# Population Growth in Random Environments: Which Stochastic Calculus?

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# Population Growth in a Random Environment: Which Stochastic Calculus?

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## 1. Introduction

Let $N = N(t)$ be the size (number of individuals, density, biomass) of a population (of animals, plants, bacteria, cells) at time $t \geq 0$ and assume the initial population size $N(0) = N_0 > 0$ is known. A general density dependent growth model assumes that the *per capita growth rate* (abbrev. *growth rate*) has the form $\frac{1}{N}\frac{dN}{dt} = f(N)$, where $f(\cdot) : (0, +\infty) \mapsto (-\infty, +\infty)$ is a continuously differentiable function such that the limit $f(0^+) := \lim_{N\downarrow 0} f(N)$ exists (may be infinite) and $F(0^+) := \lim_{N\downarrow 0} F(N) = 0$ (no spontaneous generation), where $F(N) = Nf(N)$ is the *total growth rate* of the population.

In a randomly varying environment, the growth rate $\frac{1}{N}\frac{dN}{dt}$ will have an "average" value $f(N)$ and random perturbations that we approximate by $\sigma\varepsilon(t)$, where $\varepsilon(t)$ is a standard white noise (formally the generalized function derivative of the standard Wiener process $W(t)$) and $\sigma$ is the *noise intensity*. The resulting *stochastic differential equation* (SDE) model is $\frac{1}{N}\frac{dN}{dt} = f(N) + \sigma\varepsilon(t)$ or

$$dN(t) = F(N(t))dt + V(N(t))dW(t), \tag{1}$$

where $V(N) = \sigma N$. Equation (1) is equivalent to the stochastic integral equation

$$N(t) = N_0 + \int_0^t F(N(s))ds + \int_0^t V(N(s))dW(s). \tag{2}$$

We will assume also that $f$, besides the above assumptions, is such that the boundaries $N = 0$ and $N = +\infty$ are unattainable (so that the solution of the SDE exists, is unique and has values in $(0, +\infty)$) and the moments required in this paper do exist (see Braumann, 2007a, for mild sufficient conditions).

Models of this sort have been proposed in the literature with specific forms of the function $f$. Levins (1969) was the pioneer work. Beddington and May (1977) launched the harvesting models, where a harvesting term is added to the growth equations. A list of references can be seen in Braumann (1999a,b), where, for non-harvesting and harvesting models respectively, the properties of the general model with arbitrary $f$ (satisfying only reasonable assumptions) were studied, including conditions for non-extinction and for the existence of a stationary probability density.

There is, however, a problem with these models. The second integral in (2) cannot be defined as a classical Riemann-Stieltjes integral because the Wiener process $W(t)$ is of unbounded variation. If we consider a sequence of decompositions $0 = t_{0,n} \leq t_{1,n} \leq ... \leq t_{n,n} = t$ $(n = 1, 2, ...)$ with diameters converging to zero, the Riemann-Stieltjes sums $\sum_{i=1}^{n} V(N(\tau_{i,n}))\,(W(t_{i,n}) - W(t_{i-1,n}))$ have different mean square (m.s.) limits depending on the choice of the intermediate points $\tau_{i,n} \in [t_{i-1,n}, t_{i,n}]$. Among the many possible choices, two stand out in the literature.

One is the non-anticipative choice $\tau_{i,n} = t_{i-1,n}$ that defines the *Itô integral*. Itô calculus has nice probabilistic properties but does not satisfy ordinary rules. In particular, it satisfies a different chain rule of differentiation. Namely, if $Y(t) = h(t, N(t))$, with $h(t, x)$ of class $C^{1,2}$, we get

$$(I)\quad dY = \left(\frac{\partial h(t,N)}{\partial t} + \frac{\partial h(t,N)}{\partial x}F(N) + \frac{1}{2}\frac{\partial^2 h(t,N)}{\partial x^2}V^2(N)\right)dt + \frac{\partial h(t,N)}{\partial x}V(N)dW \tag{3}$$

instead of the usual rule (applicable to Stratonovich calculus)

$$(4) \qquad (S) \quad dY = \left(\frac{\partial h(t,N)}{\partial t} + \frac{\partial h(t,N)}{\partial x}F(N)\right)dt + \frac{\partial h(t,N)}{\partial x}V(N)dW.$$

We have used "$(I)$" or "$(S)$" to distinguish between the Itô and the Stratonovich calculi. The *Stratonovich integral* is, under adequate regularity conditions, the m.s. limit of

$$\sum_{i=1}^{n}\left(\frac{V(N(t_{i-1,n}))+V(N(t_{i,n}))}{2}\right)(W(t_{i,n})-W(t_{i-1,n}))\,.$$

This integral anticipates ("guesses") a bit into the future and does not have the nice probabilistic properties of the Itô integral. The Itô and Stratonovich calculi are the ones commonly used in the literature. For more details on them, see, for instance, Arnold (1974) or Øksendal (2003).

The problem is that the solutions of SDE depend on the stochastic calculus used. For instance, when $f(N) \equiv r$ (Malthusian model), we have, under Stratonovich calculus, that extinction occurs with probability one if the "average" growth rate $r$ is negative and extinction has zero probability of occurring if $r$ is positive. This behavior is similar to the deterministic case ($\sigma = 0$). However, if one uses Itô calculus, extinction occurs with probability one when $r < \sigma^2/2$. Will a population with small (smaller than $\sigma^2/2$) positive "average" growth rate $r$ be extinct ir not?

The answer depends on the calculus used and this is a source of controversy and mistrust.

The same question can be asked for a general strictly decreasing function $f$, since Braumann (1999a) has shown, for Stratonovich calculus, that extinction occurs with probability one if $f(0^+)$ ("average" growth rate at low population sizes) is negative and occurs with zero probability (there is even a stationary probability density) if $f(0^+)$ is positive. However, for Stratonovich calculus the criteria is whether $f(0^+)$ is smaller or larger than $\sigma^2/2$.

There are recommendations, based on some limit theorems, on which calculus to use depending on whether generations are discrete and noise is white in discrete time (Itô calculus) or generations are continuous and noise is slightly colored (Stratonovich calculus) but reality is more complex than that. A paper resolving partially the controversy in the asymptotic regime is Braumann (1983). The resolution of the controversy in the Malthusian example just mentioned is in Braumann (2003). The full resolution of the controversy for models of type (1) with arbitrary $f$ is in Braumann (2007a) (see also Braumann, 2007b, for the case of harvesting models), as well as references on the history of the controversy. A brief account is made on Section 2. However, we have only considered the case of constant noise intensity $\sigma$. Here, in Section 3, we extend the resolution to cases where the noise intensity $\sigma(N)$ might vary with population size.

## 2. The resolution of the controversy for constant noise intensity

We will show that the controversy is due to the wrong presumption that $f(x)$, taken as the "average" growth rate when population size has size $x$, means the same average under the two calculi. To avoid such semantic confusion upon which rests all the controversy in the literature, we will use $f_i$ and $f_s$ to denote $f$ according to whether we use Itô or Stratonovich calculus.

Of course, for the deterministic model $\frac{dN}{dt} = F(N) = Nf(N)$, the (*per capita*) growth rate $R(x)$ when population size is $x$ at time $t$, is by definition $R(x) := \frac{1}{x}\left(\frac{dN}{dt}\right)_{N=x} = \frac{1}{x}\lim_{\Delta t\downarrow 0}\frac{N(t+\Delta t)-x}{\Delta t} = f(x)$.

However, for the stochastic models, $N(t+\Delta t)$ is a random variable and so is $R(x)$. So, we look for an average growth rate. Let us consider the *arithmetic average*, which is the usual expected value. Of course, since we are considering the situation that at time $t$ the population size is $x$, we should take the expectation conditioned on that knowledge. Let us denote it by $\mathbf{E}_{t,x}[...] = \mathbf{E}[...|N(t) = x]$. Then, the *arithmetic average growth rate* when population size is $x$ at time $t$, is defined by

$$(5) \qquad R_a(x) := \frac{1}{x}\lim_{\Delta t\downarrow 0}\frac{\mathbf{E}_{t,x}[N(t+\Delta t)]-x}{\Delta t}.$$

We could, however, consider the *geometric average growth rate* defined by

$$R_g(x) := \frac{1}{x} \lim_{\Delta t \downarrow 0} \frac{\exp\left(\mathbf{E}_{t,x}[\ln N(t+\Delta t)]\right) - x}{\Delta t}. \tag{6}$$

Consider the Itô and the Stratonovich SDE

$$(I) \quad dN(t) = f_i(N(t))N(t)dt + \sigma N(t)dW(t) \tag{7}$$

$$(S) \quad dN(t) = f_s(N(t))N(t)dt + \sigma N(t)dW(t). \tag{8}$$

The solutions (see Arnold, 1974) are homogeneous diffusion processes with common diffusion coefficient

$$b(x) := \lim_{\Delta t \downarrow 0} \frac{\mathbf{E}_{t,x}[(N(t+\Delta t) - x)^2]}{\Delta t} = V^2(x) = \sigma^2 x^2 \tag{9}$$

and drift coefficients, respectively

$$a_i(x) := \lim_{\Delta t \downarrow 0} \frac{\mathbf{E}_{t,x}[N(t+\Delta t) - x]}{\Delta t} = f_i(x)x \tag{10}$$

$$a_s(x) := \lim_{\Delta t \downarrow 0} \frac{\mathbf{E}_{t,x}[N(t+\Delta t) - x]}{\Delta t} = f_s(x)x + \frac{1}{4}db(x)/dx = (f_s(x) + \sigma^2/2)x. \tag{11}$$

Therefore, from (5), (10), and (11), we obtain the *arithmetic average growth rate* when population size is $x$ at time $t$, respectively for the Itô SDE (7) and the Stratonovich SDE (8):

$$R_a(x) = \frac{1}{x}a_i(x) = f_i(x) \tag{12}$$

$$R_a(x) = \frac{1}{x}a_s(x) = f_s(x) + \sigma^2/2. \tag{13}$$

If one makes the change of variable $Y = \ln N$, applying to equations (7) and (8) the chain rules (3) and (4), one obtains $(I)\ dY = (f_i(e^Y) - \sigma^2/2)dt + \sigma dW(t)$ and $(S)\ dY = f_s(e^Y)dt + \sigma dW(t)$, respectively. So, with $y = \ln x$, the drift coefficients $\lim_{\Delta t \downarrow 0} \frac{\mathbf{E}_{t,x}[Y(t+\Delta t) - y]}{\Delta t}$ for $Y$ are, respectively, $f_i(e^y) - \sigma^2/2$ and $f_s(e^y)$. Therefore, from (5), one obtains the *geometric average growth rate* when population size is $x$ at time $t$, respectively for the Itô SDE (7) and the Stratonovich SDE (8):

$$R_g(x) = f_i(x) - \sigma^2/2 \tag{14}$$

$$R_g(x) = f_s(x). \tag{15}$$

Conclusion: Contrary to what has been presumed in the literature, $f(x)$ **means two different "average" growth rates under the two calculi. It is the arithmetic average growth rate under Itô calculus and the geometric average growth rate under Stratonovich calculus**. Taking into account the difference between the two averages, the results of the two calculi completely coincide. In fact, the apparently different solutions of the Itô SDE (7) and the Stratonovich SDE (8) are indeed the same, namely the homogeneous diffusion process with diffusion coefficient (9) and drift coefficient $xR_a(x)$. They looked different because, instead of using a concrete average growth rate, we were expressing them in terms of an unspecified "average" wrongly assumed to be the same average under the two calculi. For the particular case of strictly decreasing growth rate $f$, extinction will occur for both calculi when the geometric average growth rate at low population sizes $R_g(0^+)$ is negative.

## *3. The case of density-dependent noise intensities*

We now consider the generalization to a density-dependent noise intensity $\sigma(N)$, assumed to be a positive continuously differentiable function for $N > 0$ such that $\sigma(0^+)$ exists and $V(0^+) = 0$, where $V(N) = \sigma(N)N$. The diffusion and drift coefficients are now

$$b(x) = V^2(x) = \sigma^2(x)x^2 \tag{16}$$

$$a_i(x) = f_i(x)x \tag{17}$$

$$a_s(x) = f_s(x)x + \frac{1}{4}\frac{db(x)}{dx} = \left(f_s(x) + \sigma^2(x)/2 + x\sigma(x)\sigma'(x)/2\right)x. \tag{18}$$

We obtain for the *arithmetic average growth rate* when population size is $x$ at time $t$

$$(19) \qquad R_a(x) = a_i(x)/x = f_i(x)$$

$$(20) \qquad R_a(x) = a_s(x)/x = f_s(x) + \sigma^2(x)/2 + x\sigma(x)\sigma'(x)/2,$$

respectively for the Itô SDE and the Stratonovich SDE. So, the arithmetic average growth rate is still $f_i(x)$ for the Itô SDE. However, $f_s(x)$ is no longer the geometric average growth rate.

The function $\phi(x) = \int_c^x \frac{1}{z\sigma(z)}dz$ (where $c$ is an fixed arbitrary positive constant) is strictly increasing for $x$ positive, and so it has an inverse $\phi^{-1}$. Let us consider the $\phi$-*average growth rate*

$$(21) \qquad R_\phi(x) := \frac{1}{x}\lim_{\Delta t\downarrow 0}\frac{\phi^{-1}\left(\mathbf{E}_{t,x}[\phi(N(t+\Delta t))]\right) - x}{\Delta t}.$$

Notice that, when $\sigma(x)$ is a constant $\sigma$, this is just the geometric average.

Under Stratonovich calculus, $Y = \phi(N)$ satisfies the SDE $(S)$ $dY = \frac{f_s(\phi^{-1}(Y))}{\sigma(\phi^{-1}(Y))}dt + dW(t)$, and so, in terms of $Y$, the drift coefficient is $\lim_{\Delta t\downarrow 0}\frac{\mathbf{E}_{t,x}[Y(t+\Delta t)-y]}{\Delta t} = \frac{f_s(\phi^{-1}(y))}{\sigma(\phi^{-1}(y))}$, where $y = \phi(x)$. Therefore, $\mathbf{E}_{t,x}[Y(t+\Delta t)] = y + \frac{f_s(\phi^{-1}(y))}{\sigma(\phi^{-1}(y))}\Delta t + o(\Delta t)$. Apply $\phi$ to both sides, expand about $y$ and notice that $\frac{d\phi^{-1}(y)}{dy} = \frac{1}{d\phi(x)/dx} = x\sigma(x)$ to obtain $\phi^{-1}\left(\mathbf{E}_{t,x}[Y(t+\Delta t)]\right) = x + xf_s(x) + o(\Delta t)$. From (21) we get

$$(22) \qquad R_\phi(x) = f_s(x).$$

Thus, for Stratonovich calculus, $f_s(x)$ is the $\phi$-*average growth rate*. Again, taking into account the difference between the arithmetic and the $\phi$-average, the results of the two calculi coincide.

## *4. Conclusion*

We have extended the resolution of the controversy on whether to use Itô or Stratonovich calculus when modeling population growth in a random environment to the case of density-dependent noise intensities. Again we show that what was thought to mean the "average" growth rate meant really different types of averages, the arithmetic average under Itô calculus and a $\phi$-average under Stratonovich calculus (coinciding with the geometric average for the case of constant noise intensity). Taking into account the difference between the two averages, the two calculi give completely coincidental results.

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