# Ito versus Stratonovich Calculus in Random Population Growth

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A general (animal or bacterial) population growth model in a randomly fluctuating environment is the stochastic differential equation (SDE) $dN_t/dt = N_t(g(N_t) + \sigma\varepsilon_t)$ **(1)**, where $N = N_t$ is the size at time $t$, $g(N)$ is the "average" *per capita* growth rate, and $\sigma\varepsilon_t$ is the effect of environmental fluctuations ($\sigma > 0$, $\varepsilon_t$ standard white noise). Models of this type have been dealt with in the literature (since [1]) for several specific functions $g(N)$. We consider the general case with any (smooth) $g(N)$.

The issue here is the use of Ito or Stratonovich calculus to interpret (1).

To show its importance, assume $g(+\infty) < 0$, $G(0^+)$=0 (with $G(N) = Ng(N)$), and $g$ strictly decreasing. Using Stratonovich calculus, the fate of the population depends upon the "average" *per capita* growth rate at low densities $g(0^+)$ being negative or positive. If negative, extinction occurs with probability 1; if positive, there is no extinction and population size has a stationary density (converges in distribution as $t \to \infty$ to a r.v. $N_\infty$ having a p.d.f.). The result is proven in [2] and extended in [3] to models with harvesting. However, if one uses Ito calculus, the fate of the population depends upon $g(0^+)$ being $< \sigma^2/2$ or $> \sigma^2/2$ (even positive "average" *per capita* growth rates at low densities can lead to extinction).

For the controversy in the literature on which calculus is more appropriate see [4] and references therein. We will show that the real issue is merely semantic and is due to the informal interpretation of $g(x)$ as being the "average" *per capita* growth rate (when population size is $x$), when indeed this rate should be defined in terms of the observed process.

For the deterministic case ($\sigma = 0$), the obvious definition of the *per capita* growth rate, at time $t$ when population size is $N_t = x$, is $g_d(x) :=$

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$\frac{1}{x}\frac{dN_t}{dt} = \frac{1}{x}\lim_{\Delta\downarrow 0}\frac{N_{t+\Delta}-x}{\Delta} = g(x)$. Let us now look at the SDE (1). $N_{t+\Delta}$ is now random and we should take some kind of average on it. Denoting by $\mathbf{E}_{t,x}$ the conditional expectation given $N_t = x$, we can use (assuming sufficient regularity), for instance, an arithmetic or a geometric average: $g_a(x) := \frac{1}{x}\lim_{\Delta\downarrow 0}\frac{\mathbf{E}_{t,x}[N_{t+\Delta}]-x}{\Delta}$ or $g_g(x) := \frac{1}{x}\lim_{\Delta\downarrow 0}\frac{\exp(\mathbf{E}_{t,x}[\ln N_{t+\Delta}])-x}{\Delta}$.

We show that the so-called (non-specified) "average" *per capita* growth rate $g(x)$ means: (a) under Ito calculus, the arithmetic average $g_a(x)$; (b) under Stratonovich calculus, the geometric average $g_g(x)$.

Taking into account the difference $\sigma^2/2$ between the two averages, the two calculi yield the same solution to the SDE (1) when written in terms of a well-defined average like (for example) $g_g(x)$. The apparent difference was due to the semantic confusion of taking the informal term "average growth rate" as meaning the same average. We now have (for both calculi!) extinction or a stationary density according to whether the geometric average *per capita* growth rate at low densities $g_g(0^+)$ is $< 0$ or $> 0$.

A further paper will consider density-dependent noise intensities $\sigma(N)$.

## References

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