Lecture 4 - Density-independent stochastic growth

Announcement:
Hand back Q1
Bring laptops next class
Today's concepts:
Stochasticity (Environmental vs. Demographic)
Expectation vs. Variance (uncertainty)
Geometric vs. Arithmetic expectation

Review: Exponential (geometric) as first-order approximation Show examples of population time series
Discrete vs. continuous Show videos

All previous equations have been deterministic
... if we start with same $N(0)$ and r we get exactly the same answer.
Add stochasticity: "Adding stochastic shell to deterministic core of our model"

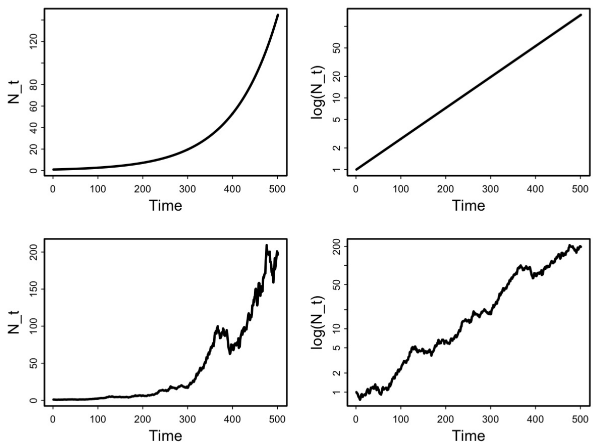
Stochastic (from the Greek for *aim* or *guess*) = random with respect to considered variables
A stochastic process is one whose subsequent state is determined by a random element.

$$N_T = N_0 e^{(r \pm noise)T} = N_0(\lambda \pm noise)^T$$

E.g., 4 years of stochastic growth

$$\begin{aligned}
N_0 &= 1 & & \\
\lambda_1 &= 2 & N_1 &= N_0\lambda_1 = 1 \cdot 2 = 2 \\
\lambda_2 &= 1 & N_2 &= N_1\lambda_2 = 2 \cdot 1 = 2 \\
\lambda_3 &= 3 & N_3 &= N_2\lambda_3 = 2 \cdot 3 = 6 \\
\lambda_4 &= 2 & N_4 &= N_0\lambda_1\lambda_2\lambda_3\lambda_4 = 12
\end{aligned}$$

Show code in R...



If we wanted to determine:
Expectation (mean) of N_T ($\bar{N}_T$) and variance of N_T ($\sigma^2_{N_T}$) over all time points:

$$\bar{N}_T = E[N_T] = \frac{1}{T}\sum_t^T N_t = \frac{1+2+2+6+12}{5} = 4.6$$

$$\begin{aligned}
\sigma^2_{N_T} = Var[N_T] &= \frac{1}{T}\sum_t^T (N_t - \bar{N}_T)^2 \\
&= \frac{(1-4.6)^2 + (2-4.6)^2 + (2-4.6)^2 + (6-4.6)^2 + (12-4.6)^2}{5} = 83.2/5 = 16.64
\end{aligned}$$

Note that σ = standard deviation
and that CV (coefficient of variation) = $\sigma^2/\bar{N}$

Environmental Stochasticity - *temporal variation in population's per capita growth rate*
Importance of distinguishing between geometric vs. arithmetic mean...
Example: Dynamics of two populations with same initial size:

$$N(3) = N_0 \lambda_1 \lambda_2 \lambda_3$$

$$\text{Population A: } N_A(3) = N_0 \cdot 2 \cdot 1 \cdot 3 = 6 \cdot N_0$$
$$\text{Population B: } N_B(3) = N_0 \cdot 2 \cdot 2 \cdot 2 = 8 \cdot N_0$$

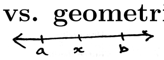
$$\bar{\lambda} = \frac{1}{T} \sum_{t}^{T} \lambda_t$$

On natural (arithmetic) scale, $\bar{\lambda}_A = \bar{\lambda}_B = 2$.

So why does population B grow more?
Appropriate measure is the geometric mean (remember: popn growth is a multiplicative process):
(No standard symbol for geometric mean)

$$\text{geometric mean } \lambda = \left(\prod_{t}^{T} \lambda_t \right)^{\frac{1}{T}} = \sqrt[T]{\prod_{t}^{T} \lambda_t}$$

$$\text{Geometric mean of } \lambda_A = \sqrt[3]{\lambda_1 \cdot \lambda_2 \cdot \lambda_3} = \sqrt[3]{2 \cdot 1 \cdot 3} = 1.817...$$
$$\text{So in fact } N_A(3) = N_0 \cdot 1.817 \cdot 1.817 \cdot 1.817 = 6 \cdot N_0$$

Side note: Contrasting arithmetic vs. geometric mean
Two numbers (expressed relative to x): 

What is x?

$$a - x = x - b \qquad\qquad \frac{a}{x} = \frac{x}{b}$$
$$a + b = 2x \qquad\qquad a \cdot b = x \cdot x$$
$$\frac{a+b}{2} = x \qquad\qquad a \cdot b = x^2$$
$$\sqrt[2]{a+b} = x$$

Will show that: *Natural log of geometric mean λ = arithmetic mean of natural log of the λ's*

$$\text{Since... } \ln(b^a) = a\ln(b) \Rightarrow \quad \ln\left(\left(\prod_{t=1}^{T} \lambda_t \right)^{1/T} \right) = \frac{1}{T} \cdot \ln(\lambda_1 \cdot \lambda_2 \ldots \lambda_T)$$
$$\text{Since... } \ln(ab) = \ln(a) + \ln(b) \Rightarrow \quad = \frac{1}{T} \left(\ln(\lambda_1) + \ln(\lambda_2) + \cdots + \ln(\lambda_T) \right)$$
$$= \frac{1}{T} \cdot T \cdot \overline{\ln(\lambda)}$$
$$= \overline{\ln(\lambda)}$$

Thus, could also calculate as:

$$\text{Geometric mean } \lambda = e^{\overline{\ln(\lambda)}}$$

An alternative approximation (provided in Case, pg. 35):

$$\text{Geometric mean } \lambda = e^{\overline{\ln(\lambda)}} \approx e^{\ln(\bar{\lambda}) - \frac{\sigma_\lambda^2}{2\bar{\lambda}^2}}$$
(*Note effects of σ_λ and of $\bar{\lambda}$.*)

Class R exercise - random vector draws - compare geometric and arithmetic means

- Effect of $\sigma = 0$, and increasing σ values:

  Geometric mean will always be less than arithmetic mean

  The more variation, the lower the geometric mean

- Effect of sample size, n:

  Little effect. very low n might have more variation in depression amount

- Effect of $\bar{\lambda}$:

  Raises and lowers, but note that at $\bar{\lambda} \approx 1$, geometric mean $\lambda < 1$ (declining population)!!

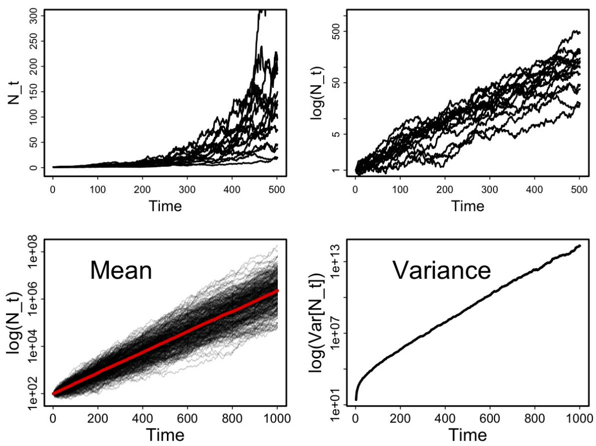
What does this mean for the dynamics of a given focal population?

Population change	Deterministic λ	Deterministic $\ln(\lambda)$	Environmental noise $\ln(\lambda \pm \text{noise})$
No change	1	0	NA
Growth	> 1	> 0	$\frac{\sigma_\lambda^2}{2\bar{\lambda}^2} < \ln(\bar{\lambda}) > 0$
Decline	< 1	< 0	$\ln(\bar{\lambda}) - \frac{\sigma_\lambda^2}{2\bar{\lambda}^2} < 0$

What are the expected mean and variance of N_T for an "average" (typical) population?
That is, we will now ask a different question...

$\Rightarrow$ What is the expected population size N_T over an ensemble of replicate populations?
(The average of n replicate populations.)

Run in R...



Will show that

$$\bar{N}_T = N_0 \bar{\lambda}^T = N_0 e^{\bar{r}t}$$

And that...
when there is *environmental variation* only:

$$\sigma^2_{ln(N_T)} = T \cdot \sigma^2_{ln(\lambda_t)}$$

when there is only *demographic variation*:

$$\sigma^2_{N_T} = \begin{cases} 2N_0\bar{b}T & \text{if } \bar{b} = \bar{d} \\ \frac{\bar{b}+\bar{d}}{\bar{b}-\bar{d}} N_0 e^{\bar{r}T}(e^{\bar{r}T} - 1) & \text{if } \bar{b} \neq \bar{d} \end{cases}$$

How to get $E[N_T]$?
Let λ be a random variable from a normal distribution.
Any given λ from this distribution is denoted by λ_t.

$$\begin{aligned}
N_T &= N_0 \prod_{t=1}^{T} \lambda_t = N_0 \cdot (\lambda_1 \lambda_2 \ldots \lambda_T) \\
E[N_T] &= N_0 \cdot E[\prod_{t=1}^{T} \lambda_t] \qquad \text{(since } N_0 \text{ is a constant)} \\
&= N_0 \cdot \prod_{t=1}^{T} E[\lambda] \\
&= N_0 \cdot E[\lambda]^T \\
&= N_0 \cdot \bar{\lambda}^T
\end{aligned}$$

How to get variance?
Transform by taking the log...

$$\ln(N_T) = \ln(N_0) + \ln\left(\prod_{t=1}^{T} \lambda_t\right) = \ln(N_0) + \boxed{\sum_{t=1}^{T} \ln(\lambda_t)}$$

Now working on the arithmetic scale!
Allows us to apply Central Limit Theorem (pg. 41 of Case):

The sum of independent, identically distributed random variables x_i tends to asymptote to the normal density distribution, no matter the underlying distribution of x_i

Under a sufficiently large number of independent random variable draws:

$$\begin{aligned}
\boxed{\sum_{i=1}^{n} x_i} &= \mathcal{N}(n \cdot E[x],\ n \cdot Var[x]) \\
&= \mathcal{N}(n\bar{x}, n\sigma_x^2)
\end{aligned}$$

The mean of the sum equals the sum of all individual means
The variance of the sum equals the sum of all individual variances

Inserting $\ln(\lambda_t)$ for x_i, we thus have

$$\begin{aligned}
\sum_{t=1}^{T} \ln(\lambda_t) &= \mathcal{N}(T \cdot E[\ln(\lambda_t)],\ T \cdot Var[\ln(\lambda_t)]) \\
&= \mathcal{N}(T \cdot \overline{\ln(\lambda_t)},\ T \cdot \sigma^2_{\ln(\lambda_t)})
\end{aligned}$$

Therefore, we have

$$E[\ln(N_T)] = \ln(N_0) + T \cdot \overline{\ln(\lambda_t)}$$

and

$$\sigma^2_{\ln(N_T)} = T \cdot \sigma^2_{\ln(\lambda_t)}$$

To translate expectation back to arithmetic scale:
Even though the expected value of N_T is $E[N_T] = N_0 \cdot \bar{\lambda}^T$,

$$N_T \sim log\mathcal{N} \text{ with median } = e^{\ln(N_0) + T \cdot \overline{\ln(\lambda)}}$$

Take-home message:
When modeling $N_{t+1} = \lambda N_t$ with environmental noise in growth rate, error must be $log\mathcal{N}$!

In Problem Set #2 you should therefore use $N_{t+1} = N_t(\lambda \pm e^{\epsilon})$, where $\epsilon \sim \mathcal{N}(0, \sigma_\epsilon^2)$.

Summary

- The solution to $Var[N_T]$ is sensitive to assumed model-formulation!
- Dependent on how stochasticity is assumed to affect λ.
- If you assume $N_T = N_0(\lambda \pm \epsilon)^T$ with $\epsilon \sim \mathcal{N}(0, \sigma_\epsilon^2)$ you'll get a different prediction!

Demographic stochasticity - Between-individual variation in per capita growth rate
Analogy of flipping a coin (not perfect, but will do).

$$H = \text{birth and } T = \text{death}$$

Q: How many H and T in 1000 flips? How many in 100? How many in 4?
For fair coin, $P(H) = P(T) = 0.5$ and $P(H) + P(T) = 1 \quad \Rightarrow$ Binomial distribution.

Class exercise in R
Number of extinctions as function of starting population size using binomial.
Going to assume:

$$P(birth) = \frac{b}{b+d}$$
$$P(death) = \frac{d}{b+d}$$

where b and d are per capita birth and death rates, such that $r = b - d$.

For true population (no longer binomial):

$$P(birth) = \frac{b}{b+d+o}$$
$$P(death) = \frac{d}{b+d+o}$$
$$P(other) = 1 - [P(b) + P(d)]$$

Won't go through derivations, but expectation of $N(t)$ is still:

$$\overline{N_t} = N_0 e^{\bar{r}t}$$

But for variance:

$$\sigma^2_{N_T} = \begin{cases} 2N_0\bar{b}T & \text{if } \bar{b} = \bar{d} \\ \frac{\bar{b}+\bar{d}}{\bar{b}-\bar{d}} N_0 e^{\bar{r}T}(e^{\bar{r}T} - 1) & \text{if } \bar{b} \neq \bar{d} \end{cases}$$

Side note...Probability of extinction:

$$P(ext) = \left(\frac{d}{b}\right)^{N_0}$$

Of course, environmental and demographic stochasticity are not mutually exclusive!
Temporal variation among individuals will also causes temporal variation in λ.
See Case for example combining the two.
