

Generalized Verhulst Laws for Population Growth

(competition)

ROBERT ZWANZIG

Institute for Fluid Dynamics and Applied Mathematics, University of Maryland, College Park Md. 20742

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ABSTRACT The growth or decay of population of a single species interacting with a large number of other species (or environment) according to the Volterra-Lotka model is investigated. When the environment is initially very close to its equilibrium level, the growth of a single species follows a generalized Verhulst law, containing hereditary effects. The derivation, modeled on statistical mechanical theories of Brownian motion, leads also to a "noise" source and to its relation to the heredity kernel. A special case, where the hereditary kernel is a damped exponential function of time, is solved numerically. When growth starts at a level much below equilibrium, the population first overshoots equilibrium and then approaches it. When decay starts at a level much higher than equilibrium, the population first decays precipitously to a very low level and then slowly grows toward equilibrium.

In mathematical treatments of population dynamics (1) two distinct models are often used. One is the Verhulst model (leading to the familiar S-shaped logistic curve); this model describes the growth or decay of a single species towards its equilibrium population. The other is the Volterra-Lotka model ("big fish eat little fish..."); this model describes the competitive interaction of several species, and generally leads to periodic fluctuations in their populations. We show here that the Verhulst model follows from the Volterra-Lotka model when certain intuitively plausible conditions are met.

This treatment actually leads to a 2-fold generalization of the Verhulst model. In the first place, we find hereditary effects of a type discussed first by Volterra (2). In the second place, we find a natural explanation for noise in Verhulst models; this provides a foundation for analyses of noise effects by Leigh (3) and by Goel *et al.* (1).

A special case of this generalized Verhulst model is solved numerically to illustrate possible consequences of hereditary effects. When a population grows from a low level, it may overshoot equilibrium and then approach it by damped oscillations. When a population decays from a high level, it may fall substantially below equilibrium in a very short time and then grow as if it were starting off at a low level. This behavior is a consequence of "remembering the past," and is not observed in the absence of hereditary effects.

The method used here was suggested by recent work on the statistical mechanical theory of Brownian motion (4). In this application, the "Brownian particle" is a particular species, and the particle's environment or "heat bath" corresponds to the set of many other species interacting with the species of interest. The interaction is governed by the equations of motion of the Volterra-Lotka model.

Verhulst model

The Verhulst model is defined as follows. Let $N_0(t)$ be the population of a single species (labeled by the subscript 0) at time t , and let Q_0 be the equilibrium population of that species. Then Verhulst's equation of motion is

$$(d/dt)N_0 = -kN_0(N_0 - Q_0) \quad [1]$$

where k is a rate constant. The main result of this article is a generalization of Eq. 1 to include hereditary and noise effects.

Volterra-Lotka model

The Volterra-Lotka model is defined as follows. We consider a set of $n + 1$ species, labeled by $j = 0, 1, 2, \dots, n$. The actual population of the j th species is $N_j(t)$. Then Volterra's equations of motion are

$$dN_j/dt = e_j N_j + b_j^{-1} \sum a_{jk} N_j N_k \quad [2]$$

Here e_j is the intrinsic birth or death rate for the j th species; b_j^{-1} is termed the "equivalence number" for that species; and a_{jk} is an antisymmetric matrix describing the interactions between species.

Let us suppose that equilibrium populations Q_j exist for all species. Then they are found from the linear equations

$$e_j + b_j^{-1} \sum a_{jk} Q_k = 0. \quad [3]$$

We may use this to eliminate the e_j and rewrite the Volterra equations in the form

$$dN_j/dt = b_j^{-1} \sum a_{jk} N_j (N_k - Q_k). \quad [4]$$

By appropriate scaling of the populations N_j and the matrix a_{jk} , the equivalence numbers can be eliminated; we assume that this has been done, and set all b_j equal to one.

It should be noted that the equilibrium populations exist in general only when the system contains an even number of species. If the number of species is odd, equilibrium populations may exist if the vector (e_0, e_1, \dots) is in the null space of the matrix a_{jk} .

The derivation

We start with the complete set of Volterra equations, and ask: Under what conditions will the evolution of one species follow an equation of the Verhulst type? No attempt will be made at mathematical rigor; intuition and heuristic arguments will be used.

We expect that the Verhulst model may apply to situations where a new species is introduced into an environment, or where some sudden change in birth rate or feeding habits causes a sudden change in the equilibrium population of a species already existing in an environment. Let us imagine that this happens at time $t = 0$. At this initial time, species 1 to n are near their equilibrium levels,

$$N_j(0) \simeq Q_j (j = 1, 2, \dots, n) \quad [5]$$

but the zeroth species may be substantially displaced from its equilibrium level,

$$N_0(0) \neq Q_0. \quad [6]$$

The evolution of the zeroth species is governed by

$$dN_0(t)/dt = N_0(t) \sum_{j=1}^n a_{0j} [N_j(t) - Q_j]. \quad [7]$$

Note that the sum ranges from $j = 1$ to $j = n$. The evolution of the j th species, where $j \neq 0$, may be separated into two parts,

$$dN_j(t)/dt = N_j(t) \sum_k' a_{jk} [N_k(t) - Q_k] + N_j(t) a_{j0} [N_0(t) - Q_0]. \quad [8]$$

In the first term on the right-hand side, the sum over k ranges from $k = 1$ to $k = n$. These equations are still exact.

Now we linearize them in the deviations $N_j - Q_j$, for $j \neq 0$. The new variables x_j are defined by

$$N_j(t) = Q_j + Q_j^{1/2} x_j(t); j \neq 0; \quad [9]$$

and a new matrix c_{jk} is defined by

$$c_{jk} = Q_j^{1/2} a_{jk} Q_k^{1/2}; j, k \neq 0. \quad [10]$$

Eq. 8 becomes

$$dx_j(t)/dt = (1 + x_j/Q_j^{1/2}) \sum_k' c_{jk} x_k + Q_j^{1/2} (1 + x_j/Q_j^{1/2}) a_{j0} (N_0 - Q_0). \quad [11]$$

According to our hypothesis about the initial state, all x_j are initially small. Let us suppose that they remain small for all subsequent times, or

$$|x_j(t)| \ll Q_j^{1/2}. \quad [12]$$

We discuss the validity of this assumption later. Then Eq. 12 may be linearized,

$$dx_j(t)/dt = \sum_k' c_{jk} x_k + Q_j^{1/2} a_{j0} (N_0 - Q_0). \quad [13]$$

This equation can be solved as an initial value problem. The solution involves the exponential matrix operator

$$U_{jk}(t) = (\exp ct)_{jk}, \quad [14]$$

where, as before, the indices are not equal to zero. The solution is

$$x_j(t) = \sum_k' \int_0^t dt' U_{jk}(t - t') Q_k^{1/2} a_{k0} [N_0(t') - Q_0] + \sum_k' U_{jk}(t) x_k(0). \quad [15]$$

When this solution is substituted into the equation for dN_0/dt ,

and terms are collected, we obtain

$$dN_0(t)/dt = -N_0(t) \int_0^t dt' K(t - t') [N_0(t') - Q_0] + N_0(t) F(t) \quad [16]$$

The kernel $K(t)$, representing hereditary effects on population growth, is given explicitly by

$$K(t) = - \sum_j \sum_k a_{0j} Q_j^{1/2} U_{jk}(t) Q_k^{1/2} a_{k0}. \quad [17]$$

The "noise" is fully determined by all of the initial deviations $x_k(0)$,

$$F(t) = \sum_j \sum_k a_{0j} Q_j^{1/2} U_{jk}(t) x_k(0). \quad [18]$$

Eqs. 16-18 are the main result of this derivation.

Kerner (5) constructed a statistical mechanical theory of Volterra-Lotka systems; this has been reviewed and extended by Goel *et al.* (1). A central feature of this theory is the use of a biological ensemble analogous to the canonical ensemble of statistical thermodynamics. The statistical properties of the noise, in Kerner's biological ensemble, are as follows. $F(t)$ is a Gaussian random variable, with zero mean value, and with the second moment

$$\langle F(t)F(t') \rangle = \theta K(t - t') \quad [19]$$

where θ is analogous to a temperature,

$$\langle x_j x_k \rangle = \theta \delta_{jk}. \quad [20]$$

The approximation

The preceding derivation was based on a semilinearization of the Volterra-Lotka equations. How reliable is this? It seems difficult to make any general statements; however, explicit calculations can be made in the two species case. Let us suppose that $N_1(0) = Q_1$. Then the condition expressed in Eq. 12 is equivalent to

$$\log Q_0/N_0(0) \ll Q_1/2Q_0 \quad [21]$$

when $N_0(0)$ is much smaller than its equilibrium value, and

$$N_0(0)/Q \ll Q_1/2Q_0 \quad [22]$$

when $N_0(0)$ is much larger than its equilibrium value. If the equilibrium population Q_1 of the other species is sufficiently large, these conditions can be met for interesting values of $N_0(0)$. In general, we may expect that the semilinearization is useful whenever all Q_j are sufficiently large (for $j \neq 0$).

The heredity kernel

The heredity kernel is determined by all of the interaction constants a_{jk} and by the equilibrium populations, and so little can be said in general about its properties. However, the matrix c_{jk} is antisymmetric; if n is even, its eigenvalue spectrum is a set of complex conjugate pairs $\pm i\omega_m$, where m ranges from 1 to $n/2$, and if n is odd, there is an extra zero eigenvalue. This means that the kernel can be written in the form

$$K(t) = \sum K_m \cos \omega_m t. \quad [23]$$

Note in particular that $K(0)$ is always positive.

Properties of functions similar to $K(t)$ were discussed by Goel *et al.* (1) in their review of Volterra systems. When the number of species is very large, and the interaction matrix

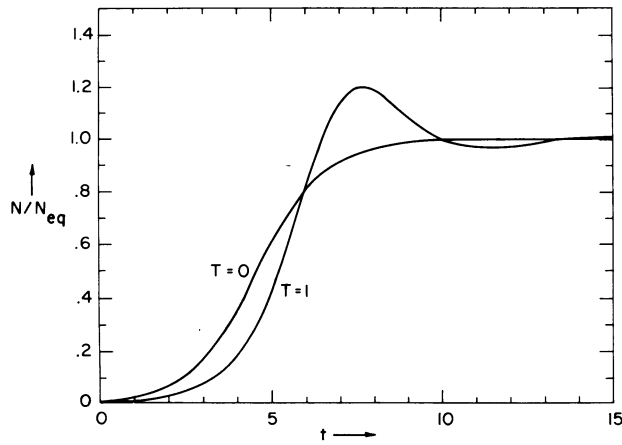


FIG. 1. Population growth from $N(0) = Q_0/100$. The Verhulst limit is labeled $T = 0$, and an example of the heredity effect is labeled $T = 1$.

(or food web) is sufficiently diverse, $K(t)$ is expected to decay from its initial value to a “noise level” of the order of $1/n^{1/2}$. This decay, which need not be monotone, takes place in a characteristic time T . At times much longer than this, recurrent behavior typical of any almost-periodic function will occur. As long as we are concerned with phenomena only on time scales of the order of T (or small multiples thereof), we may ignore the later recurrences.

During this early period, $K(t)$ is described qualitatively by two parameters, the initial value $K(0)$ and the decay time T .

An illustration

As an illustration which is expected to show the principal qualitative effects of the heredity kernel, we take a special case where $K(t)$ decays exponentially,

$$K(t) = K(0) \exp(-t/T), \tag{24}$$

and we neglect the noise term. Then the generalized Verhulst equation becomes

$$dN_0(t)/dt = -K(0)N_0(t) \int_0^t dt' \times \exp(-(t-t')/T)[N_0(t') - Q_0]. \tag{25}$$

This can be converted to a second-order differential equation as follows. We introduce a new variable $v(t)$,

$$v(t) = \log N_0(t)/Q_0 \tag{26}$$

so that

$$dv(t)/dt = -K(0)Q_0 \int_0^t dt' \times \exp(-(t-t')/T)[\exp v(t') - 1]. \tag{27}$$

On taking another time derivative, we obtain an ordinary differential equation,

$$T d^2v/dt^2 = -dv/dt - K(0)TQ_0[\exp v - 1]. \tag{28}$$

The initial conditions are

$$(v)_{t=0} = \log N_0(0)/Q_0; (dv/dt)_{t=0} = 0. \tag{29}$$

Eq. 28 may be viewed as the equation of motion of a particle. The coordinate is v , the mass is T , the potential is

$$U(v) = K(0)Q_0T[\exp v - v], \tag{30}$$

and there is an added frictional force $-dv/dt$ on the particle. This analogy suggests the kinds of behavior to be expected. For example, in the limit of infinite T , or constant $K(t)$, the motion is periodic. With large finite T , the motion is oscillatory but damped. Because of the asymmetry of the potential, motions starting with large positive $v(0)$ will be quite different from motions starting with large negative $v(0)$. The definite integral of $K(t)$ is $k = K(0)T$; this quantity is analogous to the rate constant k in the Verhulst equation. In the limit $T \rightarrow 0$, with k held constant, the second derivative term drops out of Eq. 28, and the resulting equation is precisely the Verhulst equation (in logarithmic form). When $T \neq 0$, then hereditary effects appear.

Figs. 1 and 2 show solutions of the generalized Verhulst equation, obtained by numerical integration. In both cases, we have fixed the time scale by setting k equal to unity. Also, in both cases we show results for the Verhulst limit $T = 0$, and also for $T = 1$.

In Fig. 1, a population grows from an initial value $N(0) = Q_0/100$ to the equilibrium value Q_0 . In the Verhulst limit, the growth is monotone. When $T = 1$, the growth starts out more slowly, then accelerates, overshoots, and relaxes to equilibrium.

In Fig. 2 (note the logarithmic scale here!) a population decays from an initial value $N(0) = 100 Q_0$ to the equilibrium value Q_0 . In the Verhulst limit, the decay is monotone and is essentially complete within three or four time units. When $T = 1$, the initial decay is slower and is followed by a substantial drop below equilibrium. The population is almost wiped out within two or three time units. Then it gradually grows back up to equilibrium, as if it had started out at a very low level. This striking behavior is due to the inertia associated with hereditary effects, and would not occur if the system did not “remember” its past. (Of course, the system has no choice; its behavior is fully determined by the Volterra-Lotka parameters. If this species were also to change its habits, i.e., to vary its birth rate or interactions with the environment, then the story might be different.)

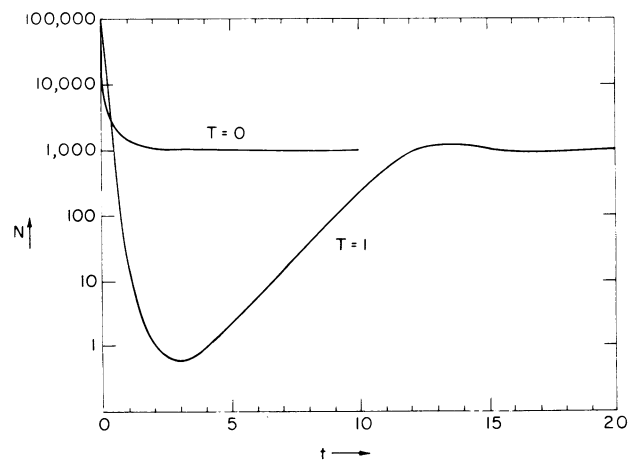


FIG. 2. Population decay from $N(0) = 100 Q_0$. Note the logarithmic scale. The Verhulst limit is labeled $T = 0$, and an example of the heredity effect is labeled $T = 1$.

Remarks

Several topics for further investigation suggest themselves immediately, but will not be treated in detail. The derivation given here can be extended trivially to the evolution of several species rather than just one. This provides a means for introducing saturation-inducing terms, with heredity, in the Volterra-Lotka equations for two or more interacting species.

Models other than that of Volterra and Lotka can be used as starting points. For example, Montrolls (6) has suggested a model in which the logarithms of populations obey linear equations. This model seems to be connected with Gompertz's law of population growth in the same way that the Volterra-Lotka model is connected with Verhulst's law. A special advantage of Montroll's model is that our semilinearization becomes exact, rather than an approximation.

Finally, we observe that it would be desirable to perform computer experiments on systems of very many interacting

species, with interaction constants and equilibrium populations chosen at random, to see what kind of hereditary kernel is actually appropriate for such systems.

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