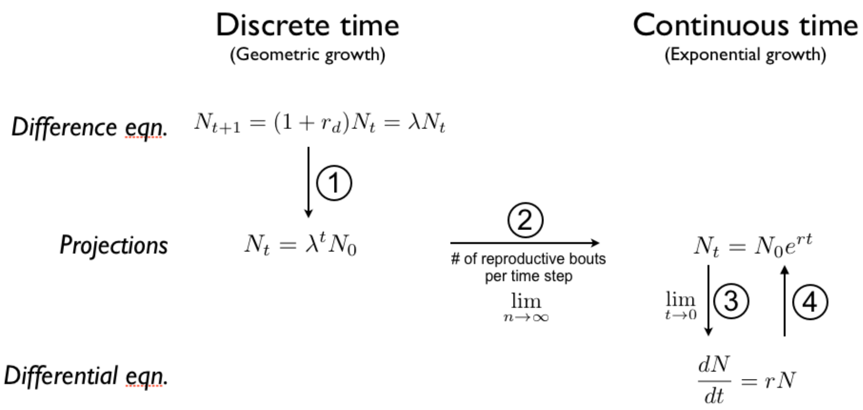
Lecture 2 - Density-independent deterministic growth

Announcements:
Today - Paper discussion until ≈ 10:45, then 5 min break, then lecture.
Next class: Bring laptop & R, having read readings & problem set
Will provide intro to R, then start problem set together.

Today's concepts:
Geometric vs. Exponential growth
Discrete vs. Continuous (Difference vs. Differential equations)
Population vs. Per capita rates of change
Simulations vs. Analytical Solutions

Overview:



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(1) Simplest possible model: Discrete time difference equation:

$$N_{t+1} = N_t + B - D + I - E$$

B-Total births; D-Total deaths; I-Immigration; E-Emigration

Let: $I = E$, $B = b_d N$, $D = d_d N$.

b_d - births per individual;
d_d - deaths per individual i.e. probability of individual dying per time-step

Thus:

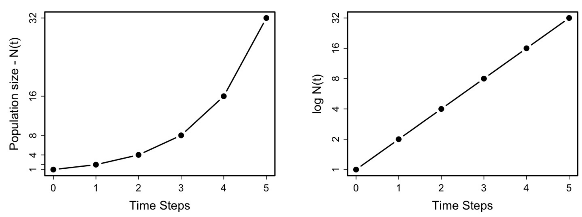
$$N_{t+1} = N_t + (b_d - d_d)N_t = (1 + b_d - d_d)N_t = (1 + r_d)N_t = \lambda N_t$$

λ - finite rate of increase - per capita rate of growth if population is growing geometrically
r_d - discrete growth factor/increment (Ted Case writes this as R).

Draw $N(t)$ vs. t on arithmetic scale on board in steps

$$N(0) = 1, \lambda = 2 \implies N(t) = 1, 2, 4, 8, 16, 32, ... \implies \textbf{Geometric growth}$$

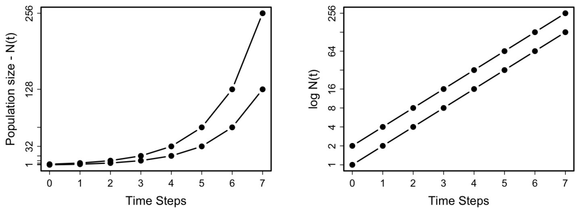
NOTE: Not just doubling! λ can be any number!
Then draw on log-scale.



Show R plots

Q: What happens if we start at different population size at same lambda?

Add points for N(0)=2 on drawing. Plot in R



Q: Why linear on log-scale?

A: On log-scale, products become sums, ratios become differences:

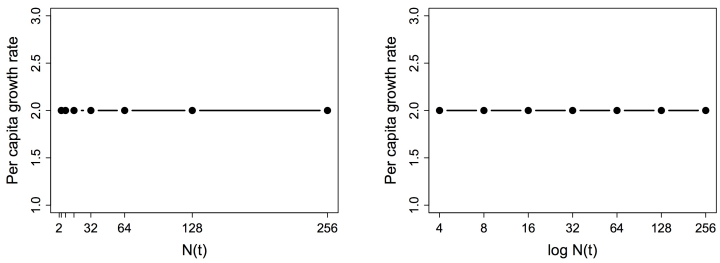
$$y = a \cdot b \qquad\qquad y = \frac{a}{b}$$

$$log(y) = log(a \cdot b) = log(a) + log(b) \qquad\qquad log(y) = log\left(\frac{a}{b}\right) = log(a) - log(b)$$

Q: Why do we call this density-independent population growth?

A: Density independence of *per capita* growth rate

Show plot of $\lambda = \frac{N_{t+1}}{N_t}$ vs. N_t



Want to predict $N(T)$: Analytical solution of $\lambda...(\lambda(\lambda N_0)) = \lambda^T N_0$

Q: What have we assumed?

A: List includes:

- synchronous discrete reproduction
- constant (non-stochastic = deterministic) growth rate
- no density-dependence

Note:
Will go back and forth between calculating per capita growth as either $\frac{N_{t+1}}{N_t}$ or $\frac{(N_{t+1}-N_t)}{N_t}$.
Why? Because:

$$N_{t+1} = \lambda N_t \implies \lambda = \frac{N_{t+1}}{N_t}$$

but also

$$N_{t+1} = \lambda N_t = (1 + r_d)N_t = N_t + r_d N_t \implies N_{t+1} - N_t = r_d N_t \implies \frac{N_{t+1} - N_t}{N_t} = r_d = \lambda - 1$$

② Discrete vs. continuous growth

Recovering the continuous from the discrete:

$$r_d = 0.5 \implies \lambda = 1.5, \quad t = 1\ year$$
$$N_1 = \lambda N_0 = (1 + 0.5)N_0$$

$$t = \frac{1}{2} year$$
$$N_1 = \lambda^2 N_0 = \left(1 + \tfrac{r_d}{2}\right)^2 N_0 = (1 + 0.25)^2 N_0$$

$$N_1 = \left(1 + \tfrac{r_d}{n}\right)^n N_0$$
$$\frac{N_1}{N_0} = \left(1 + \tfrac{r_d}{n}\right)^n$$

$$\lambda = \lim_{n\to\infty} \left(1 + \tfrac{r_d}{n}\right)^n = e^r$$

r - instantaneous per capita growth rate

R-demonstration: Euler's constant

First: $n = 1,\ N(0) = 1,\ r_d = 1$

true $e = exp(1)$

est $e = \frac{N_1}{N_0}$ ... increasing n

$$\begin{aligned}
n = 1 \Rightarrow \quad & \frac{N_1}{1} = \left(1 + \tfrac{r_d}{n}\right)^n & = \left(1 + \tfrac{1}{1}\right)^1 = 2 \\
n = 2 \Rightarrow \quad & & = \left(1 + \tfrac{1}{2}\right)^2 = 2.25 \\
n = 3 \Rightarrow \quad & & = \left(1 + \tfrac{1}{3}\right)^3 = 2.30707... \\
n = \infty \Rightarrow \quad & & = e^1 = 2.71828...
\end{aligned}$$

$$\lim_{n\to\infty} \left(1 + \tfrac{1}{n}\right)^n = e^1 = e$$

Now define natural logarithm as the anti-exponential.
Euler's constant e is the anti-log: $log(e^x) = x$.
Note that $log = log_e = ln$.
The same is true for logarithms of other bases:

$$log_{10}(10^x) = x \ \text{ (e.g., } 1, 10, 100, 1000, ...)$$
$$log_2(2^x) = x \ \text{ (e.g., } log_2(2) = 1,\ log_2(4) = 2,\ log_2(8) = 3, ...)$$

Summarize r vs. r_d vs. λ

$$(1 + r_d) = \lambda = e^r$$

And since ln is the anti-exponential (i.e. $ln(e^x) = x$), we equivalently have

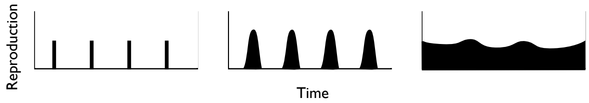
$$r = ln(\lambda) = ln(1 + r_d).$$

Thus another way to write population growth is...

$$N_t = \lambda^t N_0 = N_0 e^{rt}$$

...which is now ***exponential growth*** / *continuous reproduction*

Discussion of discrete vs. continuous as a spectrum depending on time-scale



Why emphasize this?
Empirical measurements of real populations are intrinsically discrete (we measure $N_0, N_1, N_2, ...$). Many empiricists therefore (inappropriately) default to discrete time models to estimate parameters like λ, even when biology of species exhibits continuous growth on time-scales being considered (for which estimating parameters like r is appropriate for subsequent inferences).

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(3) How to get instantaneous population-level growth rate from projection equation, $N_0 e^{rt}$?
That is, how do we show that:

$$\lim_{\Delta t \to 0} \left(\frac{\Delta N_t}{\Delta t} \right) = \frac{dN}{dt}$$

Need to take the derivative of $N_0 e^{rt}$ with respect to time t. Use Product Rule:

$$\frac{d(XY)}{dt} = \frac{d(X)}{dt} \cdot Y + X \cdot \frac{d(Y)}{dt}$$

"The derivative of a product is the sum of the product of the derivative of each term multiplied by the other term." Thus:

$$\frac{d(N_0 \cdot e^{rt})}{dt} = \frac{d(N_0)}{dt} \cdot (e^r)^t + N_0 \cdot \frac{d((e^r)^t)}{dt}$$

Note:
Derivative of a constant = 0
Derivative of $a^x = ln(a) \cdot a^x$.
Thus:

$$\begin{aligned}\frac{d(N_0 e^{rt})}{dt} &= 0 \cdot (e^r)^t + ln(e^r) \cdot (e^r)^t \cdot N_0 \\ &= r \cdot (e^r)^t \cdot N_0 \\ &= r \cdot e^{rt} \cdot N_0 \\ &= r \cdot N_0 e^{rt}\end{aligned}$$

Since $N = N_0 e^{rt}$ for any time t...

$$= rN = \frac{dN}{dt}$$

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(4) Could also go in opposite direction from $\frac{dN}{dt} \to N_0 e^{rt}$:

$$\begin{aligned}&\frac{dN}{dt} = rN \\ &\frac{1}{N}\frac{dN}{dt} = r \\ &\int_0^T \frac{1}{N}\frac{dN}{dt}\, dt = \int_0^T r\, dt \quad \text{(Think of T as a constant, and t in dt as a variable)} \\ &\int_0^T \frac{1}{N}\frac{dN}{dt} = rt|_0^T = r \cdot T - r \cdot 0\end{aligned}$$

Using $\displaystyle\int \frac{1}{x}\, dx = ln(x)$...

$$\begin{aligned}&ln(N(T)) - ln(N(0)) = rT \\ &ln\left(\frac{N(T)}{N(0)}\right) = rT \\ &\frac{N(T)}{N(0)} = e^{rT} \\ &N(T) = N(0)e^{rT}\end{aligned}$$

Q for class: Qualitative analysis of population *growth vs. decline*

Population change	λ	r_d	r
No change	1	0	0
Growth	> 1	> 0	> 0
Decline	< 1	< 0	< 0

Q: What are the units of r? A: 'Individuals *per individual* per time'
Q: What are the units of population growth rate, $\frac{dN}{dt}$? A: 'Individual per time'
Q: What are the units of per capita growth rate, $\frac{1}{N}\frac{dN}{dt}$? A: 'Individuals *per individual* per time'

Polynomial representation of $\frac{dN}{dt}$
Recall: population size as function of time as polynomial

$$N(t) = \sum_{n=0}^{\infty} \beta_n t^n = \beta_0 + \beta_1 t + \beta_2 t^2 + ...$$

Could also think of exponential growth as

$$\frac{dN}{dt} = f(N) = \sum_{n=0}^{\infty} \beta_n N^n$$
$$\text{with } \beta_0 = 0, \quad \beta_1 = r, \quad \beta_{n>1} = 0$$

It's a 'first-order' approximation.

Monod's nightmare

$$t = 20\ min., \quad N_t = 2N_0$$
$$N_t = N_0 e^{rt}$$
$$ln\left(\frac{N_t}{N_0}\right) = rt$$
$$ln(2) = rt$$
$$r = \frac{ln(2)}{t} = \frac{ln(2)}{20} \approx \frac{0.693}{20} = 0.035\% \text{ per minute}$$
