



Population Growth as a Nonlinear Stochastic Process

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Abstract—The evolution of the probability density of a biological population is described using nonlinear stochastic differential equations for the growth process and the related Fokker-Planck equations for the time-dependent probability densities.

It is shown that the effect of the initial conditions disappears rapidly from the evolution of the mean of the process. But the behaviour of the variance depends on the initial condition. It may monotonically increase, reaching its maximum in the steady state, or have a rather complicated evolution reaching the maximum near the point where growth rates (not population size) is maximal. The variance then decreases to its steady-state value.

This observation has implications for risk assessments associated with growing populations, such as microbial populations, which cause food poisoning if the population size reaches a critical level. © 2003 Elsevier Ltd. All rights reserved.

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1. INTRODUCTION

The study of growth is a central problem in biology. To describe growth, biologists have used a differential equation in the form

$$dx = (\alpha - \beta x^{m-1}) x dt, \quad m \geq 2. \quad (1)$$

Here x is the size of an organism or a biological population and α is the Malthusian growth parameter. The second term in equation (1) describes the restriction in growth, which occurs due to the effects of crowding and competition for resources, typical in biological growth. An example of this formulation is the logistic equation ($m = 2$). Another equation, which incorporates a limit on size, is the Gompertz equation

$$dx = (\alpha - \beta \ln x) x dt. \quad (2)$$

These equations are deterministic, and ignore the effect of random fluctuations on the growth of the population. It is generally assumed that such random fluctuations are independently and identically distributed about the growth path described by equation (1) or (2). In each case it is assumed that the fluctuations do not interact with the growth law described by the deterministic equation.

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A more general approach is to recognise that the fluctuations are an intrinsic part of the growth process and include them into the formulation of the equations. This approach does not involve any unreasonable assumptions of independence of the growth path and previous fluctuations. These are naturally included in dynamics.

This paper investigates the situation when the deterministic growth equations are replaced by their stochastic forms, noting particularly the relationship between the mean and the variance of the process as growth proceeds.

2. THE MODEL

There are different ways to incorporate stochastic components into deterministic models (1) or (2). In the process under consideration the fluctuations are assumed to be faster than $\tau_{\text{macro}} = 1/\alpha$, which characterises the time scale of the evolution of the macroscopic variables in these equations. Random fluctuations, such as rapid environmental changes, affect the system through external parameters. Suppose that the parameter α in equation (1) or (2) is regarded as a random variable in the form

$$\alpha_t = \alpha + \sigma \xi_t, \quad (3)$$

where α is the mean, ξ_t is Gaussian white noise, and σ is the intensity of the noise. Then equations (1) and (2) are replaced by stochastic differential equations (SDE) for the random process X_t .

$$dX_t = (\alpha - \beta X_t^{m-1}) X_t dt + \sigma X_t dW_t \quad (4)$$

and

$$dX_t = \alpha X_t \ln \left(\frac{x^*}{X_t} \right) dt + \sigma X_t dW_t, \quad (5)$$

respectively.

W_t in equations (4) and (5) is a Wiener process. For convenience, $\beta = \alpha \ln x^*$ has been substituted in equation (5) and it is assumed that the variable x is dimensionless, i.e., the equations describe changes in relative population size. Aspects of these models have been considered by different authors (see, for example, [1] and references therein, [2,3]).

The choice of an appropriate diffusion process, i.e., the choice between the Ito and Stratonovich interpretations of the above SDEs depends on the nature of the process being modelled. In the case considered here there are no qualitative differences in any of the results between either approach. However, for definiteness, the Ito stochastic calculus is used here.

3. THE RESULTS

Each solution of an SDE describes one realisation, or growth path. The ensemble of realisations generated by an SDE is described by a transitional probability density $P(x, t)$, which satisfies the corresponding Fokker-Planck equation

$$\frac{\partial P(x, t)}{\partial t} = -\frac{\partial}{\partial x} f(x)P(x, t) + \frac{\sigma^2}{2} \frac{\partial^2}{\partial x^2} x^2 P(x, t), \quad (6)$$

where $f(x) = (\alpha - \beta x^{m-1})x$ or $\alpha x \ln x^*/x$, respectively.

The steady-state probability $P_s(x)$ density can be evaluated from this. For equation (4) this is

$$P_s(x) = N_s x^{2(\alpha/\sigma^2 - 1)} \exp \left(-\frac{2\beta x^{m-1}}{\sigma^2(m-1)} \right). \quad (7)$$

And for the Gompertz model,

$$P_s(x) = N_s x^{2(\alpha \ln x^*/\sigma^2 - 1)} \exp \left(-\frac{\alpha \ln^2 x}{\sigma^2} \right), \quad (8)$$

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