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A Non-stochastic Approach for Modeling Uncertainty in Population Dynamics

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We developed a non-stochastic methodology to deal with the uncertainty in models of population dynamics. This approach assumed that noise is bounded; it led to models based on differential inclusions rather than stochastic processes, and avoided stochastic calculus. Examples of estimations of extinction times for exponential and logistic population growth with environmental and demographic noise are presented.

1. Introduction

When constructing models in population biology we are necessarily faced with the problem of uncertainty. Typically, one starts from a deterministic model, which is often described by a differential equation,

$$x'(t) = h(t, x(t)).$$

The uncertainty, or 'noise,' can be formally modeled with a parameter u appearing in the dynamics

$$x'(t) = h(t, x(t), u(t)). \tag{1}$$

There are two different approaches towards equation (1). *The stochastic approach* is commonly used, see e.g., Keiding (1975), Pielou (1977), Ricciardi (1977), Roughgarden (1979), Okubo (1980), Nisbet and Gurney (1982), Dennis *et al.*

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(1991), Lande (1993), Grasman (1996), Chesson (1994) and Foley (1994). In this setting it is assumed that the noise enters the dynamics linearly, i.e.,

$$x'(t) = f(t, x(t)) + g(t, x(t))u(t), \tag{2}$$

and $u(t)$ is the so-called *white noise*, the formal derivation (i.e., stochastic differential) of Brownian motion $w(t)$. This allows us to write (2) as a stochastic differential equation

$$dx\,(t) = f(t, x(t))\,dt + \sigma g(t, x(t))\,dw(t). \tag{3}$$

From it one can obtain a diffusion equation describing the evolution of the probability density function $p(t, x)$ for the population size x at time t

$$\frac{\partial p(t,x)}{\partial t} = -\frac{\partial}{\partial x}(m(t,x)p(t,x)) + \frac{1}{2}\frac{\partial^2}{\partial x^2}(n(t,x)p(t,x))$$

where

$$m(t,x) = f(t,x), n(t,x) = \sigma^2 g(t,x)^2,$$

see Roughgarden (1979). In order to obtain this equation, the noise must enter the dynamics in a linear way, which is not always true in population models. The solution of (3) is a stochastic process whose sample paths are nowhere differentiable functions (with unbounded variation in any time interval). This derives from the peculiarity of Brownian motion, a limit of random walks with independent steps. Although stochastic approach led to a number of useful results there was also some criticism concerning its appropriateness in models of population biology. This is mainly connected with the fact that the white noise is a mathematical construct which, though a reasonable model of the noise encountered in physics and electronics, may not be a suitable description of perturbations in biological systems. For example, Steele (1985) suggested that fluctuations in terrestrial environment are relatively well approximated by white noise over shorter periods while variations in marine environment, as well as longer-term terrestrial variations, are better approximated by 'red noise' (i.e., higher variation in low frequencies). Recently, it was suggested by Halley (1996) that so-called $1/f$ noise may be a more appropriate alternative type of noise for ecological models. While white noise emphasizes short time scales, $1/f$ noise contains equal influences for all time scales (Halley, 1996). Other situations where the use of a diffusion approximation of a discrete system is not correct are contained in Gillespie (1989). The problems arise in the limit procedure from a random walk to a continuous time process: a diffusion can be obtained only if some parameters have a particular order of magnitude, and this is not always the case. However, the use of white noise leads to mathematically tractable models, and due to the lack of experimental data, it was used as an effective representation of noise. Models which are based on (3) allow us to compute several biologically important characteristics, for example probability of reaching an extinction threshold, mean and median times to first extinction etc., which are important for conservation biology (Dennis *et al.*, 1991; Foley, 1994). However, deviations of the actual noise from the white noise in model (3) will necessarily result in discrepancies between predictions and observations. Moreover, to give a meaning to (3), standard calculus has to be replaced by stochastic calculus, where integral over stochastic processes may be defined in various ways, i.e., non-uniquely. Two commonly used interpretations of (3), namely Itô and Stratonovich stochastic integrals, lead to substantially different results, which also have different biological consequences, for example concerning mean extinction times (Roughgarden, 1979). This problem, however, may be settled at the modelling stage—since one can pass from one interpretation to the other through a correcting term in the equation—and discussions about this choice can be found in the literature (Turelli, 1977; Braumann, 1983).

In the engineering literature, another approach to uncertain systems is well established; it is called *deterministic noise*, in the sense that noise is not assumed to have any probabilistic structure whatsoever. This setting includes the so-called *unknown-but-bounded noise*, which was developed mainly in the framework of the control of uncertain systems by G. Leitmann and coworkers, as well as the H^∞ approach [see, e.g., Başar and Bernhard (1991)]. In the case of the unknown-but-bounded noise the only assumption on u in (1) is that it belongs to a prescribed bounded set U, which may depend on time or even on the state of the system. If $\mathcal{U}$ is a set of sufficiently regular functions (e.g., measurable) with values in U, then (1) becomes a *differential inclusion*

$$x'(t) \in F(t, x(t)) := \{h(t, x(t), u(t)) | u \in U\}. \tag{4}$$

The meaning of (4) is that at each point (t, x) the velocity is not uniquely given but it belongs to the set $F(t, x)$. There is no ambiguity on what 'solution' of the above differential inclusion means, since for every $u(\cdot) \in \mathcal{U}$ we have an ordinary differential equation. Thus, the collection of all possible solutions of (1), for all different (measurable) realizations of noise $u(\cdot)$, forms the solution set of (4). Moreover, since sample paths of (4) are described by (1), they are almost everywhere differentiable functions. The theory of differential inclusions is well established and does not require a special calculus (Aubin and Cellina, 1984; Aubin, 1991; Deimling, 1992). To illustrate the bounded-noise approach, let us consider the problem of extinction: let x denote population abundance, subject to a growth law and to some unknown-but-bounded noise, according to

$$x' = f(x) + cg(x)u, \quad x(0) = x_0, \quad u(t) \in [-1, 1], \tag{5}$$

and let η be a given positive extinction threshold for the population. A first question is to determine those critical values of c and x_0 for which extinction may occur, i.e., for which there are solutions of (5) that reach η. Thus, we may arrive, for example, at a qualitative conclusion, that for small c extinction does not occur, while for large c extinction is possible. Moreover, we may compute the first time of possible extinction and study its dependence on parameters, e.g., c, x_0 etc., without any information about the noise distribution. We note that, in the stochastic case, there exist trajectories of the process which reach the extinction threshold in any positive time, i.e., the first time to extinction is zero. However, since in the stochastic approach the first time to extinction is a random variable, we can ask what is the mean (median) of it, which is then called the mean (median) time to extinction. We emphasize that the computation of the mean (median) time to extinction requires us to have some information on the noise, i.e., that it is white. In the stochastic case this is assumed to be known, but model (5) does not assume such information. In fact the admissible velocities which are in the set $f(x) + cg(x)[-1, 1]$ are not distinguished one from another, i.e., all of them are 'equally likely'. In the H^∞ setting no *a priori* bound on the noise is given, but its size is penalized by a quadratic cost; more precisely, let us again consider (5). In this framework, one may consider the functional

$$J(u) = x_u^2(T) + \int_0^T u^2(t)\,dt,$$

x_u being the trajectory of (5) corresponding to the noise $u(\cdot)$. The minimum of J, among those x which are solutions of (5) and satisfy the initial condition $x(0) = x_0$, is always uniquely attained, due to the quadratic nature of J. The meaning of J is: if the unperturbed system does not lead to the given threshold, then to obtain a lower $x^2(T)$ one must spend a large u. Minimizing J is a way to balance the unboundedness of the noise: the minimizer u^* is a square integrable, but not necessarily a bounded function. The solution x^* corresponding to the minimizer u^* can be seen as a kind of worst-case solution of the perturbed equation $x' = f(x) + g(x)u, \quad x(0) = x_0$, and one may say that extinction occurs before time T if $x^*(T) \leq \eta$. This approach is effective from the point of view of calculations, even in higher dimensions and with the presence of a control [see Bardi and Capuzzo Dolcetta (1997, Appendix B)]. It is motivated also through a connection with a kind of stochastic approach, called *risk-sensitive*, containing a Gaussian noise with vanishing variance, see Whittle (1990).

An *a priori* bound on the noise, however, can sometimes be estimated from data, and model (5) takes this fact into account. Therefore, the approach with unknown-but-bounded noise seems to be very natural, when the data are too few to validate white noise as a good representation of the observed noise, but are numerous enough to estimate a bound on it. On the other hand, it may be criticized because it seems rather poor, with respect to the information which can be obtained from it. Instead, a method exists [see Bressan (1990) and Cellina and Colombo (1990)] which allows us precisely to 'distinguish' among trajectories, and so to mimic some probability-like concepts. This method relies on the definition of a function in the solution set, which is called *metric likelihood* (here the term likelihood has nothing to do with the likelihood used in probability). This function has an integral representation, which makes the approach similar to the H^∞ setting, and allows several calculations.

Here we present how the unknown-but-bounded noise approach, together with the metric likelihood, can be used to model uncertainty in population models. Since this approach does not require in principle any probabilistic knowledge of the noise, it may be applied also in those cases where insufficient data do not allow reliable estimates of the statistical properties of the noise. The only assumption which is requested is that the bound on the noise is known; this bound can be estimated from data. Our approach is an alternative to the stochastic approach and it may prove to be useful, e.g., in conservation biology. The paper is organized as follows. First, we briefly review the basic concepts concerning differential inclusions, showing that they can be good continuous approximations of the intrinsically discrete systems appearing in population dynamics. Then, we describe the metric likelihood functional, and define suitable functions, which—in this setting—are the counterpart of the probability (density) of reaching a point. With the above tools, we compute the likelihood of extinction and various extinction times for two classical models of population dynamics, the exponential and logistic growth, perturbed in different ways. Finally, using grizzly-bear data (Dennis *et al.*, 1991; Foley, 1994) we compare our results with those obtained by using the stochastic approach. We stress here that no stochastic calculus will be needed, and the methods we will use are based on deterministic approach; moreover, we do not request that the noise enters the dynamics linearly. This paper introduces a new, simple methodology and yet it produces results which are qualitatively, but not quantitatively, similar to results obtained via the theory of stochastic processes.

2. SOME BASIC MODELS

In theoretical population biology two sources of perturbations are *environmental* and *demographic* noise. The demographic noise is due to fluctuations in birth and death processes, while the environmental noise is due to unpredictable changes in environment. The difference between these two types of noise lies in the fact that the effect of demographic fluctuations decrease with increasing population size, due to the Law of Large Numbers, while in the case of environmental fluctuations all individuals are affected in the same way. Therefore, the environmental fluctuations swamp demographic ones, unless the population is small.

Let $x(t)$ denote the density of a population at time t. Two models based on (3) are thoroughly investigated in the literature: exponential and logistic growth, for which

$$f(x) = rx, \qquad f(x) = rx\left(1 - \frac{x}{K}\right). \tag{6}$$

The choice of $g(\cdot)$ depends on the nature of perturbations modeled. In the stochastic approach to demographic noise (Nisbet and Gurney, 1982),

$$g(x) = \sqrt{(b(x) + d\,(x))x},$$

where $b(x)$ and $d(x)$ are instantaneous per capita birth and death rates, respectively. For the exponential growth, this choice gives

$$g(x) \propto \sqrt{x}. \tag{7}$$

The effects of environmental noise are assumed to influence parameters r and K. Assuming that only r is affected, we are led to

$$g(x) \propto x \tag{8}$$

for exponential growth, and to

$$g(x) \propto x\left(1 - \frac{x}{K}\right) \tag{9}$$

for logistic growth. If K is affected by noise, this leads to a model in which noise u does not enter linearly:

$$x' = rx\left(1 - \frac{x}{K + cu}\right).$$

Such models are not tractable via the stochastic method. In order to overcome this difficulty, Roughgarden (1979) considers its first-order approximation in u, i.e.,

$$x' = rx\left(1 - \left(1 - \frac{cu}{K}\right)\frac{x}{K}\right)$$

which leads to

$$g(x) \propto x^2. \tag{10}$$

In stochastic differential equations the noise is represented through the white noise. Instead, we assume that the noise is bounded by a constant $c > 0$, and we consider the differential inclusion

$$x' \in f(x) + cg(x)[-1, 1]. \tag{11}$$

After introducing some general concepts we study (11) for f given by (6), and g given by (7)–(10).

3. Differential Inclusions, Fuzzy Sets and Likelihood

First we recall some facts concerning the theory of scalar differential inclusions. A set-valued map F is a map which associates with any point (t, x) the set $F(t, x)$. Having a set-valued map $F(t, x)$, a solution of the differential inclusion

$$\begin{array}{rcl} x'(t) & \in & F(t, x(t)) \\ x(0) & = & x_0 \end{array} \tag{12}$$

is an absolutely continuous function defined on an interval $I = [0, T]$, such that (12) holds for almost every $t \in I$. Several existence results for (12) are available under various continuity assumptions on the set-valued map F (Aubin and Cellina, 1984; Aubin, 1991; Deimling, 1992). In this paper we set

$$F(t, x) = h(t, x, c[-1, 1]), \tag{13}$$

or, in the linear case

$$F(t, x) = h(t, x) + cg(t, x)[-1, 1], \tag{14}$$

where h, f, g are single-valued and Lipschitz continuous maps. Under these assumptions there exist solutions of (12) for each initial condition. It is well known that the set S of all solutions of differential inclusion (12) coincides with the set of all solutions of the control system (2) for all measurable controls $u : I \mapsto [-1, 1]$, (Aubin and Cellina, 1984, p. 91). Moreover, for each time $t > 0$ the reachable set of (12)

$$R(t) := \{x(t) | x \in S\}$$

is an interval, which we denote

$$R(t) = [x_-(t), x_+(t)].$$

Then x_-, x_+ are called the minimal and the maximal solutions of (12), i.e.,

$$x'_+(t) = \max\{h(t, x_+(t), cu) | u \in [-1, 1]\}$$

$$x'_-(t) = \min\{h(t, x_-(t), cu) | u \in [-1, 1]\},$$

which gives in the linear (in u) case (we assume that g is positive)

$$x'_+(t) = f(t, x_+(t)) + cg(t, x_+(t))$$

$$x'_-(t) = f(t, x_-(t)) - cg(t, x_-(t)).$$

Any continuous model in population biology is an idealization of the real system, which is discrete in its nature. However, such models are more tractable than discrete ones, and allow us to obtain more easily some qualitative statements. To be an approximation of a discrete system, any continuous model must satisfy the following condition: as the time discretization tends to zero, the solutions of the discrete problem must approach a solution of the continuous model and vice versa (Turelli, 1977). This criterion says that if we take a sequence of piecewise-constant functions u_n which is converging to a function u, then the corresponding solutions x_n of (2) converge to a solution of (12) and, conversely, for every solution x of (12) there exists a sequence of piecewise-constant functions u_n such that the corresponding solutions x_n of (2) converge to x. This is exactly the case for our model based on differential inclusions, (Aubin and Cellina, 1984, Theorem 1, p. 60). Let us consider piecewise-constant functions u_n which may have values of only 1 or -1. This case corresponds roughly to the discrete random walk, where a particle moves either to the right, or to the left. Thus, the discrete model for population dynamics would be

$$x_{n+1} = x_n + f(t_n, x_n)\Delta + cg(t_n, x_n)u_n\Delta.$$

As Δ tends to zero, the trajectories of the above discrete model will converge to trajectories of the following differential inclusion

$$\begin{aligned} x'(t) &= f(t, x(t)) + cg(t, x(t))u(t) \\ u(t) &\in [-1, 1] \\ x(0) &= x_0. \end{aligned} \tag{15}$$

This convergence property also holds for models in which noise enters nonlinearly. The difference with the diffusion approximation is clear: the displacement is of the order of Δ instead of that of $\sqrt{\Delta}$.

We consider now the differential inclusion (12), and assume that some additional information on the noise u, besides its bound c, is available. For instance, one may assume—or obtain from data, see Section 8—that the 'extreme' values of u, namely those which are closer to the endpoints of the interval $[-1, 1]$, occur less frequently than those which are more interior; in other words, they are less likely. More generally, following Colombo and Křivan (1992), we assume that a continuous function $\rho : [-1, 1] \mapsto [0, 1]$ is given, which measures the likelihood of points in $[-1, 1]$. A prototype of a such a function on the set of perturbations, which assigns larger likelihood to smaller perturbations, is

$$\rho_q(u) = 1 - u^2. \tag{16}$$

For each solution x_u of (12) which corresponds to a function u we define its *likelihood* $\mathcal{L}(T, x_u)$ on the interval $[0, T]$ to be the average likelihood of the control function

u which represents the noise, i.e.,

$$\mathcal{L}(T, x_u) := \frac{1}{T} \int_0^T \rho(u(t))\, dt. \tag{17}$$

We remark that one can make such an assumption without supposing that the noise described by u be a stochastic process. The choice of ρ appearing in (16) also has an intrinsic interpretation, namely it takes into account 'how many' trajectories are around x. Indeed, for $\epsilon > 0$ a way to 'measure' the set of those solutions of (12) which are in the ϵ neighborhood of x is given by the following considerations. In general, the number of such solutions is infinite, and there is no standard measure defined on this set. In Bressan (1990) a measure of non-compactness (of the set of controls u which give such solutions) was chosen to this end; its limit for $\epsilon \to 0$ was defined as the likelihood of x. It was proved that, under certain conditions, this measure of non-compactness may be represented as an integral functional, which is essentially the same as (17), with $\rho = \rho_q$. In this setting, a solution is more likely than another one if there are more (according to the above concept of measure) solutions around it. The choice in (16) of ρ also keeps the analogy with the quadratic cost of the H^∞ approach; therefore, it seems to be motivated enough. We call the solution of (12) which maximizes (17) the most likely path of (12); we note that it is the solution of $x' = h(t, x, 0)$, and has likelihood 1. We call this trajectory *deterministic*.

Other choices of membership functions are also possible. With an argument similar to that of Bressan (1990), Cellina and Colombo (1990) derived a triangular membership function

$$\rho_t(u) = 1 - |u|;$$

we will make use of it in Section 8.

The function $\mathcal{L}(T, \cdot)$ maps the set of all solutions of (12) into $[0, 1]$. Note that the function ρ may be considered as a *membership function* of the fuzzy set $[-1, 1]$ (Wang and Klir, 1992). Similarly, the set S is a fuzzy set with membership function $\mathcal{L}$; in other words, (12) is a fuzzy differential inclusion (Aubin, 1990). The function $\mathcal{L}$ can be used to define the likelihood of sets. For example, the reachable set $R(T)$ at time T can also be regarded as a fuzzy set, if we define, for $\xi \in R(T)$,

$$L(T, \xi) := \sup\{\mathcal{L}(T, x) | x \in S, x(T) = \xi\}.$$

We consider L as the membership function of $R(T)$, i.e., $L(T, \xi)$ is the metric likelihood of reaching a point ξ at time T. L can be computed either by using Pontryagin's principle or the Hamilton–Jacobi equation, since it is the value function of an optimal control problem. If the integrand ρ is concave, or the dynamics is linear, the supremum is attained (see Cesari, 1983, Theorem 16.4.i). In contrast with stochastic theory, the reachable set of (12) is a bounded set. Outside of it we set L to be zero.

Let $\eta > 0$ be a given threshold of extinction. We may ask: What is the likelihood that solutions of (12) will reach the extinction threshold before some fixed time T? We define the *likelihood of extinction before time T* to be

$$L_e(T, \eta) := \sup_{t \in [T_0(x_0, \eta), T]} L(t, \eta),$$

where $T_0(x_0, \eta)$ denotes the *first time of extinction*, i.e., the first time when the minimal solution x_- of (12) reaches the extinction threshold η. If $L(\cdot, \eta)$ is an increasing function then $L_e(T, \eta) = L(T, \eta)$. By computing the supremum of $L_e(T, \eta)$ in $[T_0(x_0, \eta), +\infty)$ we obtain the likelihood that solutions of (12) will become extinct in future

$$L_e(\eta) := \sup_{T \geq T_0(x_0, \eta)} L_e(T, \eta).$$

We may also be interested to know the first extinction time T_k of trajectories of (12) which have a likelihood larger or equal to some given value k. This can be computed by solving

$$L_e(T_k, \eta) = k.$$

We note that $T_0 = T_0(x_0, \eta)$. If the time at which the deterministic solution of (12) reaches the extinction threshold is finite, then it satisfies

$$L_e(T_1, \eta) = 1.$$

All trajectories which will eventually reach the extinction threshold have a likelihood between 0 and $L_e(\eta)$. Thus, we may be interested to compute the first extinction time $T_{1/2L_e(\eta)}$ of those trajectories which have a likelihood $\frac{1}{2}L_e(\eta)$ in analogy with the median extinction time of stochastic calculus (Dennis *et al.*, 1991). We call $T_m = T_{1/2L_e(\eta)}$ *the median metric likelihood extinction time*.

4. Exponential Growth with Environmental Noise

We consider the exponential growth model, where the growth rate r undergoes unknown-but-bounded perturbations with range $c > 0$, namely

$$\begin{aligned} x' &= rx + cu\,x \\ u &\in [-1, 1] \\ x(0) &= x_0. \end{aligned} \tag{18}$$

At time $t > 0$, the reachable set is

$$R(t) = [e^{(r-c)t}x_0, e^{(r+c)t}x_0].$$

Thus, if $c < r$, both the lower and the upper bound tend to infinity when $t \longrightarrow \infty$, while for $c > r$, $R(t)$ tends to $(0, \infty)$. Let us assume that a threshold for extinction $\eta > 0$ is given. We will always assume that the initial population density x_0 is above the extinction threshold η. Then (18) predicts that, for $c > r$, extinction of the population is possible, and that the first time of possible extinction is

$$T_0(x_0, \eta) = \frac{1}{c - r} \ln(x_0/\eta). \tag{19}$$

We see that the first time of extinction is proportional to the logarithm of the initial density of the population. The use of the concept of 'likelihood' allows for some further analysis of the model. Choosing the membership function (16), for a given realization of the noise $u : [0, T] \mapsto [-1, 1]$ the likelihood of the corresponding solution x of (18) is

$$\mathcal{L}(T, x) = \frac{1}{T} \int_0^T 1 - u(t)^2 \, dt. \tag{20}$$

To find the likelihood $L(T, \xi)$ of a point ξ at time T, we have to find the solution of (18) which satisfies $x(T) = \xi$ and which has the highest likelihood. It is shown in Appendix 1 that the corresponding realization of u is constant

$$u_0 = \frac{1}{c} \left(\frac{1}{T} \ln \left(\frac{\xi}{x_0} \right) - r \right) \in [-1, 1]. \tag{21}$$

Consequently, the likelihood of reaching a point $\xi \in R(T)$ is

$$L(T, \xi) = 1 - \frac{r^2}{c^2} + \frac{1}{Tc^2} \left(2r \ln \left(\frac{\xi}{x_0} \right) - \frac{1}{T} \left(\ln \frac{\xi}{x_0} \right)^2 \right). \tag{22}$$

The likelihood of reaching the extinction threshold depends on the sign of the growth-rate parameter r. If r is negative, the deterministic trajectory $x(t) = x_0 \exp(rt)$ reaches the extinction threshold in a finite time

$$T_1 = \frac{1}{r} \ln(\eta/x_0) \tag{23}$$

and, consequently, $L_e(\eta) = 1$. If $r > 0$ then the deterministic trajectory will never reach the extinction threshold, and if $c > r > 0$ the likelihood of extinction is

$$L_e(\eta) = 1 - \frac{r^2}{c^2}.$$

Thus, we see that, for $c > r > 0$, the likelihood of extinction increases as r/c decreases. We compute the median metric likelihood extinction time T_m. According to our definition, T_m satisfies the equation

$$L(T_m, \eta) = \begin{cases} 1/2 L_e(\eta), & \text{if } c > r \geq 0 \\ 1/2, & \text{if } r < 0 \end{cases}$$

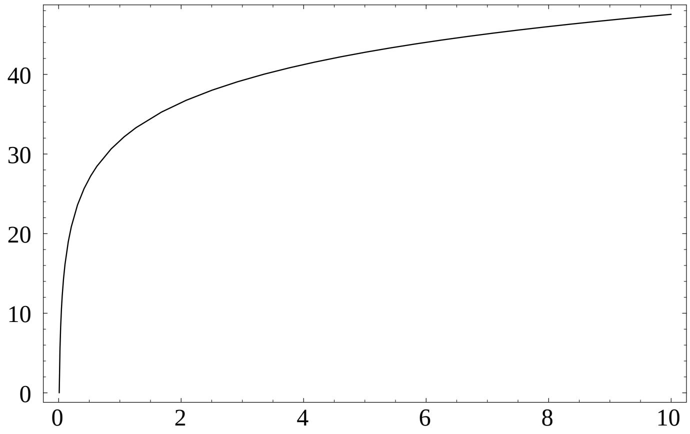

Figure 1. The median metric likelihood extinction time T_m for the exponential growth with environmental noise is plotted against the initial condition x_0. Parameters: $r = 0.25$, $c = 0.5$, $\eta = 0.01$.

i.e.,

$$T_m = \begin{cases} \ln\left(\frac{x_0}{\eta}\right) \frac{2r+\sqrt{2(c^2+r^2)}}{c^2-r^2}, & \text{if } c > r \geq 0 \\ \ln\left(\frac{x_0}{\eta}\right) \frac{\sqrt{2}}{c-\sqrt{2}r}, & \text{if } r < 0. \end{cases} \tag{24}$$

Therefore the median metric likelihood extinction time is proportional to the logarithm of the initial population, see Fig. 1.

5. Exponential Growth with Demographic Noise

We model demographic noise for the exponentially growing population by

$$x' = (r + c(x)u)x$$
$$u \in [-1, 1].$$

Here we assume that the bound $c(x)$ of the noise depends on the population density, since it is generally assumed that demographic noise decreases with respect to the density of the population. Namely, we assume that

$$c(x) = \frac{c}{\sqrt{x}}. \tag{25}$$

Thus, for $x = 0$ the noise is not bounded and it decreases for larger populations. With this choice our model for demographic noise becomes

$$x' = rx + cu\sqrt{x} \tag{26}$$
$$u \in [-1, 1],$$

which agrees with (7). We note that the above differential equation for fixed u does not uniquely define solutions from the initial condition 0. However, since our motivation comes from population biology, we assume that once the population density reaches zero, then the population cannot recover, i.e., no immigration of animals is possible. Then the reachable set at time $t > 0$ is

$$R(t) = \begin{cases} \left[\left(\dfrac{e^{rt/2}(r\sqrt{x_0} - c) + c}{r}\right)^2, \left(\dfrac{e^{rt/2}(r\sqrt{x_0} + c) - c}{r}\right)^2\right] \\ \qquad \text{if } x_0 \geq \left(\dfrac{c}{r}\right)^2 \\ \left[\left(\dfrac{e^{rt/2}(r\sqrt{x_0} - c) + c}{r}\right)^2, \left(\dfrac{e^{rt/2}(r\sqrt{x_0} + c) - c}{r}\right)^2\right] \\ \qquad \text{if } x_0 < \left(\dfrac{c}{r}\right)^2 \quad \text{and} \quad t \leq \dfrac{2}{r}\ln\left(\dfrac{c}{c - r\sqrt{x_0}}\right) \\ \left[0, \left(\dfrac{e^{rt/2}(r\sqrt{x_0} + c) - c}{r}\right)^2\right] \\ \qquad \text{if } x_0 < \left(\dfrac{c}{r}\right)^2 \quad \text{and} \quad t > \dfrac{2}{r}\ln\left(\dfrac{c}{c - r\sqrt{x_0}}\right). \end{cases}$$

Thus, we see that for

$$x_0 < \left(\frac{c}{r}\right)^2$$

there are solutions which reach zero in finite time, i.e., extinction is possible only for low initial densities. Thus, for the demographic noise we could consider the extinction threshold $\eta = 0$. However, since solutions starting from zero are not uniquely determined by (26), to avoid some additional technicalities we set the threshold for extinction $\eta > 0$. For $x_0 < (c/r)^2$, the first time of possible extinction is

$$T_0(x_0, \eta) = \frac{2}{r}\ln\left(\frac{c - r\sqrt{\eta}}{c - r\sqrt{x_0}}\right).$$

For further analysis we will use the same function ρ as for the environmental noise. To compute $L(T, \xi)$ we have to solve an optimal control problem, see Appendix 2. Let

$$x_1(t) = e^{rt}\left(-\frac{c}{2r}(1 - e^{-rt}) + \sqrt{x_0}\right)^2 \qquad \text{if} \quad \sqrt{x_0} \geq \frac{c}{2r} \quad \text{or} \quad \sqrt{x_0} < \frac{c}{2r}$$
$$\text{and} \quad t \leq t_1(x_0, 0),$$

$$x_1(t) = 0 \qquad \text{otherwise}$$

$$x_2(t) = e^{rt}\left(\frac{c}{2r}(1 - e^{-rt}) + \sqrt{x_0}\right)^2$$

where

$$t_1(x_0,\eta) = -\frac{1}{r}\ln\left(\frac{r^2}{c^2}\left(\sqrt{\eta}+\frac{\sqrt{r^2\eta - 2rc\sqrt{x_0}+c^2}}{r}\right)^2\right)$$

is the first time when x_1 reaches η. Denoting

$$A_1 := -(r\sqrt{x_0}-c)+r\sqrt{\xi}e^{-rT/2}, \quad A_2 := (r\sqrt{x_0}+c)-r\sqrt{\xi}e^{-rT/2}$$

and

$$\tau_1 = \frac{2}{r}\ln\left(\frac{A_1-\sqrt{A_1^2-c^2e^{-rT}}}{ce^{-rT}}\right), \quad \tau_2 = \frac{2}{r}\ln\left(\frac{A_2+\sqrt{A_2^2-c^2e^{-rT}}}{ce^{-rT}}\right),$$

we compute for $x_-(T) < \xi < x_+(T)$ the likelihood of reaching ξ at time T

$$L(T,\xi) = \begin{cases} \frac{1}{T}\left(T-\tau_1+\frac{1}{r}(e^{-rT}-e^{-r\tau_1})\right), & \text{if } \xi < x_1(T) \\ \frac{1}{T}\left(T+\frac{u_0^2}{r}(e^{-rT}-1)\right), & \text{if } x_1(T)\le \xi \le x_2(T) \\ \frac{1}{T}\left(T-\tau_2+\frac{1}{r}(e^{-rT}-e^{-r\tau_1})\right), & \text{if } \xi > x_2(T). \end{cases} \tag{27}$$

Now we compute the likelihood of reaching $\eta > 0$ at time T, i.e., we assume that $\sqrt{x_0} < \frac{c}{2r}$ and due to (27) we obtain

$$L(T,\eta) = \frac{1}{T}\left(T-\tau_1+\frac{1}{r}\left(e^{-rT}-e^{-r\tau_1}\right)\right), \qquad \text{if } T_0(x_0,\eta)\le T\le t_1(x_0,\eta) \tag{28}$$

and

$$L(T,\eta) = \frac{1}{T}\left(T-\frac{4rx_0}{c^2(1-e^{-rT})}\right), \qquad \text{if } t_1(x_0,\eta)\le T. \tag{29}$$

If $\sqrt{x_0} \ge \frac{c}{2r}$ then for $\eta < x_0$, $t_1(x_0,\eta) = \infty$ and $L(T,\eta)$ is given by (28). We obtain that the extinction likelihood is $L_e(\eta) = 1$. The median metric likelihood extinction time cannot be computed analytically, but numerical methods have to be used, see Fig. 2.

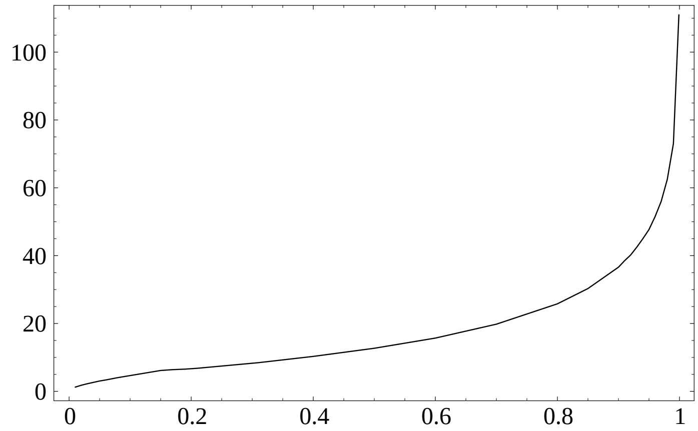

Figure 2. The median metric likelihood extinction time T_m for the exponential growth with demographic noise is plotted against the initial condition x_0. Parameters: $r = 0.25$, $c = 0.25$, $\eta = 0.01$.

6. LOGISTIC GROWTH—*r* FLUCTUATING

Now we will consider the logistic growth model with fluctuating growth rate r. Again the range of fluctuations is assumed to be bounded by a constant $c > 0$. The calculations follow those for exponential growth. Thus, the model is:

$$\begin{aligned} x' &= (r + cu)x\left(1 - \frac{x}{K}\right) \\ u &\in [-1, 1] \\ x(0) &= x_0 < K. \end{aligned} \tag{30}$$

At time $t > 0$, the reachable set is

$$R(t) = \left[\frac{Kx_0}{(K - x_0)e^{-(r-c)t} + x_0}, \frac{Kx_0}{(K - x_0)e^{-(r+c)t} + x_0}\right].$$

Thus, for $c < r$, both the lower and the upper bound tend to the carrying capacity K when $T \longrightarrow \infty$, while for $c > r$, $R(t)$ tends to $(0, K)$. Let us assume that a threshold for extinction $\eta \in (0, K)$ is given. For $x_0 > \eta$ extinction is possible if $c > r$. The first time of extinction is

$$T_0(x_0, \eta) = \frac{1}{c - r} \ln\left(\frac{(K - \eta)x_0}{(K - x_0)\eta}\right).$$

We note that the first time of extinction is increasing for increasing initial density of the population as for the exponential growth. Considering function ρ on the set of

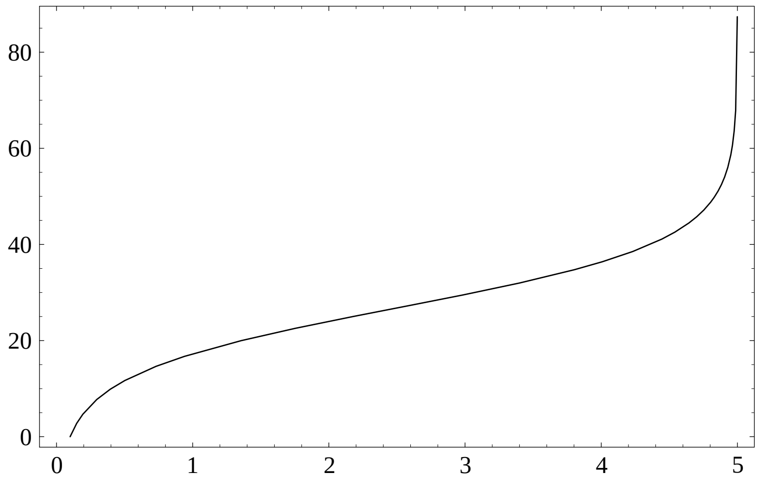

Figure 3. The median metric likelihood extinction time T_m for the logistic growth with fluctuating r is plotted against the initial condition x_0. Parameters: $r = 0.25$, $c = 0.5$, $\eta = 0.1$, $K = 5$.

perturbations and solving the corresponding optimal control problem, see Appendix 3, allows us to find the likelihood of reaching a point $\xi \in R(T)$

$$L(T, \xi) = 1 - \frac{r^2}{c^2} + \frac{1}{Tc^2}\left(2r \ln\left(\frac{(K - x_0)\xi}{(K - \xi)x_0}\right) - \frac{1}{T}\left(\ln\left(\frac{(K - x_0)\xi}{(K - \xi)x_0}\right)^2\right)\right). \quad (31)$$

Analogously to the exponential growth, we have

$$L_e(\xi) = \begin{cases} \lim_{T \longrightarrow \infty} L(T, \xi) = 1 - \frac{r^2}{c^2}, & \text{if } c > r \geq 0, \\ 1, & \text{if } r < 0, \end{cases}$$

which means that all points in the reachable set have ultimately the same likelihood. The median metric likelihood extinction time T_m is

$$T_m = \begin{cases} \ln\left(\frac{(K - \eta)x_0}{(K - x_0)\eta}\right) \frac{\left(2r + \sqrt{2(c^2 + r^2)}\right)}{c^2 - r^2}, & \text{if } c > r \geq 0, \\ \ln\left(\frac{(K - \eta)x_0}{(K - x_0)\eta}\right) \frac{\sqrt{2}}{c - \sqrt{2}r}, & \text{if } r < 0. \end{cases}$$

In this case, for small initial conditions the median metric likelihood extinction time is approximately proportional to the logarithm of the initial population density, while for x_0 tending to the carrying capacity, T_m tends to infinity, see Fig. 3.

7. Logistic Growth—*K* Fluctuating

Now we consider the logistic growth model with K fluctuating, i.e.,

$$x' = rx\left(1 - \frac{x}{K + cu}\right). \tag{32}$$

Since u does not enter the dynamics linearly, the corresponding stochastic model is not tractable. Roughgarden (1979) approximated the above dynamics by

$$\begin{aligned} x' &= rx\left(1 - \left(1 - \frac{cu}{K}\right)\frac{x}{K}\right) \\ u &\in [-1, 1] \\ x(0) &= x_0. \end{aligned} \tag{33}$$

In order to make our analysis comparable with the stochastic model, we will use the same approximation. We assume that $c < K$. At time $t > 0$, the reachable set is

$$R(t) = \left[\frac{Kx_0}{x_0(1 + c/K) + (K - x_0(1 + c/K))e^{-rt}},\right.$$
$$\left.\frac{Kx_0}{x_0(1 - c/K) + (K - x_0(1 - c/K))e^{-rt}}\right].$$

Thus, for $t \longrightarrow \infty$, $R(t)$ tends to

$$\left(\frac{K}{1 + c/K}, \frac{K}{1 - c/K}\right).$$

Let us assume that a threshold for extinction $\eta \in \left(\frac{K}{1+c/K}, \frac{K}{1-c/K}\right)$ is given. The first time of extinction is

$$T_0(x_0, \eta) = \frac{1}{r}\ln\left(\frac{\eta(K^2 - x_0(K + c))}{x_0(K^2 - \eta(K + c))}\right).$$

We note that

$$\lim_{x_0 \longrightarrow \infty} T_0(x_0, \eta) = \frac{1}{r}\ln\left(-\frac{\eta(K + c)}{K^2 - \eta(K + c)}\right),$$

i.e., the minimal solution starting from ‘infinity’ reaches η in a finite time. We compute $L(T, \xi)$ by solving the corresponding optimal control problem, see Appendix 4. Let

$$x_1(t) = \frac{2K^2 e^{rt} x_0}{ce^{r(2t-T)}x_0 + 2Kx_0e^{rt} + 2K^2 - cx_0e^{-rT} - 2Kx_0},$$

$$x_2(t) = \frac{2K^2 e^{rt} x_0}{-ce^{r(2t-T)}x_0 + 2Kx_0e^{rt} + 2K^2 + cx_0e^{-rT} - 2Kx_0}$$

and

$$A_1 = K^2\xi - e^{rT}K^2x_0 - ce^{rT}\xi x_0 - K\xi x_0 + e^{rT}K\,\xi x_0,$$

$$A_2 = K^2\xi - e^{rT}K^2x_0 + ce^{rT}\xi x_0 - K\xi x_0 + e^{rT}K\,\xi x_0,$$

$$u_0^+ = \frac{-A_1 - \sqrt{-c^2\xi^2x_0^2 + A_1^2}}{c\xi x_0},$$

$$u_0^- = \frac{-A_2 + \sqrt{-c^2\xi^2x_0^2 + A_2^2}}{c\xi x_0},$$

$$u_0 = \frac{-2K(K\,\xi - e^{rT}Kx_0 - \xi x_0 + e^{rT}\xi x_0)}{cx_0\xi - cx_0\xi e^{2rT}},$$

$$\tau_1 = \frac{1}{r}\ln\left(\frac{-1}{u_0^-}\right),$$

$$\tau_2 = \frac{1}{r}\ln\left(\frac{1}{u_0^+}\right).$$

Then for $\xi \in R(T)$ we have

$$L(T,\xi) = \begin{cases} \frac{1}{T}(\tau_2 + \frac{(u_0^+)^2}{2r}(1 - e^{2r\tau_2})), & \text{if } \xi \geq x_2(T) \\ \frac{1}{T}(T + \frac{u_0^2}{2r}(1 - e^{2rT})), & \text{if } x_1(T) < \xi < x_2(T) \\ \frac{1}{T}(\tau_1 + \frac{(u_0^-)^2}{2r}(1 - e^{2r\tau_1})), & \text{if } \xi \leq x_1(T). \end{cases} \tag{34}$$

The formula for $L(T, \xi)$ does not allow us to express the median metric likelihood extinction time analytically, but numerical methods have to be used. In Fig. 4 we compared the median metric likelihood extinction time obtained by using analytical formula for $L(T, \xi)$ (dashed line), with the approximation of the median metric likelihood extinction time obtained by approximating $L(T, \xi)$ numerically. For numerical simulations we used an algorithm for approximation of the value function of a control problem developed by Falcone [see Bardi and Capuzzo Dolcetta (1997, Appendix A)]. An implementation of the same algorithm with more than one control parameter would allow us to treat several independent noises; in particular, it is in principle possible to approximate the likelihood function for the logistic growth with both r and K independently fluctuating. The end-point constraint $u(T) = \xi$ was approximated by a penalization of the form $k(u(T) - \xi)^2$.

We now compare this result for linearized equation (33) with the result for the original, nonlinearized, equation (32). The solution set of (32) is

$$R(t) = \left[\frac{(K-c)x_0}{(K-c-x_0)e^{-rt} + x_0}, \frac{(K+c)x_0}{(K+c-x_0)e^{-rt} + x_0}\right];$$

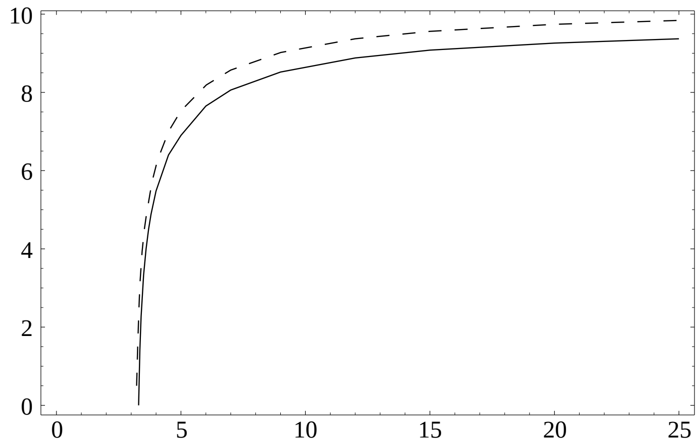

Figure 4. The median metric likelihood extinction time T_m for the linearized logistic growth with fluctuating K is plotted against the initial condition x_0. The full line is based on analytically computed formula for likelihood function (34), while the dashed line was obtained by using numerical approximation of the likelihood function. Parameters: $r = 0.25$, $c = 4$, $\eta = 3.3$, $K = 5$.

in particular, the asymptotic reachable set differs from that of (33). The first time of extinction is

$$T_0(x_0, \eta) = -\frac{1}{r} \ln \left(\frac{(K - c - \eta)x_0}{(K - c - x_0)\eta} \right).$$

The median metric likelihood extinction time cannot be computed analytically, and for its approximation we used Falcone's code, see Fig. 5. We see that the median metric likelihood extinction times based on the linearized version of the model (dashed line) are far above those which are predicted by the nonlinear model (full line).

8. Example

Here we give a simple example of how to apply to data the methodology described here. Dennis *et al.* (1991) consider the exponential growth model with the fluctuating growth-rate parameter, and, using diffusion analysis, they derive formulas for the mean extinction time, the median extinction time, the most likely time to reach the extinction threshold and for the probability to reach the extinction threshold. They apply these result to some population data sets. One data set is 3-year moving sums of the yearly estimated number of adult grizzly-bear females in the Yellowstone National Park between the years 1959 and 1987 which we will use. Dennis *et al.* (1991) deleted the transition for 1983–1984 and we do the same in order to make comparison possible. First, we simplify the exponential growth model (18)

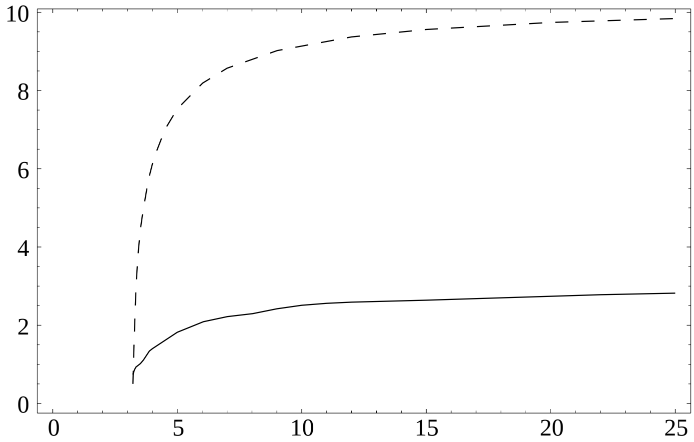

Figure 5. The median metric likelihood extinction times T_m for the logistic growth model (32) with fluctuating K (full line) and its linearized version described by (33) (dashed line) are plotted against the initial condition x_0. Parameters: $r = 0.25$, $c = 4$, $\eta = 3.3$, $K = 5$.

by using logarithmic transformation $y = \ln x$, which gives

$$y' = r + cu, \quad y(t_1) = y_1. \tag{35}$$

(Here t_1 denotes year 1959 and y_1 is the number for 1959.) For the sake of comparison we use the estimate of the growth-rate constant given in Dennis *et al.* (1991), i.e.,

$$\hat{r} = -0.007\,493.$$

We want to estimate the bound on fluctuations c in such a way that y_{i+1} belongs to the reachable set of (35) at time t_{i+1} when starting at time t_i with y_i, $i = 1, \ldots, N-1$, where $\{y_i\}_{i=1}^N$ are transformed data for the grizzly-bear population. This choice is natural in our setting, and goes towards a worst-case type analysis, since it precisely takes into account all fluctuations. We define the admissible set $A(N)$ that depends on the number of data (Křivan and Sed̆a, 1989):

$$A(N) = \{c \in \mathbb{R} \mid \|y_i - y_{i-1}(t_i - t_{i-1})\| \leq c(t_i - t_{i-1}), i = 2, \ldots, N\}.$$

The set $A(N)$ contains all values of parameter c that are consistent with measurements y_i and with model (35) in the sense that choosing any c from $A(N)$, every point y_i may be reached from y_{i-1} by a trajectory of (35). This means that using any c from the set $A(N)$, all data $\{y_i\}_{i=1}^N$ will be in the solution set of (35) with $u \in [-1, 1]$. As an estimate of c we take the minimal element of $A(N)$, i.e.,

$$\hat{c} = \min A(N).$$

For the grizzly-bear data we obtain $\hat{c} = 0.2$. The standard deviation of the growth rate computed in Dennis *et al.* (1991) is, instead, 0.09.

We compute various extinction times from the initial number of 47 bears and the extinction thresholds 10 and 1 bear. Since $\hat{r} < 0$, the likelihood of reaching extinction thresholds is 1 and the deterministic trajectory (which is the trajectory driven by $u = 0$) reaches the extinction thresholds in a finite time

$$T_1(47, 10) = 207, \quad T_1(47, 1) = 514.$$

We note that the formula for the mean time until the threshold population size is reached [Dennis *et al.* (1991, see formula (18) there)] is the same as is our formula (23) for the extinction time of deterministic solution T_1.

The first time to extinction is

$$T_0(47, 10) = 7.4, \quad T_0(47, 1) = 18.5.$$

For computations of extinction times of trajectories with a given likelihood we will use two types of membership functions: quadratic (ρ_q) and piecewise linear of a triangular shape (ρ_t). Using the least squares method implemented in Mathematica III we estimate these two membership functions:

$$\rho_q(u) = 0.225 - 0.248u^2 \quad \text{and} \quad \rho_t(u) = 0.274 - 0.264|u|.$$

In Fig. 6 frequencies of the occurrence of noise are plotted together with these two membership functions. Since both of these two membership functions are concave down, the realization of the noise which maximizes likelihood is constant by Jensen's inequality (see Appendix 1).

The median metric likelihood extinction times for the quadratic membership function are

$$T_m^q(47, 10) = 10.8, \quad T_m^q(47, 1) = 27$$

and for the triangular membership function they are

$$T_m^t(47, 10) = 13, \quad T_m^t(47, 1) = 34.5.$$

The likelihood of the trajectory of (35) which passes through points $\{y_i\}_{i=1}^N$ and which is driven by piece-wise constant controls $u_i = (y_{i+1} - y_i - r(t_{i+1} - t_i))/c$, $i = 1, \ldots, N - 1$ is approximately 0.17 and it is the same for both the quadratic and triangular membership functions. The corresponding extinction times are

$$T_{0.17}^q(47, 10) = 15.3, \quad T_{0.17}^q(47, 1) = 38,$$

$$T_{0.17}^t(47, 10) = 18.5, \quad T_{0.17}^t(47, 1) = 46.$$

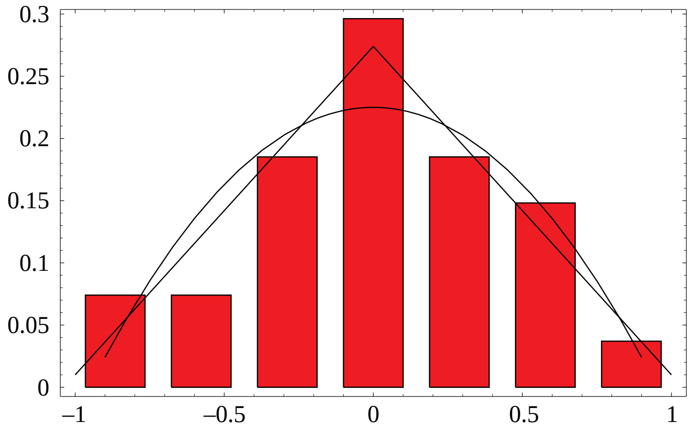

Figure 6. Estimation of the quadratic and triangular membership functions from grizzly-bear data (Foley, 1994).

We may compare these estimates with the results of Dennis *et al.* (1991) which are based on diffusion approximations. The first extinction time for the stochastic model would be 0 for any extinction threshold, in the sense that the population may become extinct before any $t > 0$—although with small probability for small t—while for the median extinction time (which is defined as time such that the probability of dying before this time is the same as is the probability of dying after this time) they obtain:

$$T_m^s(47, 10) = 152, \quad T_m^s(47, 1) = 448.$$

The mean time of extinction coincides with the time of extinction of the deterministic trajectory. We note that the median extinction time obtained with the diffusion approach is much closer to the extinction time of the deterministic solution than our T_m. This is of course due to our choice of the bound c, which takes into account all fluctuations, and is much larger than the corresponding parameter computed in the stochastic case, the standard deviation of the growth parameter. However, it is caused also by the quick growth in T of the function $L(T, \eta)$ (see Fig. 7), i.e., from our choice of the membership function. Finally, we note that the standard deviation of the mean time of extinction for the diffusion case, using formula (19) in Dennis *et al.* (1991) together with their estimate of parameters r and σ^2, gives 286 years for one bear, and 181 years for 10 bears.

Since diffusion assumes that the noise distribution is Gaussian, one may ask whether it is possible to obtain a larger median metric likelihood extinction time for bear data when substituting the quadratic (or triangular) noise membership function by $\exp(-u^2/\sigma^2)$ for $u \in [-1, 1]$. Since this membership function is not concave, the supremum in the definition of $L(T, \xi)$ may not be attained; moreover, in our case it equals the supremum of another integral functional, called the upper semicontinuous relaxed functional, which has as its integrand the smallest

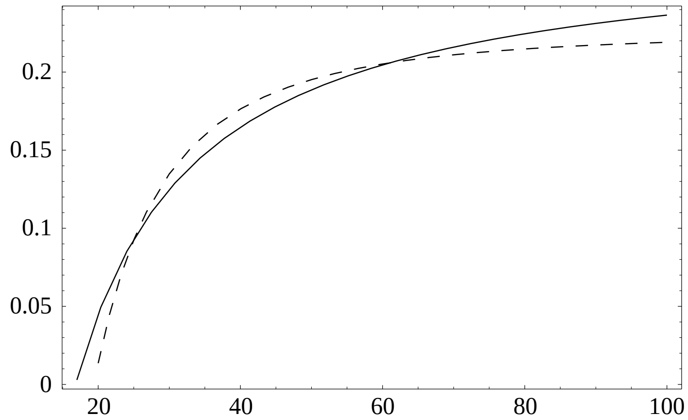

Figure 7. The likelihood of extinction at time T for the exponential growth with environmental noise is plotted against T. The heavy line corresponds to the quadratic approximation of the noise while the dashed line is for the triangular approximation of the noise. Parameters correspond to the grizzly-bear data: $r = -0.007493$, $c = 0.2$, $\eta = 1$.

concave function ρ^{**} larger than ρ [see Cesari (1983, Theorems 16.4.i, 16.2.i)]. If $\rho(u) = \exp(-u^2/\sigma^2)$, $\sigma < 1$, the graph of ρ^{**}, for $u \in [-1, 1]$ is almost triangular. Therefore, the supremum of $\int_0^T \exp(-u^2(s)/\sigma^2)\, ds$ is approximated by the supremum of $\int_0^T \rho_t(s)\, ds$ and we cannot expect to obtain a substantially larger median metric likelihood extinction time when choosing the Gaussian-like noise membership function.

9. DISCUSSION

For conservation biologists it is important to detect endangered species by categorizing them with respect to their threat of extinction. Mace and Lande (1991) proposed to redefine categories of threat in terms of the probability of extinction within a specified time period. These estimates should be based on the theory of extinction times, which in population biology has been tantamount to the use of stochastic models (Keiding, 1975; Pielou, 1977; Ricciardi, 1977; Roughgarden, 1979; Okubo, 1980; Nisbet and Gurney, 1982; Dennis *et al.*, 1991; Lande, 1993; Grasman, 1996; Chesson, 1994; Foley, 1994). Stochastic theory allows computation of the mean (or median) extinction times for simple models of population growth which are perturbed by white noise. However, as noticed in Mace and Lande (1991), in most cases there are insufficient data to verify that the noise is white. Moreover, there is some evidence that the noise may not be white (Steele, 1985; Halley, 1996). The discrepancies between the real noise and its approximation by white noise in population dynamical models may lead to substantial differences between predicted extinction times and observed extinction times. For these reasons we have envisaged a different methodology, which allows us to model uncertainty in population biology without requiring exact probabilistic knowledge of the noise. This methodology is based on the assumption that the noise is bounded and we can estimate this bound. For simple models of population growth this information alone immediately provides us with the following: (i) Which parameters lead to the possibility of population extinction? (ii) What is the first possible extinction time? The first time of extinction describes the worst possible case. The approach with unknown-but-bounded noise has been used widely in engineering literature as an alternative for modeling uncertainty. The unknown-but-bounded approach is intrinsically simpler than the stochastic approach, because it does not require any stochastic integral, but it uses standard calculus. Here we extended the unknown-but-bounded approach in the sense that if some additional information on noise distribution is known (which we here call metric likelihood), then we can also define analogs of some concepts of stochastic theory used in models of population dynamics, such as the likelihood of reaching a point, the likelihood of extinction and the median metric likelihood extinction time, which are important characteristics in conservation biology. This allows us both a qualitative and a quantitative comparison between results obtained by using the diffusion approach and ours. First, in the stochastic approach, population may become extinct in any positive time independent from the extinction threshold because white noise is not bounded. Thus, the first time of extinction when using the stochastic approach is always zero; in contrast, our approach gives a positive first extinction time. In order to compute the first extinction time no *a priori* knowledge on the noise distribution is assumed, except a bound on it. Of course, the first extinction time will be much shorter than the mean (or median) extinction time computed by diffusion approximation, since it describes the worst possible case in which perturbations are supposed to act. If the solution with maximal likelihood reaches the extinction threshold in a finite time (as in Section 8), this time may be another estimate of the extinction time. Since the most likely solution does not take into account the noise distribution, this extinction time may be quite large. For this reason we introduce another characteristic, that which we call median metric likelihood extinction time, which is larger than the first extinction time but smaller than the extinction time of the most likely trajectory. We compute these various extinction times both theoretically and numerically. For a numerical comparison we take a population of grizzly bears for which diffusion estimates were given in Dennis *et al.* (1991). This allows for comparison of various extinction times which are based on two different methodological approaches. The underlying dynamical model was in both cases exponential growth with a fluctuating growth-rate parameter. Computations show that the deterministic unknown-but-bounded approach leads to much smaller median metric likelihood extinction times than the stochastic approach, while the time of extinction of our most likely solution coincides exactly with the mean time of extinction computed in Dennis *et al.* (1991).

Attempts to extend the analytical results obtained for exponential growth, and also for logistic growth using diffusion analysis, were made by Foley (1994). However, since analytical formulas for this case cannot be obtained, he considered a simplified model by assuming that the population grows exponentially below its carrying capacity, which acts as a reflecting boundary. In contrast, our approach allows us to treat the logistic case directly. However, a comparison of our and Foley's result is difficult, because the two models differ in their dynamics. Computations similar to those for exponential growth reveal that our median metric likelihood extinction time is much smaller than Foley's mean extinction time. As initial data approach the carrying capacity, median metric likelihood extinction time starts sharply to grow to infinity, while mean extinction time converges to a finite value. However, we would like to note that there are quite big differences also between the Foley (1994) and the Dennis *et al.* (1991) results. For a qualitative comparison, we note first that typically we obtain some critical values of parameters, such that beyond them extinction is not possible, i.e., the minimum time of extinction is infinite. This effect is due to the dynamics of the original (deterministic) models, and to the boundedness of the noise. In particular, for both exponential and logistic growth with r fluctuating, extinction is possible only if the bound on the noise is larger than the intrinsic growth-rate parameter r. If this is satisfied, extinction for the exponential growth may occur from any initial population density. In the case of the logistic growth with fluctuating growth parameter extinction cannot occur from $x_0 = K$, which is an equilibrium point exactly as in the deterministic case. This is the reason why the median metric likelihood extinction time grows to infinity for x_0 tending to K. For the exponential growth with demographic noise extinction is not possible if the initial population size is above some critical value, which has a clear explanation: for larger initial populations demographic perturbations do not have enough 'strength' to counteract the positive growth tendency. The fact that the extinction time is infinite for a finite population size in some of our models is a clear difference between our approach and the stochastic one. On the other hand, our methods lead to median metric likelihood extinction times which for exponential and logistic growth increase slowly with the initial population. In particular, for fluctuating growth rate, the dependence on initial condition is logarithmic for the exponential growth and approximately logarithmic for the logistic growth with small initial densities (see formulae (19) and (24)). This qualitatively agrees with other results obtained via stochastic approach (Pakes *et al.*, 1979; Brockwell, 1985; Mangel and Tier, 1993).

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APPENDIX 1: COMPUTATIONS FOR EXPONENTIAL GROWTH WITH ENVIRONMENTAL NOISE

We note that substitution $y = \ln x$ transforms (18) to $y' = r + cu$. Moreover, we note that maximization of (20) is equivalent to minimization of $\int_0^T u^2(t)\,dt$ under the constraints $y(0) = \ln(x_0)$, $y(T) = \ln(\xi)$. Since u^2 is convex function, we can use Jensen's inequality

$$\left(\frac{1}{T}\int_0^T u(t)\,dt\right)^2 \leq \frac{1}{T}\int_0^T u^2(t)\,dt.$$

Thus the minimum of the functional is

$$\left(\frac{1}{T}\int_0^T \frac{y'(t)-r}{c}\,dt\right)^2 = \left(\frac{1}{c}\left(\frac{1}{T}\ln\left(\frac{\xi}{x_0}\right)-r\right)\right)^2,$$

which is reached by a constant control

$$u_0 = \frac{1}{c}\left(\frac{1}{T}\ln\left(\frac{\xi}{x_0}\right)-r\right) \in [-1, 1].$$

APPENDIX 2: COMPUTATIONS FOR EXPONENTIAL GROWTH WITH DEMOGRAPHIC NOISE

We note that substitution $y = \sqrt{x}$ transforms (26) to a linear control system

$$y'(t) = \tfrac{1}{2}(ry + cu). \tag{36}$$

We note that (36) together with $\int_0^T u^2(t)\,dt \to \min$ is so-called the linear regulator, for which the optimal control can be found in the feedback form

$$u(t) = -\frac{c}{2}K(t)x(t),$$

where $K(t)$ is a solution of the Riccati equation

$$K'(t) = -rK(t) + K^2(t)\left(\frac{c}{2}\right)^2,$$

(Fleming and Rishel, 1975). Considering boundary conditions $y(0) = \sqrt{x_0}$, $y(T) = \sqrt{\xi}$ we obtain optimal control

$$u(t) = u_0 e^{-r/2t}, \tag{37}$$

and the corresponding optimal trajectory is

$$x(t) = e^{rt}\left(\frac{c}{2r}u_0(1-e^{-rt}) + \sqrt{x_0}\right)^2, \tag{38}$$

where

$$u_0 = \frac{2r\left(\sqrt{\xi e^{-rT}} - \sqrt{x_0}\right)}{c(1-e^{-rT})}.$$

We note that (37) is the optimal control for the unconstrained problem, i.e., for the problem which does not consider any bound on u.

The optimal control for the constrained problem, i.e., $u \in [-1, 1]$ can be easily computed. First, we consider the set of all points which can be reached from the point x_0 by the optimal solution (38) for which the corresponding optimal control satisfies the constraint $u(t) \in [-1, 1]$. This set at time t is given by $[x_1(t), x_2(t)]$, where x_1, x_2 are optimal solutions corresponding to controls $u_1(t) = -e^{-rt/2}, u_2(t) = e^{-rt/2}$, respectively. Let

$$t_1(x_0, 0) = \frac{1}{r}\ln\left(\frac{c}{c - 2r\sqrt{x_0}}\right)$$

denote the first time when x_1 reaches zero. We note that when x_1 reaches zero, the solution is not uniquely defined due to the non-Lipschitzianity of the right-hand side of (26). We compute

$$\begin{aligned}
x_1(t) &= e^{rt}\left(-\tfrac{c}{2r}(1-e^{-rt}) + \sqrt{x_0}\right)^2, && \text{if} \quad \sqrt{x_0} \geq \tfrac{c}{2r} \quad \text{or} \quad \sqrt{x_0} < \tfrac{c}{2r} \\
& && \text{and} \quad t \leq t_1(x_0, 0), \\
x_1(t) &= 0 && \text{otherwise} \\
x_2(t) &= e^{rt}\left(\tfrac{c}{2r}(1-e^{-rt}) + \sqrt{x_0}\right)^2.
\end{aligned}$$

For $\xi = 0$ there are infinitely many solutions leading to ξ at time T. The most likely one is given by the smallest $|u_0|$, i.e.,

$$u_0 = -\frac{2r\sqrt{x_0}}{c(1-e^{-rT})}.$$

If $\xi < x_1(T)$ (or $\xi > x_2(T)$) then the optimal control is $u = -1$ on $[0, \tau_1]$ ($u = 1$ on $[0, \tau_2]$) and on $[\tau_1, T]$, ($[\tau_2, T]$) it is given by (37). Denoting

$$A_1 := -(r\sqrt{x_0} - c) + r\sqrt{\xi}e^{-rT/2}, \; A_2 := (r\sqrt{x_0} + c) - r\sqrt{\xi}e^{-rT/2}$$

we compute times τ_1 and τ_2, namely

$$\tau_1 = \frac{2}{r}\ln\left(\frac{A_1 - \sqrt{A_1^2 - c^2e^{-rT}}}{ce^{-rT}}\right), \tag{39}$$

$$\tau_2 = \frac{2}{r}\ln\left(\frac{A_2 + \sqrt{A_2^2 - c^2e^{-rT}}}{ce^{-rT}}\right).$$

APPENDIX 3: COMPUTATIONS FOR LOGISTIC GROWTH WITH r FLUCTUATING

We note that substitution $y = \ln(x/(K - x))$ transforms equation (30) to $y' = r + cu$. Using the same approach as in Appendix 1 we may prove that the optimal control is constant satisfying

$$u_0 = \frac{1}{Tc}\left(\ln\left(\frac{(K - x_0)\xi}{(K - \xi)x_0}\right) - rT\right) \in [-1, 1] \tag{40}$$

for $\xi \in R(T)$. The corresponding optimal trajectory is then

$$x(t) = \frac{Kx_0}{x_0 + (K - x_0)e^{-t(r+cu_0)}}.$$

APPENDIX 4: COMPUTATIONS FOR LOGISTIC GROWTH WITH K FLUCTUATING

After substitution $y = (K - x)/x$, system (33) is transformed to

$$y' = -ry - \frac{cr}{K}u.$$

Using the same approach as in the case of the exponential growth with demographic noise we obtain that the optimal control which minimizes the quadratic criterion is $u(t) = u_0 e^{rt}$, the corresponding optimal trajectory is

$$x(t) = \frac{2K^2 x_0 e^{rt}}{-ce^{2rt}x_0u_0 + 2Ke^{rt}x_0 + 2K^2 + cu_0x_0 - 2Kx_0}, \tag{41}$$

where

$$u_0 = \frac{-2K(K\xi - e^{rT}Kx_0 - \xi x_0 + e^{rT}\xi x_0)}{cx_0\xi(1 - e^{2rT})}. \tag{42}$$

We consider optimal solutions x_1 and x_2 on the interval $[0, T]$ which correspond to controls $u_1(t) = -e^{r(t-T)}$ and $u_2(t) = e^{r(t-T)}$, respectively. At time t, the set of all points which may be reached by the optimal trajectory which corresponds to the optimal control satisfying $u(t) \in [-1, 1]$ is $[x_1(t), x_2(t)]$. We obtain

$$x_1(t) = \frac{2K^2e^{rt}x_0}{ce^{r(2t-T)}x_0 + 2Kx_0e^{rt} + 2K^2 - cx_0e^{-rT} - 2Kx_0}$$

$$x_2(t) = \frac{2K^2e^{rt}x_0}{-ce^{r(2t-T)}x_0 + 2Kx_0e^{rt} + 2K^2 + cx_0e^{-rT} - 2Kx_0}.$$

Thus, $\lim_{t\longrightarrow\infty} x_1(t) = \frac{2K^2}{2K+c}$ and $\lim_{t\longrightarrow\infty} x_2(t) = \frac{2K^2}{2K-c}$. If $\xi > x_2(T)$ then there exists a time τ_2, $0 < \tau_2 < T$ such that the optimal control is

$$u(t) = \begin{cases} u_0 e^{rt}, & \text{for } 0 \leq t \leq \tau_2 \\ 1, & \text{for } \tau_2 \leq t \leq T. \end{cases} \tag{43}$$

We may compute both τ_2 and u_0. Denoting by

$$A_1 = K^2\xi - e^{rT}K^2x_0 - ce^{rT}\xi x_0 - K\xi x_0 + e^{rT}K\xi x_0$$

we obtain

$$u_0^+ = \frac{-A_1 - \sqrt{-c^2\xi^2x_0^2 + A_1^2}}{c\xi x_0}$$

and

$$\tau_2 = \frac{1}{r}\ln\left(\frac{1}{u_0^+}\right).$$

For $\xi < x_1(T)$ similar calculations give

$$u_0^- = \frac{-A_2 + \sqrt{-c^2\xi^2x_0^2 + A_2^2}}{c\xi x_0}$$

and

$$\tau_1 = \frac{1}{r}\ln\left(\frac{-1}{u_0^-}\right),$$

for

$$A_2 = K^2\xi - e^{rT}K^2x_0 + ce^{rT}\xi x_0 - K\xi x_0 + e^{rT}K\xi x_0.$$

Thus, for $\xi \in R(T)$ we have

$$L(T,\xi) = \begin{cases} \frac{1}{2T}(\tau_2 + \frac{(u_0^+)^2}{2r}(1 - e^{2r\tau_2})), & \text{if } \xi \geq x_2(T) \\ \frac{1}{2T}(T + \frac{u_0^2}{2r}(1 - e^{2rT})), & \text{if } x_1(T) < \xi < x_2(T) \\ \frac{1}{2T}(\tau_1 + \frac{(u_0^-)^2}{2r}(1 - e^{2r\tau_1})), & \text{if } \xi \leq x_1(T). \end{cases} \tag{44}$$

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