only by fluctuations, would necessarily exhibit approximately hyperbolic behavior (Law of Large Numbers of Ecology).

2. THE STRUCTURE DESIGN PRINCIPLE AND THE DOMINATING ROLE OF LOTKA-VOLTERRA EQUATIONS IN DYNAMIC SYSTEMS

The study of ecological systems provides us with a picture of their underlying structure in terms of a skeleton composed of chains and cycles linked by a relatively small number of feedbacks and other connections. From the functional point of view, ecological systems also contain dynamic interactions influencing the growth rates Fx_i of the corresponding state variables x_i, which represent growth indicators. The structure design principle proposed in [1] attempts to use this knowledge to obtain the structures of a huge class of systems described by ordinary differential equations.

The structure design principle is based on the following rules:

1. The logarithmic derivative function $F = d\ell n/dt$ is applied to any intermediate state variable x_i:

$$Fx_i = A_i \quad .$$

The result A_i is not introduced as a new state variable x_{i+1} as in the case of an exponential chain. Rather, A_i is in general an arithmetic expression built up from:(i) signals already known because they have appeared previously, (ii) signals unknown up to this stage of the design process, and possibly (iii) nonlinear transformations of signals of both types.

2. We identify the known signals in A_i and construct feedback loops or interconnecting arches for them; we fix in an arbitrary manner the unknown signals or nonlinear expressions of known and unknown signals as addresses of new state variables; we then continue the design process with the new signals, i.e., we operate with the logarithmic derivative function $F = d\ell n/dt$ on the newly introduced signals.

3. The structure design process comes to an end when all of its branches bear arithmetic expressions A_i containing only known signals.

We shall now demonstrate this design process for the generation of the harmonic oscillation $x_0(t) = A \sin \omega_0 t$. Following the procedure outlined above, we obtain

$$Fx_0 = \omega_0 \cos \omega_0 t / \sin \omega_0 t = \omega_0 x_1 \quad , \qquad x_1 = A \cos \omega_0 t / x_0$$

$$Fx_1 = -\omega_0 \sin \omega_0 t / \cos \omega_0 t - \omega_0 x_1 = -\omega_0 (x_2 + x_1) \quad , \quad x_2 = 1/x_1$$

$$Fx_2 = \omega_0 (x_1 + x_2)$$

Figure 2 shows the structure obtained using this design principle; it is in fact a representation of the sine signal by a completely imaginary structure. However, this has nothing to do with the numerical quality of the sine generator produced in this way. In our example the sine generator actually has quite bad properties, because it produces singularities after every quarter of a period.

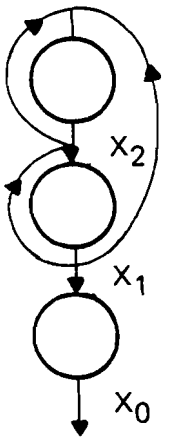

Figure 2. The structure obtained using the proposed design principle.

In general we can always direct the structure design process in such a way that linear superposition of state variables will be preserved and that all products or quotients of state variables can be replaced by linear superpositions because of the corresponding property of the logarithmic function. If this requirement is met at all stages of the structure design process we will always ultimately obtain a unified system description in the form of the well-known Lotka-Volterra equations [1,4,10]:

$$Fx_i = \sum G_{ij}x_j + \sum H_{is}y_s \quad ,$$

where the y_s represent input variables in the nonautonomous case.

The question immediately arises as to which types of ordinary differential equations can be treated with this structure design principle. There is no easy answer to this question, but the following guidelines may be useful:

1. All state variables of the original system of ordinary differential equations and all newly introduced intermediate state variables must possess a sufficient number of derivatives.

2. All zeros of the original state variables and newly introduced state variables cause singularities in the corresponding Lotka-Volterra system if they are not removed by an appropriate regularization procedure. This can usually be done by shifting the variables concerned and introducing additional state variables.

3. Assuming that conditions 1 and 2 are satisfied, all ordinary differential equations which can be defined using only the basic arithmetic operations of addition, subtraction, multiplication and division can be transformed into a Volterra representation.

There are usually many Volterra representations for a given set of ordinary differential equations because of the ambiguity introduced by choosing intermediate state variables. The procedure by which a given differential equation is transformed into a Volterra representation can be formalized using notation similar to the Backus notation familiar from algorithmic languages. We shall give here only a brief, nontechnical description of this procedure; the proof of this construction is given in [4]. Two notions are of importance: that of an arithmetic differential expression and that of an admissible differential equation.

An arithmetic differential expression is a rational function composed of constants, input variables, output variables and their derivatives up to a certain order (for example, up to order m for a certain output variable) and functions depending on one variable. The corresponding notion of a "function" is more general than that usually employed in algorithmic languages, but there are some restrictions, which are outlined below.

An admissible differential equation for a certain output variable x has the form:

$$p^n x = \text{arithmetic differential expression}, \quad p = d/dt$$

where the order m of the derivatives of the output variable x in the arithmetic differential expression must be smaller than n.

A "function" is a function f(x) which depends on one output variable and is itself a solution of an admissible differential equation with the differential operator q = d/dx.

Because the definition of a "function" in terms of an associated differential expression can itself depend on "functions" of the type introduced above, our design principle obviously produces a hierarchical procedure for the development of structures.

As another example, we shall use our structure design principle to derive the Volterra representation for a generalization of the famous Brusselator associated with the Prigogine school:

$$py = ay^k - \alpha y^\chi x^\lambda$$

$$px = \beta y^\chi x^\lambda - bx^\ell$$

where

y is the prey

x is the predator .

On the first step we obtain

$$Fy_0 = ay_0^{k-1} - \alpha y_0^{\chi-1} x_0^\lambda \quad , \quad y = y_0 \quad ,$$

$$Fx_0 = \beta y_0^\chi x_0^{\lambda-1} - bx_0^{\ell-1} \quad , \quad x = x_0 \quad .$$

We now introduce the following four variables:

$$y_1 = y_0^{k-1} \quad , \quad y_2 = y_0^{\chi-1} x_0^\lambda \quad ,$$

$$x_1 = x_0^{\ell-1} \quad , \quad x_2 = y_0^\chi x_0^{\lambda-1} \quad .$$

From this we immediately obtain the following Lotka-Volterra model:

$$Fy_0 = ay_1 - \alpha y_2 \quad , \quad Fx_0 = \beta x_2 - bx_1 \quad ,$$

$$Fy_1 = a(k-1)y_1 - \alpha(k-1)y_2 \quad , \quad Fx_1 = \beta(\ell-1)y_2 - b(\ell-1)x_1 \quad ,$$

$$Fy_2 = a(\chi-1)y_1 - \alpha(\chi-1)y_2 + \lambda\beta x_2 - \lambda b x_1 \quad ,$$

$$Fx_2 = a\chi y_1 - \alpha\chi y_2 + (\lambda-1)\beta x_2 - (\lambda-1) b x_1 \quad .$$

The expressions for the newly introduced state variables are obviously the first integrals of the final Volterra representation, i.e., we get a representation with some transparent redundancy.

3. EQUIVALENCE TRANSFORMATIONS FOR VOLTERRA REPRESENTATIONS AND THE CORRESPONDING NORMAL FORMS

Because intermediate state variables can be introduced during the structure design process in several ways, we can obtain a number of different Volterra representations for a given set of ordinary differential equations. These representations are in some sense equivalent because they all represent the trajectories of the same system.

There is a group of equivalence transformations which can be applied to Volterra representations; this is isomorphic to the group of regular affine transformations of a finite-dimensional vector space. However, it does not seem possible to introduce equivalence transformations for the Volterra equations themselves. We therefore have to embed the Volterra equations into the broader class of multinomial differential equations.

A multinomial differential equation in n state variables $x_i(t)$, $i = 1,2,\ldots,n$, is defined in the following way:

$$Fx_i = \sum_J A_{iJ} \prod_r x_r^{a_{Jr}} \prod_s y_s^{b_{Js}} \quad .$$

For simplicity we consider here only the autonomous case, i.e., without input variables. The driving force of a multinomial differential equation is apparently a superposition of terms, where each term has the form

$$\prod_r x_r^{a_{Jr}} \quad .$$

To avoid difficulties with complex numbers we have to assume that

only the behavior in the positive cone

$$x_i \geq 0$$

is of interest to us. For a given Volterra representation this condition can be met by means of an appropriate regularization procedure.

More generally, an augmented multinomial differential equation can be defined as follows:

$$\frac{d\phi(x_i)}{dt} = \sum A_{iJ}\phi^{-1}\left(\sum a_{Jr}\phi(x_r) + \sum b_{Js}\phi(y_s)\right) \quad .$$

All of the remarks made here in connection with equivalence transformations also hold in this more general case.

We now define homogeneous term-consistent coordinate transformations as linear regular affine transformations on the space spanned by $\ell n\, x_i$ (scalarization by the ℓn function):

$$x_i = \Pi z_r^{t_{ir}}$$

where $T = (t_{ir})$ is a regular matrix. The form of an autonomous multinomial differential equation is obviously preserved under such a transformation and we find that the matrix pairs $(T^{-1}A, aT)$ define a class of equivalent multinomial differential equations.

These transformations can be used to derive suitable normal forms for multinomial differential equations and also, indirectly, for Volterra representations, because every multinomial differential equation can immediately be transformed into a Volterra representation after renaming each different term.

We now have to consider which kind of normal forms are most suitable for our purpose, i.e., to simplify a given representation. We can obviously pursue simplification in a number of different ways, some of which are outlined below.

1. Matrix A should have as many zero elements as possible to minimize the number of terms occurring in the driving forces.

2. Matrix a should have as many zero elements as possible to minimize the number of times variables occur in the terms.

3. Matrix A should have as many zero rows as possible, because every zero row means that the corresponding transformed state variable is a first integral of term motion form, i.e., of power product form. This is also a means of reducing dimensionality.

4. Matrix a should have as many zero columns as possible, because every zero column represents a state variable that does not occur in the driving force, i.e., a state variable that can be eliminated. This is another means of dimension reduction.

5. Matrix a should, as far as possible, have rows equal to each other, because these rows are associated with the same terms, which can then be combined. This is obviously another way to reduce the number of different terms involved in the driving force.

To combine these various types of simplification is really a multiobjective decision problem because we are usually interested in pursuing several of these objectives simultaneously, and have as our control resource only one regular matrix T in n-dimensional space. One way of obtaining efficient solutions to this problem (in the vector-optimization sense) is outlined below.

We first use the resources T such that we reach a certain normal form which, for example, satisfies goal 3. Then we consider the subgroup of all regular affine transformations T for which this normal form is invariant, and use the rest of the resources contained in this subgroup to pursue another target, for example, goal 1.

We shall now demonstrate the use of the equivalence transformation procedure by means of a simple example: $x_0 = (1+b)\sin t$, where $\alpha < 1$, $b > 1$ are regularization parameters. It can be shown that a regular sine generator is given by the following Volterra

equations (all state variables x_i are assumed to be nonnegative):

$$
\begin{aligned}
Fx_0 &= \alpha(1+b)x_1 - b\alpha x_2 \\
Fx_1 &= -[\alpha(1+b)x_1 - b\alpha x_2] - \left(\frac{1}{\alpha(1+b)}\, x_3 - \frac{1}{\alpha(1+b)}\, x_4\right) \\
Fx_2 &= -[\alpha(1+b)x_1 - b\alpha x_2] \\
Fx_3 &= [\alpha(1+b)x_1 - b\alpha x_2] + \left(\frac{1}{\alpha(1+b)}\, x_3 - \frac{1}{\alpha(1+b)}\, x_4\right) \\
Fx_4 &= \left(\frac{1}{\alpha(1+b)}\, x_3 - \frac{1}{\alpha(1+b)}\, x_4\right) \quad .
\end{aligned}
$$

When we use the resource T^{-1} to transform A to $T^{-1}A$ we obviously have the chance to add any linear combination of rows of matrix A to any other. Thus, taking the following form of T^{-1}

$$
T^{-1} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 \\ -1 & 0 & 0 & 1 & -1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}
$$

we obtain the transformed matrix A as follows:

$$
T^{-1}A = \begin{bmatrix} 0 & \alpha(1+b) & -b\alpha & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{1}{\alpha(1+b)} & -\frac{1}{\alpha(1+b)} \end{bmatrix} .
$$

The new terms are given by the transformed matrix a:

$$
aT = T = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ -1 & 1 & 0 & 0 & -1 \\ -1 & 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} z_0 \\ z_0^{-1} z_1 z_4^{-1} \\ z_0^{-1} z_2 \\ z_0 z_3 z_4 \\ z_4 \end{bmatrix} .
$$

The new state variables z_i are related to the old ones x_i by the following coordinate transformations:

$$z_i = \Pi x_r^{t_{ir}^{-1}} \quad .$$

We therefore obtain the following expressions:

$$z_0 = x_0 \quad , \quad z_1 = x_0 x_1 x_4 \quad , \quad z_2 = x_0 x_2 \quad , \quad z_3 = x_0^{-1} x_3 x_4^{-1} \quad , \quad z_4 = x_4 \quad .$$

We see that the coordinates z_1, z_2, z_3 are first integrals, i.e., they are constant along trajectories. We have therefore reduced the dimension of the multinomial differential equation system to n = 2.

We now have to consider the following multinomial differential equations:

$$Fz_0 = \alpha(1+b) z_0^{-1} z_1 z_4^{-1} - b\alpha z_0^{-1} z_2$$

$$Fz_4 = \frac{1}{\alpha(1+b)} z_0 z_3 z_4 - \frac{1}{\alpha(1+b)} z_4 \quad .$$

By assigning new names to all of the different terms we can easily transform the multinomial differential equation into a Volterra representation. We therefore obtain the following equivalent Volterra representation:

$$Fy_0 = -\alpha(1+b) y_0 + b\alpha y_1 - \frac{1}{\alpha(1+b)} y_2 + \frac{1}{\alpha(1+b)} y_3$$

$$Fy_1 = -\alpha(1+b) y_0 + b\alpha y_1$$

$$Fy_2 = \alpha(1+b) y_0 - b\alpha y_1 + \frac{1}{\alpha(1+b)} y_2 - \frac{1}{\alpha(1+b)} y_3$$

$$Fy_3 = \frac{1}{\alpha(1+b)} y_2 - \frac{1}{\alpha(1+b)} y_3 \quad .$$

We recognize at once another first integral, $y_0 y_2 = \text{const}$. However, in this case it is not possible to reduce the order of an equivalent Volterra system still further, so that the application of an equivalence transformation actually leads to a reduction in dimensionality of one.

It should be noted that all of the rate equations in chemical reaction kinetics are multinomial differential equations, and thus it seems reasonable to seek their equivalent representations under the group of equivalence transformations described above.

If all of the exponents occurring in a multinomial differential equation are rational numbers, then the system can easily be transformed so that the transformed system contains terms with integer exponents.

4. THE RICCATI REPRESENTATION - AN EQUIVALENT REPRESENTATION OF LOTKA-VOLTERRA SYSTEMS

Suppose that we want to remove the autocatalytic term $G_{ii}x_i$ from the Volterra representation

$$Fx_i = \sum G_{ij}x_j \quad .$$

We can do this in the following way. We introduce new state variables ξ_i such that

$$F\xi_i = Fx_i - G_{ii}x_i$$

or

$$\xi_i = x_i/F^{-1}G_{ii}x_i \quad ,$$

where

$$F^{-1} = \exp(I), \; I = \int_0^t \quad .$$

If we want to solve the substituted form of the equation for variables x_i, we have to solve a special case of the Riccati differential equation. In this case a direct solution exists, namely

$$x_i = F(1-G_{ii}I\xi_i)^{-1/G_{ii}} \quad .$$

We shall now discuss this transformation, making the assumption that x_j is restricted to the positive cone $x_i \geq 0$ and that we

start the trajectory with the normalized initial condition $x_i(0) = 1$. The initial condition for ξ_i is then $\xi_i(0) = 1$.

Under this transformation, the Lotka-Volterra equation is replaced by the following integral equation:

$$\xi_i(t) = \prod_{j \neq i} (1-G_{jj}I\xi_j)^{-G_{ij}/G_{jj}} \quad .$$

If $G_{jj} = 0$ the factor $(1-G_{jj}I\xi_j)^{-G_{ij}/G_{jj}}$ reduces to $\exp(G_{ij}I\xi_j)$. This is a model containing multiplicative interactions. The components of this model show the following modes of behavior:

1. Quasihyperbolic increase (in finite time to infinity)
2. Quasiparabolic decrease (in finite time to zero)
3. Quasiparabolic saturation (in finite time to a nonzero level)
4. Quasihyperbolic decrease (in infinite time to zero)
5. Quasiparabolic increase (in infinite time to infinity)
6. Quasilogistic saturation (in infinite time to a nonzero level)

We may describe any equivalent representation (in terms of multinomial differential equations) of the form

$$\dot{u}_i = K_i \prod u_r^{k_{ir}}$$

as a Riccati representation of a Lotka-Volterra system.

From the integral equation derived above we can easily construct an equivalent Riccati representation by making the following substitutions:

$$\left.\begin{aligned} u_j &= 1 - G_{jj}I\xi_j \quad \text{for} \quad G_{jj} \neq 0 \ , \quad j \in A \\ u_j &= \exp(I\xi_j) \quad \text{for} \quad G_{jj} = 0 \ , \quad j \in \bar{A} \end{aligned}\right\} \ u_j(0) = 1 \quad .$$

For $j \in A$ we have $x_j = -(1/G_{jj})Fu_j$ and for $j \in \bar{A}$ we have $x_j = Fu_j$.

Thus we obtain the following Riccati representation for the u_j:

$$\dot{u}_j = -G_{jj} \prod_{r\in A-j} u_r^{-G_{jr}/G_{rr}} \prod_{s\in\bar{A}} u_s^{G_{js}} , \qquad j \in A$$

$$x_j = \frac{1}{u_j} \prod_{r\in A-j} u_r^{-G_{jr}/G_{rr}} \prod_{s\in\bar{A}} u_s^{G_{js}} , \qquad j \in A$$

$$\dot{u}_j = u_j \prod_{r\in A} u_r^{-G_{jr}/G_{rr}} \prod_{s\in\bar{A}-j} u_s^{G_{js}} , \qquad j \in \bar{A}$$

$$x_j = \prod_{r\in A} u_r^{-G_{jr}/G_{rr}} \prod_{s\in\bar{A}-j} u_s^{G_{js}} , \qquad j \in \bar{A} \quad .$$

It should be pointed out that in this case it is not necessary to assume initial conditions $u_i(0) = 1$ or to assume that the initial Lotka-Volterra system is restricted to the positive cone $x_i \geq 0$.

More generally, we can pass from a Lotka-Volterra representation to an equivalent Riccati representation by applying any substitution of the form

$$x_j = K_j F u_j , \qquad K_j \neq 0 \quad .$$

In the case where the motion is restricted to the positive cone we find that all of the Riccati state variables u_j are monotonic functions and therefore that all of the x_i are power products of monotonic functions.

The Riccati representation of a Lotka-Volterra system has some very useful properties:

1. The redundant state variables u_j can frequently be used to construct direct analytical solutions if they exist.

2. The poles which arise in a Lotka-Volterra system during the structure design procedure if the appropriate (regularization) measures are not taken are eliminated in the corresponding Riccati representation.

3. In the case where all of the exponents in the Riccati representation are integers, it is possible to use a special method based on graphs to examine the qualitative properties of both the Riccati representation and the original ordinary differential equation (see Section 5).

4. The Riccati representation provides a good basis for the design of an integrated processor for solving ordinary differential equations.

We shall now give two simple examples illustrating properties 1 and 2.

Example 1. We consider the Langevin differential equation [11]

$$\dot{q} = \alpha q - \beta q^3 \quad .$$

Without loss of generality we can assume that $q(0) = 1$, i.e., normalization. Then we have

$$Fq_0 = \alpha - \beta q_1 \quad , \qquad q = q_0$$

$$Fq_1 = 2\alpha - 2\beta q_1 \quad , \qquad q_1 = q_0^2 \quad .$$

The Riccati representation is

$$\dot{u}_0 = \exp(\alpha t) u_0 u_1^{-1/2} \quad , \quad q_0 = \exp(\alpha t) u_1^{-1/2}$$

$$\dot{u}_1 = 2\beta \exp(2\alpha t) \quad .$$

Integration leads directly to

$$u_1(t) = 1 + \frac{\beta}{\alpha} [\exp(2\alpha t) - 1]$$

and therefore the solution is

$$q_0(t) = \exp(\alpha t) / \left(1 + \frac{\beta}{\alpha} [\exp(2\alpha t) - 1]\right)^{1/2} \quad .$$

Example 2. In Section 2 we derived a Volterra representation for the sine function

$$x_0(t) = A \sin \omega_0 t \quad .$$

The resulting nonregular Volterra representation

$$Fx_0 = \omega_0 x_1$$

$$Fx_1 = -\omega_0 (x_1 + x_2)$$

$$Fx_2 = \omega_0 (x_1 + x_2)$$

produces a pole every quarter of a period. The corresponding Riccati representation in this case is

$$\dot{u}_0 = u_0 u_1 \ , \quad x_0 = u_1 \ ,$$

$$\dot{u}_1 = \omega_0 u_2 \ , \quad x_1 = u_2/u_1 \ ,$$

$$\dot{u}_2 = -\omega_0 u_1 \ , \quad x_2 = u_1/u_2 \ .$$

The behavior of the Riccati representation is clearly completely regular.

5. A METHOD OF GRAPHS FOR QUALITATIVE ANALYSIS, BASED ON THE RICCATI REPRESENTATION

The method presented here is applicable to any Riccati representation for which all exponents in the driving force are integer. In general, motion is not restricted to the positive cone in u-space.

We first present a general outline of the method.

Let us consider the equation

$$\dot{u}_i = K_i \prod u_r^{k_{ir}} \ , \quad i = 1,2,\ldots,n \ ,$$

where all the k_{ir} are integers. We now introduce the concepts of sign states and growth states.

A sign state is an admissible vector $(v_1, v_2, \ldots, v_n)$ where $v_i = \text{sgn } u_i$. The sign function sgn is defined as

$$\text{sgn } u = \begin{cases} +1 \text{ (or } +) & \text{if } u > 0 \\ 0 & \text{if } u = 0 \\ -1 \text{ (or } -) & \text{if } u < 0 \end{cases}$$

The fact that the vector has to be admissible means that not all sign state vectors are necessarily allowed; this takes into account possible restrictions on the x_i in the original Lotka-Volterra system.

A growth state is an admissible vector $(w_1, w_2, \ldots, w_n)$ where $w_i = \text{growth } u_i$. We define the growth function as follows:

$$\text{growth } u = \begin{cases} +1 \text{ (or } \uparrow) & \text{if } \dot{u} > 0 \\ 0 \text{ (or } \emptyset) & \text{if } \dot{u} = 0 \\ -1 \text{ (or } \downarrow) & \text{if } \dot{u} < 0 \end{cases} .$$

Again, the fact that the growth state must be admissible means that because of the configuration of driving forces in the Riccati representation not all combinations of $\uparrow$, $\downarrow$ and $\emptyset$ can necessarily occur.

The situation becomes clearer if we interpret the set of admissible sign states as the set of states of a graph game, and the set of admissible growth states as the set of states of another graph game. The two graph games are assumed to be interconnected. We now have to define the set of feasible actions for any state of a graph game; in our case this is easy because the feasible actions are specified completely by the given Riccati representation.

We shall now describe how the procedure works in practice. Assume that we start in any admissible sign state. Because of the integer exponents k_{ir} in the Riccati representation, the sign state and the power-product driving force uniquely define the growth state. Once in this growth state we can obtain the corresponding feasible new sign states from the previous sign state. Thus, the set of feasible actions is clearly specified in every state of both graph games. We therefore obtain two coupled graphs

with sign states and growth states as nodes; it is also possible (and sometimes useful) to consider the subgraphs containing only sign states or only growth states separately. These graphs can provide useful information about the qualitative behavior of a Riccati representation; the question is what sort of information they provide about the qualitative behavior of a given ordinary differential equation.

We demonstrate the use of this approach with the example of a hypercycle of order n = 2:

$$Fx_i = K_i x_{i+1} \quad , \quad i \bmod 2 \quad .$$

If we take arbitrary initial values we can remove the parameters K_i by substituting

$$y_i = K_{i-1} x_i \quad .$$

We therefore have to consider the following Riccati representation:

$$\dot{y}_0 = y_0 y_1 \quad .$$

$$\dot{y}_1 = y_1 y_0 \quad .$$

We draw the following inferences from the sign and growth graphs:

$$(+,+) \to (\uparrow,\uparrow) \to (+,+) \quad \text{(stable mode, explosive growth)}$$

$$(+,-) \to (\downarrow,\downarrow) \to (0,-) \to (\emptyset,\emptyset) \to (0,-)$$

$$(-,+) \to (\downarrow,\downarrow) \to (-,0) \to (\emptyset,\emptyset) \to (-,0)$$

$$(-,-) \to (\uparrow,\uparrow) \to (0,-) \to (\emptyset,\emptyset) \to (0,-)$$

$$\text{or} \to (-,0) \to (\emptyset,\emptyset) \to (-,0)$$

$$\text{or} \to (0,0) \to (\emptyset,\emptyset) \to (0,0) \quad .$$

Figure 3 shows the sign graph together with possible transitions caused by disturbances which influence only the value 0.

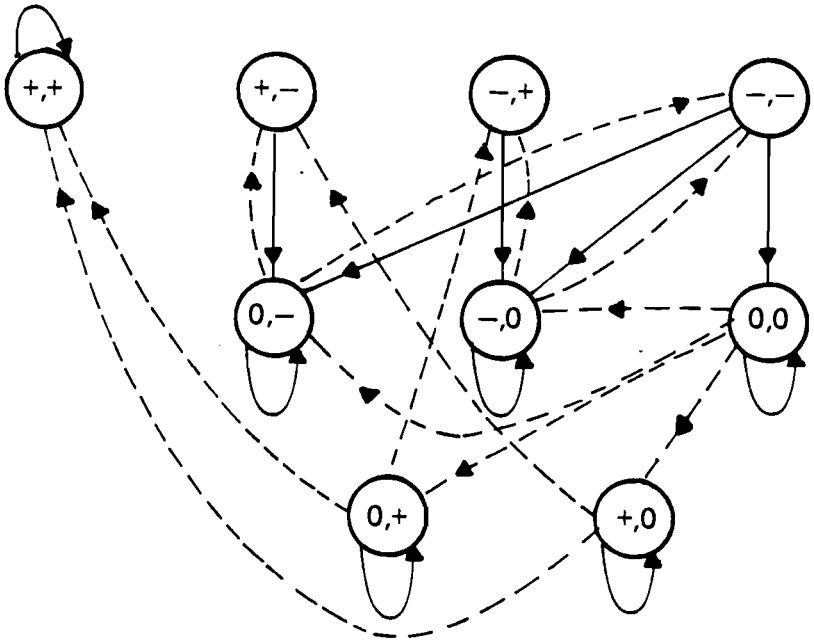

Figure 3. Sign graph and possible transitions caused by disturbances which influence only the value 0.

We see that (+,+) is the only stable focus; the other foci (which contain at least one 0) are unstable, behaving like saddle points when subject to disturbances.

6. THE HYPERLOGISTIC GROWTH MODEL AS A GENERAL MODEL FOR GROWTH FUNCTIONS

The hyperlogistic differential equation

$$\dot{x} = Kx^{k}(B-x^{w})^{\ell}$$

is a generalization of the logistic growth function (which has $k = \ell = w = 1$); many commonly used growth functions may also be represented in this general form. In addition, increases in

one-dimensional growth indicators in soft systems can usually be represented (in a phenomenological sense) by appropriate solutions of the hyperlogistic differential equation.

The analysis of many real data series using this approach is described in [4] - Figure 4 illustrates the analysis and projection of world primary energy consumption using a hyperlogistic growth model [6].

Note that only two of the three exponents k, ℓ and w are assumed to be significant, which means, for example, that w can be removed by a substitution of the form

$$y = x^w \quad .$$

It is therefore only necessary to discuss the behavior of the equation

$$\dot{x} = Kx^k(B-x)^\ell \quad .$$

With $x_0 = x$ and introducing the additional state variables

$$x_1 = x^{k-1}(B-x)^\ell \quad , \qquad x_2 = x^k(B-x)^{\ell-1}$$

we obtain the following Volterra representation:

$$\begin{aligned} Fx_0 &= Kx_1 \\ Fx_1 &= K(k-1)x_1 - K\ell x_2 \\ Fx_2 &= Kkx_1 - K(\ell-1)x_2 \end{aligned}$$

and the following Riccati representation:

$$\begin{aligned} \dot{u}_0 &= u_0 u_1^{-1/(k-1)} \quad , \qquad x_0 = u_1^{-1/(k-1)} \\ \dot{u}_1 &= -K(k-1)u_2^{-\ell/(\ell-1)} \quad , \qquad x_1 = u_2^{-\ell/(\ell-1)}/u_1 \quad , \\ \dot{u}_2 &= K(\ell-1)u_1^{-k/(k-1)} \quad , \qquad x_2 = u_1^{-k/(k-1)}/u_2 \quad . \end{aligned}$$

These representations clearly contain a second-order Lotka-Volterra model, as can be seen from Figure 2. The importance

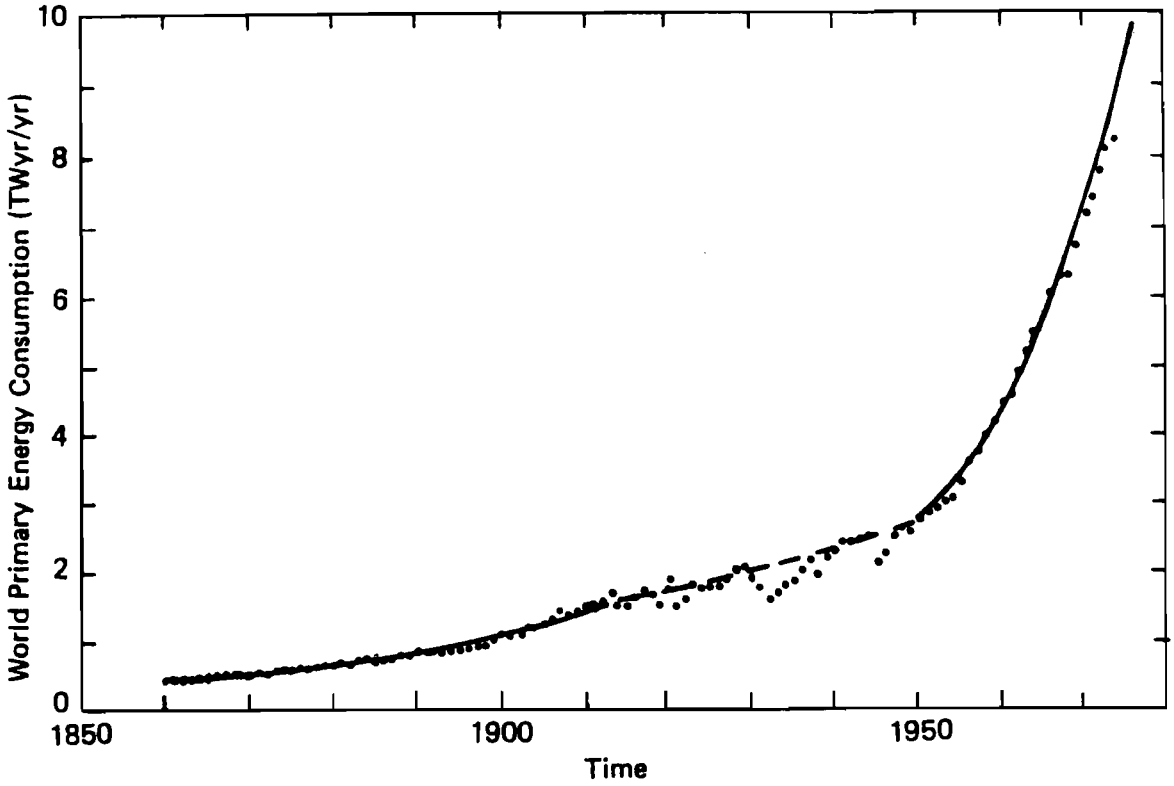

Fig. 4(a) Analysis of historical data for world energy consumption [6]. The solid line indicates the fit with a hyperlogistic growth model and the individual dots represent the observed data.

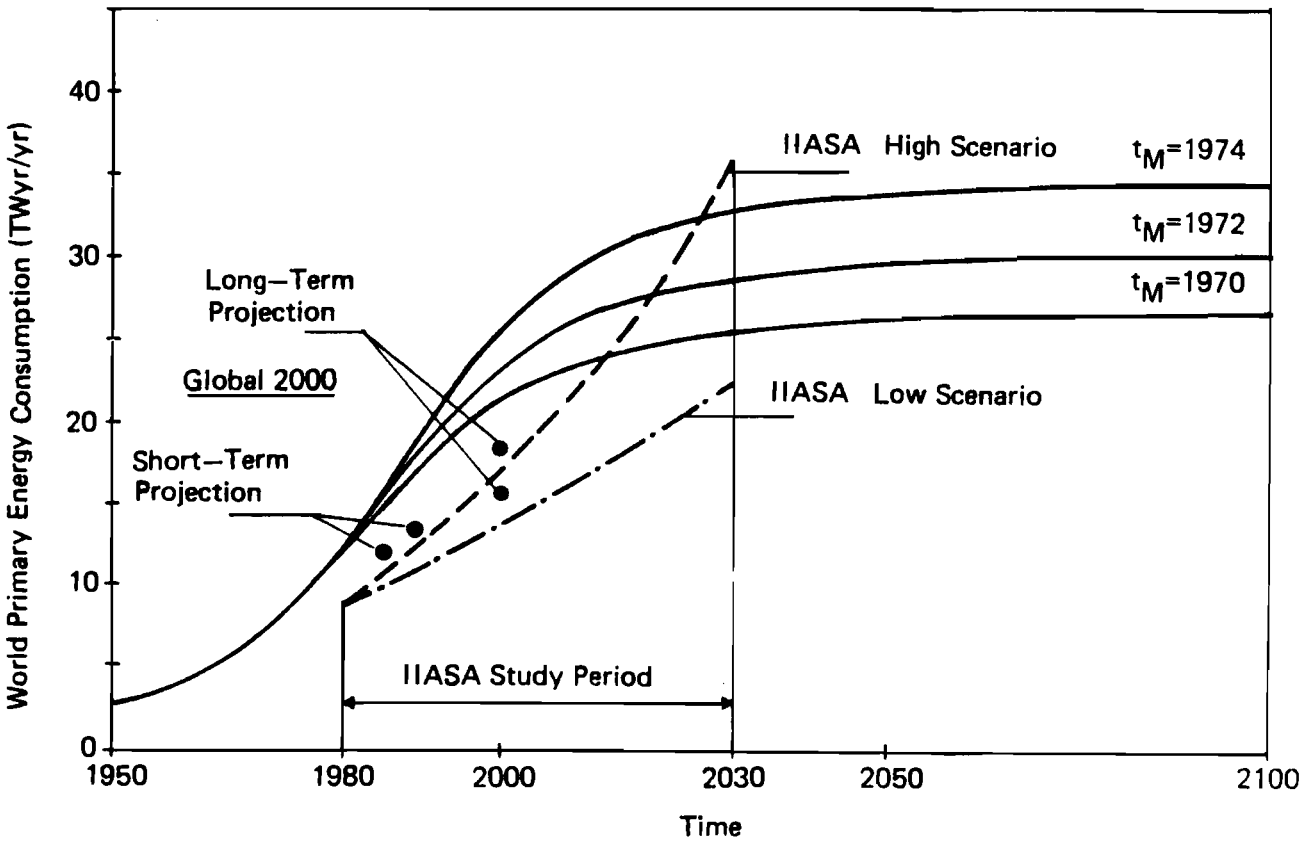

Fig. 4(b) Projection of world energy consumption [6] up to the year 2100 based on the hyperlogistic growth model presented in Fig. 4(a).

of this power-product driven model lies in the fact that in some sense it is the simplest nonlinear system exhibiting all six modes of behavior discussed in Section 4. To demonstrate this we consider the general second-order Volterra-Lotka system in the integral and differential Riccati representations. Our original Volterra equations are:

$$Fx_1 = G_{11}x_1 + G_{12}x_2$$

$$Fx_2 = G_{21}x_1 + G_{22}x_2 \quad .$$

The corresponding Riccati representations are:

$$\xi_1(t) = (1-G_{22}I\xi_2)^{-G_{12}/G_{22}}$$

$$\xi_2(t) = (1-G_{11}I\xi_1)^{-G_{21}/G_{11}}$$

which is obviously the simplest structure demonstrating all six modes of behavior, and

$$\dot{u}_1 = -G_{11}u_2^{-G_{12}/G_{22}} \quad , \quad x_1 = u_2^{-G_{12}/G_{22}}/u_1$$

$$\dot{u}_2 = -G_{22}u_1^{-G_{21}/G_{11}} \quad , \quad x_2 = u_1^{-G_{21}/G_{11}}/u_2 \quad .$$

A first integral can immediately be constructed:

$$\frac{u_1^{-G_{21}/G_{11}+1}}{G_{11} - G_{21}} - \frac{u_2^{-G_{12}/G_{22}+1}}{G_{22} - G_{12}} = C \quad .$$

We must also take into account some degenerate cases which become important later in the discussion.

For $G_{11} = G_{21}$, but $G_{22} \neq G_{12}$, the first integral becomes

$$\frac{\ell n\, u_1}{G_{11}} - \frac{u_2^{-G_{12}/G_{22}+1}}{G_{22} - G_{12}} = C \quad .$$

For $G_{12} = G_{22}$, but $G_{11} \neq G_{21}$, the first integral is

$$\frac{u_1^{-G_{21}/G_{11}+1}}{(G_{11} - G_{21})} - \frac{\ell n\, u_2}{G_{22}} = C \quad .$$

For $G_{11} = G_{21}$ and $G_{22} = G_{12}$ the first integral will be

$$\frac{\ell n\, u_1}{G_{11}} - \frac{\ell n\, u_2}{G_{22}} = C \quad .$$

In the most general case, $G_{11} \neq G_{21}$ and $G_{22} \neq G_{12}$, we introduce new variables

$$v_1 = u_1^{-G_{21}/G_{11}+1} \quad , \quad v_2 = u_2^{-G_{12}/G_{22}+1}$$

and obtain

$$\dot{v}_1 = -(G_{11}-G_{21}) v_2^{G_{12}/(G_{12}-G_{22})} v_1^{G_{21}/(G_{21}-G_{11})}$$

$$\dot{v}_2 = -(G_{22}-G_{12}) v_2^{G_{12}/(G_{12}-G_{22})} v_1^{G_{21}/(G_{21}-G_{11})}$$

so that the first integral now becomes

$$\frac{v_1}{(G_{11}-G_{21})} - \frac{v_2}{(G_{22}-G_{12})} = 0 \quad .$$

Obviously in this case both state variables v_1, v_2 have the same dynamics, determined by the general power-product driven differential equation.

We now examine the effect of introducing new variables in the other three cases.

For $G_{11} = G_{21}$, but $G_{22} \neq G_{12}$ we make the substitution

$$v_1 = \ell n\, u_1 \ , \qquad v_2 = u_2^{-G_{12}/G_{22}+1} \ .$$

The first integral will now be

$$\frac{v_1}{G_{11}} - \frac{v_2}{(G_{22}-G_{12})} = C \ .$$

The transformed differential equations are then

$$\dot{v}_1 = -G_{11}\, e^{-v_1}\, v_2^{G_{12}/(G_{12}-G_{22})}$$

$$\dot{v}_2 = -(G_{22}-G_{12})\, v_2^{G_{12}/(G_{12}-G_{22})}\, e^{-G_{21}/G_{11}v_1} \ .$$

Obviously both state variables v_1, v_2 have the same dynamics, i.e.,

$$\dot{x} = Kx^k\, e^{-\ell x} \ ,$$

which is another well-known general form for growth functions. By symmetry, the case $G_{12} = G_{22}$, $G_{11} \neq G_{21}$ yields the same result.

In the case $G_{11} = G_{21}$, $G_{22} = G_{12}$ we set

$$v_1 = \ell n\, u_1 \ , \qquad v_2 = \ell n\, u_2 \ .$$

The first integral will now be

$$\frac{v_1}{G_{11}} - \frac{v_2}{G_{22}} = C \ .$$

The transformed differential equations are then

$$\dot{v}_1 = -G_{11}\, e^{-v_1}\, e^{-v_2} \ , \qquad \dot{v}_2 = -G_{22}\, e^{-v_1}\, e^{-v_2} \ .$$

This is obviously a special case of the dynamical behavior noted previously, i.e.,

$$\dot{x} = Kx^k e^{-\ell x} \quad .$$

We have to discuss at least one more special case: that in which one of the autocatalytic terms vanishes, for example, $G_{11} = 0$. In this case we obtain

$$\dot{u}_1 = u_1 u_2^{-G_{12}/G_{22}} \quad , \quad x_1 = u_2^{-G_{12}/G_{22}}$$

$$\dot{u}_2 = -G_{22} u_1^{+G_{21}} \quad , \quad x_2 = u_1^{G_{21}}/u_2 \quad .$$

The first integral is then

$$\frac{u_1^{G_{21}}}{G_{21}} - \frac{u_2^{-G_{12}/G_{22}+1}}{(G_{22} - G_{12})} = C \quad .$$

We shall now assume $G_{21} \neq 0$ and $G_{22} - G_{12} \neq 0$. Introducing the new variables

$$v_1 = u_1^{G_{21}} \quad , \quad v_2 = u_2^{-G_{12}/G_{22}+1}$$

we obtain the following transformed differential equations:

$$\dot{v}_1 = G_{21} v_1 v_2^{G_{12}/(G_{12}-G_{22})} \quad , \quad \dot{v}_2 = (G_{22}-G_{12}) v_2^{G_{12}/(G_{12}-G_{22})} v_1 \quad .$$

Both variables show the same dynamics and the first integral now has the form

$$\frac{v_1}{G_{21}} - \frac{v_2}{(G_{22}-G_{12})} = C$$

which is obviously another special case of power-product driven dynamics.

7. THE DEVELOPMENT OF STRUCTURE AND THE LOTKA-VOLTERRA EQUATIONS

Our discussion of the development of structure is based on the following assumption: that in real systems only competition, mutation and selection determine the structure of the system - no special natural laws must be invoked. It is therefore necessary to show that structure can actually develop from these three quantitative relationships.

In this section we concentrate on the structures arising from quantitative competition in the Lotka-Volterra equations.

Schuster et al. [12] pointed out that Darwinian properties can best be studied using the replicator form of the Lotka-Volterra equations; in our opinion this is also true for the development of societies of species.

There is a standard method of transforming the Lotka-Volterra description

$$Fx_i = \sum G_{ij}x_j \quad , \qquad i = 1,2,\ldots,n$$

to the replicator form which requires us to introduce the barycentric coordinates

$$y_0 = 1/\sum x_j \quad , \qquad y_1 = x_0 x_i \quad .$$

Then, using the new coordinates y_i where $\sum_{i=1}^{n} y_i = 1$, we obtain the following differential equations:

$$Fy_i = (\sum G_{ij}y_j - \phi)/y_0 \quad , \qquad \phi = \sum y_k G_{kj} y_j \quad .$$

For $y_0 > 0$ the value of y_0 does not have an important influence on the dynamics (this is only a monotonic transformation of the time scale along the trajectories), so that for all qualitative purposes we can work with

$$Fy_i = (\sum G_{ij}y_j - \phi) \quad .$$

This is called the replication form of the Lotka-Volterra equations [12], and is qualitatively equivalent to the original Lotka-

Volterra equation. It is also possible to construct an expression quantitatively equivalent to the replicator with the help of the Riccati representation.

The Volterra representation of the replicator is

$$Fy_i = \sum_j G_{ij}y_j - \sum_{k,j} G_{kj}v_{kj}$$

$$Fv_{kj} = \sum (G_{kr}+G_{jr})x_r - 2\sum G_{kj}v_{kj}$$

where $v_{kj} = x_k x_j$. On passing to the Riccati representation we obtain the following (quantitative) equivalent to the replicator:

$$Fw_i = \sum G_{ir}w_i/w \quad , \quad y_i = w_i/w$$

where $w = \sum w_i$. All of the stationary points of the replicator equation have the form

$$y_i^* = 0 \quad \text{for} \quad i \in I \qquad (1,2,\ldots,n)$$

$$\sum G_{ij}y_j^* = \phi \quad \text{for} \quad i \in \bar{I} \quad .$$

We are interested in stable stationary points (sinks). Every stable stationary point contains a certain set I of non-vanishing species, and we consider each such set to be a possible <u>cluster</u> of the structure. The overall structure of the Lotka-Volterra system is then obtained by combining all these clusters.

This is a restricted notion of structure, because in ecology the most important clusters belong to stable limit cycles. Nevertheless, this restricted notion is very useful in solving non-linear assignment problems.

We can experiment with the structure of a Lotka-Volterra system by varying, for example, the replication rates G_{ii}. Bringing together the modified terms we obtain the following disturbed replicator equation:

$$Fy_i = \sum G_{ij}y_j - \sum G_{kj}y_k y_j + \lambda_i y_i - \sum \lambda_k y_k^2$$

or its quantitative equivalent:

$$Fw_i = \frac{\sum G_{ij}w_j + \lambda_i w_i}{w} \quad , \qquad y_i = w_i/w \quad .$$

If $\lambda_i > 0$ we call it a subvention of species i; if $\lambda_i < 0$ it becomes a tax.

As $\lambda_i \to \infty$ for all i the structure approaches a form which represents a decomposition into single species, i.e., every species forms its own cluster; by contrast, as $\lambda_i \to -\infty$ all species are grouped together into one cluster, i.e., we have a stable sink within the simplex $\sum y_i = 1$. Thus, between these two extremes, any combination of λ_i's leads to a certain configuration of clusters, the form of which is controlled by the λ_i's.

We shall now demonstrate how this cluster-building concept works for the simple example of the hypercycle of order n = 2. The quantitative equations are

$$Fw_i = \frac{K_i w_{i+1} + \lambda_i w_i}{w} \quad , \qquad i \bmod 2 \quad .$$

This leads directly to

$$F\left(\frac{w_1}{w_0}\right) = (K_1-\lambda_2)\,\frac{w_0}{w} - (K_0-\lambda_1)\,\frac{w_1}{w} \quad .$$

From this we obtain the stationary solutions

$$y_0 = \frac{K_0 - \lambda_1}{K_0 + K_1 - \lambda_1 - \lambda_0} \quad , \qquad y_1 = \frac{K_1 - \lambda_0}{K_0 + K_1 - \lambda_0 - \lambda_1} \quad .$$

For $\lambda_0 = k\lambda_1$, where k is a parameter, we obtain the result:

$$\frac{y_1}{y_0} = k + \frac{kK_0 - K_1}{\lambda_1 - K_0} \quad .$$

8. SOME GLOBAL QUALITATIVE PROPERTIES OF THE LOTKA-VOLTERRA EQUATIONS

We shall first draw some qualitative conclusions based on the transformation of the Lotka-Volterra equations to the replication form. Introducing the notion of 'biomass', defined as

$$B = \sum x_i \quad ,$$

we immediately obtain

$$\dot{B} = \psi = \sum x_k G_{kj} x_j \quad .$$

The flow ψ is obviously the driving force for the growth of the biomass B. Between this flow ψ and the flow $\phi = \sum y_k G_{kj} y_j$ introduced in the replicator equation we apparently have the relation

$$\phi = \psi / B^2 \quad .$$

However, according to Maynard-Smith most of the stationary points of the replicator equation (especially the local maxima) are evolutionary stable states, so that $d\phi/dt > 0$ in the neighborhood of these points.

In general we have:

$$F\phi = F\psi - 2FB \quad .$$

1. Let us assume that $\psi > 0$, so that the system plays the part of a predator. Because $F\phi > 0$ in the neighborhood of an evolutionary stable state we have

   $$(\psi/\psi_0) > (B/B_0)^2$$

   and

   $$B(t) > \frac{B_0}{1 - (\psi_0/B_0)t} \quad .$$

That means that the necessary input ψ is not proportional to the actual biomass but rather to the square of the biomass. Thus, the larger the system, the more inefficient is the use of this input. On the other hand, the biomass necessarily shows hyperbolic growth under these conditions - even in the case where all autocatalytic rates G_{ii} are equal to zero. We can interpret

$$\mathfrak{X} = \psi_0/B_0$$

as a measure of complexity. The growth-related complexity is high if the biomass unit absorbs much of the input (because the level of inner organization or cooperation is high). If $\mathfrak{X}$ is high, the amount of biomass "explodes" in a relatively short time.

2. Let us now assume that $\psi < 0$, so that the system as a whole represents a prey. The internal dynamics of the system are now no longer growth-oriented, but if the system nevertheless approaches an evolutionary stable state we have $d\phi/dt > 0$ so that

$$(\phi/\phi_0) < (B/B_0)^2 \quad ,$$

$$B(t) > \frac{B_0}{1 - (\psi_0/B_0)t} \quad .$$

The global biomass B is now decreasing but at a rate less than hyperbolic since $\psi_0 < 0$. This can be interpreted as meaning that the internal organization is now damping the starving process.

The biomass B will rapidly assume smaller values, we will have $B/B_0 < 1$ and the exploiting force will be greatly reduced because of the quadratic law derived above. This means that we observe a moderate exploitation of the global system by the environment, which can surely be attributed to the strength of internal links within the system.

We now pass to another global property of Lotka-Volterra systems, and consider what are known as shift cones.

We write the Lotka-Volterra equations in the form

$$Fx = \sum x_j G_{\cdot j} \quad ,$$

where $G_{\cdot j}$ is the j-th column vector of the matrix G, and restrict the motion to the positive cone $x_i \geq 0$. The vector of growth rates Fx is then a positive linear combination of the column vectors of matrix G. This leads to the following important conclusions:

1. If the zero vector is contained in the convex hull of the column vectors of matrix G,

$$0 \in H(\{G_{\cdot j}\}) \quad ,$$

then

$$0 = \sum x_j^* G_{\cdot j} \quad ,$$

where $x_j^* \geq 0$ and $\sum x_j^* = 1$. This means that the Lotka-Volterra equations have a stationary solution at which the forces driving the growth rate are vanishingly small. If, on the other hand, we have a stationary solution of the form

$$\sum \tilde{x}_j G_{\cdot j} = 0 \quad ,$$

where $\tilde{x}_j \geq 0$, then we have

$$\sum x_j^* G_{\cdot j} = 0 \quad ,$$

where $x_j^* = \tilde{x}_j / \sum \tilde{x}_s$. This means that the zero vector is again contained in the convex hull of the columns of G. In this case it is especially important that the column vectors be linearly dependent. We deduce from this that if $\det G \neq 0$ the zero vector cannot be contained in the convex hull of the column vectors $G_{\cdot j}$.

2. Let us now assume that the zero vector does <u>not</u> belong to $H(\{G_{\cdot j}\})$, i.e.,

$$0 \notin H(\{G_{\cdot j}\}) \quad .$$

In this case the zero vector and $H(\{G_{\cdot j}\})$ together span a convex cone K^* (smaller than a half-space), which we shall call a shift cone.

We now consider the trajectories of the system in the new coordinates

$$y_i = \ell n\, x_i$$

scaled by taking natural logarithms. It turns out (see Fig. 5) that for $t \geq t_0$ and any reference point $y(t_0)$, the velocity vector dy/dt of any trajectory is directed into the cone

$$y(t_0) + K^*$$

while for $t < t_0$ the velocity vector dy/dt is directed into the cone

$$y(t_0) - K^* \quad .$$

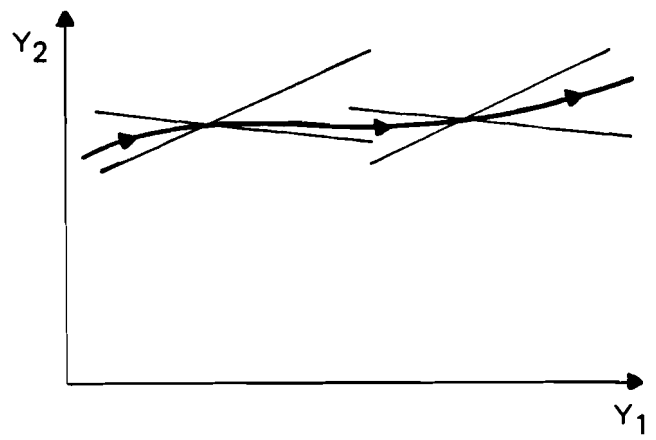

Figure 5. Trajectories of the system in the new coordinates.

This is very similar to the situation that exists with regard to "light-cones" in the theory of special relativity and is an important restriction on motion in such systems (all trajectories in this cone resemble deformed straight lines). In particular, if such a shift cone exists no cyclical motion (limit cycles, spirals or combinations of these elements) is possible.

The parameter k belongs to the cone k dual to k^* if the following relation holds for all $k^* \in K^*$:

$$(k,k^*) \geq 0 \quad .$$

The dual cone K is also a convex cone (smaller than a half space) and is spanned by a finite number of straight line generators, i.e., all vectors f^i, where

$$(f^i,G_{\cdot j}) \geq 0 \quad , \quad j = 1,2,\ldots,n \quad .$$

For every such f^i we construct a function

$$K_{f^i}(x) = \Pi x_r^{f_r^i}$$

which leads to the result

$$FK_{f^i} = \sum (f^i,G_{\cdot j})x_j \geq 0 \quad .$$

This means that the functions

$$K_{f^i}(x)$$

are Ljapunov functions which can only increase along the trajectories of the system. In particular, if det $G \neq 0$ we can choose $G_{\cdot j}$ to be a new coordinate base in n-dimensional vector space, so that we obtain the f^i as vectors of the so-called dual base where $(f^i,G_{\cdot j}) = 0$. The dual cone K is then identical with the positive cone spanned by the dual base $\{f^i\}$.

We can then apply an equivalence transformation, taking the K_{f^i} as new coordinates for the trajectories, which gives

$$FK_{f^i} = x_i \quad .$$

This means that the cone K^* is now the positive cone (Pareto cone) and in this new coordinate system we can construct the Riccati representation.

9. SOME NUMERICAL ISSUES IN THE SIMULATION OF NONLINEAR SYSTEMS USING VOLTERRA OR RICCATI REPRESENTATIONS

If we transform a given ordinary differential equation into a Volterra representation using our structure design principle it can happen that the roots of the original differential equations or the roots of the intermediate signals introduced in the design process produce poles in the Volterra representation. This occurs because we can pass from one coordinate orthant to another only through infinity. We can usually eliminate this phenomenon by suitable rescaling but then we have to introduce additional state variables, which means that the dimension of the problem increases. It is not clear whether it is always possible to get rid of these unwanted poles: some but not necessarily all of them can be removed by transforming the Volterra representation into an equivalent Riccati representation.

In the Riccati representation we have to deal with monotonically changing state variables which can either increase very quickly, leading to an overflow, or decrease very quickly, leading to a computer zero. Sometimes rapidly increasing variables are compensated analytically by rapidly decreasing variables, but this is also dangerous from the numerical point of view even if there is a finite limit - we call this the l'Hôpital catastrophe.

In some senses these properties are inherent in the representations under consideration; we have already shown that one of the specific properties of nonlinear systems is that explosion and extinction can occur in a finite time. However, we must try to overcome these numerical difficulties in some way. In the case of the Riccati representation the following rescaling is often helpful:

$$\dot{u}_i = K_i \Pi u_r^{k_{ir}} , \qquad x_i = \Pi u_r^{\ell_{ir}} .$$

We can change the scale of u_r by a factor k_r and require that x_i be invariant, i.e.,

$$0 = \sum \ell_{ir} \ell n \, k_r .$$

This makes sense only if these equations have solutions. These degrees of freedom can be used to transform the parameters of the Riccati representation as follows:

$$\dot{u}_i = \frac{K_i}{k_i} \Pi k_r^{k_{ir}} \Pi u_r^{k_{ir}} .$$

However, the best approach seems to be to look for a regular Volterra or Riccati representation.

We have found that a system of ordinary differential equations can be globally embedded into a Riccati representation; this means that all of the original trajectories then become trajectories of a single Riccati representation.

The behavior of nonlinear systems is usually approximated by a set of locally linear models using a local Taylor expansion. However, it is also possible to approximate the behavior of a given ordinary differential equation by a set of local Riccati representations. This can be done in the following way, making use of the discrete chain concept outlined in Section 1. Consider first the functions of time $x_0(t)$. We construct a first-order discrete chain

$$\frac{\ell n \, x_0(t) - \ell n \, x_0(t_0)}{\ell n (t/t_0)} = K_0$$

and determine the parameter K_0:

$$K_0 = \left. \frac{t \, d \ell n \, x_0(t)}{dt} \right|_{t = t_0} .$$

This leads to the following local model of $x_0(t)$:

$$X_{M_0}(t) = x_0(t_0)(T/T_0)^{K_0} \quad .$$

If we use a higher-order discrete chain we can determine higher-order local models in the same way, just as higher-order local models can be obtained by the Taylor series approach.

This principle can be simply extended to nonlinear ordinary differential equations. We shall consider functions of the following form (i.e., with independent arguments):

$$x = f(z_1, z_2, \ldots, z_n) \quad .$$

We first make use of the first-order discrete chain concept

$$\ell n\, f(z) = \ell n\, f(z^0) + \sum a_i \ell n (z_i / z_i^0)$$

where

$$a_i = z_i \left. \frac{\partial \ell n\, f(z)}{\partial z_0} \right|_{z = z^0} \quad .$$

This leads to the following family of local power-product models:

$$f_M(z) = f(z^0) \prod (z_i / z_i^0)^{a_i} \quad .$$

This procedure is then repeated for the driving forces of an autonomous ordinary differential equation

$$\dot{z}_i = f_i(z_1, z_2, \ldots, z_n) \quad ,$$

resulting in the following local Riccati representation:

$$\dot{z}_{iM} = f_i(z^0) \prod (z_j / z_j^0)^{a_{ij}} \quad .$$

We thus have two extreme situations which can arise when constructing a Riccati representation of a given ordinary differential equation. On the one hand we can construct a single global

Riccati representation of a given ordinary differential equation by introducing many additional state variables; on the other we can approximate the solutions of this differential equation by a family of local Riccati representations without introducing any new state variables at all. There is, of course, a whole spectrum of intermediate possibilities. We could, for example, stop the structure design process before obtaining a complete finite Lotka-Volterra representation, i.e., after having introduced a relatively small number of additional state variables, and then approximate the right-hand side with a family of local Riccati representations.

We thus conclude that it is necessary to find some compromise between the number of additional state variables and the number of local Riccati models.

10. NUMERICAL ADVANTAGES OF MODELING LINEAR SYSTEMS USING THE LOTKA-VOLTERRA APPROACH (SEE [3])

At first sight one might think that there would be no point in trying to simulate the behavior of a linear system

$$\dot{z}_i = \sum A_{ij} z_j$$

using the Lotka-Volterra approach. Why should we abandon the linear superposition principle for a higher-dimensional nonlinear representation? However, linear systems have some properties which lead very simply to regular Volterra representations.

By shifting the origin of the coordinate system we can in most cases produce a situation in which the trajectories of the linear system do not leave the positive cone $z_i \geq 0$. This is then sufficient for regularization because we cannot obtain a Volterra representation by multiple differentiation. It is then only necessary to divide the velocities $\dot{z}_i$ by z_i, which leads to

$$\frac{\dot{z}_i}{z_i} = \sum A_{ij} \frac{z_j}{z_i} \quad .$$

This is a special case of a more general Volterra quotient system of the type

$$Fz_i = \sum A_i^{rs} z_r/z_s \quad .$$

These equations can easily be transformed into a Volterra representation by introducing additional state variables

$$v_{rs} = z_r/z_s \quad ,$$

leading to the Volterra representation

$$Fz_i = \sum A_i^{rs} v_{rs}$$

$$Fv_{rs} = \sum (A_r^{mn} - A_s^{mn}) v_{mn} \quad .$$

The autocatalytic terms

$$G_{rs} = (G_r^{rs} - G_s^{rs})$$

have an important effect on the numerical properties. In particular, if all of the state variables v_{mn} (where $mn \neq rs$) are numerically stable, then the numerical stability of v_{rs} essentially depends on the sign of G_{rs}, being stable for $G_{rs} < 0$ and unstable for $G_{rs} > 0$. This property has particular advantages when dealing with linear systems, since in this case the following hypothesis is likely to be true (under certain minor additional conditions):

If $A = (A_{ij})$ is the matrix of a stable linear system, i.e., all roots of the characteristic equation $\det(A-\lambda E)$ possess negative real parts, then the Volterra representation derived above always contains at least n equations with negative autocatalytic or resource parameters.

We will demonstrate this for a linear system of order n = 2:

$$\dot{z}_1 = A_{11}z_1 + A_{12}z_2$$

$$\dot{z}_2 = A_{21}z_1 + A_{22}z_2 \quad .$$

In this case we have the following Volterra representation:

$$Fz_1 = A_{11} + A_{12}v_{21}$$

$$Fz_2 = A_{21}v_{12} + A_{22}$$

$$Fv_{21} = A_{21}v_{12} - A_{12}v_{21} + A_{22} - A_{11}$$

$$Fv_{12} = - A_{21}v_{12} + A_{12}v_{21} + A_{11} - A_{22} \quad .$$

The characteristic equation of the linear system is

$$\lambda^2 - \lambda(A_{11}+A_{22}) + A_{11}A_{22} - A_{12}A_{21} = 0 \quad .$$

The linear system is stable under the conditions

$$A_{11} + A_{22} < 0$$

$$A_{11}A_{22} - A_{12}A_{21} > 0 \quad .$$

At least one of the elements A_{11} or A_{22} must be negative. If only one of them is negative, then necessarily $\mathrm{sgn}(A_{12}A_{21}) < 0$, so that a linear equation and a v-equation are damped; if both elements A_{11} and A_{22} are negative, then both linear equations are damped. It is obviously necessary to distinguish between damping by autocatalytic terms and damping by "resources" in these linear equations.

If the system is unstable, for example if it fulfills the condition

$$A_{11} + A_{22} > 0 \quad ,$$

then this would be consistent with $A_{12} < 0$ and $A_{21} < 0$.

11. CONCLUSIONS

The approach presented in this paper is based on the observation that ecological systems can be described by chains and cycles of rate-coupled evolving systems. Applying this description to arbitrary nonlinear nonstationary systems governed by sets of ordinary differential equations leads to a new flexible structure design procedure which makes it possible to describe the original system by a system of Volterra equations (a Volterra representation). Using a nonlinear transformation, the Volterra equations can be converted into a system of differential equations, where the right-hand side consists only of a power product of states (Riccati representation). This unified system description in terms of Volterra or Riccati representations allows us to apply mathematical tools developed for the analysis of Volterra systems to a large class of nonlinear systems. The Riccati representation provides a means of characterizing the dynamics of the original system using only a few basic modes of growth. The advantages of this new approach from both the theoretical and the practical point of view have been demonstrated by examples (replication equation, analysis of world energy consumption and world population growth [4,6]).

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