Consequences of an incorrect model specification for population growth in random environments

Carlos A. Braumann

braumann@uevora.pt

Universidade de Évora – Portugal

Department of Mathematics www.dmat.uevora.pt

CIMA - Research Center in Math. and Appl. www.cima.uevora.pt

Clara Carlos

Instituto Politécnico de Setúbal – Portugal

Escola Superior de Tecnologia do Barreiro

clara.carlos@estbarreiro.ips.pt

Summary

- We use general form stochastic differential equations (SDE) models of population growth in a randomly varying environment.
- So, we obtain properties concerning existence of a stationary density and extinction behavior, that are model robust. This is nice, since the “true” model is unknown.
- However, when applying to data, we often use, as an approximation of the “true” model, classical specific simple models, like the logistic or the Gompertz SDE models, and use them to make predictions.
- Can we trust predictions based on the classical (simpler but approximate) models within a certain degree of accuracy?
- We study the effect of the gap between the approximate and the "true" model, on model predictions, particularly on asymptotic behavior and mean and variance of the population time to extinction.

Deterministic population growth models

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

$$\frac{1}{X(t)} \frac{dX(t)}{dt} = f(X(t)) \qquad X(0) = x > 0 \quad \text{is known}$$

$f(X)$ (*per capita*) growth rate (when population size is X)

$F(X) = f(X)\, X$ *total growth rate*

Examples

Malthusian	$f(X) = r$ *not realistic*
Logistic	$f(X) = r\,(1 - X/K)$
Gompertz	$f(X) = r \ln (K/X)$

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r intrinsic growth parameter
K carrying capacity of the environment (deterministic equilibrium)

Randomly fluctuating environment

Effect of environmental random fluctuations on the growth rate

Add noise to the growth rate $\varepsilon(t)$ standard white noise

autonomous Stochastic Differential Eq. (SDE)

Example: logistic model

$$\frac{1}{X(t)}\frac{dX(t)}{dt} = r\left(1 - \frac{X}{K}\right) + \sigma\varepsilon(t) = f(X) + \sigma\varepsilon(t)$$

Example: Gompertz model

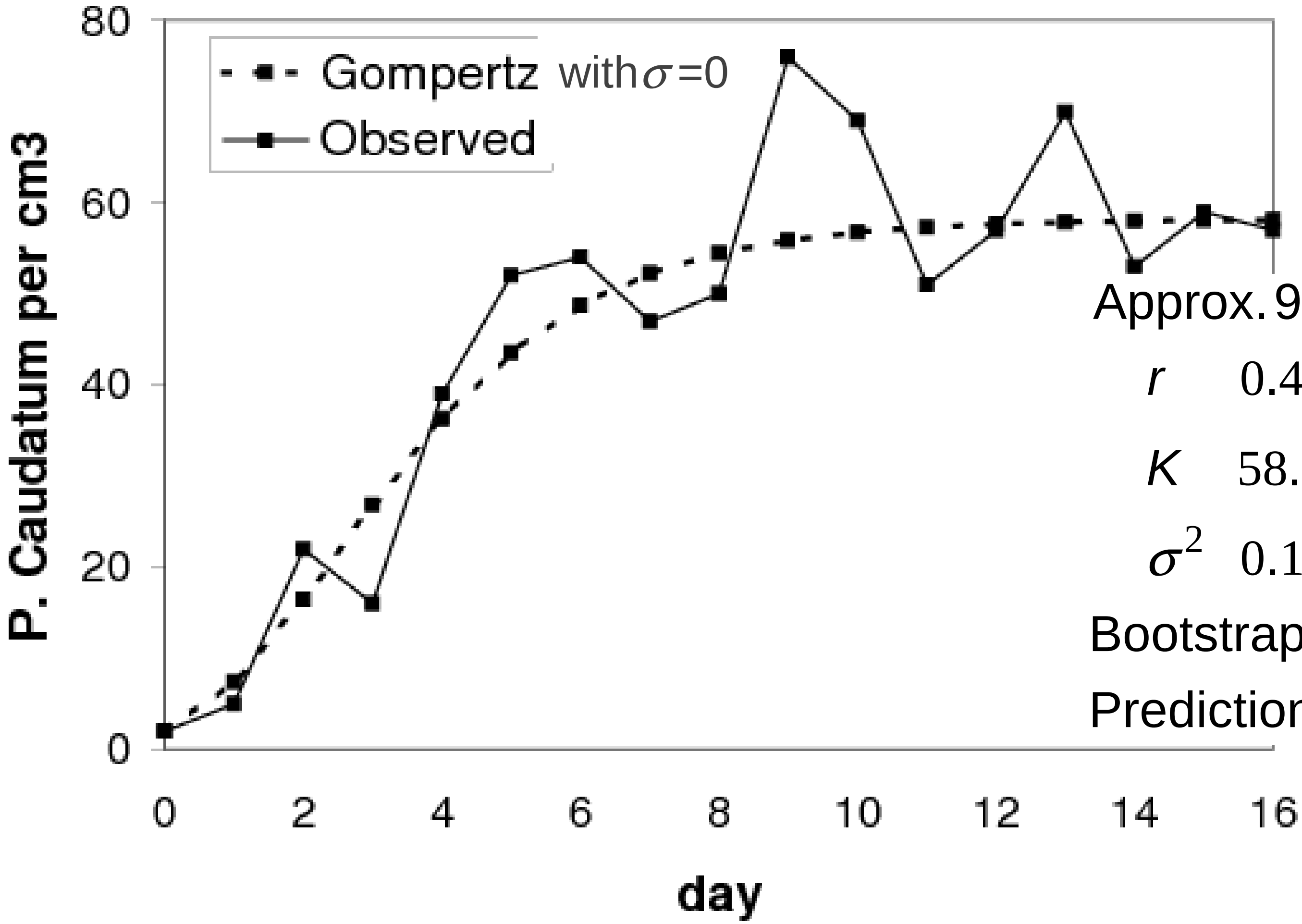
$$\frac{1}{X(t)}\frac{dX(t)}{dt} = r\ln\frac{K}{X} + \sigma\varepsilon(t) = f(X) + \sigma\varepsilon(t)$$

But, in the "true" model, $f(X)$ may have a different form and the noise intensity may not be a constant σ but rather a density-dependent function $\sigma(X)$.

Since we aim at model robust properties, instead of considering specific models we will now consider a general model in which $f(X)$ and $\sigma(X)$ are arbitrary functions satisfying only biologically determined assumptions and mild technical assumptions.

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

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



Approx. 95% conf. intervals (ML)

r $\quad 0.49 \pm 0.15$ per day

K $\quad 58.2 \pm 23.2$ individuals per cm^3

σ^2 $\quad 0.137 \pm 0.096$ per day

Bootstrap can be used

Prediction of future pop. sizes possible

General SDE model

$$(S)\quad \frac{1}{X(t)}\frac{dX(t)}{dt} = f(X(t)) + \sigma(X)\varepsilon(t) \qquad X(0) = x > 0 \text{ known}$$

$$(S)\quad dX(t) = F(X(t))\,dt + V(X(t))\,dW(t)$$

$W(t) = \int_0^t \varepsilon(t)\,dt$ is the standard Wiener process

$f(X)$	geometric average growth rate
$F(X)=f(X)X$	total "average" growth rate
$\sigma(X)>0$	noise intensity
$V(X)=\sigma(X)X$	total noise intensity

General growth model

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

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

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

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

(A) $\int_{0^+}^{x_*}\frac{1}{\sigma(x)x}dx=+\infty$ for some $x_*>0$;

(B) $\int_{y_*}^{+\infty}\frac{1}{\sigma(x)x}dx=+\infty$ for some $y_*>0$.

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

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

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

General growth model

The solution exists and is unique up to an explosion time

The solution is a homogeneous diffusion process with

Diffusion coefficient

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

Drift coefficient

$$a(x) = f(x)x + \frac{1}{4}\frac{db(x)}{dx}$$

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General growth model

$$(S) \qquad \frac{dX}{dt} = \big(f(X) + \sigma(X)\varepsilon(t)\big)X$$

Scale density

$$s(X) := \exp\left(-\int_{x_*}^{X} \frac{2a(\theta)}{b(\theta)} d\theta\right) = \frac{V(x_*)}{V(X)} \exp\left(-2\int_{x_*}^{X} \frac{F(\theta)}{V^2(\theta)} d\theta\right) \quad (x_* > 0 \text{ arbitrary})$$

Scale function $\qquad S(X) = \int_{x_{**}}^{X} s(z)dz \quad (x_{**} > 0 \text{ arbitrary})$

Speed density

$$m(X) := \frac{1}{s(X)b(X)} = \frac{1}{V(x_*)V(X)} \exp\left(2\int_{x_*}^{X} \frac{F(\theta)}{V^2(\theta)} d\theta\right)$$

Speed function $\qquad M(X) = \int_{x_{**}}^{X} m(z)dz \quad (x_{**} > 0 \text{ arbitrary})$

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

$$u(x) = \mathbf{P}\left[T_b < T_a \middle| X(0) = x\right] = \frac{S(x) - S(a)}{S(b) - S(a)}$$

General growth model

$$(S)\quad \frac{dX}{dt} = \left(f(X) + \sigma(X)\varepsilon(t)\right)X$$

Boundary X=0 is non-attractive

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

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

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

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

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

Similarly, the boundary $X = +\infty$ is non-attractiveness iff $S(+\infty) = +\infty$

With our assumptions we prove that:

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

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

General growth model

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 $f(0^+)>0$.

CONCLUSIONS:

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

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

Realistic extinction

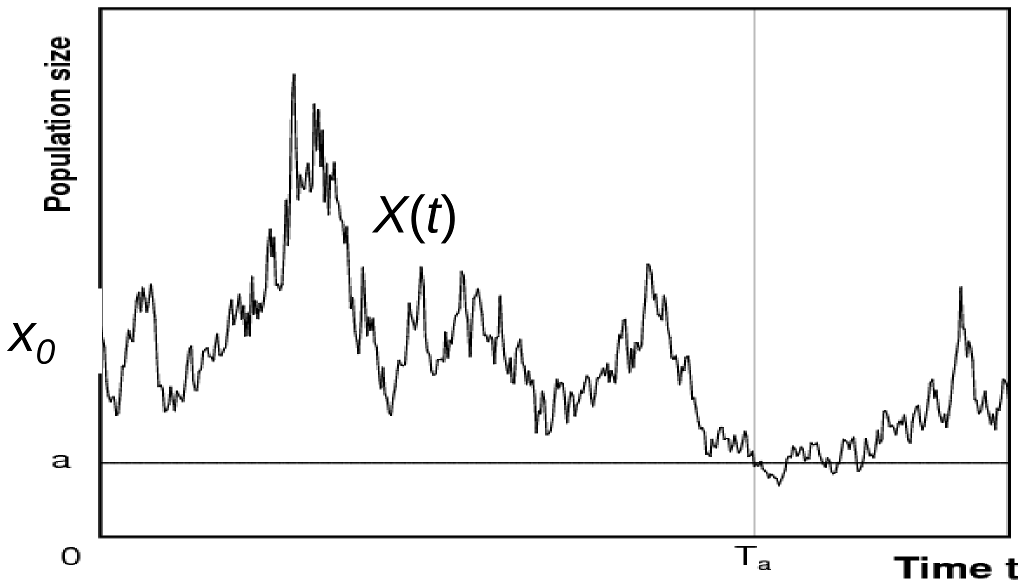
When $f(0^+) > 0$, there is a zero probability of “mathematical” extinction

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

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

“Realistic” extinction occurs if ever $X(t)$ reaches the threshold.

The **extinction time** is the first passage time $T_a = \inf\{t > 0 : X(t) = a\}$



Since the process is ergodic, it will (sooner or later) with probability 1 reach the extinction threshold *a.* So, with this general density-dependent model, extinction always occurs w.p. 1.

The distribution of the extinction time can be obtained

(Braumann 1985, Carlos and Braumann 2005,2006).

Approximate and "true" models

We always use Stratonovich calculus and drop the "(S)"

SDE approximate models:

Autonomous stochastic differential equation (SDE)

$$\frac{1}{X}\frac{dX(t)}{dt} = f(X) + \sigma\varepsilon(t) \quad \text{or} \quad dX(t) = X(t)\ \left(f(X(t))dt + \sigma dW(t)\right)$$

with	Logistic	$f(x) = r\,(1 - x/K)$	with $r>0$, $\sigma>0$, $K>0$
or	Gompertz	$f(x) = r\ \ln(K/x)$	with $r>0$, $\sigma>0$, $K>0$

SDE "true" models

$$dX(t) = X\ \left(f(X)\,dt + \sigma(X)\,dW(t)\right)$$

$f(x) = r\,(1 - x/K) + \alpha(x)$ and $\sigma(x) = \sigma$

or

$f(x) = r\ \ln(K/x) + \alpha(x)$ and $\sigma(x) = \sigma$

α is a C^1 function s.t. $|\alpha(x)|\,/\,r < \delta$

$f(x) = r\,(1 - x/K)$ and $\sigma(x) = \sigma + \alpha(x)$

or

$f(x) = r\ \ln(K/x)$ and $\sigma(x) = \sigma + \alpha(x)$

α is a C^2 function s.t. $|\alpha(x)|\,/\,\sigma < \delta$

Model behavior

With the assumption $f(0^+) > 0$, we have the same qualitative properties for both the “true” model and the approximate logistic or Gompertz SDE models (in this case, $f(0^+) > 0$ is insured with $r > 0$), namely:

- The state space has boundaries $X=0$ and $X=+\infty$.
- On can see that $X=0$ and $X=+\infty$ are non-attracting.
- “Mathematical” extinction has zero probability of occurring. “Realistic” extinction will, however, occur with probability one.
- Explosions can not occur and the solution exists and is unique for all $t>0$.
- There exists a stationary density $p(y)$, because

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

First passage times

- Let $a < x < b$.
- The first passage time of the population size $X(t)$ by a us denote by T_a . Similarly define T_b .

$$T_a = \inf\{t > 0 : \ X(t) = a\} \qquad T_b = \inf\{t > 0 : \ X(t) = b\}$$

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

- The probability of $X(t)$ to reach a before reaching b is

$$u(x) = \mathbf{P}\left[T_a < T_b \middle| X(0) = x\right] = \frac{S(x,b)}{S(a,b)}$$

Time to extinction

$$U_k(x) = \mathbf{E}\left[(T_{ab})^k \middle| X(0) = x\right] \qquad k\text{ - th order moment}$$

Diffusion operator $\mathscr{D} = a(x)\frac{d}{dx} + \frac{1}{2}b^2(x)\frac{d^2}{dx^2} = \frac{1}{2}\frac{d}{dM(x)}\left(\frac{d}{dS(x)}\right)$

$$\mathscr{D}\, U_k(x) + kU_{k-1}(x) = 0$$

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

$$U_k(a) = U_k(b) = 0 \quad (k = 1,2,\ldots) \qquad U_0(x) \equiv 1$$

$$U_k(x) = 2u(x)\int_x^b S(\xi,b)kU_{k-1}(\xi)m(\xi)d\xi + 2(1-u(x))\int_a^x S(a,\xi)kU_{k-1}(\xi)m(\xi)d\xi$$

Since boundaries are unattainable, if we let $b \uparrow +\infty$, we obtain as limit of U_k(x)

$$V_k(x) = \mathbf{E}\left[(T_a)^k \middle| X(0) = x\right] = 2\int_a^x s(\xi)\left(\int_\xi^{+\infty} kV_{k-1}(\theta)m(\theta)d\theta\right)d\xi$$

Time to extinction

For k=1

$$\mathbf{E}\left[T_a \middle| X(0)=x\right]=V_1(a)=2\int_a^x s(\xi)\left(\int_\xi^{+\infty} m(\theta)d\theta\right)d\xi$$

Replacing in the equation for k=2 we obtain $V_2(x)$ and then

$$\mathbf{VAR}\left[T_a \middle| X(0)=x\right]=\int_a^x s(\xi)\int_\xi^{+\infty} s(\mu)\left(\int_\mu^{+\infty} m(\theta)d\theta\right)^2 d\mu d\xi$$

These have to be numerically integrated.

Logistic model, approximate drift coefficient

$$\left|\beta(X)\right| = \frac{\left|\alpha(X)\right|}{r} \le \delta, \quad R = \frac{r}{\sigma^2}, \quad d = \frac{a}{K}, \quad z = \frac{x}{a}$$

$$r\,\mathbf{E}_x[T_a] = 2R\int_{2Rd}^{2Rdz} y^{-2R-1}e^{y}\left(\int_y^{+\infty} t^{2R-1}e^{-t}\exp\left(2R\int_y^t \frac{\beta(\frac{Kv}{2R})}{v}dv\right)dt\right)dy$$

$$r^2\mathbf{VAR}_x[T_a] = 8R^2\int_{2Rd}^{2Rdz} y^{-2R-1}e^{y}\int_y^{+\infty} u^{-2R-1}e^{u}\left(\int_u^{+\infty} t^{2R-1}e^{-t}\exp\left(2R\int_y^t \frac{\beta(\frac{Kv}{2R})}{v}dv\right)dt\right)$$

$$\left(\int_u^{+\infty} t^{2R-1}e^{-t}\exp\left(2R\int_u^t \frac{\beta(\frac{Kv}{2R})}{v}dv\right)dt\right)dudy$$

Logistic model

For the logistic model $\alpha(x) = 0$

$$r\ \mathbf{E}_x^{Logistic(R,d)}\left[T_a\right] = 2R\int_{2Rd}^{2Rdz} y^{-2R-1}e^y\,\Gamma(2R,y)\,dy$$

$$r^2\mathbf{VAR}_x^{Logistic(R,d)}\left[T_a\right] = 8R^2\int_{2Rd}^{2Rdz} y^{-2R-1}e^y\int_y^{+\infty} u^{-2R-1}e^u\left(\Gamma(2R,u)\right)^2 du\,dy$$

with $\Gamma(c,x) = \int_x^{+\infty} t^{c-1}e^{-t}dt$

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Logistic model, approximate drift coefficient

$$R^* = R(1-\delta) \qquad d^* = d/(1-\delta)$$

$$R^{**} = R(1+\delta) \qquad d^{**} = d/(1+\delta),$$

$$r\ \mathbf{E}_x[T_a] \ge \frac{1}{1-\delta} 2R^* \int_{2R^*d^*}^{2R^*d^*z} y^{-2R^*-1} e^y \Gamma(2R^*, y)\,dy = \frac{1}{1-\delta} r\ \mathbf{E}_x^{Logistic(R^*,d^*)}[T_a]$$

$$r\ \mathbf{E}_x[T_a] \le \frac{1}{1+\delta} 2R^{**} \int_{2R^{**}d^{**}}^{2R^{**}d^{**}z} y^{-2R^{**}-1} e^y \Gamma(2R^{**}, y)\,dy = \frac{1}{1+\delta} r\ \mathbf{E}_x^{Logistic(R^{**},d^{**})}[T_a]$$

$$r^2 \mathbf{VAR}_x[T_a] \ge \frac{1}{(1-\delta)^2} 8R^{*2} \int_{2R^*d^*}^{2R^*d^*z} y^{-2R^*-1} e^y \int_y^{+\infty} u^{-2R^*-1} e^u \left(\Gamma(2R^*, u)\right)^2 du\,dy$$

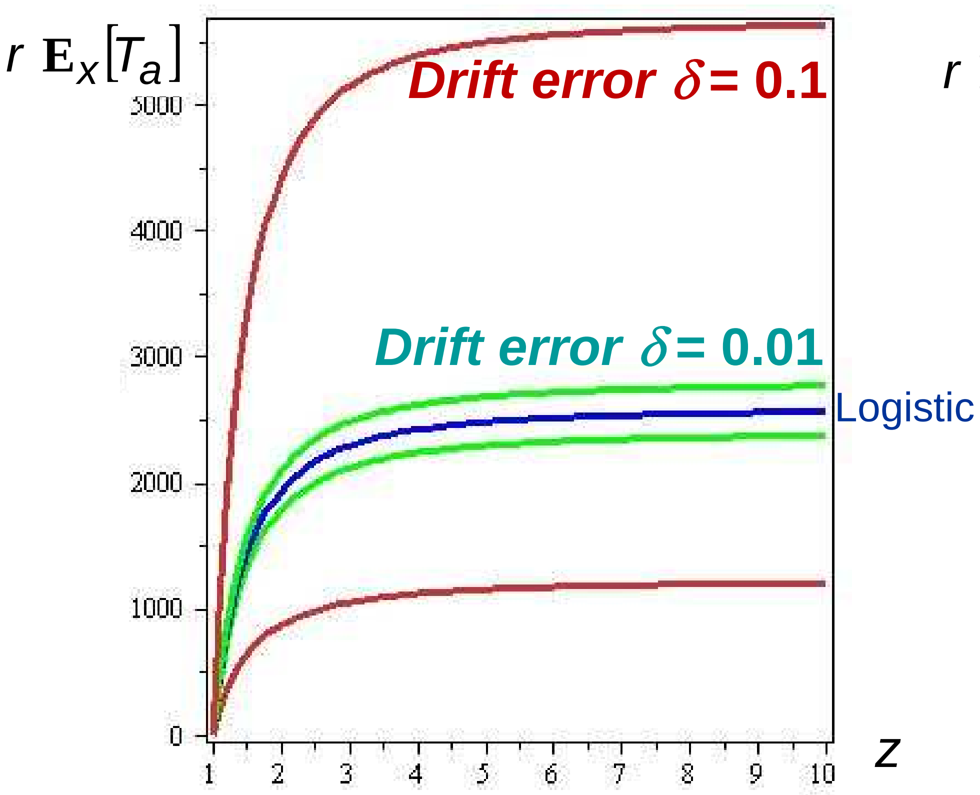
$$= \frac{1}{(1-\delta)^2} r^2 \mathbf{VAR}_x^{Logistic(R^*,d^*)}[T_a]$$

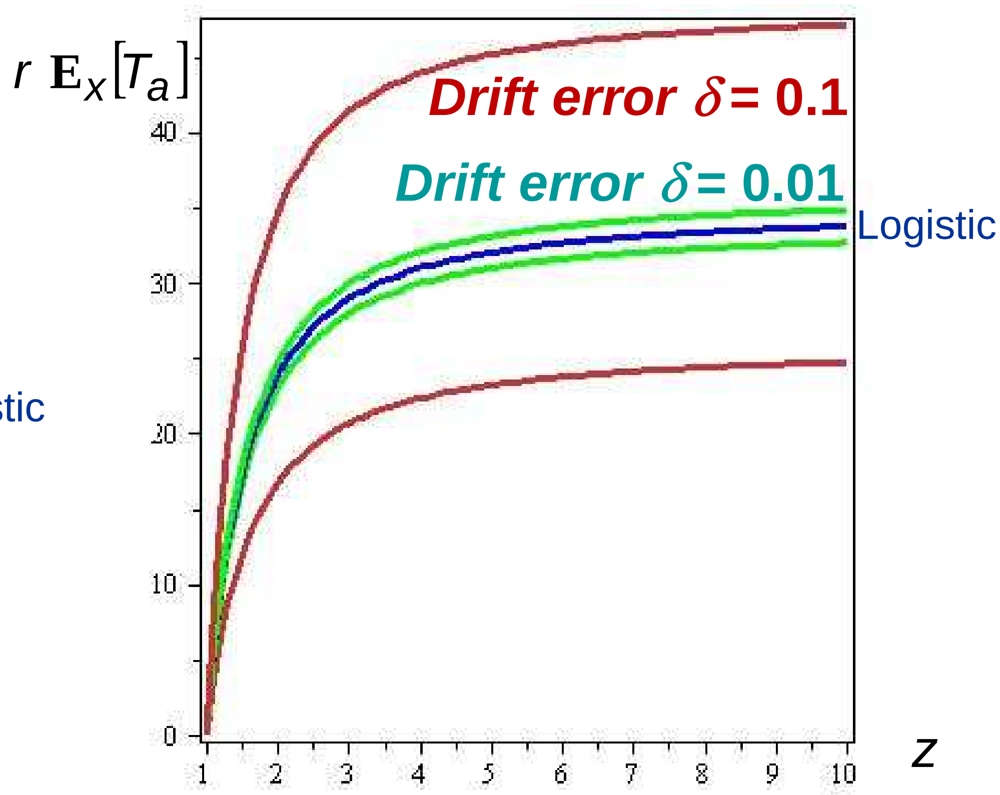
$$r^2 \mathbf{VAR}_x[T_a] \le \frac{1}{(1+\delta)^2} 8R^{**2} \int_{2R^{**}d^{**}}^{2R^{**}d^{**}z} y^{-2R^{**}-1} e^y \int_y^{+\infty} u^{-2R^{**}-1} e^u \left(\Gamma(2R^{**}, u)\right)^2 du\,dy$$

$$= \frac{1}{(1+\delta)^2} r^2 \mathbf{VAR}_x^{Logistic(R^{**},d^{**})}[T_a]$$

Example

Behavior of *r* times the **mean of the population extinction time** as a function of *z=x/a*



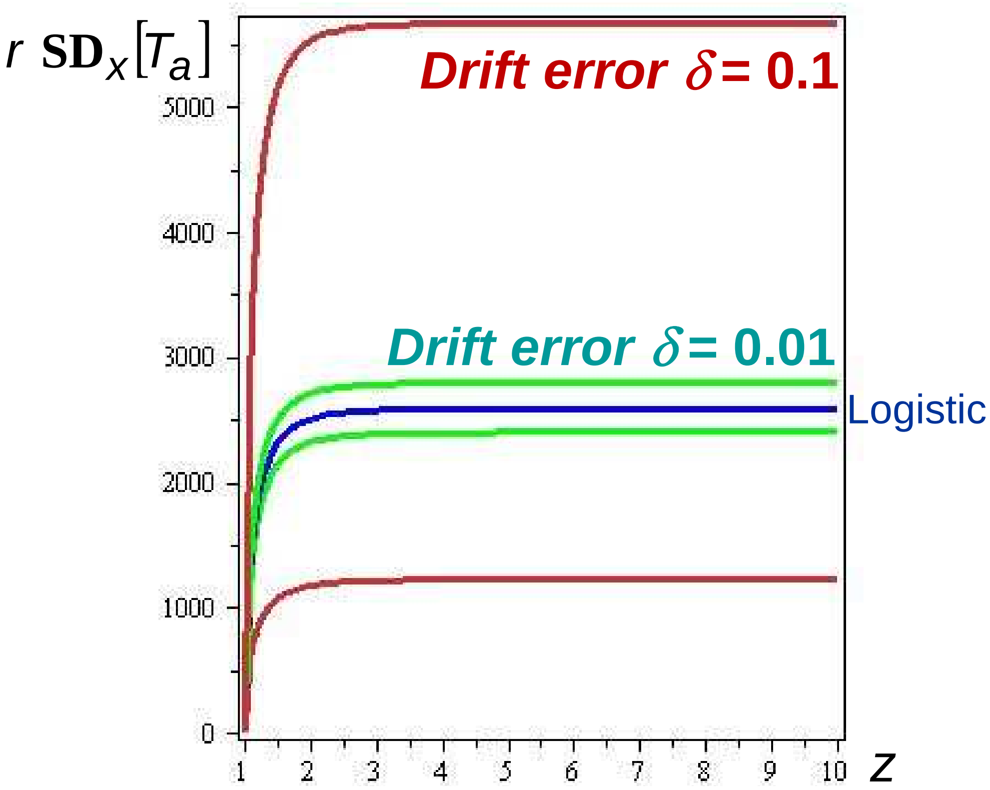


R=1 ($r = \sigma^2$)
d=0.01 (a=K/100)

R=1 ($r = \sigma^2$)
d=0.1 (a=K/10)

Example

Behavior of *r* times the **standard deviation of the population extinction time** as a function of *z=x/a*



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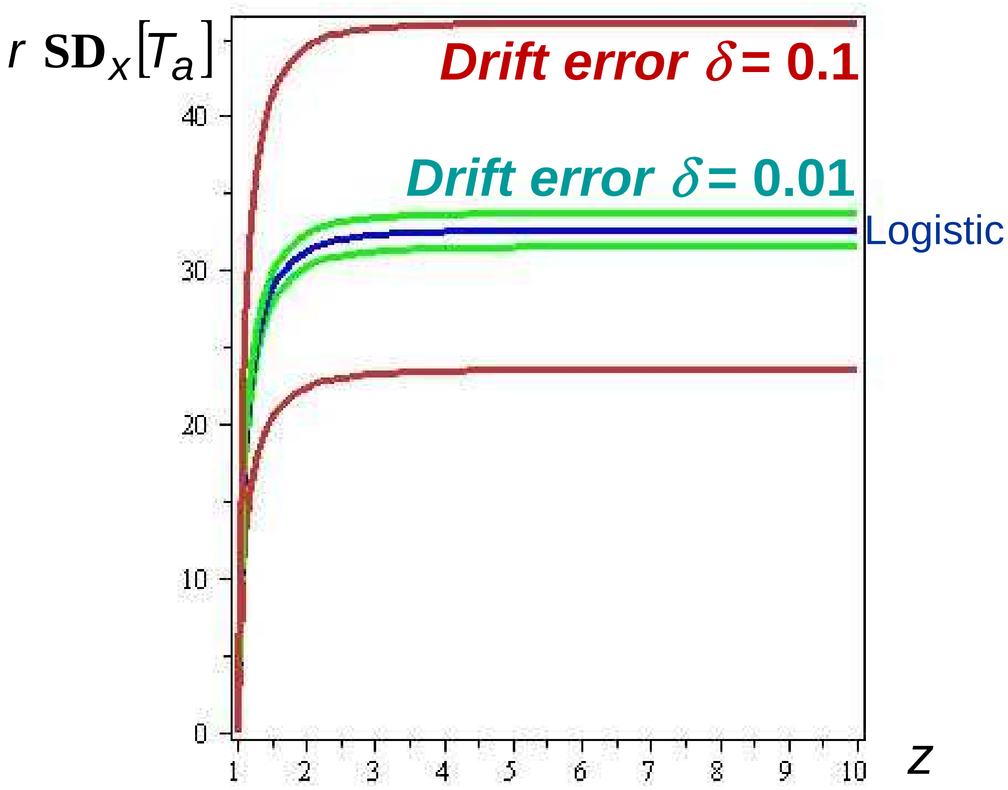


R=1 ($r = \sigma^2$)
d=0.1 (a=K/10)

Gompertz model, approximate drift coefficient

$$\left|\beta(X)\right| = \frac{\left|\alpha(X)\right|}{r} \leq \delta, \quad R = \frac{r}{\sigma^2}, \quad d = \frac{a}{K}, \quad z = \frac{x}{a}$$

$$r\, \mathbf{E}_x\left[T_a\right] = 2\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} e^{y^2} \int_y^{+\infty} e^{-t^2} \exp\left(2\sqrt{R}\int_y^t \beta\left(K\exp\left(\frac{v}{\sqrt{R}}\right)\right)dv\right) dt\,dy$$

$$r^2\mathbf{VAR}_x\left[T_a\right] = 8\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} e^{y^2} \int_y^{+\infty} e^{u^2}\left(\int_u^{+\infty} e^{-t^2} \exp\left(2\sqrt{R}\int_y^t \beta\left(K\exp\left(\frac{v}{\sqrt{R}}\right)\right)dv\right) dt\right)$$
$$\left(\int_u^{+\infty} e^{-t^2} \exp\left(2\sqrt{R}\int_u^t \beta\left(K\exp\left(\frac{v}{\sqrt{R}}\right)\right)dv\right) dt\right) du\,dy$$

Gompertz model

For the Gompertz model $\alpha(x) = 0$

$$r\ \mathbf{E}_x^{Gompertz(R,d)}[T_a] = 2\sqrt{\pi}\int_{\sqrt{R}\ln(d)}^{\sqrt{R}\ln(dz)} e^{y^2}\left(1-\Phi(\sqrt{2}y)\right)dy$$

$$r^2\mathbf{VAR}_x^{Gompertz(R,d)}[T_a] = 8\pi\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} e^{y^2}\int_y^{+\infty} e^{u^2}\left(1-\Phi\left(\sqrt{2}u\right)\right)^2 du dy$$

with $\Phi(x) = \int_{-\infty}^{x}\frac{1}{\sqrt{2\pi}}e^{-t^2/2}dt$ standard Gaussian d.f.

Gompertz model, approximate drift coefficient

$$d^* = d\, e^{\delta}$$

$$d^{**} = d\, e^{-\delta}$$

$$r\ \mathbf{E}_x[T_a] \geq 2\sqrt{\pi}\int_{\sqrt{R}\ln(d^*)}^{\sqrt{R}\ln(d^* z)} e^{y^2}\left(1-\Phi(\sqrt{2}y)\right)dy = r\ \mathbf{E}_x^{Gompertz(R,d^*)}[T_a]$$

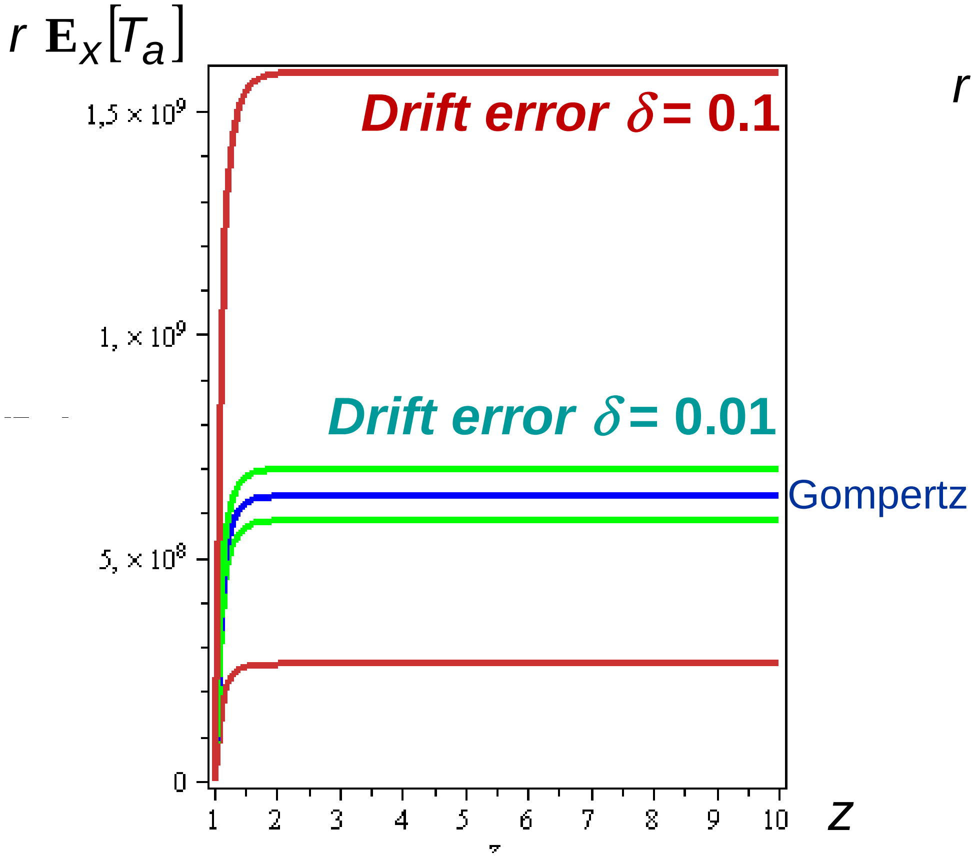
$$r\ \mathbf{E}_x[T_a] \leq 2\sqrt{\pi}\int_{\sqrt{R}\ln(d^{**})}^{\sqrt{R}\ln(d^{**} z)} e^{y^2}\left(1-\Phi(\sqrt{2}y)\right)dy = r\ \mathbf{E}_x^{Gompertz(R,d^{**})}[T_a]$$

$$r^2 Var_x[T_a] \geq 8\pi\int_{\sqrt{R}\ln d^*}^{\sqrt{R}\ln(d^* z)} e^{y^2}\int_y^{+\infty} e^{u^2}\left(1-\Phi\left(\sqrt{2}u\right)\right)^2 du dy = r^2\mathbf{VAR}_x^{Gompertz(R,d^*)}[T_a]$$

$$r^2\mathbf{VAR}_x[T_a] \leq 8\pi\int_{\sqrt{R}\ln d^{**}}^{\sqrt{R}\ln(d^{**} z)} e^{y^2}\int_y^{+\infty} e^{u^2}\left(1-\Phi\left(\sqrt{2}u\right)\right)^2 du dy = r^2\mathbf{VAR}_x^{Gompertz(R,d^{**})}[T_a]$$

Example

Behavior of r times the **mean of the population extinction time** as a function of $z=x/a$



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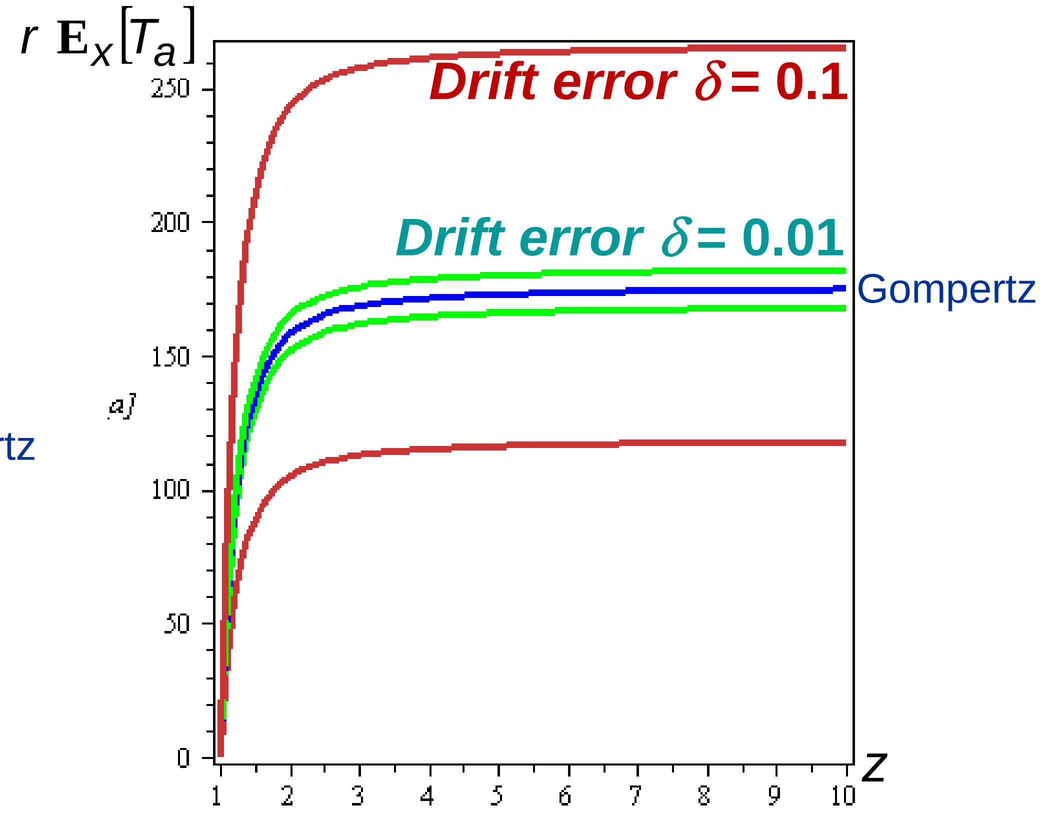

R=1 ($r = \sigma^2$)
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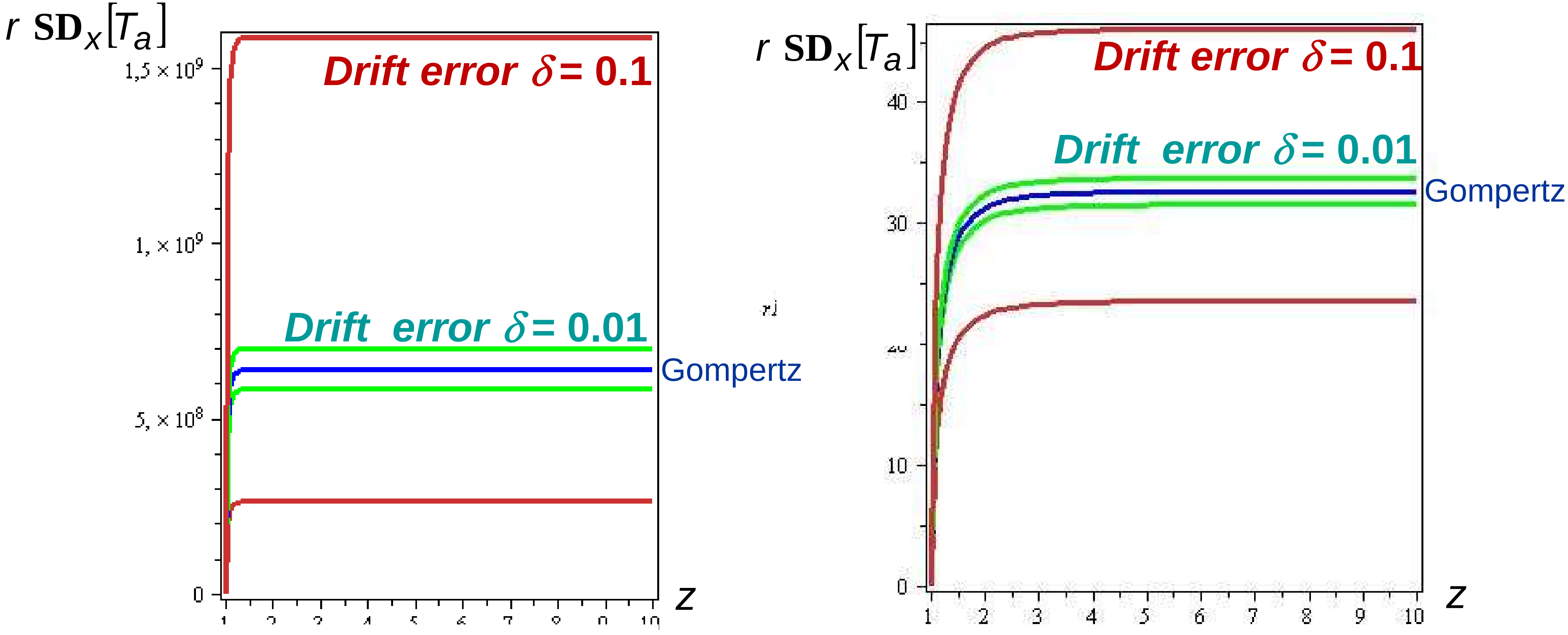
Example

Behavior of *r* times the **standard deviation of the population extinction time** as a function of *z=x/a*



R=1 ($r = \sigma^2$)
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R=1 ($r = \sigma^2$)
d=0.1 (a=K/10)

Logistic model, approximate diffusion coefficient

$$|\beta(X)| = \frac{|\alpha(X)|}{\sigma} \le \delta, \quad R = \frac{r}{\sigma^2}, \quad d = \frac{a}{K}, \quad z = \frac{x}{a}$$

$$r\,\mathbf{E}_x[T_a] = 2R\int_{2Rd}^{2Rdz} \frac{1}{\left(1+\beta\left(\frac{Ky}{2r}\right)\right)y} \int_y^{+\infty} \frac{1}{\left(1+\beta\left(\frac{Kt}{2r}\right)\right)t} \exp\left(\int_y^t \frac{\frac{2R}{v}-1}{\left(1+\beta\left(\frac{Kv}{2r}\right)\right)^2} dv\right) dt\,dy$$

$$r^2\mathbf{VAR}_x[T_a] = 8R^2\int_{2Rd}^{2Rdz} \frac{1}{\left(1+\beta\left(\frac{Ky}{2r}\right)\right)y} \int_y^{+\infty} \frac{1}{\left(1+\beta\left(\frac{Ku}{2r}\right)\right)u} \left(\int_u^{+\infty} \frac{1}{\left(1+\beta\left(\frac{Kt}{2r}\right)\right)t} \exp\left(\int_y^t \frac{\frac{2R}{v}-1}{\left(1+\beta\left(\frac{Kv}{2r}\right)\right)^2} dv\right) dt\right)$$
$$\left(\int_u^{+\infty} \frac{1}{\left(1+\beta\left(\frac{Kt}{2r}\right)\right)t} \exp\left(\int_u^t \frac{\frac{2R}{v}-1}{\left(1+\beta\left(\frac{Kv}{2r}\right)\right)^2} dv\right) dt\right) du\,dy$$

Logistic model

For the logistic model $\alpha(x) = 0$

$$r\ \mathbf{E}_x^{Logistic(R,d)}\left[T_a\right] = 2R\int_{2Rd}^{2Rdz} y^{-2R-1}e^{y}\Gamma\left(2R,y\right)dy$$

$$r^2\mathbf{VAR}_x^{Logistic(R,d)}\left[T_a\right] = 8R^2\int_{2Rd}^{2Rdz} y^{-2R-1}e^{y}\int_{y}^{+\infty} u^{-2R-1}e^{u}\left(\Gamma\left(2R,u\right)\right)^2 du dy$$

with $\Gamma\left(c,x\right) = \int_{x}^{+\infty} t^{c-1}e^{-t}dt$

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Logistic model, approximate diffusion coefficient

$$R^* = R/(1+\delta)^2 \qquad d^* = d(1+\delta)^2/(1-\delta)^2$$

$$R^{**} = R/(1-\delta)^2 \qquad d^{**} = d(1-\delta)^2/(1+\delta)^2$$

$$r\ \mathbf{E}_x[T_a] \geq 2R^* \int_{2R^*d^*}^{2R^*d^*z} y^{-2R^*-1} e^y \Gamma(2R^*, y)\,dy = r\ \mathbf{E}_x^{Logistic(R^*,d^*)}[T_a]$$

$$r\ \mathbf{E}_x[T_a] \leq 2R^{**} \int_{2R^{**}d^{**}}^{2R^{**}d^{**}z} y^{-2R^{**}-1} e^y \Gamma(2R^{**}, y)\,dy = r\ \mathbf{E}_x^{Logistic(R^{**},d^{**})}[T_a]$$

$$r^2 \mathbf{VAR}_x[T_a] \geq 8R^{*2} \int_{2R^*d^*}^{2R^*d^*z} y^{-2R^*-1} e^y \int_y^{+\infty} u^{-2R^*-1} e^u \left(\Gamma(2R^*, u)\right)^2 du\,dy$$

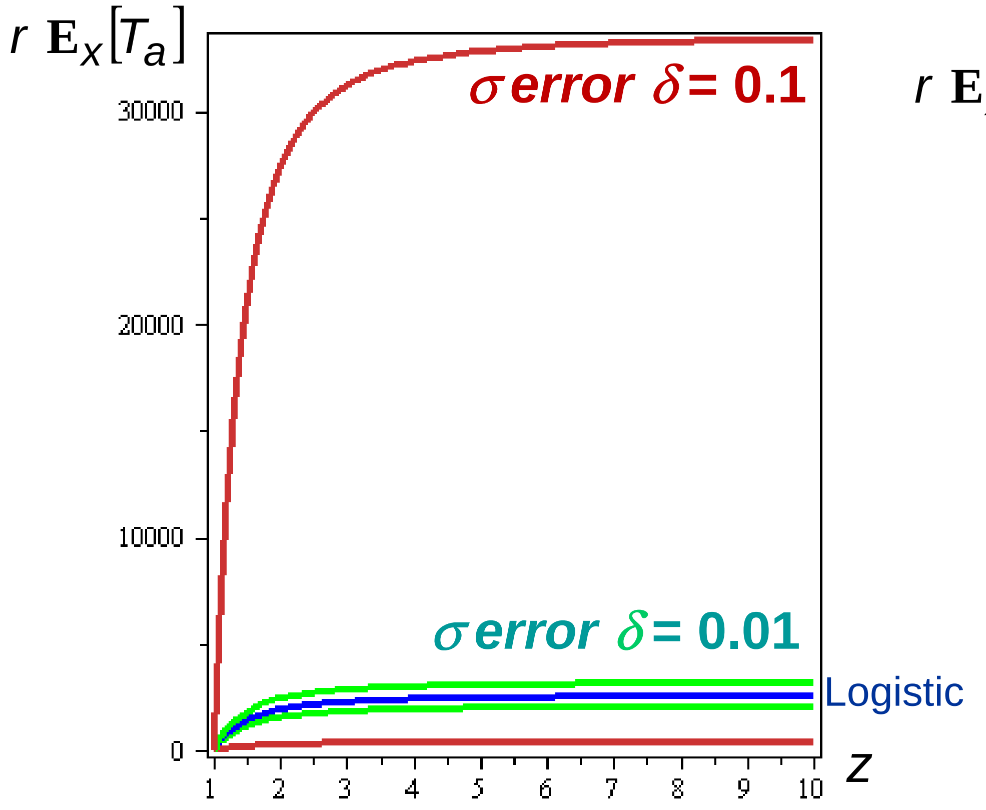
$$= \frac{1}{(1-\delta)^2} r^2 \mathbf{VAR}_x^{Logistic(R^*,d^*)}[T_a]$$

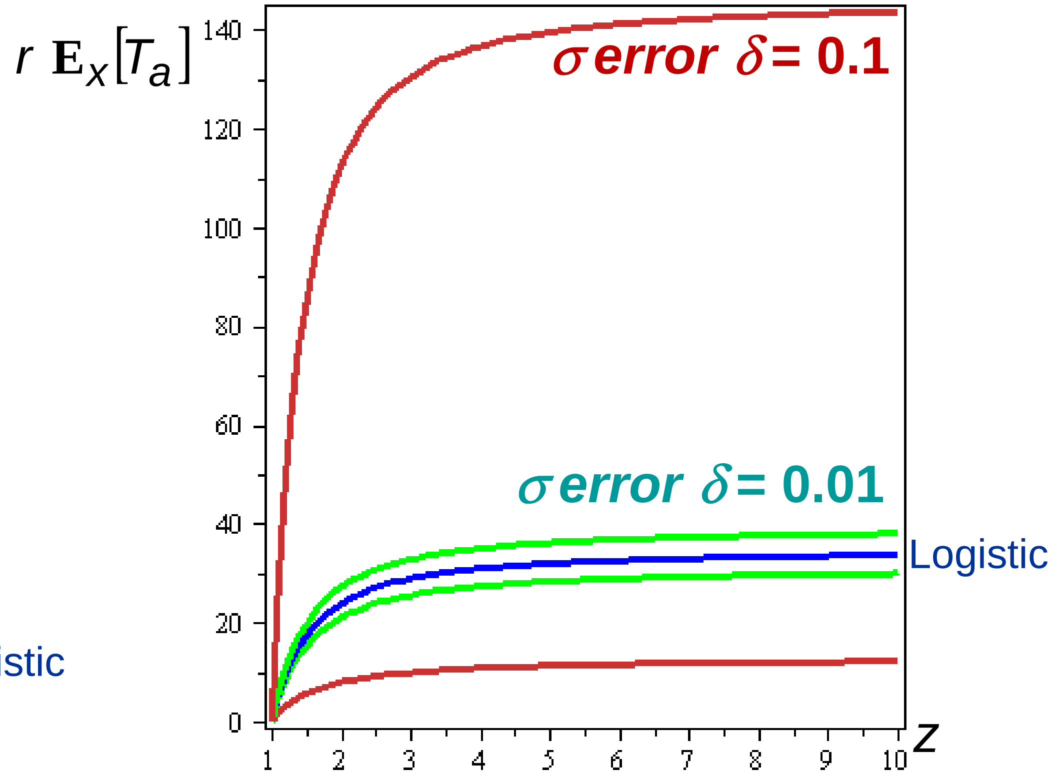
$$r^2 \mathbf{VAR}_x[T_a] \leq 8R^{**2} \int_{2R^{**}d^{**}}^{2R^{**}d^{**}z} y^{-2R^{**}-1} e^y \int_y^{+\infty} u^{-2R^{**}-1} e^u \left(\Gamma(2R^{**}, u)\right)^2 du\,dy$$

$$= \frac{1}{(1+\delta)^2} r^2 \mathbf{VAR}_x^{Logistic(R^{**},d^{**})}[T_a]$$

Example

Behavior of r times the **mean of the population extinction time** as a function of $z=x/a$



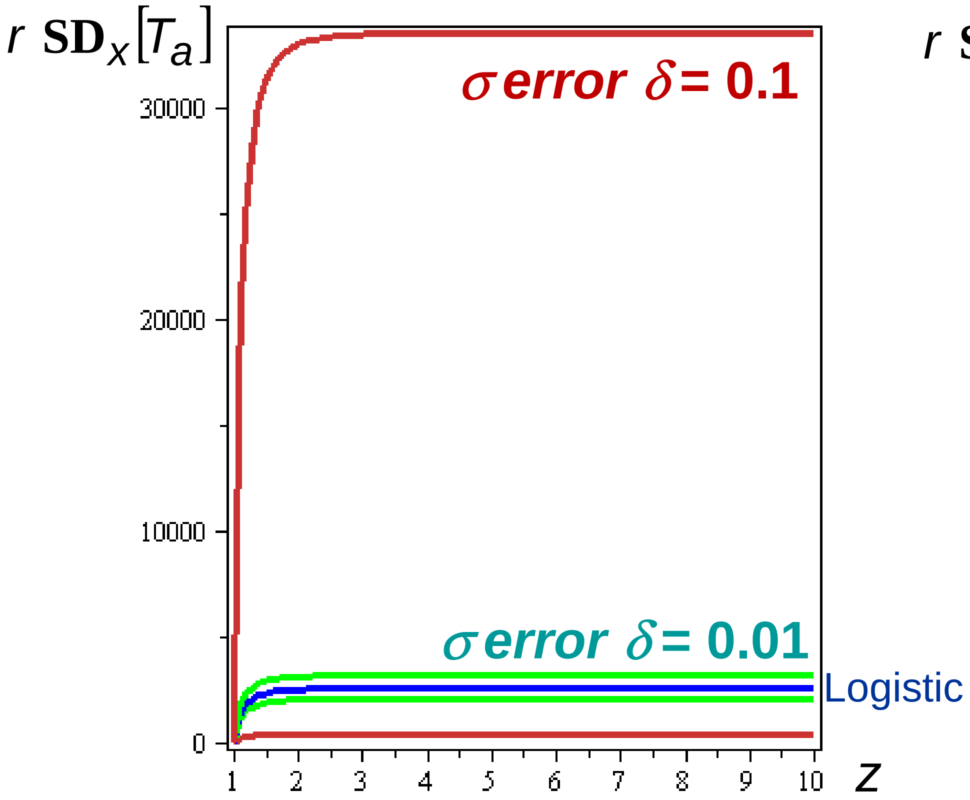


R=1 ($r = \sigma^2$)
d=0.01 ($a=K/100$)

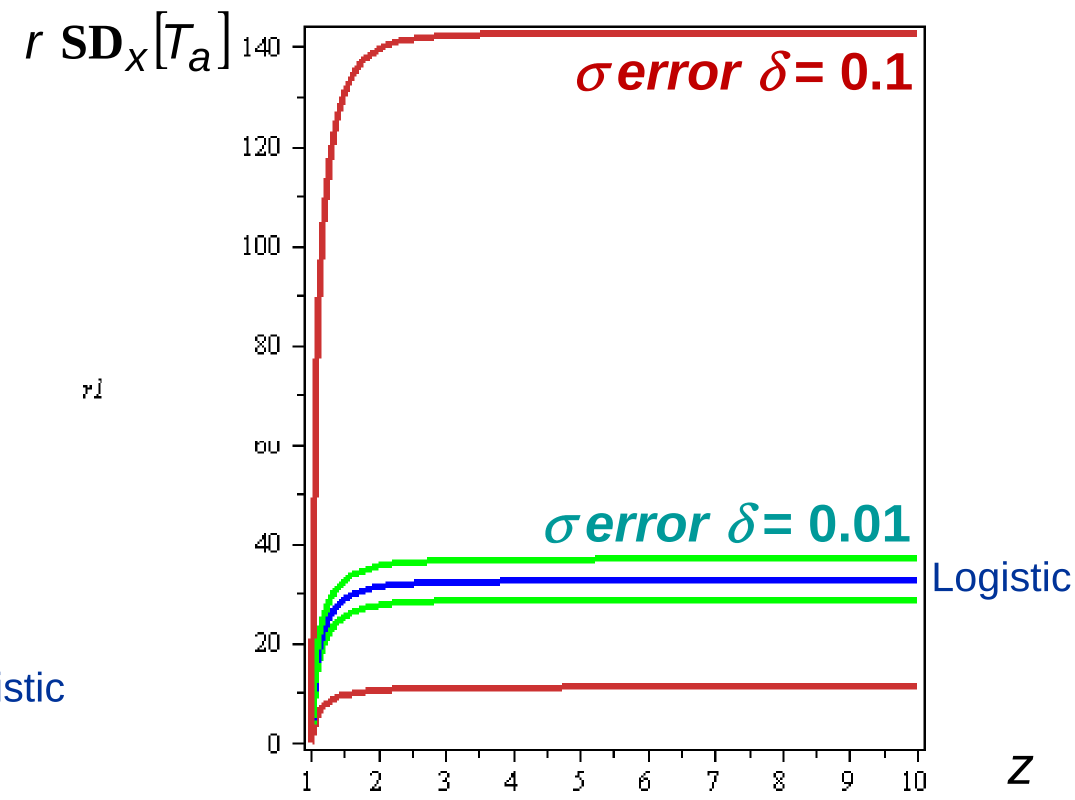
R=1 ($r = \sigma^2$)
d=0.1 ($a=K/10$)

Example

Behavior of *r* times the **standard deviation of the population extinction time** as a function of *z=x/a*



R=1 ($r = \sigma^2$)
d=0.01 (a=K/100)



R=1 ($r = \sigma^2$)
d=0.1 (a=K/10)

Gompertz model, approximate diffusion coefficient

$$|\beta(X)| = \frac{|\alpha(X)|}{\sigma} \le \delta, \quad R = \frac{r}{\sigma^2}, \quad d = \frac{a}{K}, \quad z = \frac{x}{a}$$

$$r\,\mathbf{E}_x[T_a] = 2\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} \frac{1}{\left(1+\beta\left(K\exp\left(y/\sqrt{R}\right)\right)\right)} \int_y^{+\infty} \frac{1}{\left(1+\beta\left(K\exp\left(t/\sqrt{R}\right)\right)\right)} \exp\left(-2\int_y^t \frac{v}{\left(1+\beta\left(K\exp\left(v/\sqrt{R}\right)\right)\right)^2}dv\right)dt\,dy$$

$$r^2\mathbf{VAR}_x[T_a] = 8\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} \frac{1}{\left(1+\beta\left(K\exp\left(y/\sqrt{R}\right)\right)\right)} \int_y^{+\infty} \frac{1}{\left(1+\beta\left(K\exp\left(u/\sqrt{R}\right)\right)\right)} \left(\int_u^{+\infty} \frac{1}{\left(1+\beta\left(K\exp\left(t/\sqrt{R}\right)\right)\right)} \exp\left(-2\int_y^t \frac{v}{\left(1+\beta\left(K\exp\left(v/\sqrt{R}\right)\right)\right)^2}dv\right)dt\right) \left(\int_u^{+\infty} \frac{1}{\left(1+\beta\left(K\exp\left(t/\sqrt{R}\right)\right)\right)} \exp\left(-2\int_u^t \frac{v}{\left(1+\beta\left(K\exp\left(v/\sqrt{R}\right)\right)\right)^2}dv\right)dt\right)du\,dy$$

Gompertz model

For the Gompertz model $\alpha(x) = 0$

$$r\ \mathbf{E}_X^{Gompertz(R,d)}[T_a] = 2\sqrt{\pi}\int_{\sqrt{R}\ln(d)}^{\sqrt{R}\ln(dz)} e^{y^2}\left(1-\Phi(\sqrt{2}y)\right)dy$$

$$r^2\mathbf{VAR}_X^{Gompertz(R,d)}[T_a] = 8\pi\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} e^{y^2}\int_y^{+\infty} e^{u^2}\left(1-\Phi\left(\sqrt{2}u\right)\right)^2 du dy$$

with $\Phi(x) = \int_{-\infty}^{x}\frac{1}{\sqrt{2\pi}}e^{-t^2/2}dt$ standard Gaussian d.f.

Gompertz model, approximate diffusion coefficient

$$r\,\mathbf{E}_x[T_a] \geq \frac{2}{(1+\delta)^2}\sqrt{\pi}\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} \exp\left(\frac{y^2}{(1+\delta)^2}\right)\left(\int_y^0 \exp\left(-\frac{t^2}{(1+\delta)^2}\right)dt + \int_0^{+\infty}\exp\left(-\frac{t^2}{(1-\delta)^2}\right)dt\right)dy$$

$$r\,\mathbf{E}_x[T_a] \leq \frac{2}{(1-\delta)^2}\sqrt{\pi}\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} \exp\left(\frac{y^2}{(1-\delta)^2}\right)\left(\int_y^0 \exp\left(-\frac{t^2}{(1-\delta)^2}\right)dt + \int_0^{+\infty}\exp\left(-\frac{t^2}{(1+\delta)^2}\right)dt\right)dy$$

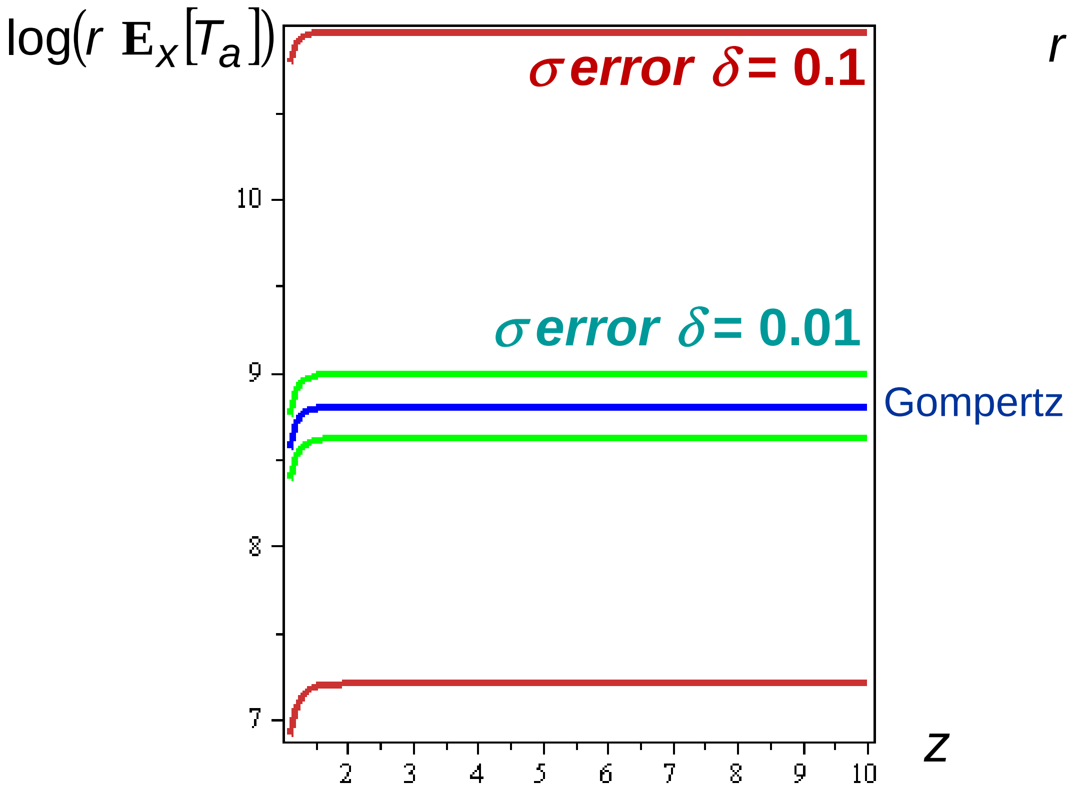
$$r^2\mathbf{VAR}_x[T_a] \geq \frac{8}{(1+\delta)^4}\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} \exp\left(\frac{y^2}{(1+\delta)^2}\right)\int_y^0 \exp\left(\frac{u^2}{(1+\delta)^2}\right)\left(\int_u^0 \exp\left(-\frac{t^2}{(1+\delta)^2}\right)dt + \int_0^{+\infty}\exp\left(-\frac{t^2}{(1-\delta)^2}\right)dt\right)^2 du\,dy$$
$$+\frac{8}{(1-\delta)^4}\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} \exp\left(\frac{y^2}{(1+\delta)^2}\right)\int_0^{+\infty} \exp\left(\frac{u^2}{(1-\delta)^2}\right)\left(\int_u^{+\infty} \exp\left(-\frac{t^2}{(1-\delta)^2}\right)dt\right)^2 du\,dy$$

$$r^2\mathbf{VAR}_x[T_a] \leq \frac{8}{(1-\delta)^4}\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} \exp\left(\frac{y^2}{(1-\delta)^2}\right)\int_y^0 \exp\left(\frac{u^2}{(1-\delta)^2}\right)\left(\int_u^0 \exp\left(-\frac{t^2}{(1-\delta)^2}\right)dt + \int_0^{+\infty}\exp\left(-\frac{t^2}{(1+\delta)^2}\right)dt\right)^2 du\,dy$$
$$+\frac{8}{(1-\delta)^4}\int_{\sqrt{R}\ln d}^{\sqrt{R}\ln(dz)} \exp\left(\frac{y^2}{(1-\delta)^2}\right)\int_0^{+\infty} \exp\left(\frac{u^2}{(1+\delta)^2}\right)\left(\int_u^{+\infty} \exp\left(-\frac{t^2}{(1+\delta)^2}\right)dt\right)^2 du\,dy$$

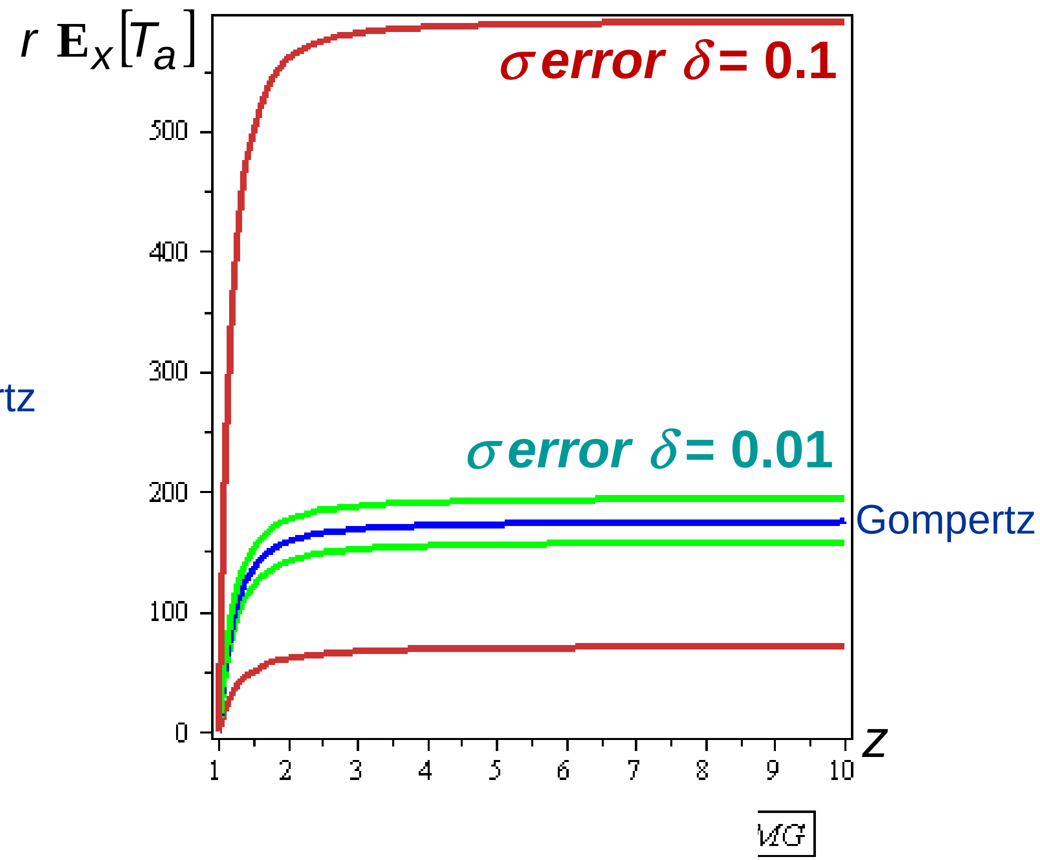
There are “nicer” but not so good bounds

Example

Behavior of r times the **mean of the population extinction time** as a function of $z=x/a$



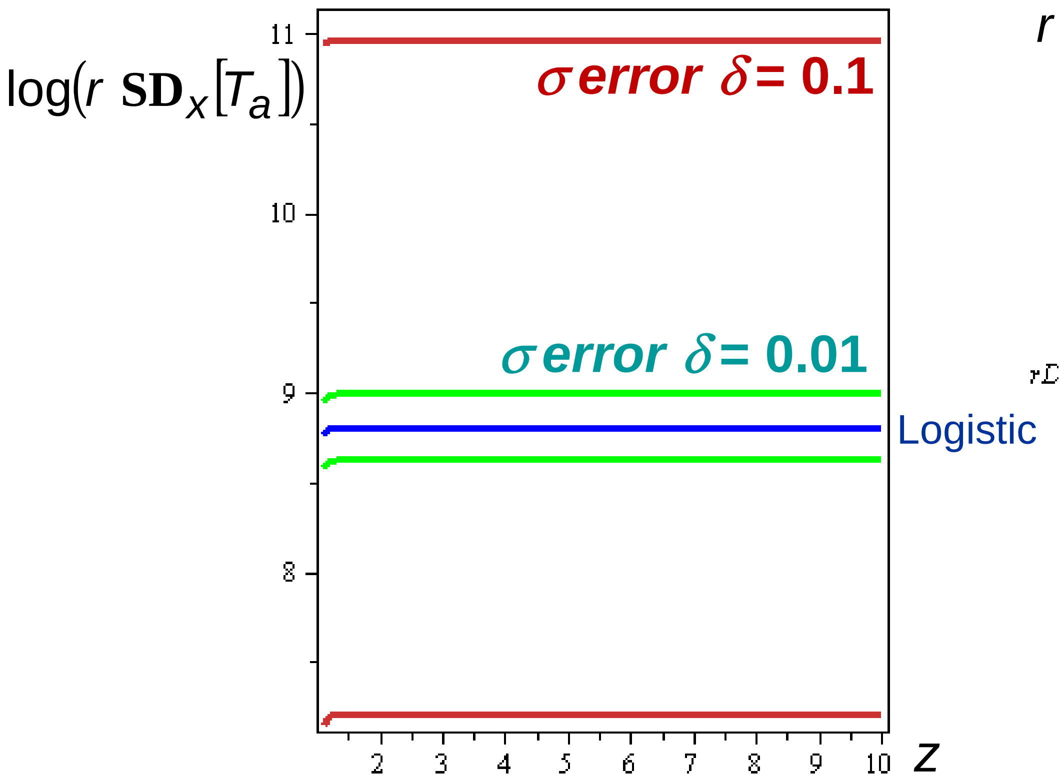
R=1 ($r = \sigma^2$)
d=0.01 (a=K/100)

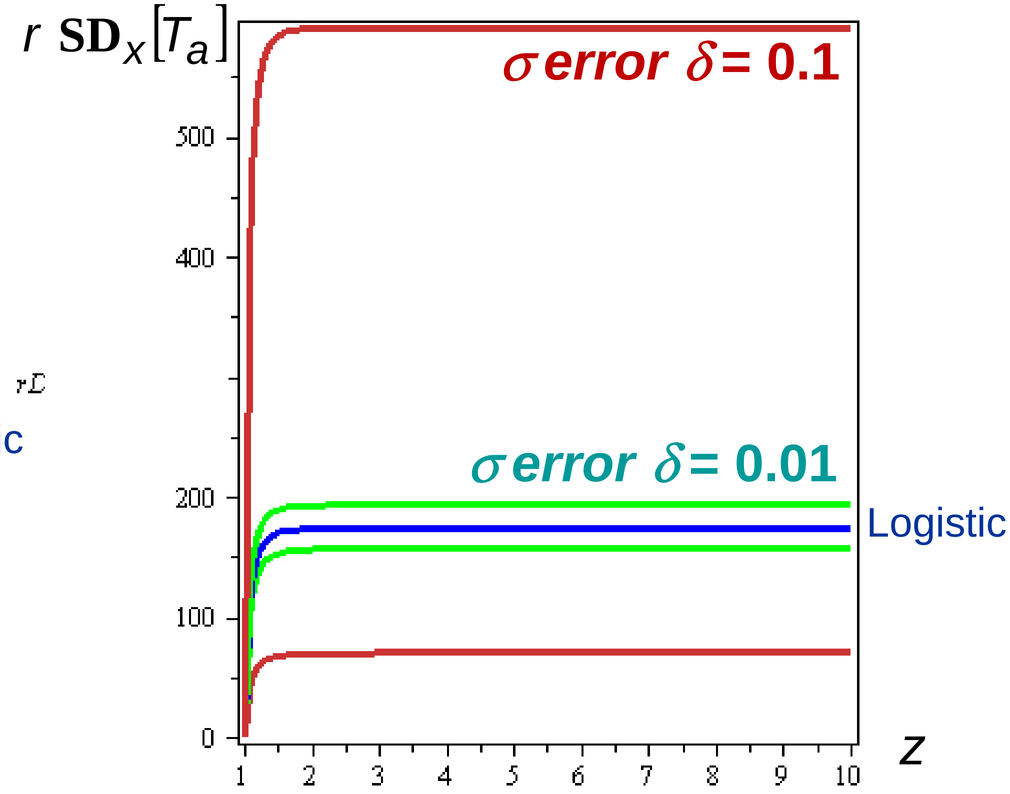


R=1 ($r = \sigma^2$)
d=0.1 (a=K/10)

Example

Behavior of r times the **standard deviation of the population extinction time** as a function of $z=x/a$





R=1 ($r = \sigma^2$)
d=0.01 (a=K/100)

R=1 ($r = \sigma^2$)
d=0.1 (a=K/10)

Harvesting models

$$(S) \quad \frac{1}{X}\frac{dX}{dt} = f(X) + \sigma(X)\varepsilon(t) - h(X)$$

$h(X)$	harvesting effort (when population size is X)
$q(X)=f(X)-h(X)$	net growth rate

Conclusions

- We have studied **general ("true")** models of population growth in random environments so that properties obtained are not model specific.

- 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) always occurs. We obtained explicit expressions for the mean and standard deviation of the extinction time, which are of the same order of magnitude. So, use of means alone is not very informative.

- If the true average growth rate or the true environmental noise intensity are very close to the standard model (logistic or Gompertz), the mean and standard deviation of the extinction time are close to the ones of the standard model. One can then use a standard model, which is much simpler to deal with, as a convenient approximation. One can even have bounds for the error committed.

- Otherwise, the use of the approximate model may lead to values quite different from the true ones.

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Gracias

Thank you