Remark on the Lotka–Volterra Model

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The Lotka–Volterra equations for the population growth of a system of interacting species are linearized around equilibrium. The linear equations are solved for a special choice of the coefficients. It is shown that, in the limit of a large number of species, each one of them obeys a Langevin equation without memory. Subsequently, following Zwanzig, one species is added that is treated without linearization. The character of the equation governing its population is materially dependent on the special choice of the interaction coefficients. It is concluded that no general statement can be made concerning the stochastic behavior of the solutions of the Lotka–Volterra equations without being more specific about the coefficients than has been customary so far.

1. INTRODUCTION

Consider an ecological system of S species feeding on one another. A simplified mathematical model is provided by the Lotka–Volterra equations

$$dN_s/dt = k_s N_s + (1/\beta_s) \sum_{r=1}^{S} a_{sr} N_s N_r$$

N_s is the number of individuals of species s and k_s is its intrinsic growth rate. The quadratic term describes how an encounter between species s and r results in an increase of one at the expense of the other. Accordingly, one

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supposes $a_{sr} = -a_{rs}$ and supplies a positive "equivalence number" β_s^{-1} to account for the fact that the loss of an individual r only adds a fraction of an individual to species s. Admittedly this is a crude model, but it is hoped that it may serve to gain insight in more complex situations. For background information and literature we refer to the review paper of Goel et al.[1]

   This set of S coupled nonlinear differential equations can be solved for $S = 1$ and treated graphically for $S = 2$, but little is known about the solutions for larger S. Kerner suggested that for very large S statistical methods might be used in analogy with those of statistical mechanics. Such methods, however, are always based on rather drastic assumptions concerning randomness or absence of correlations, which even in the case of statistical mechanics are sometimes open to doubt. For this reason it is of interest to study an even more simplified model, which can be solved exactly and may therefore serve as a touchstone for the statistical assumptions.

   One such simplification was recently studied by Zwanzig.[2,3] First suppose that there is a time-independent solution $N_s^{eq} > 0$ obeying

$$\beta_s k_s + \sum_r a_{sr} N_r^{eq} = 0$$

Then write $N_s = N_r^{eq} + \Delta N_s$, so that (1) takes the form

$$\Delta \dot{N}_s = \beta_s^{-1}(N_s^{eq} + \Delta N_s) \sum_r a_{sr} \Delta N_r$$

It is then possible to study small deviations from the equilibrium solution by neglecting the quadratic terms, or else to linearize all equations but one and study the nonlinear behavior of that one species as affected by the others. We shall do both for a special choice of the matrix (a_{sr}) for which the linear equations can be solved explicitly.

2. THE SPECIAL CHOICE FOR a_{sr}

   We omit all terms quadratic in the ΔN_s and apply a scale transformation

$$\Delta N_s = (N_s^{eq}/\beta_s)^{1/2} x_s, \qquad a_{sr} = (N_s^{eq} N_r^{eq}/\beta_s \beta_r)^{1/2} c_{sr}$$

The resulting set of S coupled linear equations is

$$\dot{x}_s = \sum_r c_{sr} x_r$$

The solution for given initial values $x_s(0)$ can formally be written in terms of an evolution matrix $\mathbf{U}(t)$,

$$x_s(t) = \sum_r U_{sr}(t) x_r(0), \qquad \mathbf{U} = \exp(\mathbf{c}t)$$

Note that there is a constant of the motion

$$\tfrac{1}{2} \sum_s x_s^2 = E$$

In order to solve the equations explicitly we have to choose a special antisymmetric **c** that can be diagonalized. In order that the large number of species will actually have the effect of a random heat bath, they should all interact, that is, there must not be too many zeros among the c_{sr}. We choose therefore

$$\mathbf{c} = \begin{pmatrix} 0 & 1 & 1 & 1 & \cdots & 1 \\ -1 & 0 & 1 & 1 & \cdots & 1 \\ -1 & -1 & 0 & 1 & \cdots & 1 \\ & & & & & \\ -1 & -1 & -1 & -1 & \cdots & 0 \end{pmatrix}$$

This describes a hierarchy of species: each species is eaten by all its predecessors and eats all its successors.

The eigenvalues $i\omega_p$ and normalized eigenvectors $X_s^{(p)}$ of **c** are given by $(p = 1, 2, ..., S)$

$$\omega_p = \cot[\pi(p + \tfrac{1}{2})/S], \qquad X_s^{(p)} = S^{-1/2} \exp[2\pi i(p + \tfrac{1}{2})s/S]$$

This provides an explicit expression for the evolution matrix:

$$U_{sr}(t) = \sum_{p=1}^{S} X_s^{(p)} X_r^{(p)*} e^{i\omega_p t}$$

$$= \frac{1}{S} \sum_p \exp\left[\frac{2\pi i(p + \tfrac{1}{2})}{S}(s - r) + it \cot \frac{\pi(p + \tfrac{1}{2})}{S} \right]$$

For large S the sum tends to the integral

$$U_{sr}(t) \simeq (1/\pi) \int_0^\pi \exp[2i(s - r)\varphi + it \cot \varphi] \, d\varphi$$

The integration can be performed and gives for $t > 0$

$$U_{sr}(t) = 0 \qquad\qquad\qquad\qquad\qquad \text{for} \quad s < r$$
$$= e^{-t} \qquad\qquad\qquad\qquad\quad\, \text{for} \quad s = r$$
$$= e^{-t} \sum_{\nu=0}^{s-r-1} \binom{s - r - 1}{\nu} \frac{(-2t)^{\nu+1}}{(\nu + 1)!} \qquad \text{for} \quad s > r$$

This result demonstrates that, although for finite S all normal modes are oscillatory, in the limit $S \to \infty$ an irreversible damping appears.

3. THE LANGEVIN EQUATION FOR INDIVIDUAL SPECIES

For any particular species k one has

$$x_k(t) = e^{-t}x_k(0) + G(t)$$

where $G(t)$ only involves the initial values of other species,

$$G(t) = \sum_{r \neq k} U_{kr}(t)x_r(0)$$

Accordingly, one also has, putting $G + \dot{G} = L$,

$$\dot{x}_k(t) = -x_k(t) + L(t)$$

This has the form of a Langevin equation, although so far L does not have the properties of a Langevin force but is merely some linear expression in the initial values of the other species.

Now consider an ensemble of solutions determined by a canonical distribution of the initial values in x space,

$$P(x_1, x_2, ..., x_s) = \text{const} \times e^{-E/\theta}$$

Extract the subensemble in which x_k has its assigned initial value $x_k(0)$. Averaging over this subensemble, one finds of course $\langle L(t) \rangle = 0$, and furthermore

$$\begin{aligned}
\langle G(t)G(t') \rangle &= \sum_{r,s \neq k} U_{kr}(t)U_{ks}(t')\theta\,\delta_{rs} \\
&= \theta U_{kk}(t - t') - \theta U_{kk}(t)U_{kk}(t') \\
&= \theta\{\exp(-|t - t'|) - \exp(-t - t')\}
\end{aligned}$$

From this one easily derives

$$\langle L(t)L(t') \rangle = 2\theta\,\delta(t - t')$$

Thus *in the limit of large S each species obeys the Langevin equation, the Langevin force L being supplied by the interaction with other species.* This result implies that there is no memory in the behavior of $x_k(t)$.

4. ZWANZIG'S MODEL

We now add one more species x and do not linearize its equation:

$$\dot{x} = (1 + \alpha x)\sum_s c_s x_s$$

$$\dot{x} = \sum_r c_{sr}x_r - c_s x$$

Here $\alpha = (N^{eq}/\beta)^{-1/2}$ and the c_s are some set of constants. Following Zwanzig,[2] we have omitted terms involving products $x_s x$ as well.

Substitution of the solution of the second line into the first line yields an equation for $x(t)$ alone of the form

$$\dot{x} = (1 + \alpha x)\left\{ -\int_0^t K(t - t')x(t')\, dt' + F(t) \right\}$$

The memory kernel K and the force F are

$$K(t) = \sum_{sr} c_s U_{sr}(t)c_r = \sum_p e^{i\omega_p t}\left| \sum_s c_s X_s^{(p)} \right|^2$$
$$F(t) = \sum_{sr} c_s U_{sr}(t)x_r(0)$$

For a canonical ensemble, $\langle F(t) \rangle = 0$ and one easily verifies

$$\langle F(t)F(t') \rangle = \theta K(t - t')$$

The quantities $\sum c_s X_s^{(p)}$ arise from the c_s by a unitary transformation and can therefore be given almost any value by suitably choosing the c_s, subject only to the restriction that these must be real. Hence the function $K(t)$ may have almost any form, subject to the restriction that its Fourier transform is positive (as befits a correlation function). We consider two special cases.

First take all c_s equal to 1 (the added species eats all others) or all equal to -1 (the added species is eaten by all others). Then for large S one finds

$$K(t) = 2\,\delta(t)$$

so that the equation for x has no memory. Rather, its probability density obeys a Fokker–Planck equation

$$\frac{\partial P(x, t)}{\partial t} = 2\frac{\partial}{\partial x} x(1 + \alpha x)P + \theta\frac{\partial^2}{\partial x^2}(1 + \alpha x)^2 P$$

If one takes $c_s = 1$ for $\alpha S < s < \beta S$ and zero outside, one finds

$$K(t) = (2\pi i t)^{-1}(e^{it\cot\beta\pi} - e^{it\cot\alpha\pi})$$

which approximates a delta function for $\beta \to 1$, $\alpha \to 0$, but otherwise has a memory.

As the second case, suppose that the c_s consist of a random row of $+1$ and -1. Since there are many terms in each frequency interval, this amounts to writing

$$K(t) = \sum_p e^{i\omega_p t} \sum_{s,r} X_s^{(p)} X_r^{(p)*}\overline{c_s c_r}$$
$$= \sum_p e^{i\omega_p t} \sum_s |X_s^{(p)}|^2 = S e^{-|t|}$$

Owing to the factor S, the evolution of $x(t)$ is very rapid, and we scale the time accordingly: $t = S^{-1/2}\tau$.

$$\frac{dx}{d\tau} = (1 + \alpha x)\left\{-\int_0^\tau \left(\exp -\frac{\tau - \tau'}{\sqrt{S}}\right) x(\tau')\, d\tau' + \Phi(\tau)\right\}$$

where $\Phi(\tau) = S^{-1/2}F(t)$. For large S this reduces to

$$\frac{dx}{d\tau} = (1 + \alpha x)\left\{-\int_0^\tau x(\tau')\, d\tau' + \Phi(\tau)\right\}$$

with

$$\langle\Phi(\tau)\rangle = 0, \qquad \langle\Phi(\tau)\Phi(\tau')\rangle = \theta$$

These equations indicate that (on the time scale on which x evolves) *the memory is complete*, in the sense that the influence of past values of x does not die out.

On the other hand, the memory is very limited, in the sense that it can be eliminated at the expense of introducing one higher derivative:

$$\frac{d}{d\tau}\frac{1}{1 + \alpha x}\frac{dx}{d\tau} = -x$$

The substitution $1 + \alpha x = e^u$ yields the equation

$$d^2u/d\tau^2 = 1 - e^u$$

This is the equation of motion for a classical particle in a potential $V(u) = e^u - u$, from which it follows that all solutions are periodic.

Our general conclusion is that the results depend strongly on the special form of the matrix (a_{rs}), and that no universal statements about the behavior in time are possible without a more detailed specification of that matrix.

REFERENCES

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