Can populations live forever?

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Outline

Can populations live for ever?

- We look first at deterministic models.
- Two sources of stochasticity:
  - **Demographic stochasticity** due to sampling variations in births and deaths (birth-and-death processes, branching processes)
  - **Environmental stochasticity** due to the effect of random environmental fluctuations on the growth rate (stochastic differential equations-SDE)
- Compare the models for the sources of stochasticity for the **density-independent** (Malthusian) growth benchmark
- Obtain results on **extinction** and **existence of a stationary density** for density-dependent SDE models.

  In order for our results to be robust with respect to model choice, we will not use specific models (as is usual in the literature), We will use **general density-dependent** SDE growth models.
- Compare with the demographic stochasticity density-dependent models.

Deterministic population growth models

$X(t)$ Population size at time t

$$\frac{1}{X(t)}\frac{dX(t)}{dt} = g(X(t)) \qquad X(0) = x_0 > 0 \quad \text{is known}$$

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

$G(X) = g(X)\,X$ *total growth rate*

Examples

DENSITY-INDEPENDENT

Malthusian $g(X) = r$

DENSITY-DEPENDENT

Logistic $g(X) = r\,(1-X/K)$

Gompertz $g(X) = r \ln (K/X)$

……………………………………….

r intrinsic growth parameter

K carrying capacity of the environment (deterministic equilibrium)

Randomly fluctuating environment

affecting the growth rate

What has appeared in the literature? (since Levins (1969))

autonomous Stochastic Differential Eq. (SDE) using $\varepsilon(t)$ standard white noise

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

However, we aim at obtaining model robust properties and so, instead of using a specific model, we consider a general model

$$\frac{1}{X(t)}\frac{dX(t)}{dt} = g(X)+\sigma\varepsilon(t)$$

in which $g(X)$ is an arbitrary function satisfying only biologically determined assumptions and mild technical assumptions

Since this is a multiplicative type phenomenon, it is more “natural” to work with a geometric average growth rate $g(X)$.

Therefore (Braumann 2007 Math. Biosc.; Braumann 2007 J. Theor. Biol), I am going to use Stratonovich calculus

Randomly fluctuating environment

affecting the growth rate

$$\frac{1}{X(t)}\frac{dX(t)}{dt} = g(X) + \sigma\varepsilon(t)$$

$g(X)$	geometric average growth rate (*per capita*)
$G(X)=g(X)X$	total geometric average growth rate
σ	noise intensity (later generalized to a density-dependent realistic noise intensity $\sigma(X)$)
$V(X)=\sigma X$	total noise intensity

$$\frac{dX(t)}{dt} = G(X(t)) + V(X(t))\varepsilon(t)$$

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

$$dX(t) = G(X(t))\,dt + V(X(t))\,dW(t)$$

Solution

$$dX(t) = G(X(t))\,dt + V(X(t))\,dW(t)$$

Under appropriate regularity conditions on *G* and *V*, the solution exists, is unique and is a homogeneous diffusion process with

Drift coefficient

Infinitesimal mean

$$a(x) = \lim_{\Delta t \downarrow 0} \frac{\mathrm{E}_{t,x}[X(t+\Delta t)] - x}{\Delta t} = G(x) + \frac{1}{4}\frac{db(x)}{dx}$$

$$= \text{total arithmetic average growth rate}$$

Diffusion coefficient

Infinitesimal variance

$$b(x) = \lim_{\Delta t \downarrow 0} \frac{\mathrm{VAR}_{t,x}[X(t+\Delta t)]}{\Delta t} = V^2(x)$$

Malthusian SDE model

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

r	geometric average growth rate
$\sigma > 0$	noise intensity (constant)
$G(X) = r\,X$	total geometric average growth rate
$V(X) = \sigma X$	total noise intensity

$$dX(t) = G(X(t))\,dt + V(X(t))\,dW(t)$$

The solution is a homogeneous diffusion process with

Drift coefficient $a(X) = (r + \sigma^2/2)x = R\,x$

Diffusion coefficient $b(x) = V^2(x) = \sigma^2 x^2$

Solution

$$X(t) = x_0 \exp\left(r\,t + \sigma W(t)\right) \xrightarrow{t\to+\infty} \begin{cases} +\infty & \text{if } r > 0 \\ 0 & \text{if } r < 0 \end{cases}$$

Malthusian model - Realistic extinction

So, the probability of "mathematical" extinction is

- 0 if $r > 0$
- 1 if $r < 0$

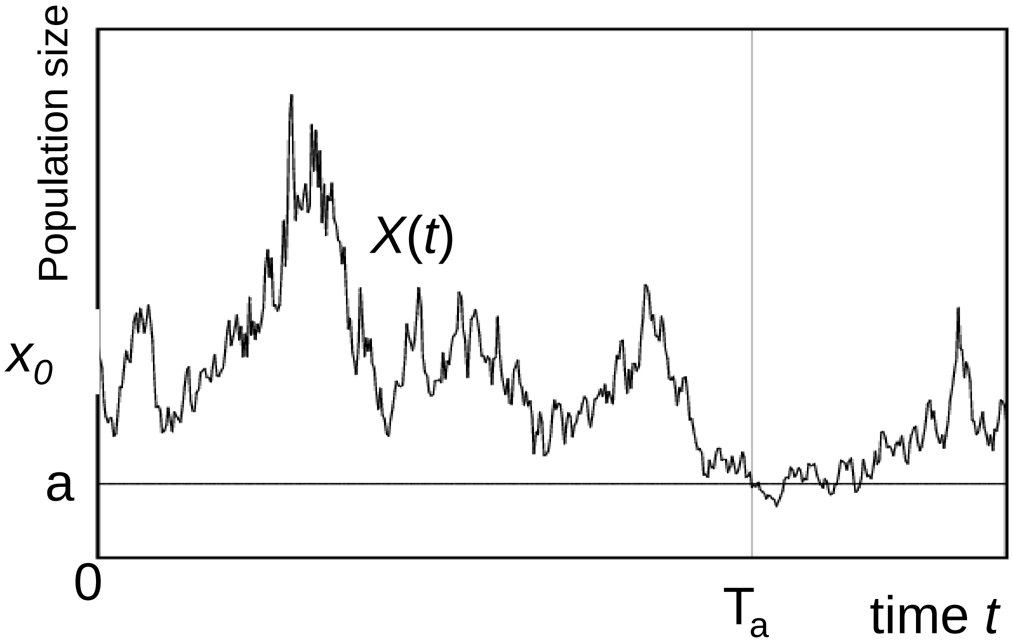
What about a population of 0.4 individuals? What about Allee effects?

Set extinction threshold $a>0$. We assume $a<x_0$.

Note: To study pest outbreaks, we could also consider $a>x_0$

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

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



The probability of realistic extinction is

- $(a/x_0)^{2r/\sigma^2} < 1$ se $r > 0$
- 1 se $r \le 0$

We can also determine the distribution of the extinction time (inverse Gaussian)

Galton-Watson process
(Malthusian branching process)

A branching process is a discrete-time Markov chain X_n representing the population size at generation *n.*

The offspring of the individuals in generation *n* will form generation *n*+1.

Denoting by ξ_{nj} the r.v. representing the number of offspring of the individual number *j* (*j*=1,2,…, X_n) of generation *n,* we have

$$X_{n+1} = \sum_{j=1}^{X_n} \xi_{nj}$$

The Galton-Watson process is the particular density-independent case where all ξ_{nj} are i.i.d. with common distribution (the progeny size distribution) defined by

$$p_i = \mathrm{P}\left[\xi_{nj} = i\right] \quad (i = 0,1,2,\cdots) \text{ with } p_0 + p_1 + p_2 + \cdots = 1$$

Let m and s be the expected value and standard deviation of that distribution.

Let the generation time be Δt . For comparison with continuous-time models, we will, for a fixed time *t,* put $\boldsymbol{t=n\Delta t}$ **and** $\boldsymbol{X(t)=X_n}$ and let $\boldsymbol{\Delta t}\to 0$ **and** $\boldsymbol{n} \to +\infty$.

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Simple (Malthusian) birth and death process

A birth and death process is a continuous-time Markov chain *X*(*t*) representing the population size at time *t* with transition probabilities

$$P\left[X(t+\Delta t)=j \mid X(t)=i\right]=\begin{cases} \lambda_i \Delta t + o(\Delta t) \text{ if } j=i+1 \text{ (one birth)} \\ \mu_i \Delta t + o(\Delta t) \text{ if } j=i-1 \text{ (one death)} \\ 1-(\lambda_i+\mu_i)\Delta t + o(\Delta t) \text{ if } j=i \\ o(\Delta \text{t}) \quad \text{otherwise} \end{cases}$$

The simple birth and death process is the particular (Malthusian) case of density-independence and assumes that

$$\lambda_i = i\lambda$$
$$\mu_i = i\mu$$

where the *per capita* birth and death rates λ and μ are constant, irrespective of population size.

Malthusian model – comparisons

	Malthusian determi-nistic model (no noise $\sigma=0$)	**Malthusian SDE** (environmental noise) r =geometric average growth rate $\sigma>0$ Noise intensity	**Galton-Watson process** m=average progeny size in a gener. Δt $r=\frac{\ln m}{\Delta t}$	**Simple birth and death process** λ (μ)= *per capita* birth (death) rate $r=\lambda-\mu$
Subcritical $r<0$	Extinction	Extinction with probability 1	Extinction with probability 1	Extinction with probability 1
Critical $r=0$	No extinction Constant size	Extinction with probability 1	Extinction with probability 1	Extinction with probability 1
Supercritical $r>0$	No extinction Exponential growth	Extinction with prob.<1: $(a/x_0)^{2r/\sigma^2}$	Extinction with prob. <1: first positive root of progeny size pgf	Extinction with prob. <1: $(\mu/\lambda)^{x_0}$

Malthusian model – comparisons

x=current population size	Determi-nistic model	Malthusian SDE model	Galton-Watson process ***s*** = st.dev. progeny size	Simple birth & death process
Infinitesimal mean per capita $\frac{1}{x}\lim_{\Delta t\downarrow 0}\frac{\mathrm{E}_{t,x}[X(t+\Delta t)]-x}{\Delta t}$	r	$R=r+\sigma^2/2$=arith-metic average growth rate R	$r=\frac{\ln m}{\Delta t}$ r	$r=\lambda-\mu$ r
Infinitesimal stand. deviation per capita $\frac{1}{x}\sqrt{\lim_{\Delta t\downarrow 0}\frac{\mathrm{VAR}_{t,x}[X(t+\Delta t)]}{\Delta t}}$	0	σ	$\sigma^2\approx\frac{s^2}{\Delta t}$ $\sigma/\sqrt{x}$	$\sigma=\sqrt{\lambda+\mu}$ $\sigma/\sqrt{x}$

General Density-dependent SDE model
(constant noise intensities)

$$\frac{1}{X(t)}\frac{dX(t)}{dt} = g(X(t)) + \sigma\varepsilon(t) \qquad X(0) = x_0 > 0 \text{ known}$$

$$dX(t) = G(X(t))\,dt + V(X(t))\,dW(t)$$

$g(X)$	**geometric** average growth rate
$G(X)=g(X)X$	total **geometric** average growth rate
$\sigma>0$	noise intensity (constant)
$V(X)=\sigma X$	total noise intensity

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

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

General Density-dependent SDE model
(constant noise intensities)

The solution exists and is unique up to an explosion time

The solution is a homogeneous diffusion process with

Drift coefficient

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

Diffusion coefficient

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

General Density-dependent SDE model
(constant noise intensities)

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

Scale density

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

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

Speed density

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

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

$$0 < a < x_0 < b < +\infty$$

$$u(x_0) = \mathbf{P}\left[T_b < T_a \middle| X(0) = x_0\right] = \frac{S(x_0) - S(a)}{S(b) - S(a)}$$

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General Density-dependent SDE model
(constant noise intensities)

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

Boundary X=0 is <u>non-attractive</u>

if there is a right-neighborhood R=]0,y[of zero such that, for any $0<x_0<n\in R$,

$$\mathrm{P}\left[T_{0^+} \le T_n \middle| X(0) = x_0\right] = 0$$

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, the boundary $X = +\infty$ is non-attractive 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 $g(0^+) < 0$ and non-attractive if $g(0^+) > 0$.

General Density-dependent SDE model
(constant noise intensities)

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 (Braumann 1999a+b+2008 Math. Biosc./Proc. Plovdiv/C&MwA)

- When $g(0^+) < 0$, "mathematical" extinction occurs a.s.
- When $g(0^+) > 0$, 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).

However, 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, realistic extinction always occurs w.p. 1.

General density-dependent growth model

with realistic density-dependent noise intensity

$$\sigma(X)$$

(Braumann 2002+2008)

Same conclusions with the extra 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) $|\sigma(X)/g(X)|$ is bounded in a right neighborhood of 0.

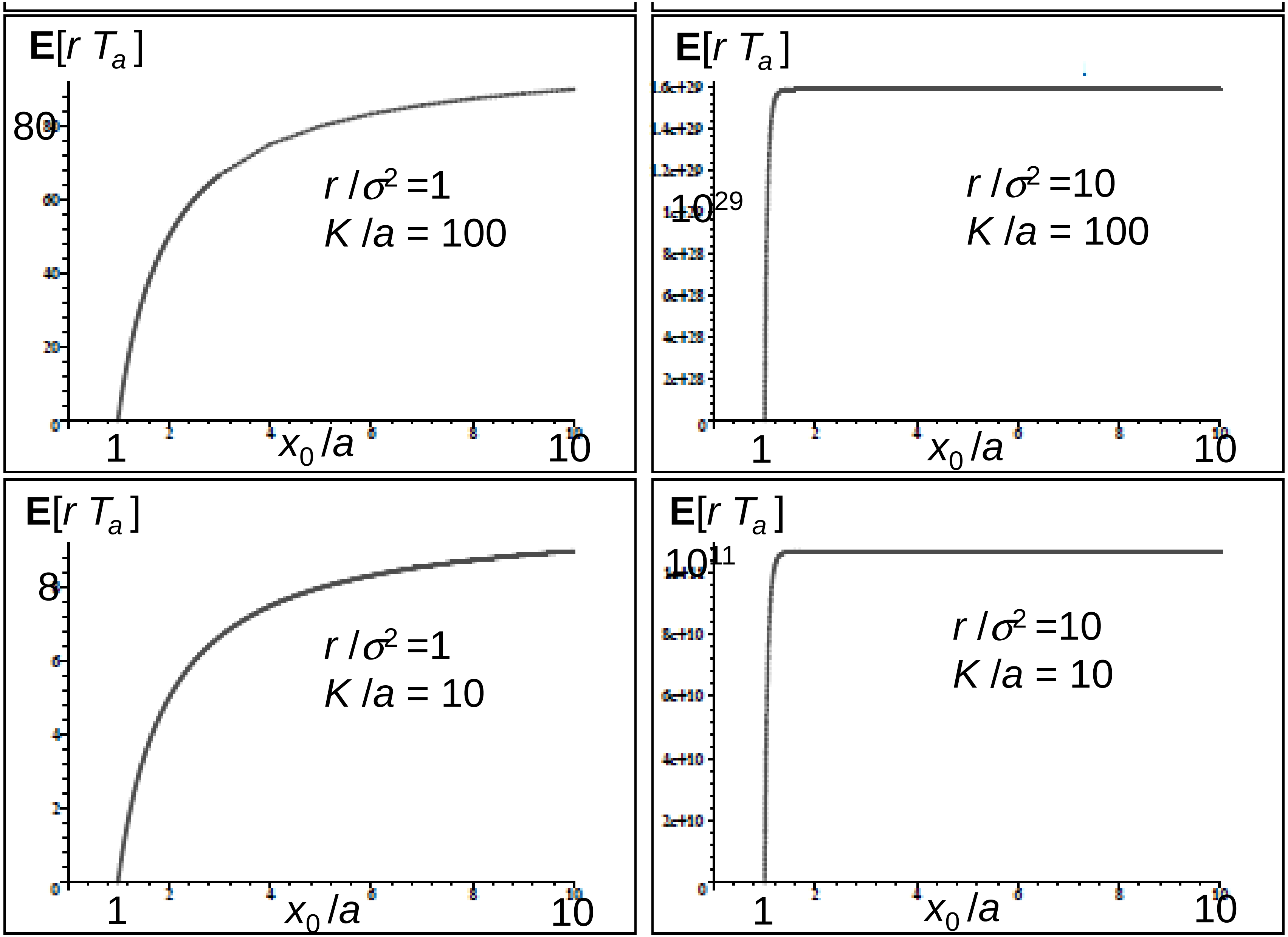
(D) $|\sigma(X)/g(X)|$ is bounded in a neighborhood of $+\infty$.

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

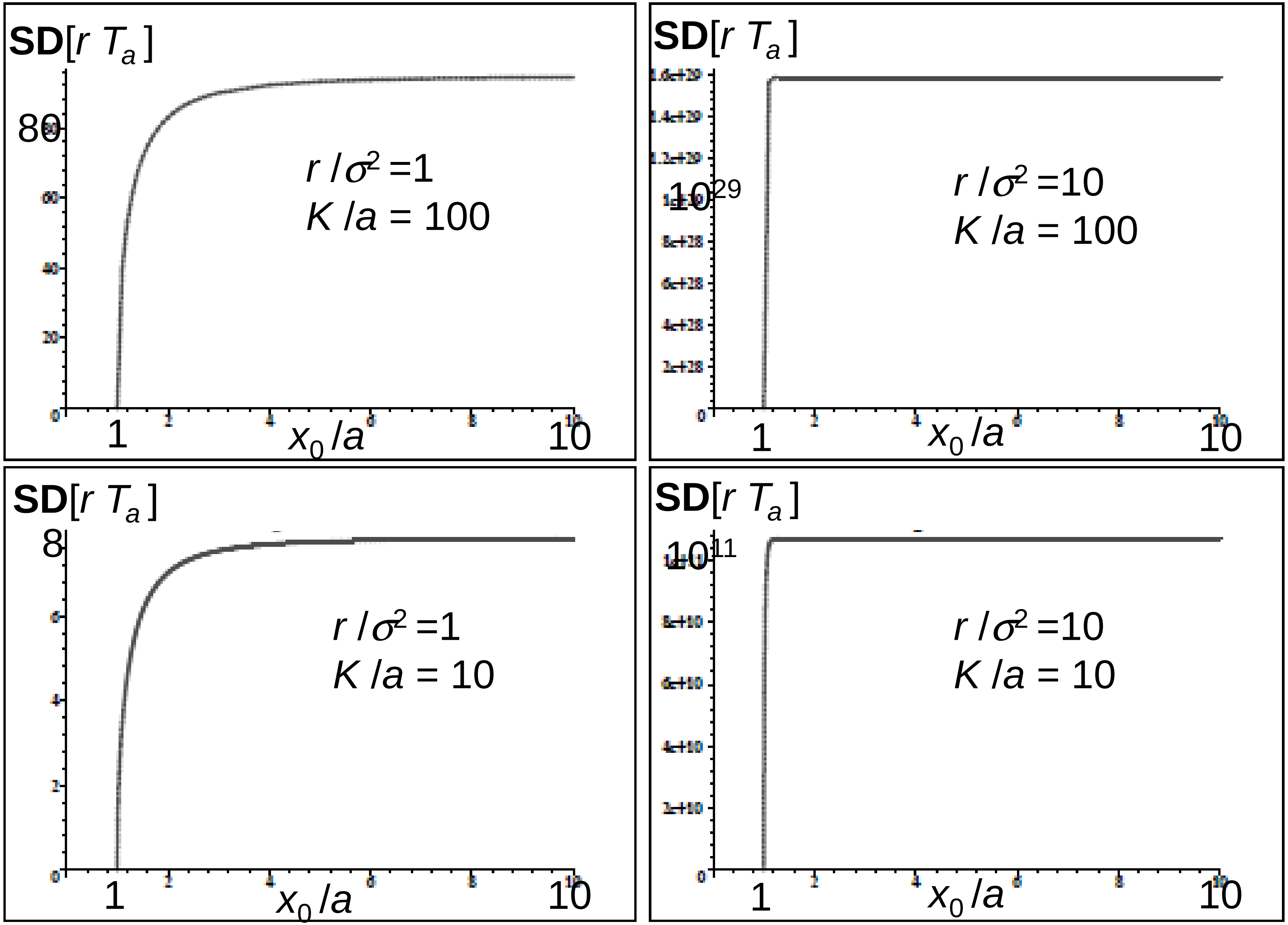
Density-dependence and extinction

- Under environmental stochasticity, density-dependence leads to extinction
- The same has been shown for some specific demographic stochasticity models and we speculate that it is true for general models with reasonable assumptions.
- For branching processes that is certainly the case if there is a finite maximum population size, but this assumption is a bit too strong. What assumptions would we need? We may take the average number of progeny $m(X)$ decreasing with increasing population size X and being <1 for populations beyond a certain size.
- For birth and death processes, we may assume a decreasing per capita birth rate $\lambda(X)$ and an increasing per capita death rate $\mu(X)$, such that the difference becomes negative for large enough populations.
- The issue is how long does it take for extinction to occur.
- For environmental stochasticity, we have obtained (Braumann 1985, Carlos & Braumann 2005,2006, Carlos, Braumann & Filipe 2013) explicit expressions for the mean and standard deviation of the extinction time. We will illustrate its behavior for the logistic model, but the exercise can be made for other models

Mean time for extinction (logistic model)



Standard deviation of extinction time (logistic model)



Density-dependence and extinction

- The mean and standard deviation of the number of "generations" before extinction are of the same order of magnitude and increase with:
  - the relative initial population x_0/a when initial population is close to the extinction threshold; otherwise, is almost constant
  - relative intrinsic growth rate r/σ^2
  - relative carrying capacity K/a
- Extinction can take a very long time, in which case there are long periods where the population size stays in the vicinity of the carrying capacity. By a large deviation argument, one can show that the duration of one such period grows exponentially with r/σ^2.
- For demographic stochasticity that duration grows exponentially with K [Jagers and Klebaner (2011) showed it for a general class of models that include birth-and-death processes and continuous-time branching processes; the form of density-dependence is general with a bit restrictive shape assumptions]

Harvesting models with constant noise intensity

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

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

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

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

CONCLUSIONS (Braumann 1999b Math. Biosc.)

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

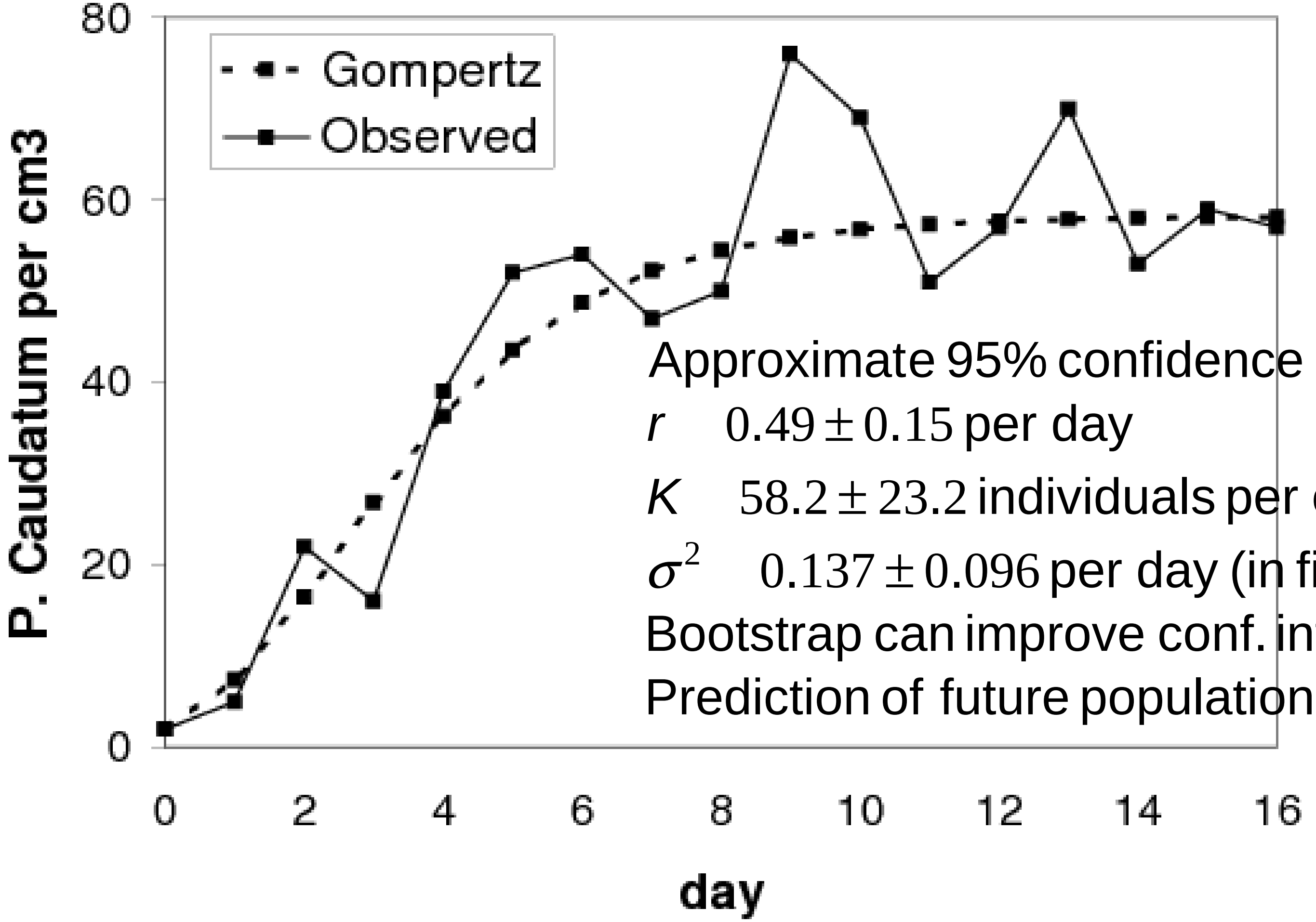
When $q(0^+) > 0$, there is 0 probability of extinction and there is a stationary density (the mode of which approximately coincides with the deterministic equilibrium when the noise intensity is small).

Itô and Stratonovich: Braumann 2007c J.Theor. Biol.

Optimal harvesting: Lungu e Oksendal 1997, Alvarez e Shepp 1997, Alvarez 2000

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

$$\frac{1}{X(t)}\frac{dX(t)}{dt} = r\ln\frac{K}{X} + \sigma\varepsilon(t) \quad \text{with } r>0, K>0, \sigma>0, X(0)=x_0>0$$



Approximate 95% confidence intervals (ML)

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)

Bootstrap can improve conf. int. for small sample sizes

Prediction of future population sizes is also possible

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Conclusions

•We have compared, for the Malthusian growth benchmark, the extinction probabilities and the infinitesimal mean and variance for

- the SDE model (environmental noise)
- the Galton-Watson process (demographic noise)
- the simple birth and death process (demographic noise)

•We have then considered a general density-dependent SDE model and shown that “mathematical” extinction occurs with probability one if the geometric average growth rate at low population densities is negative. If it is positive, “mathematical” extinction has zero probability of occurring and there is a stationary density.

•We have also shown that, for such general density-dependent SDE models, ”realistic” extinction (population dropping to a positive low extinction threshold) always occurs a.s.

Conclusions

•We can speculate that extinction would also always occur in general density-dependent models with demographic stochasticity and with both demographic and environmental stochasticity, although some work is still required.

•The issue is how long does it take for extinction to occur.

•For SDE models (environmental stochasticity), extinction time distributions can be obtained. Looking at the average time for extinction, one can see that extinction can be fast for certain parameter values and can take a very long time for other parameter values.

•For SDE models, parameter estimation and prediction can be done. Applications to harvesting (fishing, hunting, forestry) is possible.

Can populations live forever?

Let me answer with another question:

how long is forever?

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Obrigado

Thank you