Exponential Growth: Part I

EFB 370: Population Ecology

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Goals

(concepts / buzzwords / jargon)

- The Population Equation
- Closed vs. Open Population
- Unconstrained (density independent) Growth
- Geometric Growth = Exponential Growth
- Discrete Time vs. Continuous Time Models
- Difference Equations vs. Differential Equations
- Population growth parameters:
  - continuous / discrete / per capita / per unit time
- Amazing properties of exponential and log.

Suggested reading

- Gotelli: Chapter 1 (first half)
- Neal: Chapter 4

Meet … *Enhydra lutris*

The largest …

- **Mustelid**

The smallest …

Marine mammal

By far the furriest …

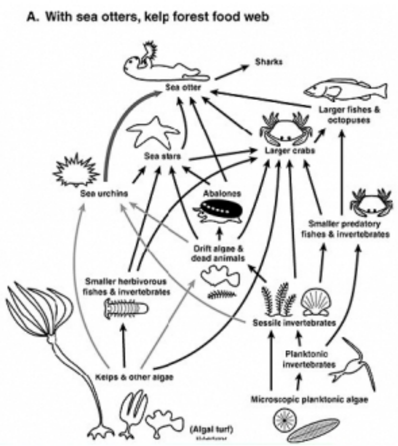
Guess how may hairs / sq. inch ?
(*Hint, humans are born with ~100,000 TOTAL.*)

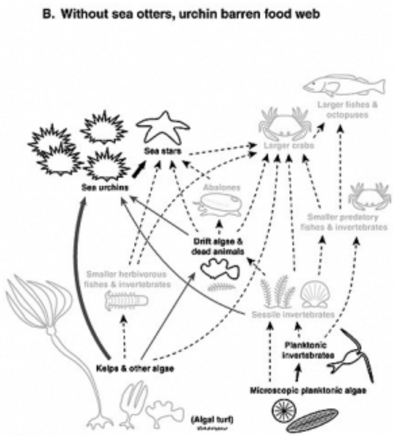
1,000,000

Sea otters: Range

Littorally the entire North Pacific

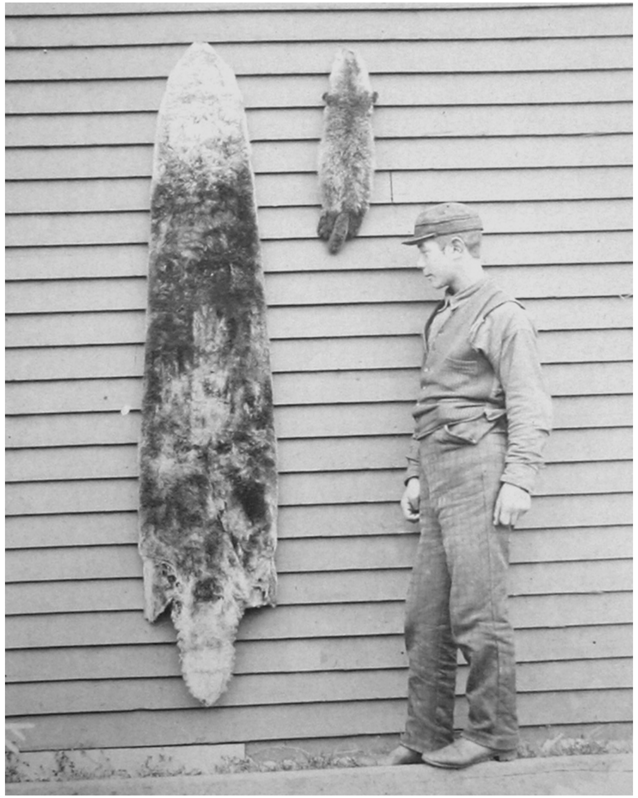
Sea otters: Keystone Species





(Estes et al. 1974)

Sea otters: Furriness > Cuteness

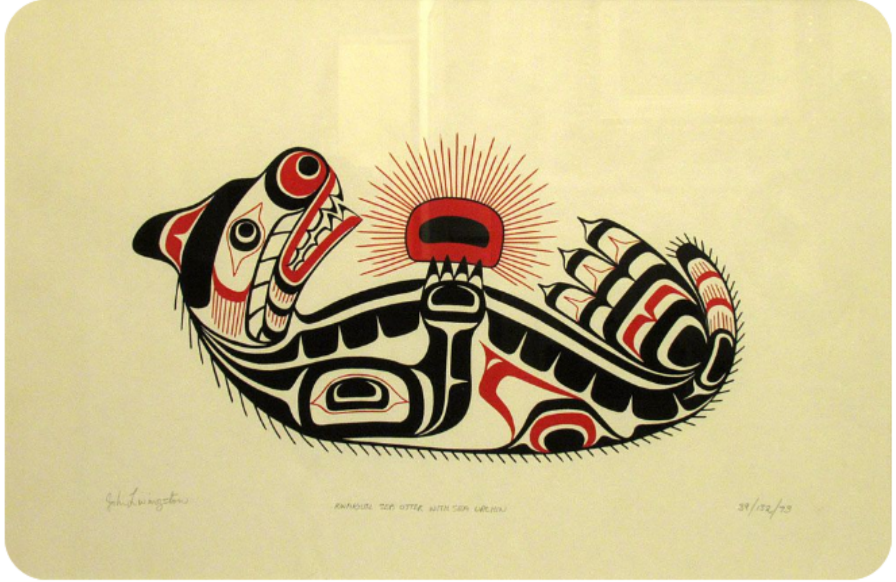


- Fur trade (Russian -> British -> American) leads to near **extirpation** across the entire range.
- **> 300,000 in 1740 … < 2,000 in 1900**.
- Displacement and indenturing of Indigeneous fishermen (esp. Aleut)

> *… the rush for the otters' "soft gold" was a predictable boom and bust … a cautionary example of unsustainable resource use, and a socioeconomic driver of Western — mainly American — involvement in the Pacific region,* (Loshbaugh 2021)

Sea otters: Not totemic

> … a sea otter hunter who was “lazy, spiteful, malicious or disregarded the teaching of the elders” would find his prey “cavorting around his baidarka … teas[ing] and splash[ing] him with water.” *(Innokentiy Venianimov, 1840)*



art by John Livingston

… but culturally significant

See: https://www.youtube.com/watch?v=ZyYH4KBHKU4

across N. Pacific …

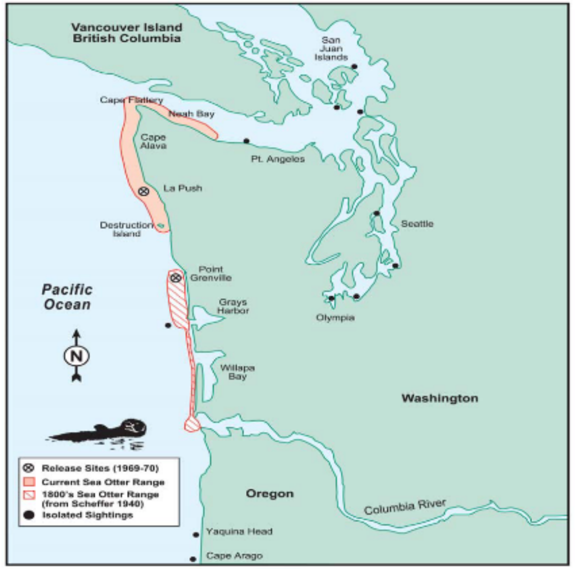
culture	name
Ainu	Esaman
Koryak	Kalan (also Russian)
Aleut	Chngatux
Alutiiq	Arhnaq

culture	name
Tlingit	Yáxwch’
Haida	Ku
Nuu chah nulth	Kwak̓aƛ
Siletz	Elakha

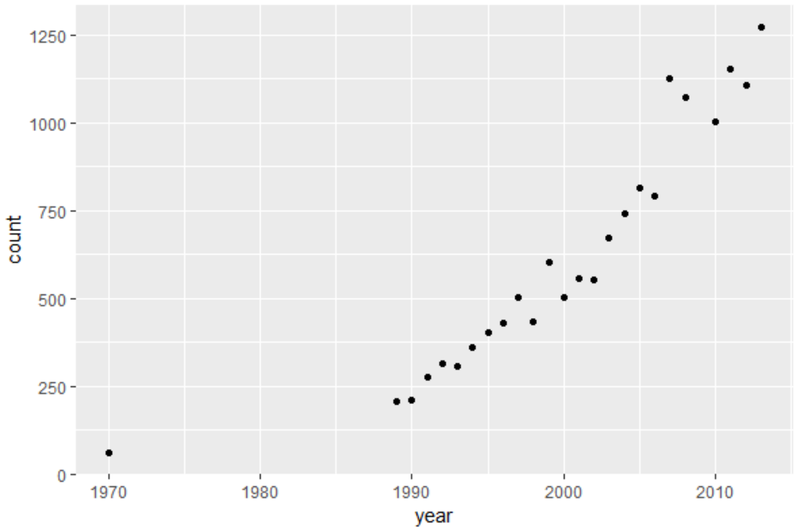
Sea otter reintroduction: Pacific NW

Remnant populations from Aleutian Islands … released in OR, WA, BC and SE-AK 1969 – 1972.

Sea otter reintroduction: Washington State ...



1970: 60 otters



2010's: over 1000

Successful!

Population ecology is all about ...

$$N$$

but where? when?

Here! Now! ..

$$N_t$$

but how many were there?

That many, then Δt ago!

$$N_t = N_{t-\Delta t} + \Delta N$$

slight rearrangement:

$$N_{t+1} = N_t + \Delta N$$

For now, $\Delta t = 1$, i.e. it's the discrete unit that we measure population change. VERY TYPICALLY - whether because of biology or field seasons:

$$\Delta t = 1 \text{ year}$$

.

How does population change?

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

Birth

Death

Immigration

Emigration

Assumption 1: no one's getting on or off the bus

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

Birth

Death

~~Immigration~~

~~Emigration~~

This is a **closed** (vs. **open**) **population** ...

Assumption 2: the important one

The number of *Births* and *Deaths* is proportional to *N*.

$$N_{t+1} = N_t + bN_t - dN_t$$

What does that mean?

- Every female gives birth to the same number of offspring?
- Every female has the same *probability* of giving birth?
- Every female has the same *probability* of giving birth to the same *distribution* of offspring?

- A fixed proportion of all individuals dies?
- Every individual has the same *probability* of dying?
- the *distribution* of probabilities of dying is constant?

Some math ....

Define

$$r_0 = b - d$$

r_0: **discrete growth factor**,

$$N_{t+1} = N_t + r_0 N_t$$

$$N_{t+1} = (1 + r_0)N_t$$

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

λ is **rate of growth (or decrease)**

- If $d > b$, $\lambda < 1$.
- If $b > d$, $\lambda > 1$.

Cranking this forward

$$N_{t+1} = \lambda(N_t)$$

$$N_{t+2} = \lambda(N_{t+1}) = \lambda^2 N_t$$

$$N_{t+3} = \lambda^3 N_t$$

Solution:

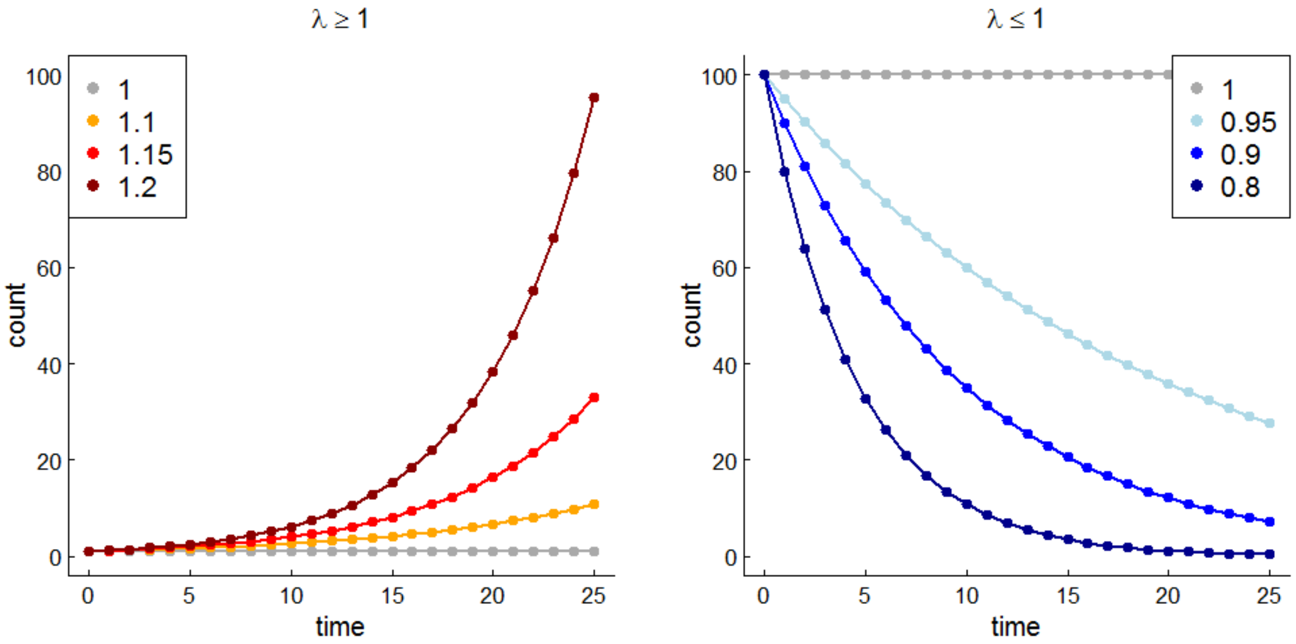
$$N_{t+y} = \lambda^y N_t$$

or

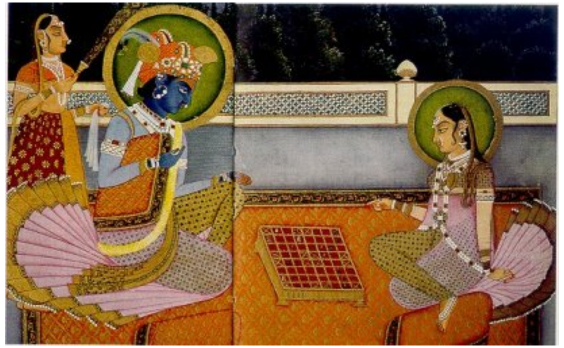
$$N_t = \lambda^t N_0$$

Geometric (same as ***Exponential***) growth.

Some examples



How fast is exponential/geometric growth?

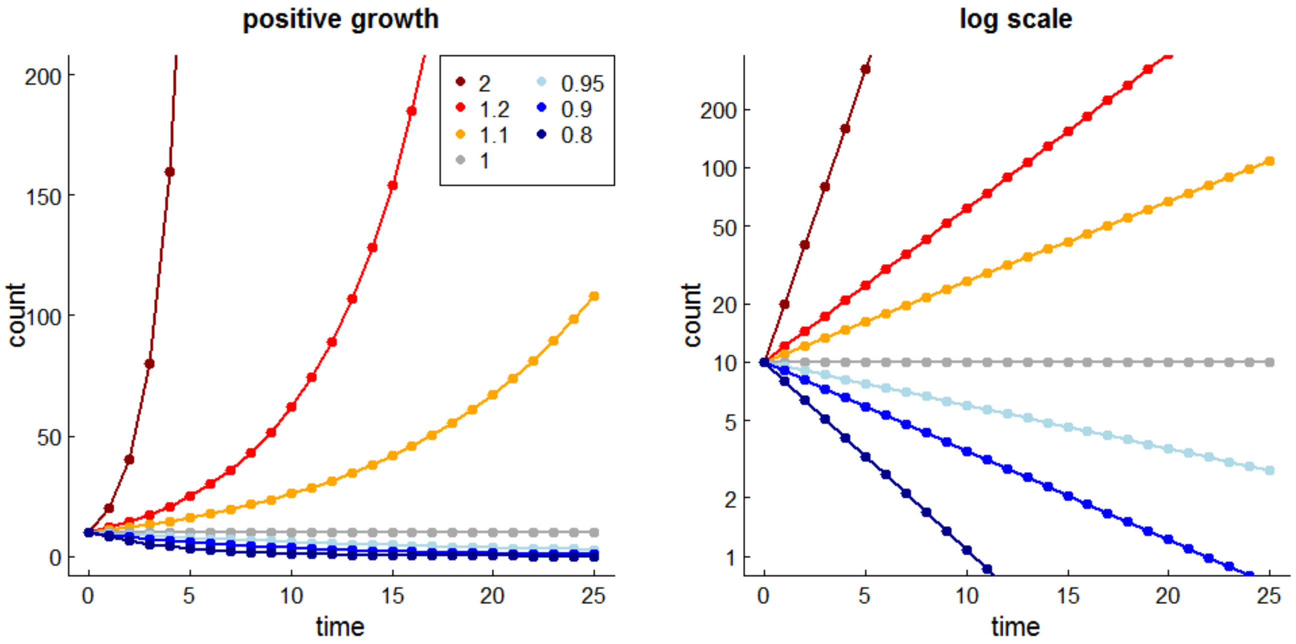


Legend says the inventor of chess (in India) so delighted the raja, he was offered anything he wanted.

Inventor said, not much. One grain of rice on one square, 2 on the next, 4 on the next and so on till the board is filled.

Not only is there not enough rice in India to fill such a chessboard, **there are not enough atoms on earth**.

Note what the log-scale does



Estimating some rates ... discrete

The amazing thing is, if you have an equation "solved", you only need 2 points on the curve to compute.

Let's use the discrete equation:

$$N_{t+y} = \lambda^y N_t$$

$$1000 = 60 \times \lambda^{40}$$

$$16.7 = \lambda^{40}$$

$$2.81 = 40 \times \log(\lambda)$$

$$0.07025 = \log(\lambda)$$

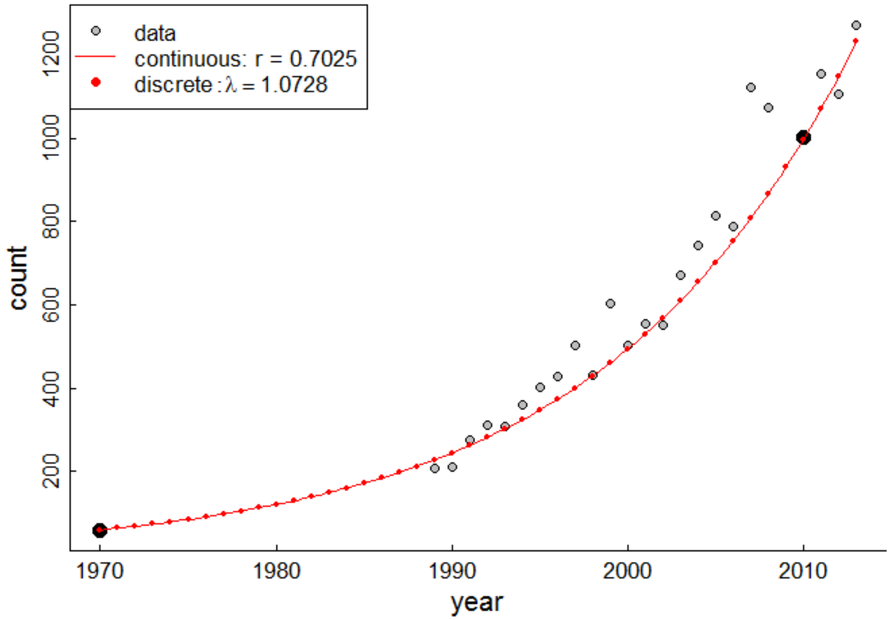
$$\lambda = \exp(0.07025) = 1.0728$$

i.e. population increase about

$$7.28\%/\text{year}$$

.

Washington sea otter fit to data (7.025% discrete growth)



This is an EXCELLENT fit

but why isn't it *perfect*?

What are some potential sources of **variation**?

Discrete Model to Continuous Model

Let's do some trickery, starting with:

$$N_{t+1} = (1 + r_0)\, N_t$$

$$N_{t+1} - N_t = r_0 N_t$$

$$N_{t+\Delta t} - N_t = r_{\Delta t} N_t$$

$$\lim_{\Delta t \to 0} \frac{\Delta N}{\Delta t} = \lim_{\Delta t \to 0} \frac{r_{\Delta t}}{\Delta t} N$$

Magically define:

$$\frac{r_\Delta}{\Delta t} = r$$

and rewrite Δ as d:

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

This is a ***differential*** (vs. difference) equation

Solve this:

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

where:

$$N(t=0) = N_0$$

Integration is fun! (*but you don't need to know how to do this*)

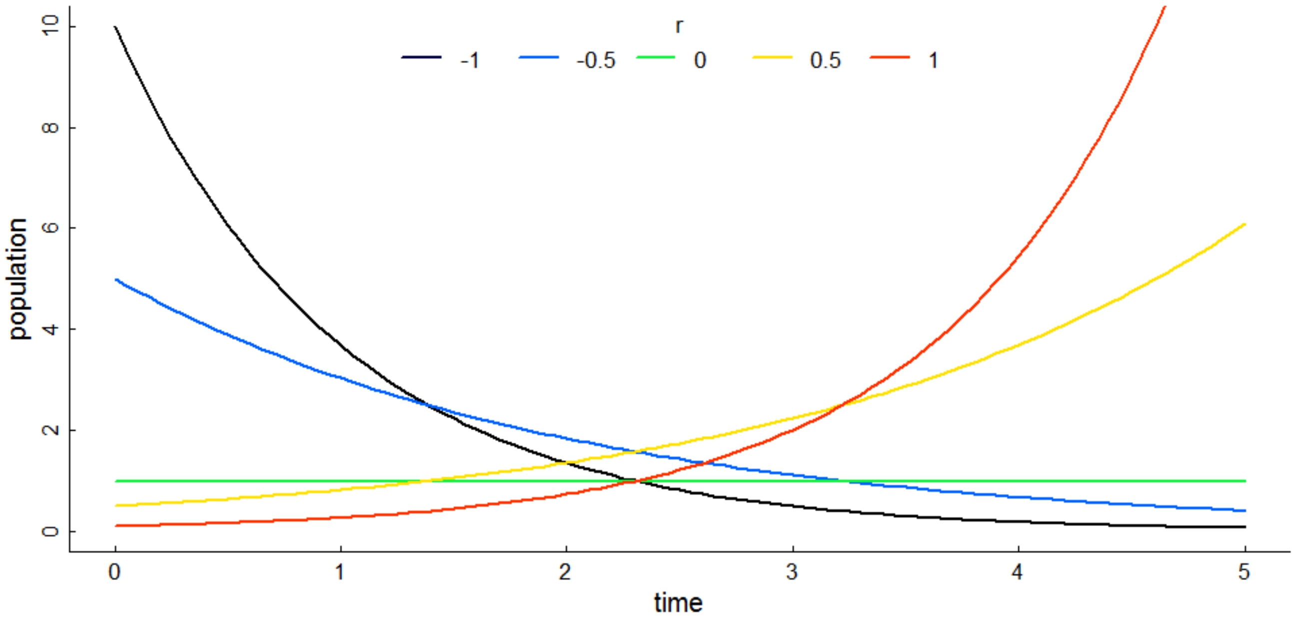
$$\begin{aligned}
\frac{1}{N} dN &= r dt \\
\int_{t'=t_0}^{t} \frac{1}{N(t)} dN &= \int_{t'=t_0}^{t} r dt \\
\log(N) &= rt + C_0 \\
N &= e^{rt+C_0}
\end{aligned}$$

Solution:

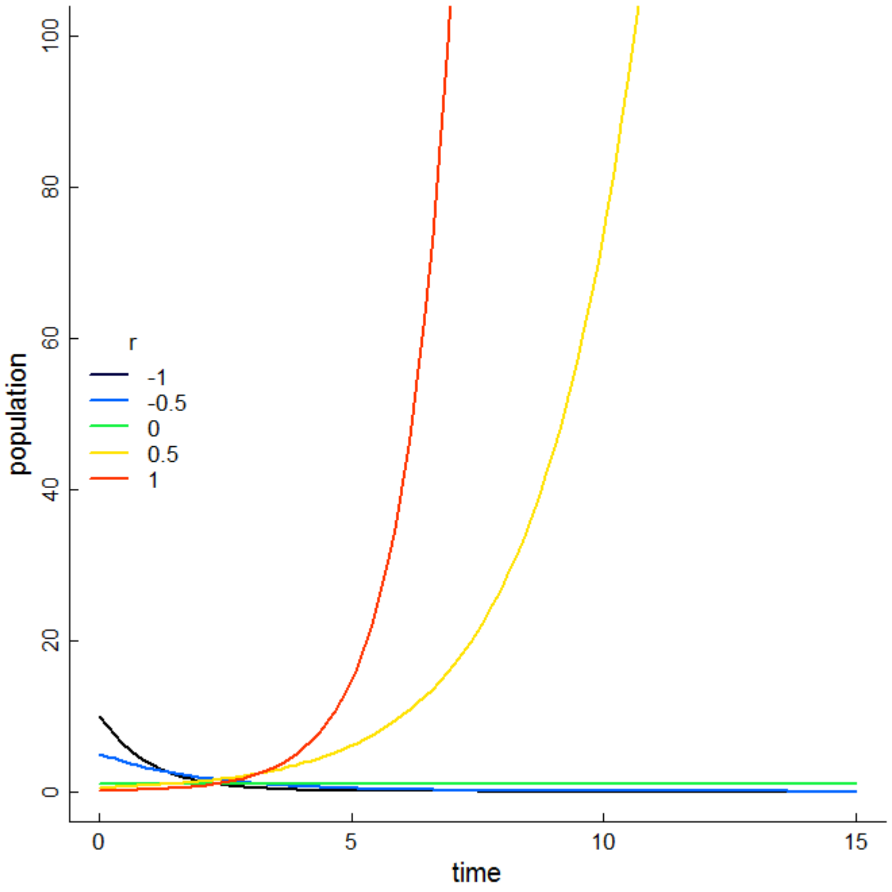
$$N(t) = N_0 e^{rt}$$

> **Incredibly Interesting And Important Fact:** The exponential function is the ONLY function whose derivative is proportional to itself.

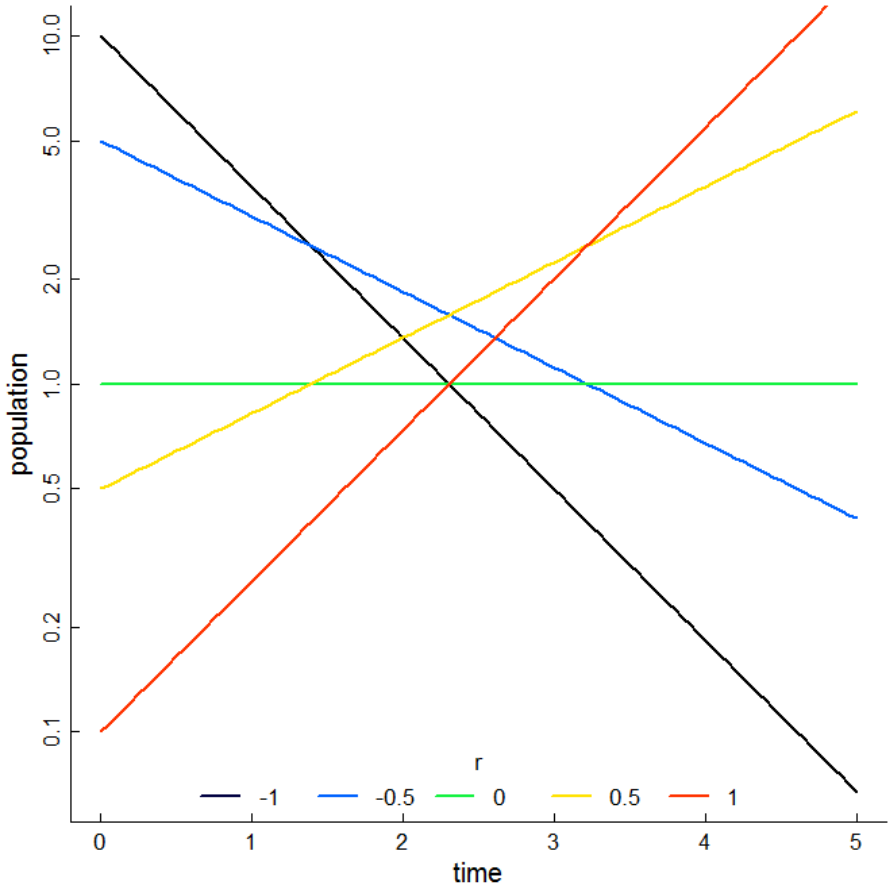
Some examples



Note crazy fast growth



and how straight on a log-scale



Discrete vs. Continuous Modeling

Difference equations

$$N_{t+\Delta t} - N_t = \lambda_{\Delta t} N_t$$

think of *absolute change*

Pros:

- Reflects (often) biological reproduction patterns, practical sampling schedule (esp. annual)
- Intuitive

Cons:

- Depends on discretization timescale
- Surprisingly difficult to analyze

Differential equations

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

think of *rates* (change/time).

Pros

- Easier "elegant" mathematical analysis
- Scales nicely

Cons

- Unbiological
- Unintuitive

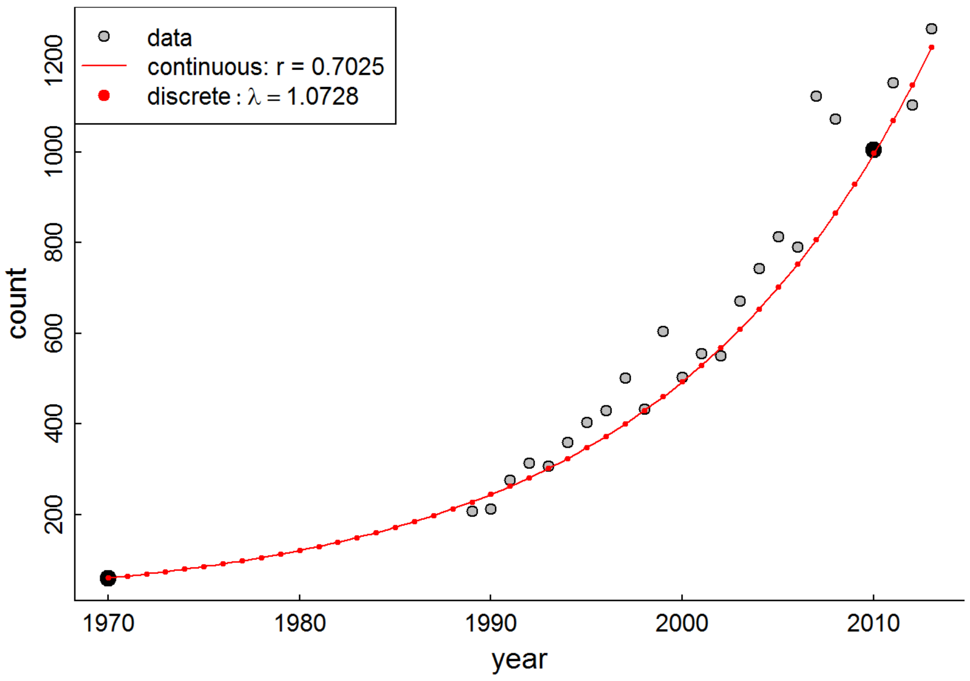
Estimating some rates ... continuous

Let's use the continuous equation:

$$
\begin{aligned}
1000 &= 60 \times e^{40\,r} \\
16.7 &= e^{40\,r} \\
2.81 &= 40 \times r \\
r &= 0.07025
\end{aligned}
$$

Intrinsic growth rate = 0.07025.

Washington sea otter fit to data



Note: dots for **discrete**, lines for **continuous** ...

but really there is NO difference in the two curves

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How long does it take for a population to double?

solve for doubling time t_d

Continuous:

$$2N = Ne^{rt_d}$$

$$\log(2) = rt_d$$

$$t_d = \log(2)/r$$

Discrete:

$$2N = N\lambda^{t_d}$$

$$\log(2) = \log(\lambda)t_d$$

$$t_d = \log(2)/\log(\lambda)$$

Sea otter population doubles in ~10 years.

Sea otter references

- J. A. Estes, J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. Science 185, 1058–1060. (link)
- Loshbaugh S. 2021. Sea Otters and the Maritime Fur Trade. In: Davis R.W., Pagano A.M. (eds) *Ethology and Behavioral Ecology of Sea Otters and Polar Bears. Ethology and Behavioral Ecology of Marine Mammals.* (link)
- Gilkinson, A.K., Pearson, H.C., Weltz, F. and Davis, R.W., 2007. Photo-identification of sea otters using nose scars. *The Journal of Wildlife Management*, 71(6), pp.2045-2051. (link)
- Veltre, D.W. *Unangax̂: Coastal People of Far Southwestern Alaska*. (link)

If you want to disabuse yourself of "sea otters are cute" - read about why the females have nose scars.