

Growth and extinction in randomly varying environments: modelling and optimization using stochastic differential equations

Crecimiento y extinción en ambientes que varían aleatoriamente: modelamiento y optimización mediante ecuaciones diferenciales estocásticas

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Abstract—This paper presents a brief overview of a range of applications of stochastic differential equations (SDE) in describing the growth of wildlife populations living in randomly varying environments and the associated risks of extinction, including profit optimization issues in the particular case of fish or other populations subjected to harvesting. The same basic ideas apply also to the growth of individual animals and how to optimize the profit of the farmers that raise such animals.

Keywords—Stochastic differential equations, random environments, population growth models, extinction, fisheries, individual growth models, profit optimization

Resumen— Este artículo presenta una breve descripción de una gama de aplicaciones de las ecuaciones diferenciales estocásticas (SDE) para describir el crecimiento de poblaciones de vida silvestre que viven en condiciones ambientales que varían aleatoriamente y los riesgos asociados de extinción, incluidos los problemas de optimización de ganancias en el caso particular de peces u otras poblaciones sometido a recolección. Las mismas ideas básicas se aplican también al crecimiento de animales individuales y cómo optimizar las ganancias de los granjeros que crían tales animales.

Palabras clave— Ecuaciones diferenciales estocásticas, ambientes aleatorios, modelos de crecimiento poblacional, extinción, pesquerías, modelos de crecimiento individual, optimización de ganancias

INTRODUCTION

The growth of a wildlife population over time or the growth of an individual animal from birth to maturity are often described by a deterministic growth curve, usually the solution of an ordinary differential equation (ODE) that describes the dynamics of the growth process. For example, if we have Gompertz growth dynamics, the size $X(t)$ of the population at time $t \geq 0$ or of an individual animal at age

$t \geq 0$ would be described by the ODE

$$\frac{dX(t)}{dt} = rX(t) \ln \frac{K}{X(t)},$$

where $K > 0$ is the asymptotic size and $r > 0$ is a speed of growth parameter, the solution of which is the Gompertz curve $X(t) = K \left(\frac{x_0}{K}\right)^{\exp(-rt)}$, where $x_0 = X(0) > 0$ is the initial size. Of course, $X(t) \rightarrow K$ when $t \rightarrow +\infty$ and K is called the *carrying capacity* of the environment in the population growth literature and it is the *size at maturity* for

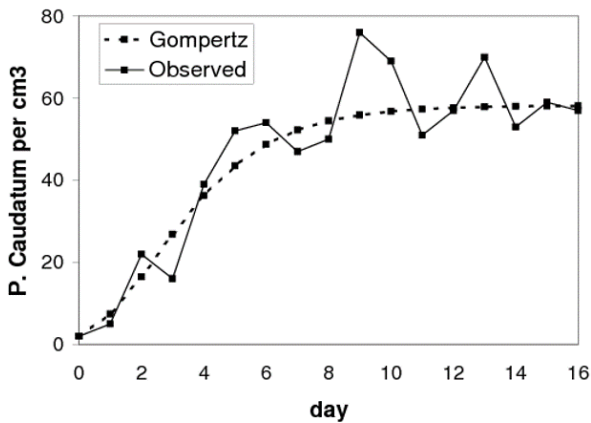


Figure 1: Time evolution of the population size (measured in individuals per cm^3) of a lab protozoan population (data from (Gause, 1934)). The solid broken line represents the observed data and the dashed smooth curve is the estimated Gompertz curve.

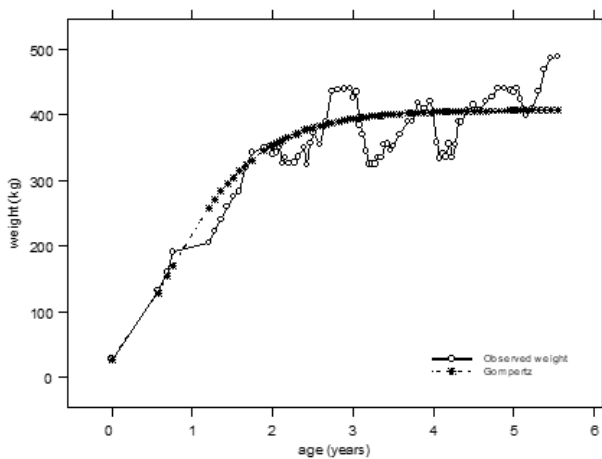


Figure 2: Age evolution of the size (in kg) of an individual cow of the Mertolengo breed (data from (Filipe et al., 2007)). The solid broken line represents the observed data and the dashed smooth curve is the estimated Gompertz curve.

an individual animal growth.

However, when we look at the data, what we observe is not this nice very smooth growth curve but rather a more irregular curve somewhat fluctuating around it, accompanying the effect of the random fluctuations that occur in nature on the internal and external environmental conditions. In Figures 1 and 2 we can see the observed irregular data for the size (in individuals per cm^3) of a lab population of the protozoan *Paramecium caudatum* (data from (Gause, 1934)) and for the size (in kg) of a cow of the Mertolengo breed raised in the Alentejo region of Portugal (data taken from (Filipe et al., 2007)), respectively, together with the estimated smooth Gompertz curve that would occur under constant environmental conditions.

The usual literature on individual animal growth considers a growth curve (the Gompertz curve or some other function of age) and uses a regression model in which, typically, the observed deviations from the curve are assumed to be

independent and identically distributed. That would be quite appropriate if they were due to measurement errors, which are negligible with our weighting apparatus. With such a model, looking at a cow that has now a weight quite below the growth curve, the prediction for its weight next week will be the weight given by the growth curve, a miraculous weight recovery in just a week. The deviations from the growth curve are, in fact, due to fluctuations in the growth rate induced by internal and external random environmental conditions and so, a good prediction for the weight next week should instead use today's weight as a starting point and project it to next week using the growth dynamics given by the differential equation. But we have to take into account that the growth rate is not exactly given by the deterministic differential equation because it keeps suffering the influence of the environmental conditions, which will introduce some amount of uncertainty on the prediction.

To take into account the influence of the random environmental fluctuations on the growth rate, that influence should be included in the differential equation that drives the growth process dynamics, making it a *stochastic differential equation* (SDE). The same applies to population growth dynamics.

There are many other dynamical phenomena in Biology and in several other different areas of Science and Technology where the descriptive variable(s) change in time according to some rules concerning its rate of change (i.e., its time derivative), rules that are conveniently described by an ODE. For simplicity of notation, we consider here the unidimensional case of a single variable $X(t)$ following the ODE

$$\frac{dX(t)}{dt} = F(t, X(t)) \quad \text{or} \quad dX(t) = F(t, X(t)) dt,$$

with initial condition $X(0) = X_0$ (we consider for simplicity 0 as the starting time, but it can be replaced by some other time t_0). The extension to the multidimensional case is relatively simple, working with the column vector of the several descriptive variables involved.

Such dynamical phenomena are often influenced by many other variables not considered in the model, either for parsimonious reasons due to their less relevant effect or for the simple reason that they are unknown or impossible to measure and predict. But such factors have an effect on the rate of change of $X(t)$. So, it is quite natural to group that effect in a single temporal variable having a necessarily random behavior, i.e., a *stochastic process*, and include it as an additional term in the equation. So, the original terms in the equation describe the deterministic dynamics that result from the variables explicitly considered in the model and the additional term describes the perturbation caused on such dynamics by other factors. That is similar to the probabilistic treatment we use to describe the result of throwing a coin instead of trying to model the gravity, air resistance and hand movement forces involved.

Assuming that there are many such perturbing factors that affect the rate of change of $X(t)$, when grouping their effect on a single stochastic process the central limit theorem

would lead to an approximately Gaussian behavior, and so we assume here that such stochastic process is Gaussian.

Let us look at the integral of such stochastic process, i.e. the stochastic process of the accumulated perturbations between time 0 and time $t \geq 0$. It is likely that the effect of the perturbations acting on a given time interval is approximately independent of the effect of the perturbations on another non-overlapping time interval, so we will assume that this stochastic process, besides being Gaussian, has independent increments. If the many perturbations have approximately independent additive effects and occur with a relatively uniform frequency, the number of perturbations occurring in a time interval is approximately proportional to the interval's length and so their accumulated effect on that time interval has a variance also approximately proportional to the length of the interval. Even if such proportionality is not correct and the "constant" of proportionality is in fact variable with time and $X(t)$, we can incorporate such variability in a multiplicative factor $G(t, X(t))$ that modifies an underlying perturbing process truly proportional and for which we can choose the constant of proportionality to be $= 1$. From all of the above, and assuming time continuity of the perturbations, we can assume that the underlying process behind the accumulated perturbations in the time interval $[0, t]$ is a Wiener process, the only continuous Gaussian processes with independent increments and variance of the increment over a time interval exactly proportional to the interval's length. Since obviously the accumulated effect of perturbations on the time interval $[0, 0]$ should be $= 0$ and we can choose the constant of proportionality to be $= 1$ (so that the increment on a time interval has variance equal to the length of the interval), we can take as underlying process the standard Wiener process $W(t)$, also known in the literature as *Brownian motion* (since it was used as a model of the Brownian motion of a particle suspended in a fluid). The square of the multiplicative factor $G^2(t, X(t))$ should take care of the variance of the perturbations per unit time and it may be constant or may depend on t and $X(t)$.

In an infinitesimal time interval dt , the effect of the perturbations will then be given by the effect of the underlying perturbations, i.e. the increment $dW(t)$ of the cumulative underlying process on that time interval, multiplied by the multiplicative factor $G(t, X(t))$. So, our general initial ODE becomes the general stochastic differential equation

$$dX(t) = F(t, X(t)) dt + G(t, X(t)) dW(t), \quad (1)$$

with the same initial condition $X(0) = X_0$; since the initial value X_0 may in some cases be unknown, nothing prevents X_0 from being a random variable, as long as it is independent of the Wiener process $W(t)$.

All this can be generalized to the multidimensional case (with also multidimensional Wiener processes) and also to non-continuous underlying processes (processes with jumps).

The randomness of the perturbations is associated to a probability space $(\Omega, \mathcal{F}, \mathcal{P})$, where Ω can be considered the set of all possible environmental "states", from which an observed state $\omega \in \Omega$ is "chosen by chance" according to the probability law P , which is defined for the sets of states belonging to the σ -algebra \mathcal{F} . Notice that a state

ω describes a concrete whole history of environmental conditions over the full time span for which we are using the SDE. The stochastic process $W(t)$ depends also on "chance", i.e. on ω , so $W(t)$ is an abbreviation of $W(t, \omega)$. For a fixed ω , $W(t, \omega)$ is a function of time (called a trajectory, realization or sample path) that describes the evolution over time of the underlying cumulative effect of the perturbations between time 0 and time t when the state of the environment is ω . Different states will in general have different trajectories. Of course, a solution (when it exists) of the SDE is also a stochastic process and so, when we write $X(t)$, that should be taken as an abbreviation of $X(t, \omega)$. When we make predictions about a future fixed time t , we should remember that they must assume a probabilistic nature since $X(t) = X(t, \omega)$ is a random variable.

One may think that there are always perturbing factors not explicitly considered in a ODE deterministic model and so one should always use SDE models to take the uncertainty they cause in due consideration. Indeed, there are cases (sometimes even with relatively small G values) where the results obtained using the SDE model are quantitatively, and sometimes qualitatively, quite different from the results obtained using the ODE model with mean values of the variables or of the parameters, making the ODE models useless. That is certainly the case in many biological phenomena, in epidemiology, in seismology, in finance (stocks, futures, options, etc.) or in telecommunications. However, considering the added complexity of SDE models, it is not worth using them if the perturbing factors are relatively irrelevant.

In the next section we give a brief introduction to the treatment of stochastic differential equations following the steps of (Braumann, 2018). Of course, the reader interested in using SDE should follow up using a textbook like, for example, (Braumann, 2019), (Arnold, 1974) or (Øksendal, 2003).

Among the many areas of application, we are here just illustrating some biological applications related to population growth and individual animal growth. We start by looking at the modeling of population growth in a randomly varying environment and the associated extinction issues. The particular case of populations subject to harvesting, like it is the case in fisheries and forestry, is treated next, focusing on how to optimize the profit from the harvesting activity. After that, we deal with individual growth models for farm animals and some issues on profit optimization for farmers raising those animals. Finally, we present some conclusions and suggest further reading on related issues.

BRIEF INTRODUCTION TO STOCHASTIC DIFFERENTIAL EQUATIONS

The solution of the SDE (1) with the initial condition $X(0) = X_0$ is the solution of the corresponding integral equation

$$X(t) = X_0 + \int_0^t F(s, X(s)) ds + \int_0^t G(s, X(s)) dW(s). \quad (2)$$

Please keep in mind that W and X both depend also on ω , although we use the common convention of not writing

that dependence explicitly. But, if we fix the trajectory ω , we will only have functions of time and, under sufficient regularity conditions, the first integral in (2) can be interpreted as an ordinary Riemann integral. However, the second integral cannot be interpreted as a Riemann-Stieltjes integral since the integrator $W(t)$ has unbounded variation for almost all trajectories. For that reason, when we approximate the second integral (the stochastic integral) by Riemann-Stieltjes sums for a sequence of tagged partitions $0 = t_{n,0} < t_{n,1} < \dots < t_{n,n-1} < t_{n,n} = t$ ($n = 1, 2, \dots$) of the $[0, t]$ interval with mesh $\delta_n = \max_{k=1, \dots, n} (t_{n,k} - t_{n,k-1})$ converging to zero, the limit of such sums depends on the choice of the tags (i.e. the intermediate points $\tau_{n,k} \in [t_{n,k-1}, t_{n,k}]$) where the integrand function $G(s, X(s))$ is computed. Different choices lead to different stochastic integrals.

If, for each subinterval k of the partition, we choose as tag $\tau_{n,k} = t_{n,k-1}$ the initial point of the subinterval, that has the advantage of being *non-anticipative* (the present dynamics is not affected by the future random fluctuations) and we obtain, assuming appropriate regularity conditions, the *Itô integral*

$$\int_0^t G(s, X(s)) dW(s) = \text{l.i.m.} \sum_{k=1}^n G(t_{n,k-1}, X(t_{n,k-1})) (W(t_{n,k}) - W(t_{n,k-1})), \quad (3)$$

where we have used the mean square limit (L^2 convergence with respect to ω), represented by l.i.m., of the Riemann-Stieltjes sums. Under appropriate regularity conditions on G , the Itô integral has excellent probabilistic properties, like having a null mathematical expectation $\mathbb{E} \left[\int_0^t G(s, X(s)) dW(s) \right] = 0$, having variance equal to $\int_0^t \mathbb{E}[G^2(s, X(s))] ds$ and being a martingale as a function of t . However, it does not follow the ordinary calculus rules and we need a new calculus, the *Itô stochastic calculus*, which is characterized by the following differentiation chain rule:

Itô formula (or *Itô theorem*). Let $h(t, x)$ be $C^{1,2}$ (have a continuous partial derivative in t and first and second order continuous partial derivatives in x), assume F and G satisfy appropriate regularity conditions, let $X(t)$ be unique solution of the SDE (1) and consider the stochastic process $Y(t) = h(t, X(t))$. Its differential, contrary to ordinary calculus rules (based on first order expansions), is based on the second order expansion in x , $dY(t) = \frac{\partial h}{\partial t} dt + \frac{\partial h}{\partial x} dX(t) + \frac{1}{2} \frac{\partial^2 h}{\partial x^2} (dX(t))^2$. Note that the second order term $(dX(t))^2$ would be of lower order than dt in ordinary calculus and, therefore, would not appear, but, due to the irregularity of the trajectories of the Wiener process $W(t)$, this is not true here (note that $\mathbb{E}[(W(t + \Delta t) - W(t))^2] = \Delta t$). Therefore, now $(dX(t))^2 = (F dt + G dW(t))^2 = F^2 (dt)^2 + 2FG dt dW(t) + G^2 (dW(t))^2 = 0 + 0 + G^2 dt$ (since the first two terms are of lower order than dt but the third term is of the same order as dt). Replacing $dX(t)$ and $(dX(t))^2$ by their expressions and collecting terms, we obtain the *Itô chain rule* (with F , G and h and their derivatives computed at the point $(t, X(t))$):

$$dY(t) = \left(\frac{\partial h}{\partial t} + \frac{\partial h}{\partial x} F + \frac{1}{2} \frac{\partial^2 h}{\partial x^2} G^2 \right) dt + \frac{\partial h}{\partial x} G dW(t). \quad (4)$$

There are other stochastic integrals corresponding to other (anticipative) choices or combinations of choices of the tag points used in the Riemann-Stieltjes sums. The most popular of them is the *Stratonovich integral*

$$\begin{aligned} (S) \int_0^t G(s, X(s)) dW(s) &= \text{l.i.m.} \sum_{k=1}^n G \left(t_{n,k-1}, \frac{X(t_{n,k-1}) + X(t_{n,k})}{2} \right) (W(t_{n,k}) - W(t_{n,k-1})). \end{aligned} \quad (5)$$

Since this expression contains a trajectory smoothing, the Stratonovich integral follows the ordinary rules of calculus, but in general lacks the nice probabilistic properties of the Itô integral. Also, for the same functions F and G , the solution of the Stratonovich SDE (i.e. the solution of the SDE one obtains by using Stratonovich integrals) is in general different from the Itô SDE solution. Using (3) and (5), it is easy to show that the Itô SDE $dX = F dt + G dW$ is equivalent to (has the same solution as) the Stratonovich SDE $(S) dX = F^* dt + G dW$ with $F^* = F - \frac{1}{2} G \frac{\partial G}{\partial x}$.

Whether one uses Itô calculus or Stratonovich (ordinary rule) calculus, existence and uniqueness of the corresponding SDE requires some regularity conditions on F and G and, with appropriate conditions, the solution is even a Markov process and a diffusion process, satisfying therefore the Kolmogorov equations. In the particular case of *autonomous* SDE, i.e., when $F(t, x) \equiv F(x)$ and $G(t, x) \equiv G(x)$, the solution is even a homogeneous diffusion process. For these issues, the reader can consult, for instance (Braumann, 2019).

The two calculi, Itô or Stratonovich, can give apparently different results, leading even to qualitative different conclusions. For example, in population growth models in a random environment, one calculus may predict, under certain conditions, the extinction of the population with probability one, while the other, under apparently the same conditions, may predict a zero probability of population extinction. Therefore, there has been some controversy in the literature on applications concerning which calculus is more appropriate to certain type of applications. Illustrating with population growth models (with and without harvesting), the controversy is solved in (Braumann, 2007a,b,c) by showing that the apparent discrepancy in results is due to the incorrect implicit assumption that $F(t, x)$ (“average” population growth rate) has the same meaning under both calculi. That is not true since F always represents the arithmetic average when one uses Itô calculus but (except when the function G does not depend on x) it usually represents a different average under the Stratonovich calculus; in the illustrative models, it represented the geometric average when Stratonovich calculus was used. When one attends to the difference between the averages represented by F in the two calculi, the results of the two calculi completely coincide. The moral of the story is that one can use either calculus indifferently but should be careful when choosing the expression of F ; it should be the correct expression for the arithmetic mean of the rate of change if one uses Itô calculus and it should be the correct expression for the appropriate mean (the geometric

mean in the illustrative models) of the rate of change if one uses Stratonovich calculus. More on that can be seen on (Braumann, 2019). Here we will use Itô calculus.

Let us now focus on Itô unidimensional autonomous SDE models

$$dX(t) = F(X(t)) dt + G(X(t)) dW(t), \quad (6)$$

with known initial condition $X(0) = x_0$ and with functions $F(x)$ and $G(x)$ of class C^1 . It can be proved that the solution exists and is unique up to a possible explosion time and, if we can show that the probability of explosion is zero, then, with probability one, the solution exists and is unique for all $t \geq 0$ and is a homogeneous diffusion process with drift coefficient $a(x) = F(x)$ and diffusion coefficient $b(x) = G^2(x)$ (so the process satisfies the Kolmogorov equations). If the state space, i.e. the space where $X(t)$ takes values, has boundaries r_1 and r_2 with $-\infty \leq r_1 < r_2 \leq +\infty$ and $G(x) > 0$ for $x \in]r_1, r_2[$, we can define, for $x \in]r_1, r_2[$, the *scale density* $s(x)$ and the *speed density* $m(x)$ given by

$$s(x) = \exp\left(-\int_z^x \frac{2a(u)}{b(u)} du\right) \\ m(x) = \frac{1}{b(x)m(x)}, \quad (7)$$

where z is a fixed but arbitrarily chosen point in the interior of the state space. A necessary and sufficient condition for the boundary r_1 to be *non-attractive* is that $\int_{r_1}^{c_1} s(x) dx = +\infty$ for some $c_1 \in]r_1, r_2[$ (it is enough to check for one such c_1 , because, if its true for some c_1 , it is true for all). Similarly, the boundary r_2 is non-attractive iff $\int_{c_2}^{r_2} s(x) dx = +\infty$ for some $c_2 \in]r_1, r_2[$. When both boundaries are non-attractive, whenever the process approaches a boundary, it is pushed away towards the interior of the state space and so it is possible that the transient probability distribution of $X(t)$ may reach a stochastic equilibrium as $t \rightarrow +\infty$ in the sense of converging in distribution to a stationary distribution. If so, the pdf of such distribution is called the *stationary density* $p(x)$ and is a time-invariant solution of the forward Kolmogorov equation. Indeed, it can be proved that, if both boundaries are non-attractive and the speed density is integrable, then the process is ergodic and such stochastic equilibrium occurs and has a stationary density given by

$$p(x) = \frac{m(x)}{\int_{r_1}^{r_2} m(z) dz} \quad (r_1 < x < r_2). \quad (8)$$

More details can be seen, for example, in (Braumann, 2019).

POPULATION GROWTH AND EXTINCTION IN RANDOMLY VARYING ENVIRONMENTS

Let $X(t)$ be the size (number of individuals, biomass, density) of a wildlife population (of animals, plants or bacteria) at time t with known initial size $X(0) = x_0$. In the deterministic case, the contribution of an individual to the growth of the population is given by the *per capita* growth rate (abbreviately, growth rate, difference between the birth rate and the death rate) $R = \frac{dX(t)/dt}{X(t)}$, which expression may depend on the time t and the population size x at that time,

i.e. $R = R(t, x)$. So, we have the deterministic ODE model $\frac{dX(t)/dt}{X(t)} = R(t, X(t))$ or $\frac{dX(t)}{X(t)} = R(t, X(t))dt$.

Assuming from now on a stable environment, we can assume an $R = R(x)$ and obtain the autonomous ODE $\frac{dX(t)}{X(t)} = R(X(t))dt$. The function R may be constant if resources are unlimited but, since usually the available resources are limited, the amount of resources available per individual (*per capita*) tends to decrease when the population size x increases and, therefore, $R(x)$ should be a strictly decreasing function. Several models satisfying this property have been proposed like the logistic $R(x) = r(1 - x/K)$ or the Gompertz $R(x) = r \ln(K/x)$ (considered at the beginning of this paper), in which $r > 0$ is a speed of growth parameter and $K > 0$ is the *carrying capacity* of the environment, i.e. the stable equilibrium size towards which the population size $X(t)$ converges when $t \rightarrow +\infty$.

If the environment has random fluctuations that affect the *per capita* growth rate, their cumulative effect in a time interval $[0, t]$ can be described by an underlying standard Wiener process $W(t)$ multiplied by an intensity factor $\sigma(x) \geq 0$. So we obtain the general SDE population growth model

$$\frac{dX(t)}{X(t)} = R(X(t)) dt + \sigma(X(t)) dW(t)$$

or, written in the traditional format,

$$dX(t) = R(X(t)) X(t) dt + \sigma(X(t)) X(t) dW(t). \quad (9)$$

We will assume the initial population size $X(0) = x_0$ known. Many specific models, i.e. models with specific forms of the functions $R(x)$ (logistic, Gompertz, generalized logistic, etc.) and $\sigma(x)$ (constant or proportional to $R(x)$), have been proposed in the literature, starting with the pioneering works of (Levins, 1969; May, 1973; Capocelli and Ricciardi, 1974; Goel and Richter-Dyn, 1974; Kiester and Barakat, 1974; Tuckwell, 1974; Roughgarden, 1975).

Let us illustrate (see (Braumann, 2008)) with the Gompertz SDE model $R(x) = r \ln(K/x)$ with constant noise intensity $\sigma(x) \equiv \sigma > 0$:

$$dX(t) = r \left(\ln \frac{K}{X(t)} \right) X(t) dt + \sigma X(t) dW(t) \quad (10)$$

with known initial condition $X(0) = x_0 > 0$. Let us make the change of variable $Y(t) = \ln(X(t)/K)$ and use Itô formula to obtain, after simplifying,

$$dY(t) = \left(-rY(t) + \frac{\sigma^2}{2} \right) dt + \sigma dW(t).$$

Another change of variable $Z(t) = e^{rt}Y(t)$ and Itô formula lead to

$$dZ(t) = \frac{\sigma^2}{2} e^{rt} dt + \sigma e^{rt} dW(t)$$

and, by direct integration, to $Z(t) = \ln \frac{x_0}{K} + \frac{\sigma^2}{2} (e^{rt} - 1) + \sigma \int_0^t e^{rs} dW(s)$, from which we get

$$Y(t) = \left(\ln \frac{x_0}{K} \right) e^{-rt} + \frac{\sigma^2}{2} (1 - e^{-rt}) + \sigma e^{-rt} \int_0^t e^{rs} dW(s) \quad (11)$$

$$X(t) = K \left(\frac{x_0}{K} \right)^{\exp(-rt)} \exp \left(\frac{\sigma^2}{2} (1 - e^{-rt}) + \sigma e^{-rt} \int_0^t e^{rs} dW(s) \right). \quad (12)$$

When $\sigma = 0$, we retrieve the solution $X(t) = K \left(\frac{x_0}{K} \right)^{\exp(-rt)}$ of the deterministic Gompertz curve, but, while in the deterministic case, $X(t) \rightarrow K$ as $t \rightarrow +\infty$ (a stable deterministic equilibrium population size), this is not happening in the stochastic case. To see that, it is easier to work with $Y(t)$ because it has a Gaussian distribution with mean $\left(\frac{x_0}{K} \right) e^{-rt} + \frac{\sigma^2}{2} (1 - e^{-rt})$ and variance $\frac{\sigma^2}{2r} (1 - e^{-2rt})$. This comes from (11) and the fact that the stochastic integral $\int_0^t e^{rs} dW(s)$ is Gaussian (because the integrand is deterministic) and has variance $\int_0^t e^{2rs} ds = \frac{1}{2} (e^{2rt} - 1)$. Of course, $X(t) = K \exp(Y(t))$ has a lognormal distribution. In this case, $Y(t)$ has a stationary distribution towards which it converges as $t \rightarrow +\infty$, which is Gaussian with mean $\frac{\sigma^2}{2}$ and variance $\frac{\sigma^2}{2r}$. The stationary distribution in terms of the X process is lognormal and its pdf, called *stationary density*, is therefore

$$p(x) = \frac{1}{x \sqrt{2\pi \frac{\sigma^2}{2r}}} \exp \left(-\frac{\left(\ln \frac{x}{K} - \frac{\sigma^2}{2} \right)^2}{2 \frac{\sigma^2}{2r}} \right) \quad (x > 0). \quad (13)$$

So, for the Gompertz model, while in the deterministic case the population size $X(t)$ settles down for large t at the deterministic equilibrium K , in the stochastic case the environmental fluctuations will keep the population fluctuating randomly somewhat around K . It is rather a stochastic equilibrium, where what settles down is not $X(t)$ but its probability distribution, which settles down to the stationary distribution.

Using the techniques at the end of the previous section and noting that $a(x) = r \left(\ln \frac{x}{K} \right) x$ and $b(x) = \sigma^2 x^2$, one can easily show that the boundaries $r_1 = 0$ and $r_2 = +\infty$ are both non-attractive and that the speed density is integrable. So, without solving the equation, we could have concluded that the solution exists and is unique always (because we have C^1 functions and the non-attractiveness of the $+\infty$ boundary prevents explosions), that “mathematical” extinction of the population (in the sense of population size converging to zero) has zero probability of occurring and that there is a stochastic equilibrium with a stationary density. For large t , the pdf of the $X(t)$ distribution can be approximated by the stationary density.

This observation is particularly important since, like for ODE, we are often unable to determine the explicit solution of an SDE model. We can also, like in ODE, use numerical methods. In the SDE case, we recur to Monte Carlo techniques (taking advantage of the Markov property) to simulate trajectories. That technique, or the numerical solution of the forward Kolmogorov equation, can be used to approximate the transient probability distribution of $X(t)$ when t is not large enough to use the stationary distribution as an approximation.

The specific models considered in the literature are certainly useful. However, one would like to have model robust properties that do not depend on the specific model considered but rather on the biological properties and so it is better to use general functions $R(x)$ and $\sigma(x)$ (defined

for $x \in]0, +\infty[$) satisfying only assumptions dictated by biological considerations and mild technical assumptions. From now on, we use the general model (9) and assume $R(x)$ to be of class C^1 , strictly decreasing, with limit $R(+\infty) < 0$ (since, due to limited resources, a very large population must have a negative growth rate) and with $\lim_{x \rightarrow 0^+} R(x)x = 0$ (closed to immigration). We assume $\sigma(x) > 0$ and of class C^1 . In (Braumann, 1999), using the techniques described at the end of last Section, we studied the properties of this general SDE model (also in the case of harvested populations) for the particular case of constant $\sigma(x) \equiv \sigma > 0$ and in (Braumann, 2002, 2008) we have extended to general C^1 functions $\sigma(x) > 0$ satisfying an additional mild technical assumption (which all bounded functions automatically satisfy). Now the drift coefficient is $a(x) = R(x)x$ and the diffusion coefficient is $b(x) = \sigma^2(x)x^2$.

We have shown first that the solution exists and is unique. Notice that the *per capita* growth rate is affected by the random environmental fluctuations and so we should look at some appropriate average. What matters for the fate of the population in terms of “mathematical” extinction is its average in the limit when population size $\rightarrow 0^+$, when the population grows at the fastest rate *per capita* since resource limitations have almost no effect. But, being growth a multiplicative process, we should not look at the arithmetic average $R(0^+)$ (implied in the Itô calculus we are using here), but rather to the geometric average given by $R(0^+) - \frac{\sigma^2(0^+)}{2}$. If this quantity is negative, it means that even the fastest growth is negative on the appropriate average and “mathematical” extinction will occur with probability one. If that quantity is positive, then “mathematical” extinction has zero probability of occurring, the process is ergodic and there is a stochastic equilibrium with stationary density, which we can compute using (7) and (8).

There is always some approximation involved when one uses continuous state models, like ODE or SDE, for the population size $X(t)$. For large populations sizes, having a non-integer number of individuals is, in relative terms, a negligible error and so we can use these models as excellent approximations. But that is not the case when the population is very small, particularly so when we are talking about extinction. We have spoken about “mathematical” extinction (population size converging to zero) and, under certain conditions, we saw that it does not happen, but, since the process is ergodic under those conditions, the solution $X(t)$ of the SDE will sooner or later take values like 0.4 individuals before coming back to higher numbers. When that happens, although not “mathematically” extinct, the population is extinct in realistic terms. If we set up a small extinction threshold a with $0 < a < x_0$ and consider realistic extinction happens when the population crosses the threshold, then all populations will become realistically extinct, even those that have a zero probability of becoming ‘mathematically’ extinct.

So, the real issue is not whether realistic extinction will occur (it will), but rather how long does it take, i.e., we are interested in the *extinction time* T_a , the first passage time of $X(t)$ through the extinction threshold a . We can also study

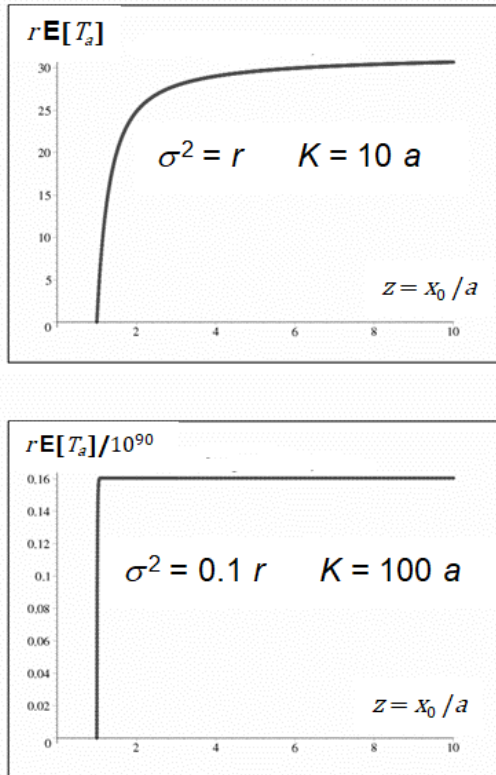


Figure 3: Plot of $r\mathbb{E}[T_a]$ as a function of $z = x_0/a$ for the SDE Gompertz model (10) and two parameter combinations. Notice that the vertical axis in the bottom plot is not in the natural scale, so the mean number of ideal generations to extinction is of the order of 10^{90} . Figure taken from (Carlos and Braumann, 2006).

T_b when b is a high threshold $b > x_0$, as well as $T_{a,b}$, the first passage time through either threshold. Expressions for the moments and the study of the behavior of the expected value and the variance of such passage times for these type of models and its applications can be seen in (Carlos and Braumann, 2005, 2006; Carlos et al., 2013; Braumann, 2008; Filipe et al., 2015; Braumann, 2019). As a function of x_0 , the mean extinction time is very low when x_0 is close to a but, as x_0 increases, it rapidly reaches a plateau and becomes almost insensitive to the initial population size. Depending on the specific models and parameters, that plateau can range from a few generations to times far larger than the age of the universe. For the SDE Gompertz model (10), Fig. 3 plots $r\mathbb{E}[T_a]$ (expected value of T_a measured in number of “ideal” generations, since $1/r$ is a proxy of generation time) as a function of $z = x_0/a$ (so values of z close to one correspond to x_0 close to a) for two parameter combinations.

Some populations, however, are subjected to Allee effects (see (Allee et al., 1949)), in which small population sizes, instead of having the highest *per capita* growth rates as would be expected since resource limitations barely affect them, have on the contrary depressed growth rates. That may be due to individuals having difficulty in finding mating partners (being few they might be very dispersed geographically) or requiring a minimum population size to mount an effective group defense from predators or, the other way around, requiring a minimum size to effectively

group hunt their prey. With Allee effects, $R(x)$ will only be strictly decreasing due to resource limitations for population sizes above a certain threshold size L but, for sizes lower than L , Allee effects will prevail and $R(x)$ will be an increasing function (since Allee effects will become weaker, and so the growth rate less depressed, as the population size increases). Specific models were studied, for instance, by (Dennis, 2002; Engen et al., 2003). The study of Allee effect models with a general $R(x)$ function was held in (Carlos and Braumann, 2017).

HARVESTING AND HARVESTING OPTIMIZATION

If the population (say a population of fish, but it could be a population of trees or of wild birds) is being harvested, we can use the general model

$$dX(t) = (R(X(t)) - qE(t, X(t)))X(t) dt + \sigma(X(t))X(t) dW(t), \tag{14}$$

where $qE(t, x)$ is, at time t when the population has size x , the additional *per capita* mortality rate of the population caused by the harvesting activity. It is assumed proportional to the *harvesting effort* $E(t, x) \geq 0$ (measured, in the case of fishing effort, by the number of fishing vessels adjusted by their efficiency and fraction of time they are in use). The constant of proportionality $q > 0$ is called the *catchability* in the fishing literature. Now, the arithmetic average of the *per capita* growth rate is the arithmetic average of the *net growth rate* $R(x) - qE(t, x)$, the difference between the arithmetic average natural growth rate $R(x)$ and the additional mortality rate $qE(t, x)$ caused by fishing. The amount of fish caught per unit time is $H(t, x) = qE(t, x)x$ and is called the *yield* in the harvesting literature.

The pioneer works (Beddington and May, 1977; Gleit, 1978; May, 1973; Braumann, 1985) were on specific models assuming specific functions $R(x)$ and $\sigma(x)$. They also assumed the fishing efforts to depend only on the size of the population, i.e. $E(t, X(t)) \equiv E(X(t))$, so that the SDE (14) would become autonomous and we could determine conditions on the effort to avoid “mathematical” extinction of the fish population and to allow for a stochastic equilibrium with a stationarity density.

The study of general autonomous models with arbitrary $R(x)$ and $\sigma(x)$ satisfying the assumptions mentioned in the previous Section and arbitrary C^1 autonomous effort $E(x)$ can be seen in (Braumann, 1999) for the case of constant noise intensity σ and in (Braumann, 2002) for the most general case. The conclusions are similar to the general SDE population growth models, except that now one should use, instead of the natural growth rate of the population, its net growth rate (natural growth rate minus the additional mortality rate caused by fishing).

If, for vanishing population sizes, the geometric average net growth rate $R(0^+) - \frac{\sigma^2(0^+)}{2} - qE(0^+)$ is negative, “mathematical extinction” of the population will occur with probability one. That happens if we are overfishing, i.e. if,

when the population size is small, the fishing effort $E(0^+)$ is so high that the additional mortality rate caused by fishing $qE(0^+)$ exceeds the geometric average natural growth rate $R(0^+) - \frac{\sigma^2(0^+)}{2}$.

If we are not overfishing, i.e. if the geometric average net growth rate at small population sizes is positive, “mathematical” extinction has zero probability of occurring and the process is ergodic with a stochastic equilibrium and a stationary density $p(x)$ (pdf of the limiting probability distribution as $t \rightarrow +\infty$). Let $X(+\infty)$ denote the equilibrium random variable having pdf $p(x)$. One can then study the effect at the stochastic equilibrium of the fishing effort $E(x)$ on the expected yield $\mathbb{E}[H(+\infty, X(+\infty))] = \int_0^{+\infty} qE(x)x p(x)dx$ or on the expected profit. Usually, one takes a simple profit structure in which the profit per unit time is $\Pi(t, x) = p_1H(t, x) - c_0 - c_1E(x)$ (where $p_1 > 0$ is the unit price, for example the price per kg, at which the fish is sold, $c_0 \geq 0$ are the fixed costs and $c_1 > 0$ is the cost per unit effort) and looks at $\mathbb{E}[\Pi(+\infty, X(+\infty))] = \int_0^{+\infty} (p_1qE(x)x - c_0 - c_1E(x)) p(x)dx$.

Another approach tries to keep adjusting the effort $E(t, x)$ over time according to the evolution of the population size in order to maximize the overall expected profit (with a discount rate $\delta > 0$ that takes care of depreciation costs such as the cost of opportunity of the investment) over some time horizon $[0, T]$ (where T can be finite or infinite). So, it tries to optimize $\mathbb{E}\left[\int_0^T e^{-\delta t} \Pi(t, X(t)) dt\right]$, called the *present value*, not caring if the optimal policy leads or not to the extinction of the population. We can cite pioneering works of (Lungu and Øksendal, 1997; Alvarez and Shepp, 1997; Alvarez, 2000).

One of the techniques, considering that we can control the effort $E(t, x)$ and so can use it as a control, is based on *stochastic optimal control theory* and the use of the Hamilton-Jacobi-Bellman (HJB) equation. In (Brites and Braumann, 2017) and (Brites and Braumann, 2019b) that technique was used, together with Monte Carlo simulations of the SDE and a Crank-Nicholson discretization of the HJB equation, for the case of constant noise intensity $\sigma(x) \equiv \sigma$ and a more complex profit structure $\Pi(t, x) = (p_1 - p_2H(t, x))H(t, x) - c_0 - (c_1 + c_2E(t, x))E(t, x)$ (with $p_2 \geq 0$ and $c_2 > 0$). Those papers consider the application to specific real fisheries using, respectively, the logistic model $R(x) = r\left(1 - \frac{x}{K}\right)$ and the Gompertz model $R(x) = r\ln\left(\frac{K}{x}\right)$. The growth parameters r and K and the cost and price parameters of those specific fisheries came from (Hanson and Ryan, 1998) and (Kar and Chakraborty, 2011), respectively.

In those papers, one can see in the optimal variable effort policy (the one obtained from stochastic optimal control theory that maximizes the present value, i.e. the expected discounted profit over a time horizon) a serious applicability problem not found when using optimal control theory in deterministic models. Namely, the optimal effort $E^*(t, x)$ keeps changing all the time accompanying the random fluctuations of population size induced by the effect of environmental fluctuation on the natural growth rate. Those changes include

frequent periods with zero or low effort (where the fishery stops or has very little activity) and periods of fishing at the highest possible effort. Therefore, since in practice it is operationally not possible to keep changing the fishing effort all the time and so abruptly, this optimal fishing policy is not applicable. Also, in the periods of no or low fishing, fishermen unemployment occurs, with the corresponding social problems (or hidden unemployment compensation costs not taken into account in the used profit structure). Furthermore, at every time, we need to know the population size of fish since we need it to compute the optimal fishing effort to apply at that time. But estimating the population size cannot be done all the time because it is a difficult and costly process (another hidden cost not contemplated in the profit structure); also, the estimates are inaccurate, so we may compute an inaccurate value for the fishing effort to apply.

In those papers, it was also determined what would happen if one applies a constant effort fishing policy with $E(t, x) \equiv E$. This is operationally extremely easy to apply because the fishing effort is the same all the time and does not change with the changes in the population size. So, there are no periods of zero or low effort and so there are no social problems or hidden costs. There is also no need to estimate the population size all the time since it is not required in the computation of the effort. We chose the optimal sustainable effort, i.e. the value E^{**} of the constant effort E that maximizes the expected profit at the stochastic equilibrium $\mathbb{E}[\Pi(+\infty, X(+\infty))] = \int_0^{+\infty} ((p_1 - p_2 qEx) qEx - c_0 - (c_1 + c_2E) E) p(x)dx$, which can be easily obtained. Then we compare this sustainable policy with the previous optimal variable effort policy in terms of their present values in a $T = 50$ years horizon. Of course, the previous optimal variable effort policy, if it could be applied in practice, would maximize the present value and so it gives a better present value than the optimal sustainable policy. The question is: how worse is the present value of the sustainable constant effort policy (which is easily applicable and free of social problems) compared to the present value of the (inapplicable) optimal variable effort policy? It is only 4,1% worse for the logistic model and 1,5% worse for the Gompertz model! For lack of information, those papers did not take into account the hidden costs of the inapplicable policy, but it is possible that, if they did, it might turn out that the sustainable constant effort policy would be better even in terms of profit.

Fig. 4, taken from (Brites and Braumann, 2017), shows the comparison for the logistic model of the two policies in terms of population size, effort and profit per unit time dynamics. The thin lines correspond to one simulated trajectory chosen at random and correspond to what the fishermen will typically experience (maybe they will experience a different trajectory but with a similar typical behavior). The solid lines are the average over 1000 simulated trajectories, which is a good approximation of the expected values. Looking at the effort, one can see the problems with the optimal variable effort policy. Looking at the profit per unit time, although the optimal effort policy has usually a better expected value (as seen looking at the solid lines), if we look at the thin lines

to see what the fishermen will typically experience, it is obvious that the profit is very unsteady over time in the optimal variable effort policy. On the contrary, although not having a constant profit (even though the effort is constant, the population size fluctuates and so does the profit), one can see that the constant effort policy provides a much steadier profit.

Other fishing policies, somewhere in between the constant effort and the optimal variable effort, could be used to try to improve the profit in comparison with the constant effort policies while attenuating the problems of the optimal variable effort policy we have mentioned. Their study can be seen in (Brites and Braumann, 2019a,b,c). The treatment of fish populations having Allee effects can be seen in (Brites and Braumann, 2020).

INDIVIDUAL ANIMAL GROWTH MODELS IN RANDOM ENVIRONMENTS

In the Introduction we have mentioned that the traditional use of regression models based on growth curves to study the individual growth of animals (or, for that matter, of plants, particularly trees) is inappropriate because it ignores the dynamics of the growth process and the influence on the growth rate of random variations in internal and external environmental conditions. We have even given as example of a typical deterministic growth curve used in the literature, the Gompertz curve and showed on Fig. 2 that the observed evolution of the size of a cow indicates the existence of such fluctuations. The Gompertz growth curve in fact results from growth dynamics governed by a Gompertz ODE model $\frac{dX(t)}{dt} = rX(t) \ln \frac{K}{X(t)}$, where $X(t)$ is the size of the animal, $K > 0$ is the size at maturity and $r > 0$ is a parameter that characterizes the speed of approach to maturity. So, if one takes into account the effect of random fluctuations, one should use an SDE model. This was proposed by (Garcia, 1983) and applied to the growth of trees.

But the Gompertz curve is just one of the several deterministic models proposed in the literature for individual growth. However, as also shown in (Garcia, 1983), the classical most used deterministic growth curves can be described as the result of growth dynamics driven by a common ODE model $\frac{dY(t)}{dt} = r(A - Y(t))$ with $r > 0$, where $Y(t)$ is not the actual size of the individual at age t but rather a modified size by some strictly increasing C^1 function h , i.e. $Y(t) = h(X(t))$, where $X(t)$ is the actual size. When $h(x) = x$ we get the monomolecular growth curve, when $h(x) = x^c$ ($c > 0$) we get the Bertalanffy-Richards curve, when $h(x) = \ln x$ we get the Gompertz curve (which can be considered a limiting case of the Bertalanffy-Richards curve when $c \rightarrow 0^+$), and when $h(x) = -1/x$ we get the logistic curve. Of course, the modified size at maturity is $A = h(K)$, where $K > 0$ is the actual size at maturity. Then, one can consider also a common SDE model that takes into account the effect of environmental fluctuations on the growth process, namely

$$dY(t) = r(A - Y(t)) dt + \sigma dW(t) \quad (t \geq t_0, Y(t_0) = y_0), \tag{15}$$

where $\sigma > 0$ measures the intensity of the effect on Y of the environmental fluctuations, t_0 is the age of the initial (assu-

med known) size observation $X(t_0) = x_0$ and $y_0 = h(x_0)$. The solution of (15) is, for $t > t_0$,

$$Y(t) = A + e^{-r(t-t_0)}(y_0 - A) + \sigma e^{-r(t-t_0)} \int_{t_0}^t e^{rs} dW(s). \tag{16}$$

Notice that $Y(t)$ is Gaussian with mean $A + e^{-r(t-t_0)}(y_0 - A)$ and variance $\frac{\sigma^2}{2r} (1 - e^{-2r(t-t_0)})$. Likewise, since $Y(t)$ is a homogeneous diffusion process, the transition distribution between two ages s and $t > s$ (both $\geq t_0$), given the value of $Y(s) = y_s$, is also Gaussian with mean $A + e^{-r(t-s)}(y_s - A)$ and variance $\frac{\sigma^2}{2r} (1 - e^{-2r(t-s)})$. The stationary distribution of Y , obtained by letting $t \rightarrow +\infty$, is also Gaussian with mean A and variance $\frac{\sigma^2}{2r}$. Of, course, using the transformation h , one can easily obtain from the transient, transition and stationary distributions of the Y process the corresponding distributions of the actual size process X .

Modifications of this model have been proposed. We might have two (or more) growth phases (as may happen in cows before and after weaning due to different food diets) with two different growth parameters, r_1 for ages $t \leq u$ and r_2 for $t > u$; these *biphasic models* were studied in (Filipe et al., 2012). It is also possible that, due to genetic differences for instance, different animals have different parameter values, say different maturity sizes K ; so, when we study a certain animal breed, we may need to take that into account and assume, for example that the modified maturity size A varies randomly among the individual animals of the breed, with a Gaussian distribution. These are *mixed models* that have been studied and applied to the Mertolengo breed of cows (data provided by the producer's association ACBM, Associação de Criadores de Bovinos Mertolengos) in (Braumann et al., 2009).

For the applications, one needs to deal with statistical issues of estimation, model choice and prediction, which pose more complex issues for modified models (like the biphasic or the mixed models), but can be easily handled for the basic model (15) if we have (as we do) a reasonable number and age range of observed sizes for many different animals (Filipe et al., 2010; Braumann et al., 2009). We may assume different animals correspond to independent realizations of the stochastic process so that the likelihood function of the observations is just the product of the likelihoods of the individual animals. By the Markov property of the Y process, the likelihood function for one animal is just the product of the transition densities between the consecutive observations made on that animal, and such transition densities are, as we have seen, Gaussian. So, one easily obtains the likelihood function and can maximize it to obtain the maximum likelihood estimates of the parameters r , A and σ ; their approximate confidence intervals can be obtained by the traditional method, using the inverse of the empirical Fisher information matrix. For example, from the data on 16201 bovine Mertolengo males provided by ACBM and using the Gompertz model, the 95% confidence intervals were 630.1 ± 6.4 kg for $K = e^A$, 1.422 ± 0.012 per year for r and 0.340 ± 0.002 per year^{1/2} for σ , as can be seen in (Filipe, 2018).

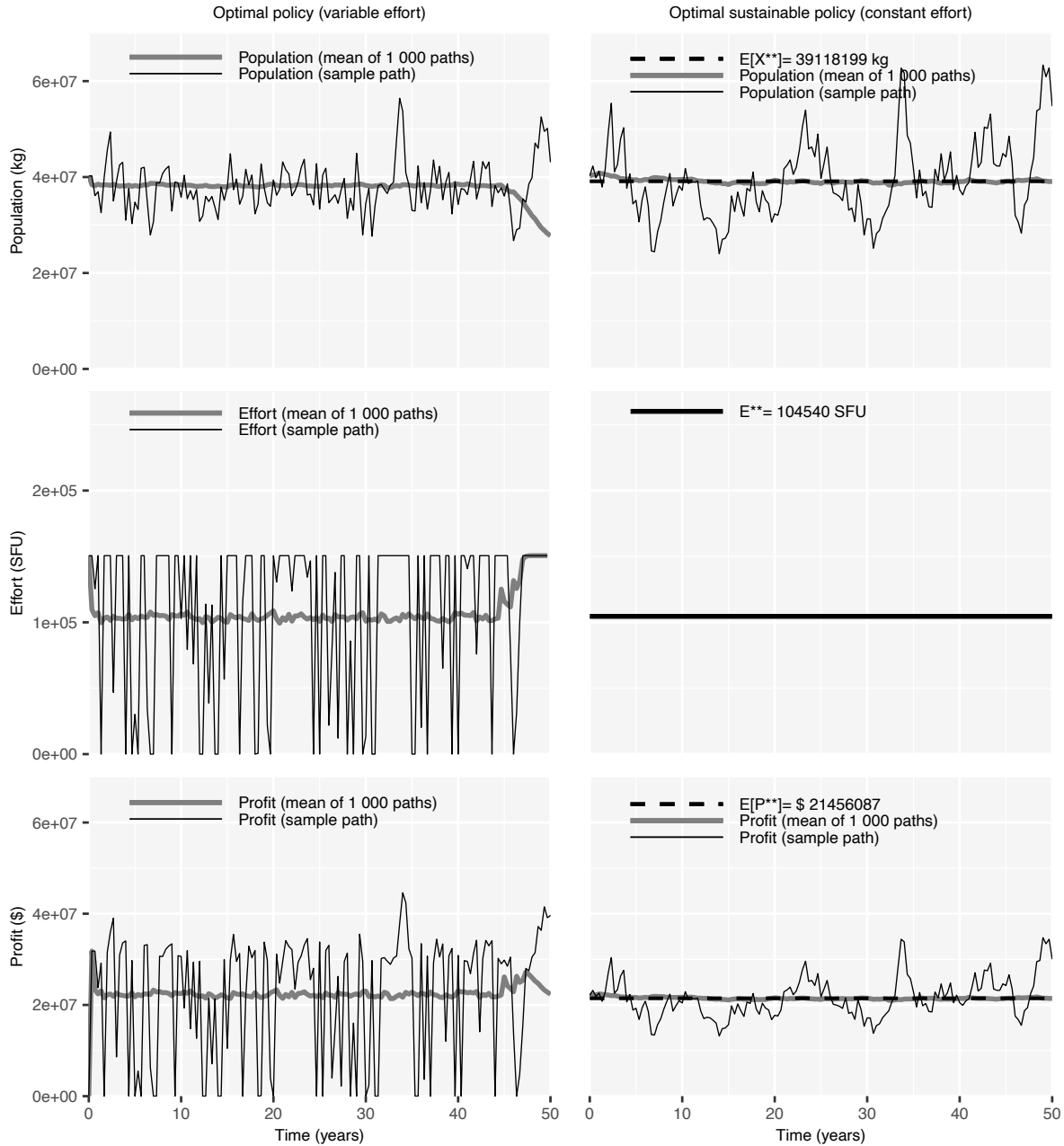


Figure 4: On the left is the optimal variable effort policy and on the right the optimal sustainable constant effort policy. Thin lines correspond to one randomly chosen simulated trajectory (representing what fishermen typically experience) and solid lines to the average of a 1000 simulated trajectories (an approximation of the expected values). The Figure is taken from Brites and Braumann (2017) and shows, using the application of an SDE logistic model with fishing, the evolution with time (in years) of the population size (on top, in kg), of the fishing effort (in the middle, in standardized fishing units) and of the profit per unit time (at the bottom, in US dollars per year).

If we have enough data and no assumptions on the growth dynamics, we may wish to use a general model $dY(t) = f(Y(t))dt + \sigma(Y(t))dW(t)$ and estimate the drift coefficient $f(y)$ and the diffusion coefficient $\sigma^2(y)$ by nonparametric methods; this was done in (Filipe et al., 2010), where it turned out that the estimated coefficients were relatively close to the coefficients of the Gompertz model and also of the Bertalanffy-Richards model with $c = 1/3$, so that this specific models were somewhat “validated” as reasonable models. Actually, comparisons of several specific models using AIC show that these two models have the best performances.

Prediction issues were discussed in (Filipe et al., 2013).

In (Filipe et al., 2015), a farmer optimization issue was studied. Suppose a farmer buys an animal having weight x_0 at age t_0 (usually right after weaning) in order to raise (finishing phase) and sell it to the meat market at a later age $t > t_0$ with weight $X(t)$ yet unknown. In the process, the farmer makes a profit $\Pi(t) = p_1X(t) - c_0 - c_1(t - t_0)$, where p_1 is the selling price per kg of live weight, c_0 are the fixed costs (like, for example, the price the farmer paid for the animal at age t_0 , transportation costs, veterinary costs, certain licenses and taxes) and c_1 are the variable costs per unit time of raising the animal (such as feeding and handling costs). The paper shows how to determine the optimal selling age t in order to maximize the expected profit $\mathbb{E}[\Pi(t)]$ and ap-

plies the results to the Mertolengo breed using information on typical costs and market meat prices. Instead of choosing a fixed age t (preferably the optimal one) to sell the animal, one could alternatively choose a fixed weight M and sell the animal when it reaches that weight (irrespective of its age). To choose the optimal M , one needs to maximize the expected profit $\mathbb{E}[P(M)]$ where $P(M) = p_1M - c_0 - c_1(T_M - t_0)$ and T_M is the first age at which the animal reaches the weight M . That problem was also solved in (Filipe et al., 2015) using the study made on first passage times T_M in (Carlos et al., 2013). Curiously, this second approach turns out to give a slightly better average profit than the first approach, but it has the inconvenience of having to keep weighting the animal until it reaches the target optimal weight.

CONCLUSIONS

We have given a general birds eye view on how to model the growth of a wildlife population living in a randomly varying environment by using stochastic differential equations, and use the models to study important issues such as the risk of extinction. Since we are dealing with similar models, the paper also presents the modeling of the growth of individual animals (or plants like trees). These models have many important applications, for which we gave two examples concerning profit optimization in fisheries and in animal production farming.

Many other biological applications could be given, in ecosystems management, in epidemiology, in physiology, in medical applications, in demography and in many other areas traditionally handled by ordinary differential equation models but for which random fluctuations in non-directly modelled internal and external environmental factors do require a stochastic differential equation approach.

On the technical side, here we have just treated unidimensional models where the “underlying environmental noise” can be handled (in its cumulative form over time) by a Wiener process, which is characterized by the continuity of its trajectories and by its independent increments. There are, however, extensions to multidimensional models (for instance, if we have to consider different interacting populations). There are also extensions to “noises” with jumps or with correlated increments, although for most practical applications, the approach taken here of using a Wiener process approximation, besides being much simpler, is sufficiently accurate.

Also the statistical issues were just briefly mentioned and only for an ideal situation in which we can explicitly obtain the likelihood function, which involves the exact knowledge of the transition densities. But, in most cases, one cannot solve explicitly the SDE and needs to use approximate expressions for the transition densities or recur to Monte Carlo simulation techniques, issues that are out of the scope of this paper.

Of course, in order to give the reader a flavor on SDE, we have also given here a quick and dirty introduction to its theory, but, for those interested in pursuing work on mode-

ling with SDE, we recommend further consolidating reading, like, for example, (Braumann, 2019), (Arnold, 1974) or (Øksendal, 2003). The reading of a few papers from the ones recommended in the References or others in application subjects that might interest the reader will be also recommended.

I am sure the reader understands that my main purpose is not to give a comprehensive treatment, nor that would be feasible in a short dissemination paper. Rather, the aim is to introduce the subject, using mostly material that I have worked with, to give a rough idea of its usefulness and potential range of applications to the reader not yet acquainted with it. If this managed to attract a few readers to the subject and maybe drive some to develop further ideas and new areas of application, all the better.

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REFERENCES

- [1] Allee, W. C., Emerson, A. E., Park, O., Park, T., and Schmidt, K. P. (1949). *Principles of animal ecology*. Saunders.
- [2] Alvarez, L. H. R. (2000). “On the option interpretation of rational harvesting planning”. *Journal of mathematical biology*, 40:383–405.
- [3] Alvarez, L. H. R. and Shepp, L. A. (1997). “Optimal harvesting in stochastically fluctuating populations”. *Journal of mathematical biology*, 37:155–177.
- [4] Arnold, L. (1974). *Stochastic differential equations: Theory and applications*. Wiley.
- [5] Beddington, J. R. and May, R. M. (1977). “Harvesting natural populations in a randomly fluctuating environment”. *Science*, 197:463–465.
- [6] Braumann, C. A. (1985). “Stochastic differential equation models of fisheries in an uncertain world: Extinction probabilities, optimal fishing effort, and parameter estimation”, pages 201–206. In: *Mathematics in biology and medicine*. Springer.
- [7] Braumann, C. A. (1999). “Variable effort fishing models in random environments”. *Mathematical biosciences*, 156:1–19.
- [8] Braumann, C. A. (2002). “Variable effort harvesting models in random environments: generalization to density-dependent noise intensities”. *Mathematical biosciences*, 177 & 178:229–245.
- [9] Braumann, C. A. (2007a). “Harvesting in a random environment: Itô or Stratonovich calculus?” *Journal of theoretical biology*, 244:424–432.
- [10] Braumann, C. A. (2007b). “Itô versus Stratonovich calculus in random population growth”. *Mathematical biosciences*, 206:81–107.
- [11] Braumann, C. A. (2007c). “Population growth in random environments: which stochastic calculus?” *Bulletin of the International Statistical Institute*, LXII:5802–5805.
- [12] Braumann, C. A. (2008). “Growth and extinction of populations in randomly varying environments”. *Computers and mathematics with applications*, 56:631–644.
- [13] Braumann, C. A. (2018). “Breve introdução às equações diferenciais estocásticas”. *Boletim Sociedade Portuguesa de Estatística*, outono de 2018:81–88.

- [14] Braumann, C. A. (2019). *Introduction to stochastic differential equations with applications to modelling in biology and finance*. Wiley.
- [15] Braumann, C. A., Carlos, C., Filipe, P. A., and Roquete, C. J. (2009). "Growth of individuals in randomly fluctuating environments". In: Vigo-Aguiar, J., Alonso, P., Oharu, S., Venturino, E., and Wade, B., editors, *Proc. of the 2009 International Conference in Computational and Mathematical Methods in Science and Engineering*. CMMSE, pages 201–212.
- [16] Brites, N. M. and Braumann, C. A. (2017). "Fisheries management in random environments: Comparison of harvesting policies for the logistic model". *Fisheries research*, 195:238–246.
- [17] Brites, N. M. and Braumann, C. A. (2019a). "Harvesting policies with stepwise effort and logistic growth in a random environment", pages 95–110. In: *Dynamical systems in biology and natural sciences*, volume 21. SEMA SIMAI Springer Series.
- [18] Brites, N. M. and Braumann, C. A. (2019b). "Fisheries management in randomly varying environments: comparison of constant, variable and penalized efforts policies for the Gompertz model". *Fisheries research*, 216:196–203.
- [19] Brites, N. M. and Braumann, C. A. (2019c). "Harvesting in a random varying environment: optimal, stepwise and sustainable policies for the Gompertz model". *Statistics, optimization and information computing*, 7:533–544.
- [20] Brites, N. M. and Braumann, C. A. (2020). "Stochastic differential equations harvesting policies: Allee effects, logistic-like growth and profit optimization". *Applied stochastic models in business and industry*, 36:825–835.
- [21] Capocelli, R. M. and Ricciardi, L. M. (1974). "A diffusion model for population growth in random environments". *Theoretical population biology*, 5:28–41.
- [22] Carlos, C. and Braumann, C. A. (2005). "Tempos de extinção para populações em ambiente aleatório", pages 133–142. In: *Estatística jubilar*. Edições SPE.
- [23] Carlos, C. and Braumann, C. A. (2006). "Tempos de extinção para populações em ambiente aleatório e cálculos de Itô e Stratonovich", pages 229–238. In: *Ciência estatística*. Edições SPE.
- [24] Carlos, C. and Braumann, C. A. (2017). "General population growth models with Allee effects in a random environment". *Ecological complexity*, 30:26–33.
- [25] Carlos, C., Braumann, C. A., and Filipe, P. A. (2013). "Models of individual growth in a random environment: study and application of first passage times", pages 103–111. In: *Advances in regression, survival analysis, extreme values, Markov processes and other statistical applications*. Springer.
- [26] Dennis, B. (2002). "Allee effects in stochastic populations". *Natural resources modelling*, 96:389–401.
- [27] Engen, S., Lande, R., and Sæther, B.-E. (2003). "Demographic stochasticity and Allee effects in populations with two sexes". *Ecology*, 84(9):2378–2386.
- [28] Filipe, P. A. (2018). "Modelos de equações diferenciais estocásticas e modelos mistos em crescimento individual". *Boletim Sociedade Portuguesa de Estatística*, outono de 2018:76–80.
- [29] Filipe, P. A., Braumann, C. A., Brites, N. M., and Roquete, C. J. (2010). "Modelling animal growth in random environments: an application using nonparametric estimation". *Biometrical journal*, 52(5):653–666.
- [30] Filipe, P. A., Braumann, C. A., Brites, N. M., and Roquete, C. J. (2013). "Prediction for individual growth in a random environment", pages 193–201. In: *Recent developments in modeling and applications in statistics*. Springer.
- [31] Filipe, P. A., Braumann, C. A., and Carlos, C. (2015). "Profit optimization for cattle growth in a randomly fluctuating environment". *Optimization*, 64(6):1393–1407.
- [32] Filipe, P. A., Braumann, C. A., and Roquete, C. J. (2007). "Modelos de crescimento de animais em ambiente aleatório", pages 401–410. In: *Estatística ciência interdisciplinar*. Edições SPE.
- [33] Filipe, P. A., Braumann, C. A., and Roquete, C. J. (2012). "Multiphase individual growth models in random environments". *Methodology and computing in applied probability*, 14(1):49–56.
- [34] Garcia, O. (1983). "A stochastic differential equation model for the height of forest strands". *Biometrics*, 39:1059–1072.
- [35] Gause, G. F. (1934). *The struggle for existence*. Williams and Wilkins.
- [36] Gleit, A. (1978). "Optimal harvesting in continuous time with stochastic growth". *Mathematical biosciences*, 41:112–123.
- [37] Goel, N. S. and Richter-Dyn, N. (1974). *Stochastic models in biology*. Academic Press.
- [38] Hanson, F. B. and Ryan, D. (1998). "Optimal harvesting with both population and price dynamics". *Mathematical biosciences*, 148(2):129–146.
- [39] Kar, T. K. and Chakraborty, K. (2011). "A bioeconomic assessment of the Bangladesh shrimp fishery". *World journal of modelling and simulation*, 7(1):58–69.
- [40] Kiester, A. R. and Barakat, R. (1974). "Exact solutions to certain stochastic differential equation models of population growth". *Theoretical population biology*, 6:199–216.
- [41] Levins, R. (1969). "The effect of random variations of different types on population growth". *Proc. National Academy of Sciences USA*, 62:1061–1065.
- [42] Lungu, E. M. and Øksendal, B. (1997). "Optimal harvesting from a population in a stochastic crowded environment". *Mathematical biosciences*, 145:47–75.
- [43] May, R. M. (1973). "Stability in randomly fluctuating versus deterministic environments". *American naturalist*, 107:621–650.
- [44] Øksendal, B. (2003). *Stochastic differential equations. An introduction with applications (6th edition)*. Springer.
- [45] Roughgarden, J. (1975). "A simple model for population dynamics in stochastic environments". *American naturalist*, 109:713–736.
- [46] Tuckwell, H. C. (1974). "A study of some diffusion models of population growth". *Theoretical population biology*, 5:345–357.