Growth and extinction of populations in a randomly varying environments

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Outline

- Population growth in a random environment can be modeled using stochastic differential equations (SDE).
- Instead of considering specific models, we will study a general model in what concerns extinction and existence and existence of stationary densities. That model is a generalization of previously studied specific models.
- Which stochastic calculus is more appropriate: Itô or Stratonovich?
- Extension to general harvesting models
- Further generalization to density-dependent noise intensities.
- Time to extinction
- Application (including estimation and prediction)

Deterministic model

$N(t)$ Population size at time $t > 0$

$$\frac{1}{N(t)}\frac{dN(t)}{dt} = g(N(t)) \qquad N(0) = N_0 > 0 \quad \text{is known}$$

$g(N)$	(*per capita*) growth rate (when population size is N)
$G(N) = g(N)\,N$	*total growth rate*

Examples

Malthusian	$g(N) = r$
Logistic	$g(N) = r\,(1-N/K)$
Gompertz	$g(N) = r \ln(K/N)$

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Randomly fluctuating environment

Effect of environmental random fluctuations on the growth rate

What has appeared in the literature

• Additive noise Add noise to the growth rate of a specific model

Example: logistic model

$$\frac{1}{N(t)}\frac{dN(t)}{dt} = r\left(1-\frac{N}{K}\right) + \sigma\varepsilon(t)$$

$\varepsilon(t)$ standard white noise

• Add noise to a parameter of a specific model

Example: Add noise to the r in the logistic model

$$\frac{1}{N(t)}\frac{dN(t)}{dt} = (r + \sigma\varepsilon(t))\left(1-\frac{N}{K}\right) = r\left(1-\frac{N}{K}\right) + \sigma\left(1-\frac{N}{K}\right)\varepsilon(t)$$

Sometimes unrealistic model

Randomly fluctuating environment

Several specific models (specific functions $g(N)$) have been proposed in the literature starting with Levins (1969) and, for the case of harvesting, with Beddington and May (1977).

Question: Are the properties obtained model specific or real properties of the population?

Our work:

- See if you can obtain properties for general models (arbitrary functions $g(N)$ satisfying only biologically determined assumptions and some mild technical assumptions). We seek properties on extinction or non-extinction and on existence of stationary densities.
- We consider realistic noise intensities
  - First: additive noise (constant noise intensities)
  - Later: density-dependent noise intensities that are positive for positive population sizes

General SDE model with constant noise intensity

$$\frac{1}{N(t)}\frac{dN(t)}{dt} = g(N(t)) + \sigma\varepsilon(t) \qquad N(0) = N_0 > 0 \quad \text{is known}$$

$$dN(t) = G(N(t))\,dt + V(N(t))\,dW(t)$$

$W(t) = \int_0^t \varepsilon(s)ds$ standard Wiener process

$g(N)$ "average" growth rate

$G(N)=g(N)N$ total "average" growth rate

$\sigma>0$ noise intensity (constant)

$V(N)=\sigma N$ total noise intensity

Assumptions on $g(\cdot):(0,+\infty)\mapsto(-\infty,+\infty)$

- continuously differentiable strictly decreasing
- the limit $g(0^+) := \lim_{N\downarrow 0} g(N) \neq 0$ (may be infinite)
- $g(+\infty) < 0$
- $G(0^+) = 0$

Stochastic integration

$$dN(t) = G(N(t))\,dt + V(N(t))\,dW(t) \qquad N(0) = N_0 > 0 \quad \text{is known}$$

$$N(t) = N_0 + \int_0^t G(N(s))ds + \int_0^t V(N(s))dW(s)$$

Decompositions with diameter converging to 0

$$0 = t_{0,n} < t_{1,n} < \cdots < t_{n-1,n} < t_{n,n} = t \quad (n = 1,2,\cdots)$$

Intermediate points

$$\tau_{i,n} \in [t_{i-1,n}\,,\, t_{i,n}]$$

The Riemann-Stieltjes sums

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

have m.s. limits that depend on the choice of the intermediate points.

Stochastic integration

Itô integral (non-anticipative choice $\tau_{i,n}=t_{i\,-1,n}$)

$$\int_0^t V(N(s))\,dW(s) = \underset{n\to+\infty}{\text{l.i.m.}} \sum_{i=1}^{n} V(N(t_{i-1,n}))\left(W(t_{i,n}) - W(t_{i-1,n})\right)$$

Nice probabilistic properties. Does not follow ordinary calculus rules.

Itô chain rule for $Y(t) = h(t,N(t))$ with $h(t,x)$ of class $C^{1,2}$

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

Stratonovich integral

$$(S)\int_0^t V(N(s))\,dW(s) = \underset{n\to+\infty}{\text{l.i.m.}} \sum_{i=1}^{n} \left(\frac{V(N(t_{i-1,n})) + V(N(t_{i,n}))}{2} \right)\left(W(t_{i,n}) - W(t_{i-1,n})\right)$$

We will use Stratonovich calculus.

General growth model with constant noise intensity

$$(S) \quad \frac{dN}{dt} = \big(g(N) + \sigma\varepsilon(t)\big)N$$

The solution exists and is unique up to an explosion time

The solution is a homogeneous diffusion process with

Diffusion coefficient

$$b(x) := V^2(x) = \sigma^2 x^2$$

Drift coefficient

$$a(x) := g(x)x + \frac{1}{4}\frac{db(x)}{dx} = \left(g(x) + \sigma^2/2\right)x$$

Note: With Itô calculus $a(x) := g(x)x$

General growth model with constant noise intensity

$$(S)\quad \frac{dN}{dt} = (g(N) + \sigma\varepsilon(t))N$$

Scale density

$$s(N) := \exp\left(-\int_{y_0}^{N} \frac{2a(\theta)}{b(\theta)} d\theta \right) = \frac{V(y_0)}{V(N)} \exp\left(-2\int_{y_0}^{N} \frac{G(\theta)}{V^2(\theta)} d\theta \right) \quad (y_0 > 0 \text{ arbitrary})$$

Scale function $S(N) = \int_{x_0}^{N} s(z)dz \quad (x_0 > 0 \text{ arbitrary})$

Speed density

$$m(N) := \frac{1}{s(N)b(N)} = \frac{1}{V(y_0)V(N)} \exp\left(2\int_{y_0}^{N} \frac{G(\theta)}{V^2(\theta)} d\theta \right)$$

Speed function $M(N) = \int_{x_0}^{N} m(z)dz \quad (x_0 > 0 \text{ arbitrary})$

$$0 < a < N_0 < b < +\infty$$

$$u(x) = \mathbf{P}\left[T_b < T_a \middle| N_0 = x\right] = \frac{S(x) - S(a)}{S(b) - S(a)}$$

General growth model with constant noise intensity

$$(S) \quad \frac{dN}{dt} = \left(g(N) + \sigma\varepsilon(t)\right)N$$

Boundary N=0 is non-attractive

if there is a right-neighborhood R=]0,y[of zero such that, for any 0<x<n∈R,

$$\mathrm{P}\left[T_{0^+} \leq T_n \middle| N(0) = x\right] = 0$$

T_z - first passage time by z $\quad T_{0^+} = \lim_{z\downarrow 0} T_z$

Necessary and sufficient condition $S(0^+) = -\infty$

This implies (Karlin and Taylor 1981) non-extinction a.s.

Similarly, for non-attractiveness of the boundary $N = +\infty$

With our assumptions we prove that:

The boundary $N = +\infty$ is non-attractive (which implies non-explosion, i.e., existence and uniqueness of the solution for all times).

The boundary $N = 0$ is attractive if $g(0^+) < 0$ and non-attractive if $g(0^+) > 0$.

General growth model with constant noise intensity

$$(S) \quad \frac{dN}{dt} = \left(g(N) + \sigma\varepsilon(t)\right)N$$

When both boundaries are non-attractive and

$$M(0,+\infty) = \int_0^{+\infty} m(z)dz < +\infty,$$

the process is ergodic and there is a stationary density given by

$$p(x) = \frac{m(x)}{M(0,+\infty)} \quad (0 < x < +\infty).$$

With our assumptions, we prove that happens when $g(0^+)>0$.

CONCLUSIONS:

- When $g(0^+) < 0$, extinction occurs a.s.
- When $g(0^+) > 0$, there is a zero probability of extinction and there is a stationary density

  (the mode of which approximately coincides with the deterministic equilibrium when the noise intensity is small).

General growth model with constant noise intensity

What happens if we use Itô calculus?

$$(I) \quad \frac{dN}{dt} = \left(g(N) + \sigma\varepsilon(t)\right)N$$

CONCLUSIONS:

- When $g(0^+) < \sigma^2/2$, extinction occurs a.s.
- When $g(0^+) > \sigma^2/2$, there is a zero probability of extinction and there is a stationary density

So, we can have extinction even when the “average” growth rate at low densities is positive.

Which calculus is right?

Recipes

Resolution of the controversy

for constant noise intensity

$$\frac{dN}{dt} = \left(g(N) + \sigma\varepsilon(t)\right)N$$

Deterministic model (σ=0)

(per capita) growth rate $R(x)$ when population size is x at time t

$$R(x) := \frac{1}{x}\left(\frac{dN}{dt}\right)_{N=x} = \frac{1}{x}\lim_{\Delta t \downarrow 0}\frac{N(t+\Delta t) - x}{\Delta t} = g(x)$$

Stochastic models

$$(I) \quad \frac{dN}{dt} = \left(g_i(N) + \sigma\varepsilon(t)\right)N \qquad\qquad (S) \quad \frac{dN}{dt} = \left(g_s(N) + \sigma\varepsilon(t)\right)N$$

Arithmetic average growth rate $R_a(x)$ when population size is x at time t

$$R_a(x) := \frac{1}{x}\lim_{\Delta t \downarrow 0}\frac{\mathrm{E}_{t,x}[N(t+\Delta t)] - x}{\Delta t} = \frac{1}{x}a(x) = \begin{cases} g_i(x) & \text{Itô} \\ g_s(x) + \sigma^2/2 & \text{Stratonovich} \end{cases}$$

Resolution of the controversy

for constant noise intensity

Geometric average growth rate $R_g\,(x)$ when population size is x at time t

$$R_g(x) := \frac{1}{x} \lim_{\Delta t \downarrow 0} \frac{\exp\big(\mathrm{E}_{t,x}[\ln N(t+\Delta t)]\big) - x}{\Delta t} = \begin{cases} g_i(x) - \sigma^2/2 & \text{Itô} \\ g_s(x) & \text{Stratonovich} \end{cases}$$

CONCLUSION (Braumann 2007a)

$g(x)$ means two different “average” growth rates under the two calculi.

It is the arithmetic average growth rate when we use Itô calculus.

It is the geometric average growth rate when we use Stratonovich calculus.

Taking into account the difference between the two averages, the two calculi completely coincide.

In both, we have extinction or stationary density according to whether the geometric average growth rate at low densities $R_g(0^+)$ is negative or positive.

Harvesting models with constant noise intensity

$$(S) \quad \frac{1}{N}\frac{dN}{dt} = g(N) + \sigma\varepsilon(t) - h(N)$$

$h(N)$	harvesting effort (when population size is N)
$H(N)= h(N)N$	yield (total harvesting rate)
$q(N)=g(N)-h(N)$	net growth rate

Assumptions on $h(\cdot):(0,+\infty)\mapsto[0,+\infty)$

- continuously differentiable non-negative
- the limit $q(0^+) := \lim_{N\downarrow 0} q(N)$ exists and is $\neq 0$ (may be infinite) can be weakened
- $H(0^+) = 0$

CONCLUSIONS (Braumann 1999b)

When $q(0^+) < 0$, extinction occurs a.s.

When $q(0^+) > 0$, there is 0 probability of extinction and there is a stationary density (the mode of which approximately coincides with the deterministic equilibrium when the noise intensity is small).

Itô and Stratonovich: Braumann (2007c).

Optimal harvesting (Lungu e Oksendal 1997, Alvarez e Shepp 1997, Alvarez 2000)

General growth model with density-dependent noise intensity

$$\sigma(N)$$

Assumptions on $\sigma(\cdot):(0,+\infty)\mapsto(0,+\infty)$:

- strictly positive twice continuously differentiable
- $V(0^+)=0$, where $V(N)=\sigma(N)N$

(A) $\int_{0^+}^{x_0}\frac{1}{\sigma(N)N}dN=+\infty$ for some $x_0>0$;

(B) $\int_{y_0}^{+\infty}\frac{1}{\sigma(N)N}dN=+\infty$ for some $y_0>0$.

(C) $|\sigma(N)/g(N)|$ is bounded in a right neighborhood of 0.

(D) $|\sigma(N)/g(N)|$ is bounded in a neighborhood of $+\infty$.

If noise intensity is bounded, it satisfies (A), (B), (C) and (D).

General growth model with density-dependent noise intensity

$$R_a(x) = \frac{1}{x} a(x) = \begin{cases} g_i(x) & \text{Itô} \\ g_s(x) + \sigma^2(x)/2 + x\sigma(x)\sigma'(x) & \text{Stratonovich} \end{cases}$$

ϕ - average

$$\phi(x) = \int_c^x \frac{1}{z\sigma(z)} dz \quad (c \text{ fixed arbitrary constant})$$

$$R_\phi(x) := \frac{1}{x} \lim_{\Delta t \downarrow 0} \frac{\phi^{-1}\left(\mathrm{E}_{t,x}[\phi(N(t+\Delta t))]\right) - x}{\Delta t} = g_s(x) \quad \text{for Stratonovich}$$

CONCLUSION (Braumann 2007b)

g(*x*) means two different “average” growth rates under the two calculi.

It is the arithmetic average growth rate when we use Itô calculus.

It is the ϕ–average growth rate when we use Stratonovich calculus (coincides with the geometric average when *N* approaches 0).

Taking into account the difference between the two averages, the two calculi completely coincide.

General growth model with density-dependent noise intensity

Proof of $R_\phi(x) := \frac{1}{x}\lim_{\Delta t\downarrow 0}\frac{\phi^{-1}\left(\mathrm{E}_{t,x}[\phi(N(t+\Delta t))]\right)-x}{\Delta t} = g_s(x)$ for Stratonovich

Under Stratonovich calculus, $Y=\phi(N)$ satisfies the SDE

$$(S) \quad dY = \frac{g_s(\phi^{-1}(Y))}{\sigma(\phi^{-1}(Y))}dt + dW(t)$$

In terms of Y, the drift coefficient is, with $y=\phi(x)$, $\lim_{\Delta t\downarrow 0}\frac{1}{\Delta t}\mathrm{E}_{t,x}\left[Y(t+\Delta t)-y\right] = \frac{g_s(\phi^{-1}(y))}{\sigma(\phi^{-1}(y))}$

Therefore $\mathrm{E}_{t,x}\left[Y(t+\Delta t)\right] = y + \frac{g_s(\phi^{-1}(y))}{\sigma(\phi^{-1}(y))}\Delta t + o(\Delta t)$.

Apply ϕ to both sides, expand about y and notice that $\frac{d\phi^{-1}(y)}{dy} = \frac{1}{d\phi(x)/dx} = x\sigma(x)$

to obtain $\phi^{-1}\left(\mathrm{E}_{t,x}[Y(t+\Delta t]\right) = x + xg_s(x) + o(\Delta t)$, from which the result follows

General growth model with density-dependent noise intensity

$$\sigma(N)$$

With the assumptions made, the same conclusions hold:

• When the geometric average growth rate at low densities is negative, extinction occurs a.s.

• When the geometric average growth rate at low densities is positive, there is a zero probability of extinction and there is a stationary density

For harvesting models see Braumann 2001

Time to extinction

$$(S) \quad \frac{1}{N(t)}\frac{dN(t)}{dt} = g(N(t)) + \sigma\varepsilon(t) \qquad N(0) = N_0 = x > 0 \quad \text{is known}$$

with the assumptions made on g and $g(0^+)>0$.

There is no "mathematical" extinction and there is a stationary density.

What about a population of 0.4 individuals? What about Allee effects?

Set extinction threshold $a>0$. We assume $a<N_0$.

Note: To study pest outbreaks, we could also consider $a>N_0$

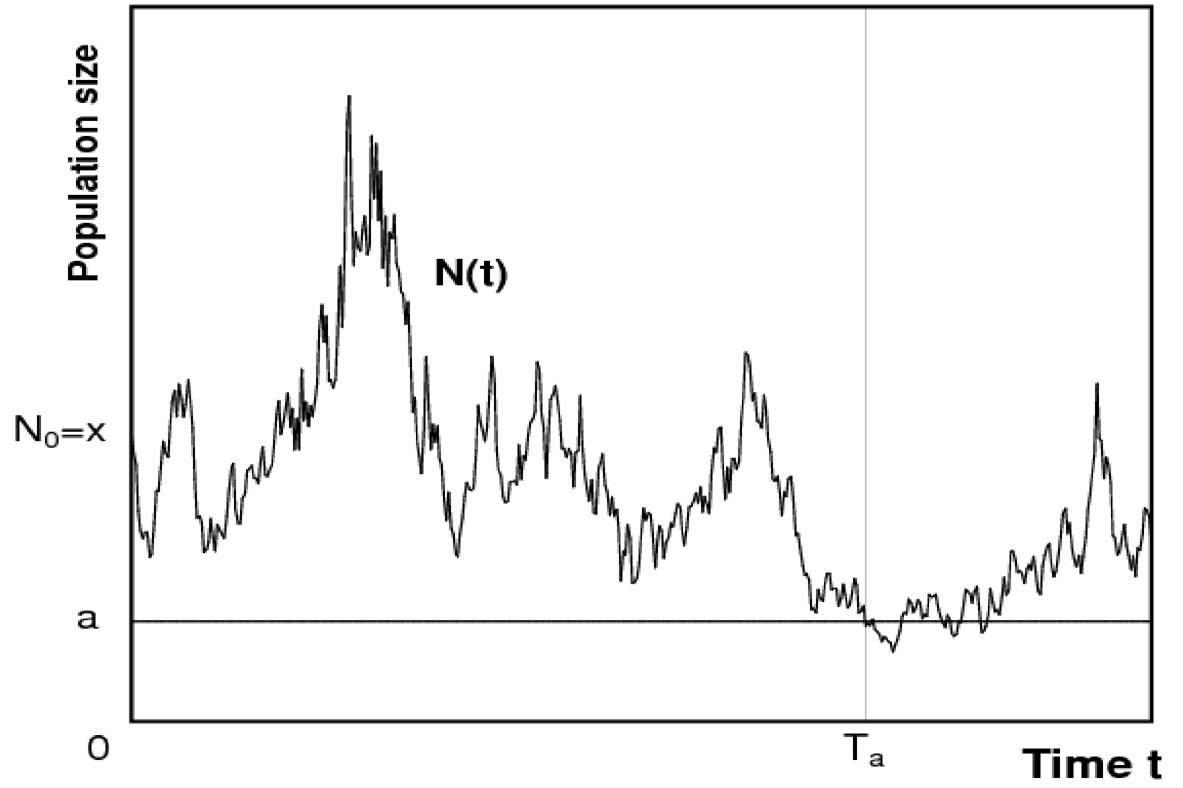
"Realistic" extinction occurs if ever $N(t)$ reaches the threshold

Since the process is ergodic it will do it (sooner or later) with probability one.

So, "realistic" extinction occurs a.s.

How long does it take? (Braumann 1985, Carlos and Braumann 2005,2006)

Time to extinction



To the first passage time

$$T_a = \inf\{t > 0 : \; N(t) = a\}$$ we call **extinction time**

Time to extinction

$$a(x) = \left(g(x) + \sigma^2 / 2\right)x \qquad b(x) = (\sigma x)^2$$

$$0 < a < N_0 < b < +\infty$$

$$T_{ab} = \min\{T_a, T_b\}$$

$$u(x) = \mathbf{P}\left[T_b < T_a \middle| N_0 = x\right] = \frac{S(x) - S(a)}{S(b) - S(a)}$$

$$V_k(x) = \mathbf{E}\left[(T_{ab})^k \middle| N_0 = x\right] \qquad \text{k - th order moment}$$

$$\frac{1}{2} b(x) \frac{d^2 V_k(x)}{dx^2} + a(x) \frac{dV_k(x)}{dx} + kV_{k-1}(x) = 0$$

$$\frac{1}{2} \frac{d}{dM(x)} \left(\frac{dV_k(x)}{dS(x)} \right) + kV_{k-1}(x) = 0$$

$$V_k(a) = V_k(b) = 0 \quad (k = 1,2,\ldots) \qquad V_0(x) \equiv 1$$

$$V_k(x) = 2u(x) \int_x^b (S(b) - S(\xi)) kV_{k-1}(\xi) m(\xi) d\xi$$

$$+ 2(1 - u(x)) \int_a^x (S(\xi) - S(a)) kV_{k-1}(\xi) m(\xi) d\xi$$

Time to extinction

We can also obtain an ODE for the Laplace transform

$$U_\lambda(x) = \mathbf{E}\left[\exp(-\lambda T_{ab}) \middle| N_0 = x\right]$$

$$\frac{1}{2}\frac{d}{dM(x)}\left(\frac{dU_\lambda(x)}{dS(x)}\right) - \lambda U_\lambda(x) = 0$$

$$U_\lambda(a) = U_\lambda(b) = 0$$

Solving the equation and inverting the Laplace transform, one obtains the p.d.f. of T_{ab}

Time to extinction

Since the process is ergodic, if we let $b \uparrow +\infty$, we obtain as limit of $V_k(x)$

$$\underline{V}_k(x) = \mathbf{E}\left[(T_a)^k \middle| N_0 = x\right]$$

So, we obtain (after some indeterminations are removed)

$$\underline{V}_k(x) = 2\int_x^{+\infty} (S(x) - S(a)) k V_{k-1}(\xi) m(\xi) d\xi$$

$$+ 2\int_a^x (S(\xi) - S(a)) k V_{k-1}(\xi) m(\xi) d\xi$$

$$= 2\int_a^x s(\xi)\left(\int_\xi^{+\infty} k V_{k-1}(\theta) m(\theta) d\theta\right) d\xi$$

Application

Gompertz model with additive noise

$$(S)\quad \frac{1}{N(t)}\frac{dN(t)}{dt} = r\ln\frac{K}{N} + \sigma\varepsilon(t) \quad \text{with } r>0, K>0, \sigma>0, N_0>0$$

$$g(N) = r\ln\frac{K}{N} \qquad \sigma(N)\equiv\sigma$$

satisfy all the assumptions and $g(0^+) = +\infty > 0$

$$a(x) = \left(r\ln\frac{K}{x} + \frac{\sigma^2}{2}\right)x \qquad b(x) = (\sigma x)^2$$

choosing $y_0 = K$

$$s(x) = \frac{K}{x}\exp\left(-\frac{r}{\sigma^2}\left(\ln\frac{x}{K}\right)^2\right) \qquad m(x) = \frac{1}{\sigma^2 Kx}\exp\left(\frac{r}{\sigma^2}\left(\ln\frac{x}{K}\right)^2\right)$$

Application

Extinction has 0 probability of occurring and there is a stationary density proportional to $m(n)$ with support $n>0$, the mode of which is $K\exp(\sigma^2/(2r))$.

Change of variable

$$y = \ln(n/K)$$

$Y(t) = \ln(N(t)/K)$ has stationary density proportional to $m(n)\, dn/dy$, which one immediately sees to be Gaussian with mean 0 and variance $\sigma^2/(2r)$.

We can obtain the transient p.d.f. of $Y(t)$

$Y(t)$ satisfies the SDE

$$(S) \quad dY = -rYdt + \sigma dW(t)$$

$$(S) \quad e^{rt}dY + re^{rt}Ydt = \sigma e^{rt}dW(t)$$

$$Y(t)e^{rt} = Y_0 + (S)\int_0^t \sigma e^{rs}dW(s) \quad \text{with} \quad Y_0 = \ln(N_0/K)$$

Application

$$Y(t) = Y_0 e^{-rt} + \sigma e^{-rt} \int_0^t e^{rs} dW(s)$$

$$\text{Gaussian}\left(Y_0 e^{-rt}, \sigma^2 e^{-2rt} \int_0^t e^{2rs} ds = \frac{\sigma^2}{2r}\left(1 - e^{-2rt}\right)\right)$$

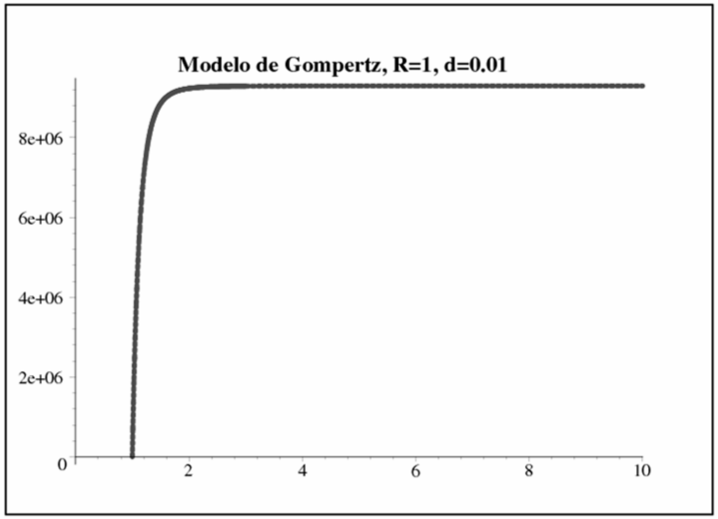
$$\to \text{Gaussian}\left(0, \frac{\sigma^2}{2r}\right) \quad \text{as} \quad t \to +\infty.$$

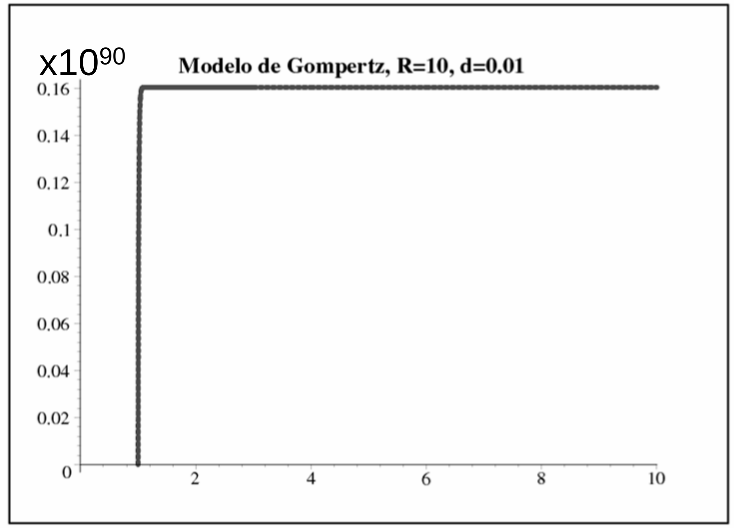
$$\underline{V}_1(x) = \mathbf{E}\left[T_a \middle| N_0 = x\right] = \frac{2\sqrt{\pi}}{r} \int_\alpha^\gamma (1 - \Phi(\sqrt{2}\, t))\, e^{t^2} dt$$

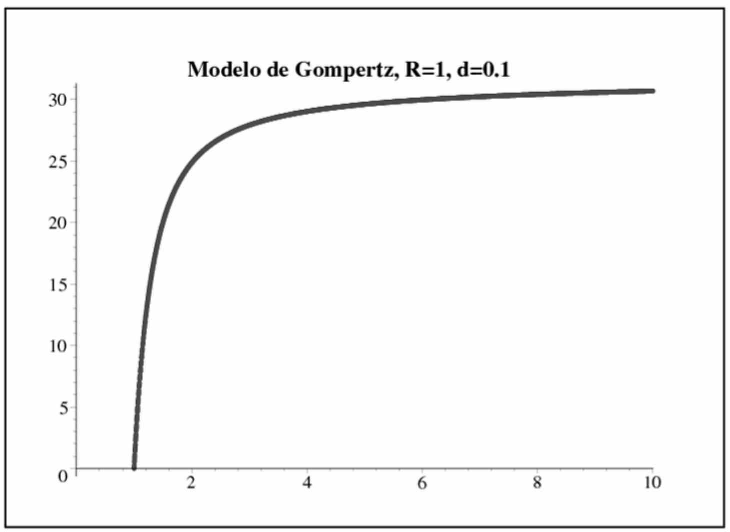
$$\underline{V}_2(x) = \mathbf{E}\left[(T_a)^2 \middle| N_0 = x\right] = \frac{8\sqrt{\pi}}{r^2} \int_\alpha^\gamma e^{s^2} \int_s^{+\infty} \int_\alpha^t (1 - \Phi(\sqrt{2}\, z))\, e^{z^2} dz e^{-t^2} dt ds$$

$$\text{with} \quad \alpha = \frac{\sqrt{r}}{\sigma} \ln \frac{a}{K} \quad \text{and} \quad \gamma = \frac{\sqrt{r}}{\sigma} \ln \frac{x}{K}$$

Gráfico de $r\,\mathbf{E}[T_a]$ como função de N_0/a. Aqui $R=r/\sigma^2$ e $d=a/K$.







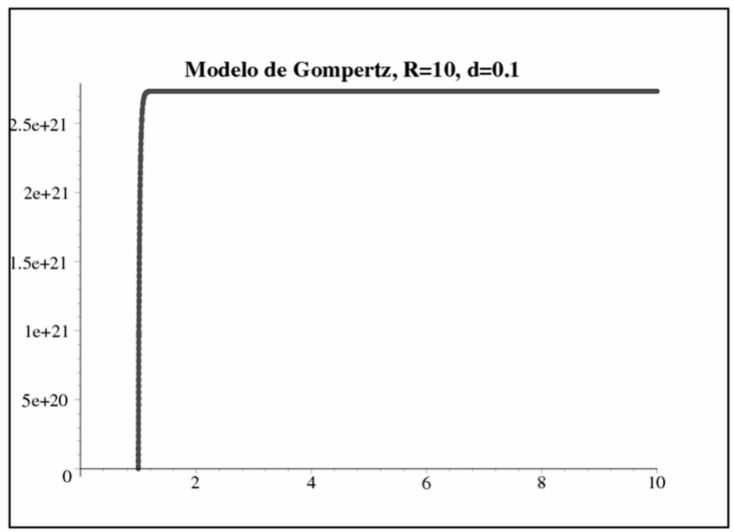
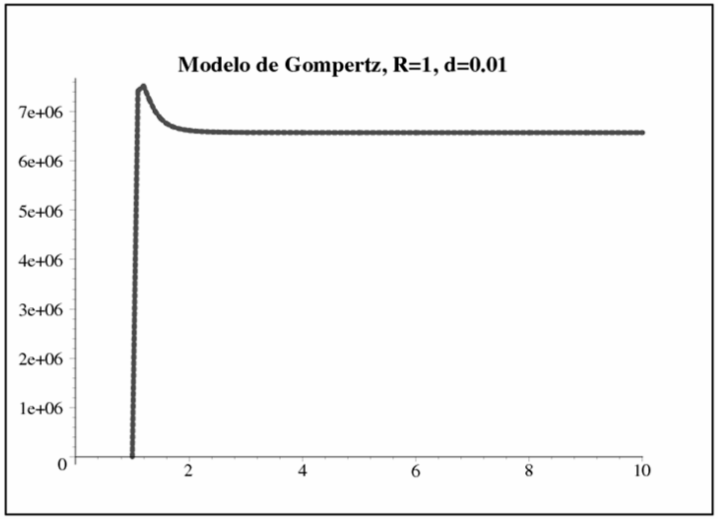
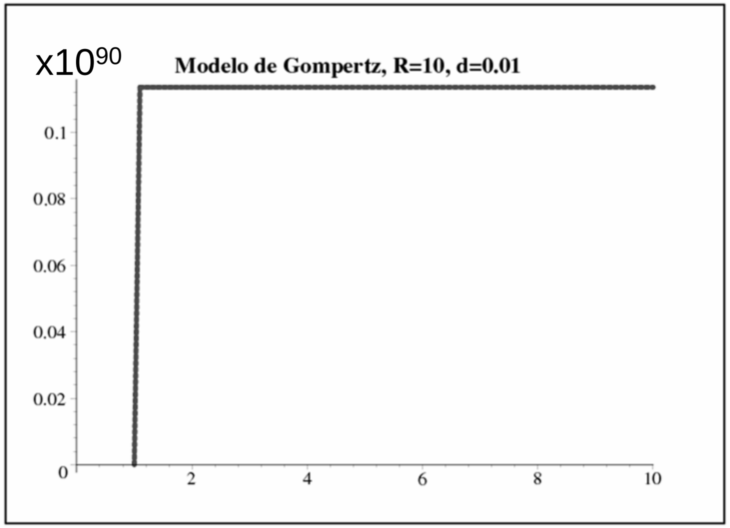
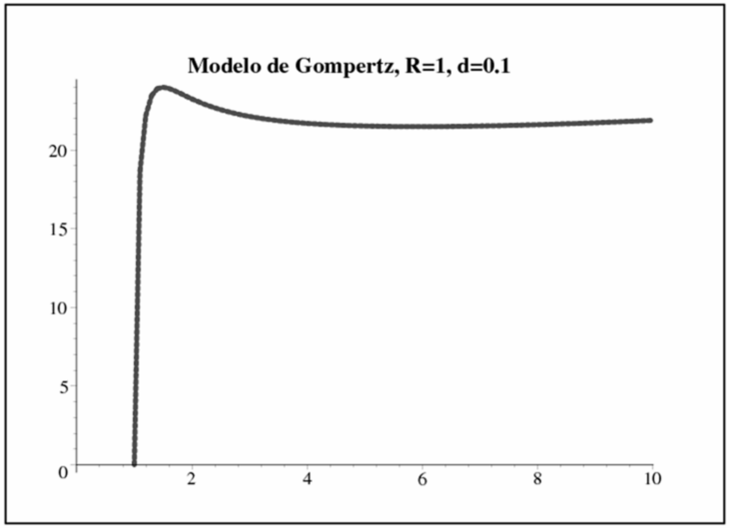
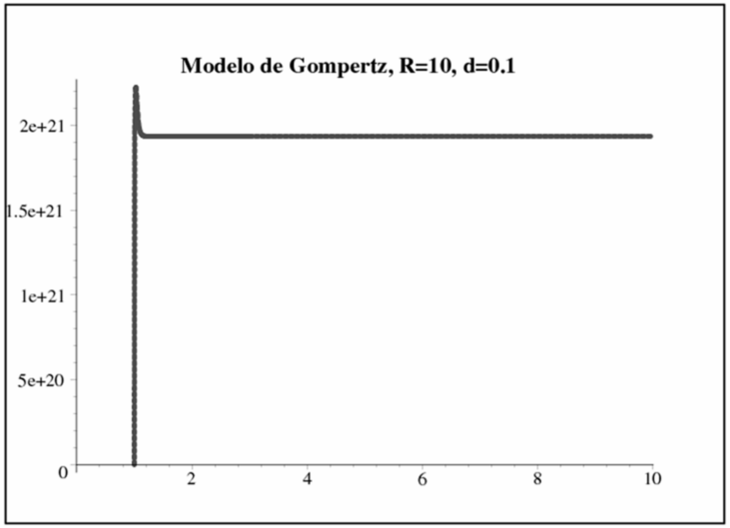


Gráfico de r **DP**[T_a] como função de N_0/a. Aqui $R=r/\sigma^2$ e $d=a/K$.









Case of logistic model

If we use instead the logistic model with additive noise

$$(S)\quad \frac{1}{N(t)}\frac{dN(t)}{dt} = r\left(1-\frac{N}{K}\right)+\sigma\varepsilon(t)\quad \text{with } r>0, K>0, \sigma>0, N_0>0$$

$$g(N) = r\left(1-\frac{N}{K}\right)\qquad \sigma(N)\equiv\sigma$$

satisfy all the assumptions and $g(0^+) = r > 0$

$$a(x) = \left(r\left(1-\frac{x}{K}\right)+\frac{\sigma^2}{2}\right)x \qquad b(x) = (\sigma x)^2$$

choosing $y_0 = K$

$$s(x) = \frac{K}{x}\exp\left(-\frac{2r}{\sigma^2}\left(\ln\frac{x}{K}+1-\frac{x}{K}\right)\right) \qquad m(x) = \frac{1}{\sigma^2 Kx}\exp\left(\frac{2r}{\sigma^2}\left(\ln\frac{x}{K}+1-\frac{x}{K}\right)\right)$$

Case of logistic model

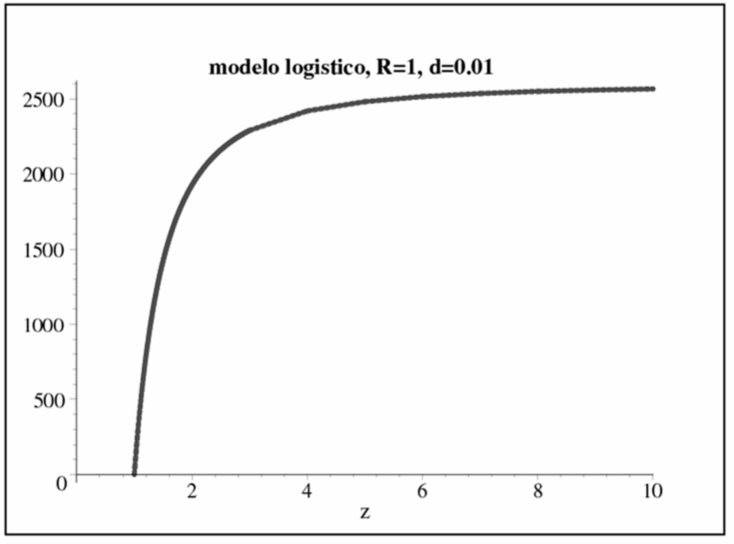
$$\underline{V}_1(x) = \mathbf{E}\left[T_a \middle| N_0 = x\right] = \frac{2}{\sigma^2} \int_{\alpha'}^{\gamma'} \Gamma\left(\frac{2r}{\sigma^2}, y\right) y^{-2r/\sigma^2 - 1} e^y dt$$

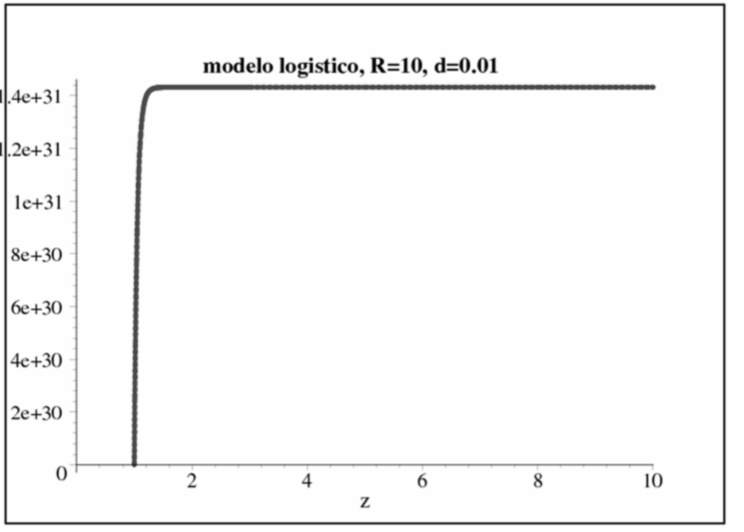
$$\underline{V}_2(x) = \mathbf{E}\left[\left(T_a\right)^2 \middle| N_0 = x\right]$$

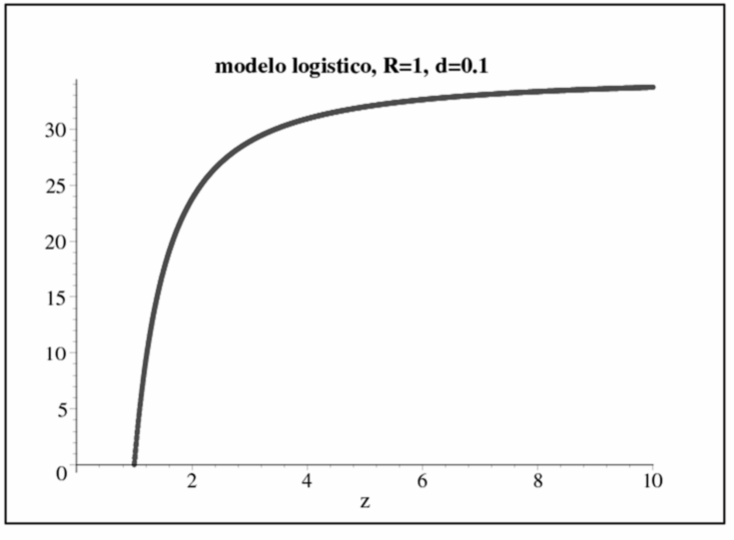
$$= \frac{8}{\sigma^4} \int_{\alpha'}^{\gamma'} s^{-2t/\sigma^2 - 1} e^s \int_s^{+\infty} \int_{\alpha'}^{t} \Gamma\left(\frac{2r}{\sigma^2}, y\right) y^{-2r/\sigma^2 - 1} e^y dy\, t^{2r/\sigma^2} e^{-t} dt ds$$

with $\alpha' = \frac{2r}{\sigma^2 K} a$ and $\gamma' = \frac{2r}{\sigma^2 K} x$

Gráfico de $r\,\mathbf{E}[T_a]$ como função de N_0/a. Aqui $R=r/\sigma^2$ e $d=a/K$.







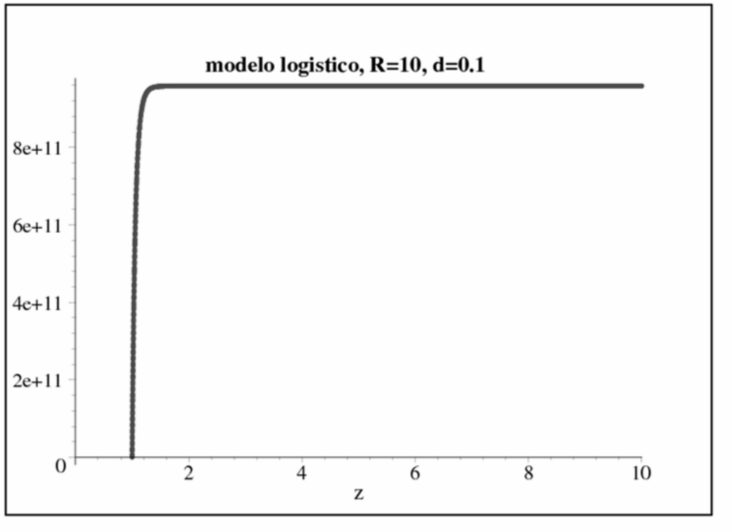
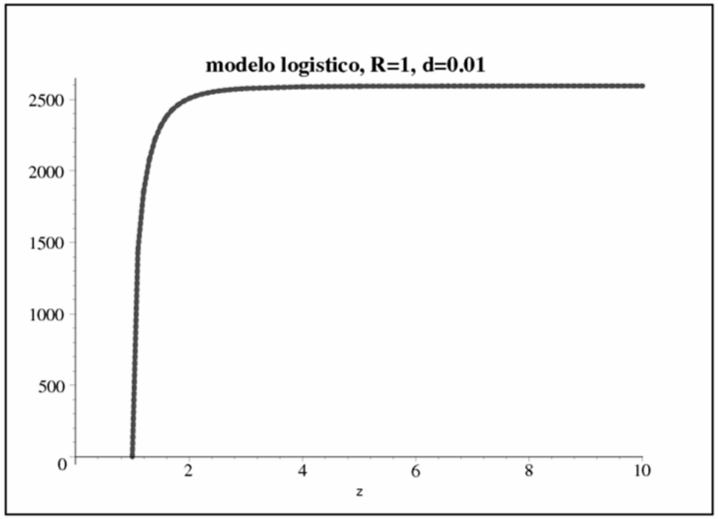
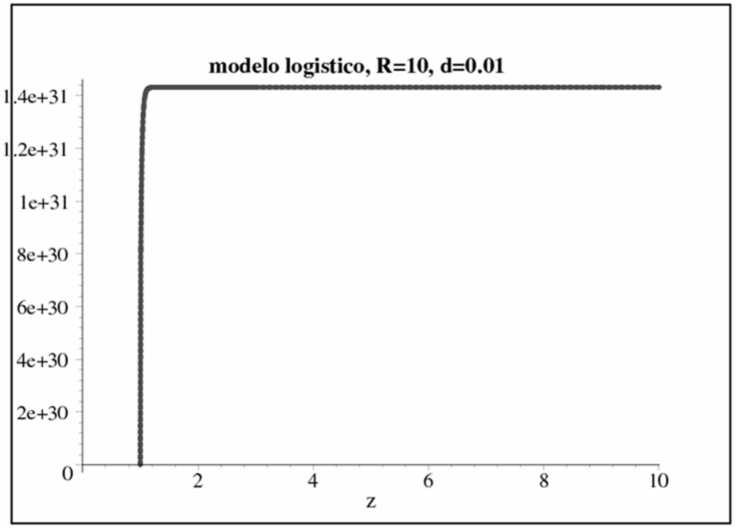
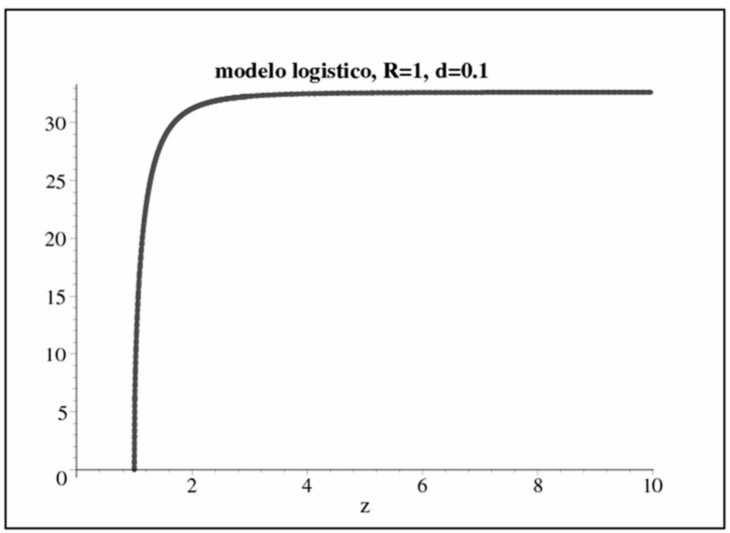
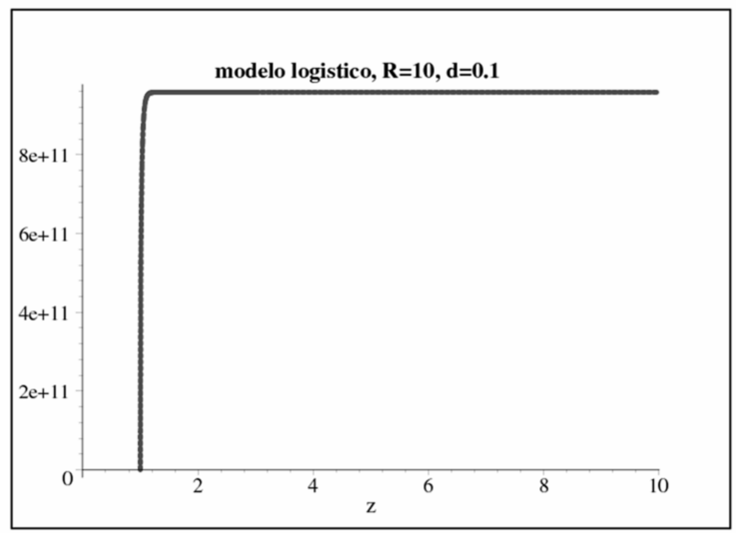


Gráfico de r **DP**[T_a] como função de N_0/a. Aqui $R=r/\sigma^2$ e $d=a/K$.

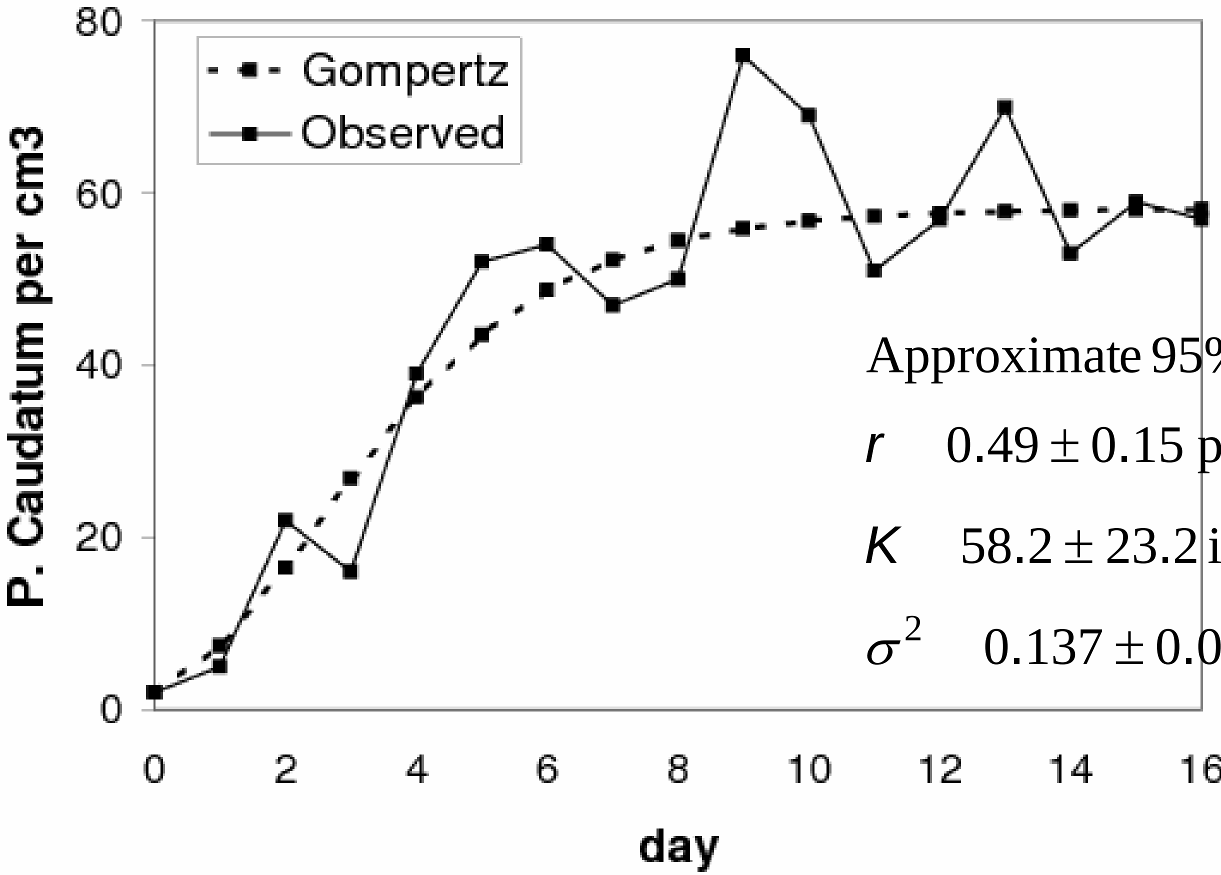








Application of Gompertz additive noise model to Gause´s 1934 data on *Paramecia caudatum*



Approximate 95% confidence intervals

r 0.49 ± 0.15 per day

K 58.2 ± 23.2 individuals per cm^3

σ^2 0.137 ± 0.096 per day (in figure set to 0)

Estimation for Gompertz additive noise model

Assume we have observations in a single trajectory at times

$$t_0 = 0 < t_1 < t_2 < ... < t_k$$

$N_0, N_1, N_2, ..., N_k$ com $N_i = N(t_i)$ $Y_0, Y_1, Y_2, ..., Y_k$ com $Y_i = Y(t_i) = \ln(N_i / K)$

$n_0 = N_0, n_1, n_2, ..., n_k$ concrete observations $y_0, y_1, y_2, ..., y_k$ com $y_i = \ln(n_i / K)$

$$p_{i|i-1}(n|n^*) = p^Y_{i|i-1}(y|y^*)\frac{e^{-y}}{K}$$

$p_{i|i-1}(n|n^*)$ transition p.d.f. of N_i given that $N_{i-1} = n^*$

$p^Y_{i|i-1}(y|y^*)$ transition p.d.f. of Y_i given that $Y_{i-1} = n^*$

with $y = \ln\frac{n}{K}$ and $y^* = \ln\frac{n^*}{K}$

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Estimation for Gompertz additive noise model

From the Markov property, we obtain the log-likelihood function

$$L(r,K,\sigma \mid n_1,\ldots,n_k) = \sum_{i=1}^{k} p_{i|i-1}(n_i \mid n_{i-1}) = \sum_{i=1}^{k} p_{i|i-1}^{Y}(y_i \mid y_{i-1}) \frac{e^{-y_i}}{K}$$

From $Y(t) = Y_0 e^{-rt} + \sigma e^{-rt} \int_0^t e^{rs} dW(s)$ one obtains

$$Y_i = Y_{i-1} e^{-r\Delta_i} + \sigma e^{-rt_i} \int_{t_{i-1}}^{t_i} e^{rs} dW(s) \text{ with } \Delta_i = t_i - t_{i-1}$$

and so

$$p_{i|i-1}^{Y}(y \mid y^*) = \frac{1}{\sqrt{2\pi \frac{\sigma^2}{2r}\left(1-e^{-2r\Delta_i}\right)}} \exp\left(- \frac{\left(y - y^* e^{-r\Delta_i}\right)^2}{2\frac{\sigma^2}{2r}\left(1-e^{-2r\Delta_i}\right)} \right)$$

from which one obtains

Estimation for Gompertz additive noise model

$$L(r,K,\sigma|n_1,\ldots,n_k)=\frac{k}{2}\left(\ln\pi-\ln r+2\ln\sigma-2\ln K\right)$$

$$-\sum_{i=1}^{k}\left(\ln\frac{n_i}{K}+\frac{1}{2}\ln\left(1-e^{-2r\Delta_i}\right)+\frac{r}{\sigma^2}\frac{\left(\ln\frac{n_i}{K}-e^{-r\Delta_i}\ln\frac{n_{i-1}}{K}\right)^2}{1-e^{-2r\Delta_i}}\right)$$

Maximizing we obtain the ML estimators

$$(\hat\theta_1,\hat\theta_2,\hat\theta_3)=(\hat r,\hat K,\hat\sigma)\quad\text{of}\quad(\theta_1,\theta_2,\theta_3)=(r,K,\sigma).$$

$(\hat\theta_1,\hat\theta_2,\hat\theta_3)=(\hat r,\hat K,\hat\sigma)$ is asympt. Gaussian with mean $(\theta_1,\theta_2,\theta_3)=(r,K,\sigma)$

and variance $\left[-\mathbf{E}\left[\frac{\partial^2 L}{\partial\theta_i\partial\theta_j}\right]\right]_{i,j=1,\ldots,k}$ allowing computation of approx. conf. intervals

For small sample sizes, bootstrap methods are advisable.

Prediction for Gompertz additive noise model

For prediction of population size at a future time $t > t_k$ it is better to work with the Gaussian random variable $Y(t)$.

A good predictor is

$$\hat{Y}(t) = \hat{\mathbf{E}}\left[Y(t) \middle| Y_1, ..., Y_k\right] = \hat{\mathbf{E}}\left[Y(t) \middle| Y_k\right] = \hat{Y}_k e^{r(t-t_k)}$$

with $\hat{Y}_k = \ln \frac{N_k}{\hat{K}}$

from which

$$\hat{N}(t) = \hat{K} \exp(\hat{Y}(t)).$$

Conclusions

•We have studied general models of population growth in random environments so that properties obtained are not model specific. We have first considered constant noise intensity and then allowed density-dependent noise intensity.

•For the general model considered, we have shown that “mathematical” extinction occurs if the geometric average growth rate at low population densities is negative. If it is positive, “mathematical” extinction does not occur and there is a stationary density.

•”Realistic” extinction (population dropping to a positive low extinction threshold) allways occurs and one can obtain explicit expressions for the moments of the extinction time (the extinction time pd.f. can also be obtained numerically). We have applied to the Gompertz model with additive noise and obtain graphs of the mean and standard deviation of the extinction time. The same ideas can apply to high threshold crossing times (study of pest outbreaks).

•For the same specific model we have illustrated using real data the issues of parameter estimation and prediction.

Conclusions

•We have also resolved the controversy on whether to use Itô or Stratonovich calculus, which was a major obstacle to the use of these models.

Indeed, we have shown that it was due to the implicit wrong assumption that the deterministic term of the SDE meant the same average growth rate under the two calculi. We have shown that it means two different averages and that, taking into account the difference between them, the two calculi give completely coincidental results.

•We have also considered the case of harvesting models.

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