Exponential Growth Part III: Randomness and Stochasticity

EFB 370: Population Ecology

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Goals (concepts / buzzwords)

- **I. Random variables:**

    - mean / variance / standard deviation / distributions / expected value

    - Binomial and Normal distributions
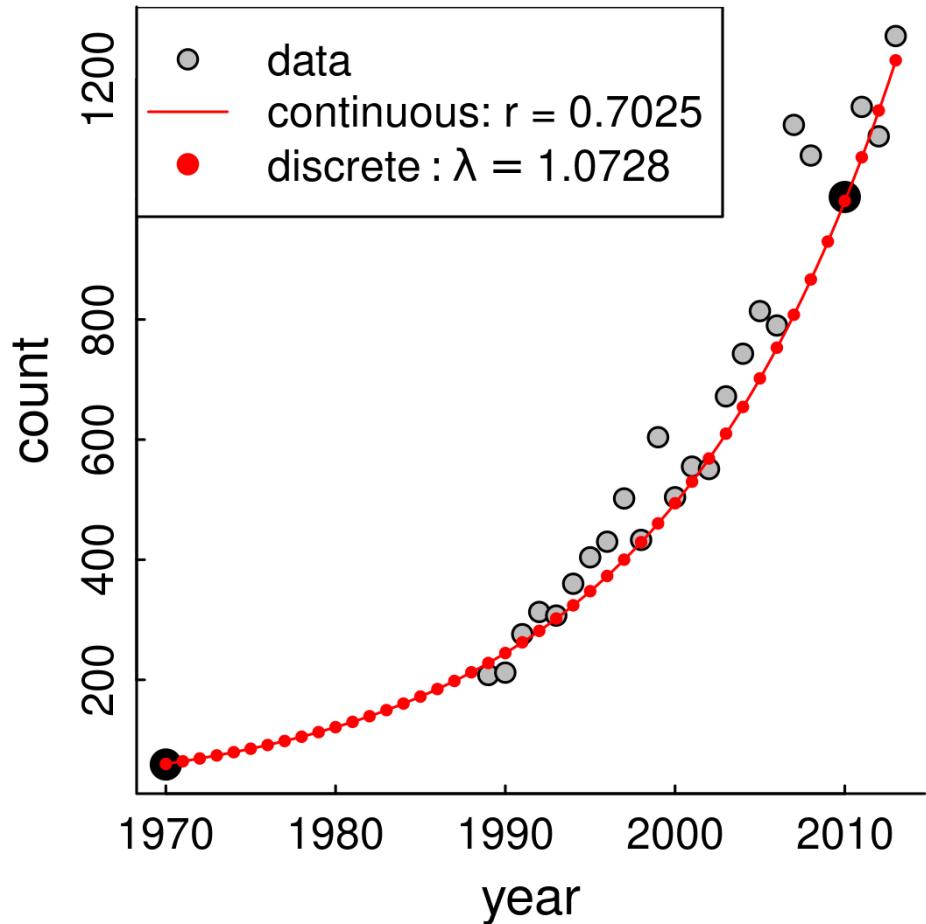
- II **stochastic** = randomness in time

    - **demographic stochasticity** = randomness in individual processes

    - **environmental stochasticity** = randomness affecting populations

Suggested reading:

- Gotelli: Chapter 1 (second half)
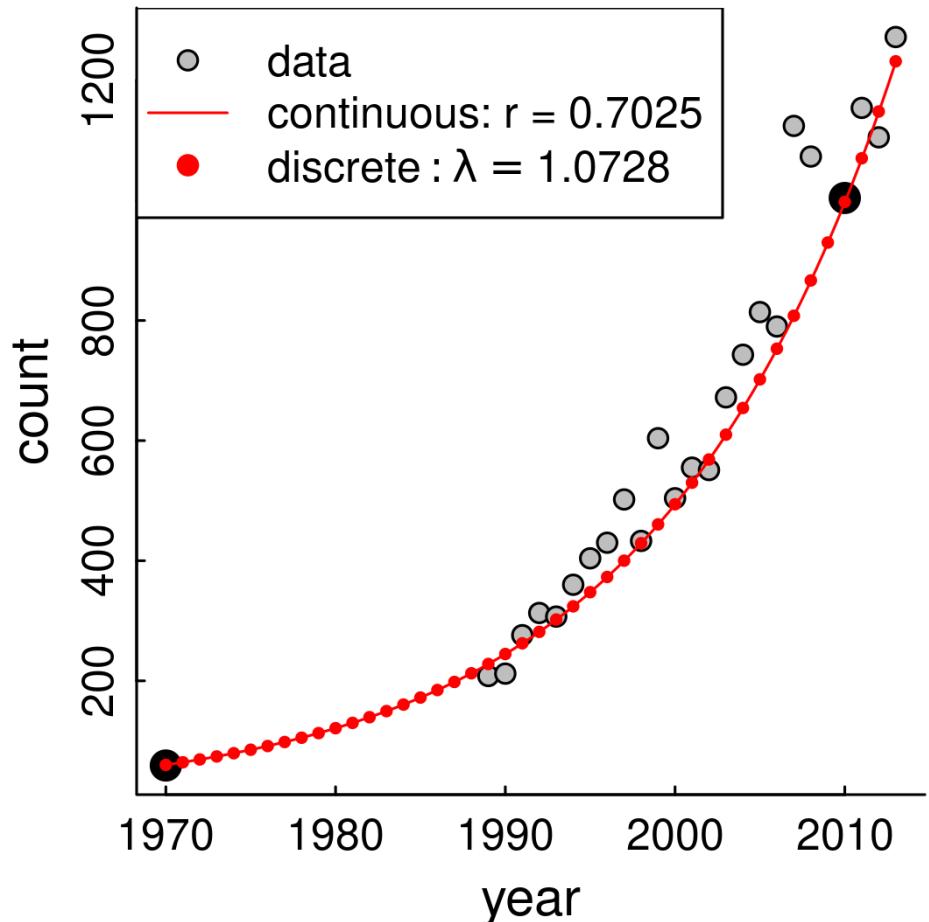
If the exponential model is so tidy ... why isn't it *perfect?*

Because ... *randomness!(?)*

What are some potential sources of "randomness" in the sea otter population process?

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*What are some potential sources of "randomness" in the sea otter population process?*

- Environment good / bad affecting all animals ...
- Randomness in birth-death affecting individual animals ...
- Unexpected immigration / emigration ...
- Observation error ...

Brief Intro to Random Variables

Easiest problem in boring arithmetic:

$$1 + 1 = 2$$

Easiest problem in random arithmetic:

 $+$ $= ?$

One coin flip is Random

Random variables have *possible events* associated with *probabilities*.

event	numeric	probability
	0	1/2
	1	1/2
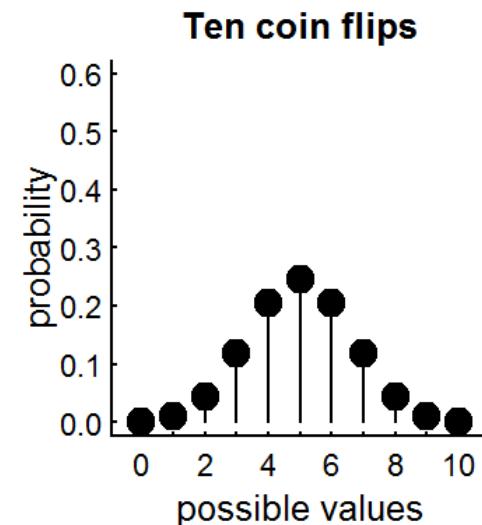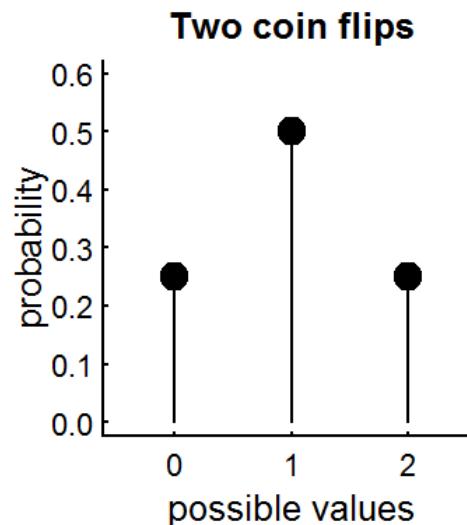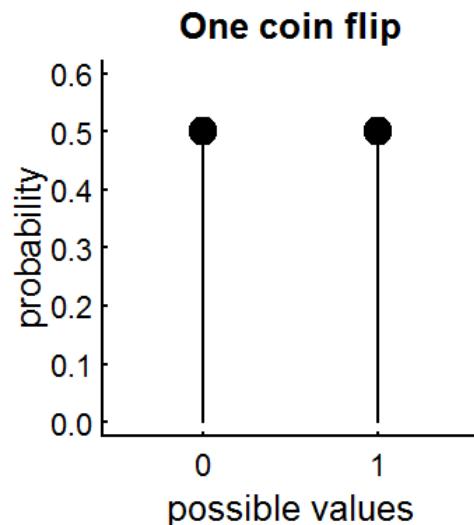
# Two coin flips is also Random

Random variables have *possible events* associated with *probabilities*.

event	numeric	probability
	0	1/4
OR	1	1/2
	2	1/4

Random variables...

... are described by **Probability Distributions**. **Probability Distributions** have **names** and **parameters** that describe the distribution.

| **One flip**	=	$X \sim Bernoulli(p = 1/2).$
Two flips	=	$X_1 + X_2 = Y \sim Binomial(p = 1/2, n = 2).$
n **flips**	=	$\sum_{i=1}^{n} X_i = Y \sim Binomial(p = 1/2, n = n).$
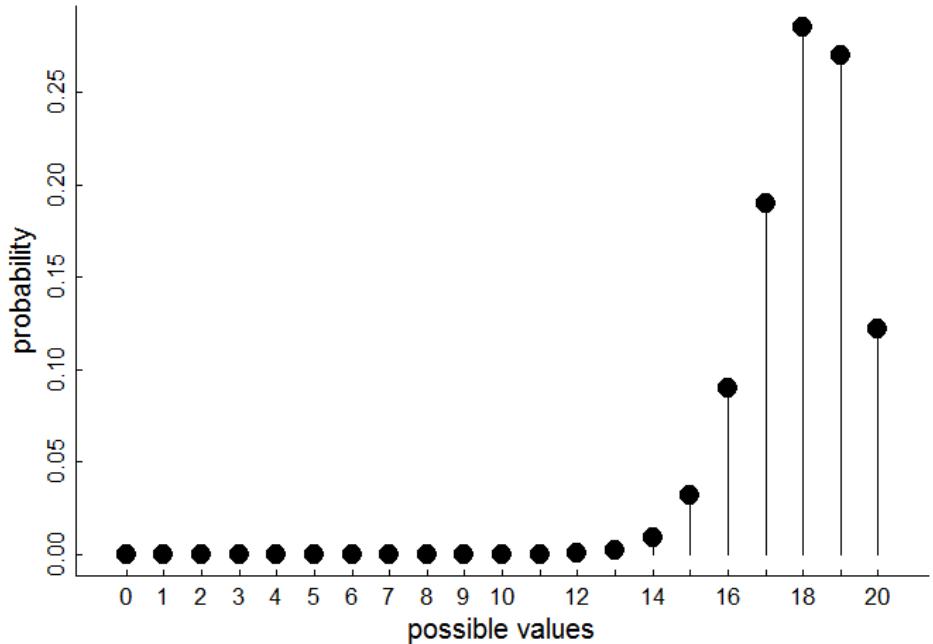
A bit about the binomial distribution

$X \sim Binomial(n, p)$ describes the sum of n random events, each of which has probability p.

Pop ecology example:

If you have 20 sea otters ($X_t = 20$), each with a 90% probability of survival / year, how many next year?

Answer: A random variable with distribution: $X_{t+1} \sim Binomial(n = 20, p = 0.9)$

Key questions about a random variable:

$$X_{t+1} \sim Binomial(n = X_t, \ p = p_{surv})$$

Q1. How many would you *expect* to survive?

$$E(X) = \mu_X = np = 0.9 \times 20 = 18$$

This value is the **Expectation** of the distribution: $E(X)$ or $\mu(X)$. It would be the *mean* value if you could repeat the experiment an infinite amount of times.

Q2. How much *variability* is there in this process?

$$SD(X) = \sigma_x = \sqrt{n\,p(1-p)} = 1.34$$
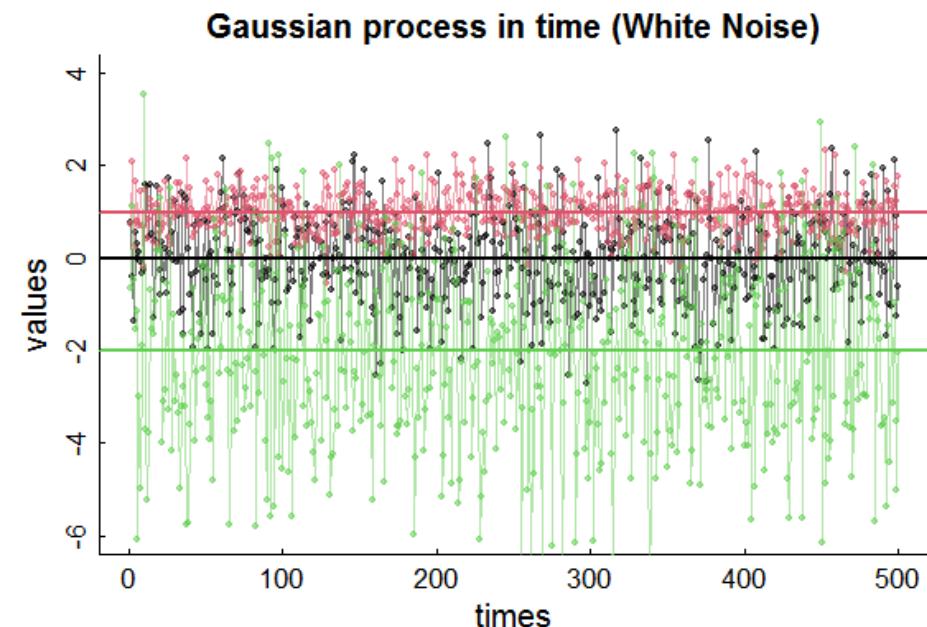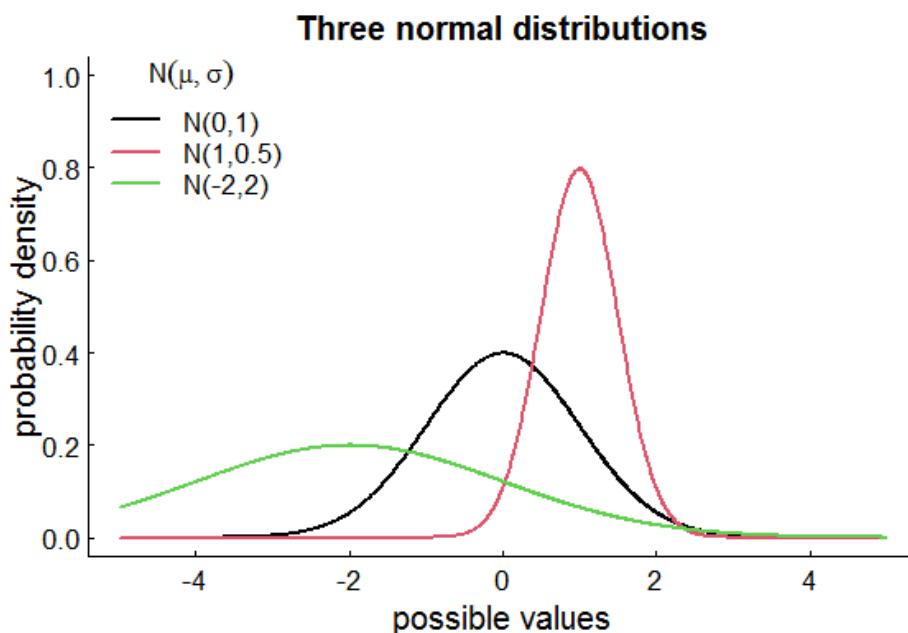
The **standard deviation** of a random variable: $SD(X)$ or σ_x quantifies how concentrated the distribution is around the *mean. Approximately* 95% of the probability is within 2 standard deviations.

Continuous random variables

There are a bunch. The most famous is the **Normal** or **Gaussian** distribution:

$$X \sim \mathcal{N}(\mu, \sigma)$$

It has two parameters: μ and σ with are - unsurprisingly - the *mean* (expectation) and *standard deviation* (spread) of the variable.

Once upon a time in Germany ....

Some probability distributions

We use these to **model** random processes:

name	notation	possible values	models	mean	standard deviation
Normal	$\mathcal{N}(\mu, \sigma)$	$(-\infty, \infty)$	bell-shaped	μ	σ
Exponential	$Exp(\lambda)$	$[0, \infty)$	random events	$\frac{1}{\lambda}$	$\frac{1}{\lambda}$
Poisson	$Poisson(\lambda)$	$[0, \infty)$	positive count data (e.g. births)	λ	$\sqrt{\lambda}$
Bernoulli	$Bernoulli(p)$	$[0, 1)$	binary outcomes (e.g. deaths)	p	$\sqrt{p(1-p)}$
Binomial	$Binomial(n, p)$	$[0, n)$	many binary outcomes	np	$\sqrt{np(1-p)}$

Demographic Stochasticity

- *Stochasticity* means: **Randomness** in **time**.

- *Demography* is the **Science of Population Dynamics**. Often it refers specifically to **births** and **deaths** (and **movements** ... but we're still looking at closed population).

- Individually, *all* demographic processes are stochastic. An individual has some *probability* of dying at any moment. An individual has some *probability* of reproducing at a given time.

Q: How important is *individual* randomness for a *population* process?

More specific Q: **What is the probability of extinction?**

Human Experiment with Life and Death

- 15 students

- Flip a survival coin.

  - If you die (**TAILS**) sit down, if you live (**HEADS**) stay standing

- Flip a reproduction coin.

  - If you reproduce (**HEADS**) call on another student to stand

What do we predict from this experiment?

Starting with N_t: expected number of survivors (S):

$$E(S) = p_s N_t$$

Expected number of new individuals (babies - B):

$$E(B) = p_b E(S)$$

New population equals survivals + new babies:

$$E(N_{t+1}) = E(S) + E(B) = p_s N_t + p_b \, p_s N_t = p_s (1 + p_b) N_t$$

So (in our coin flip example)
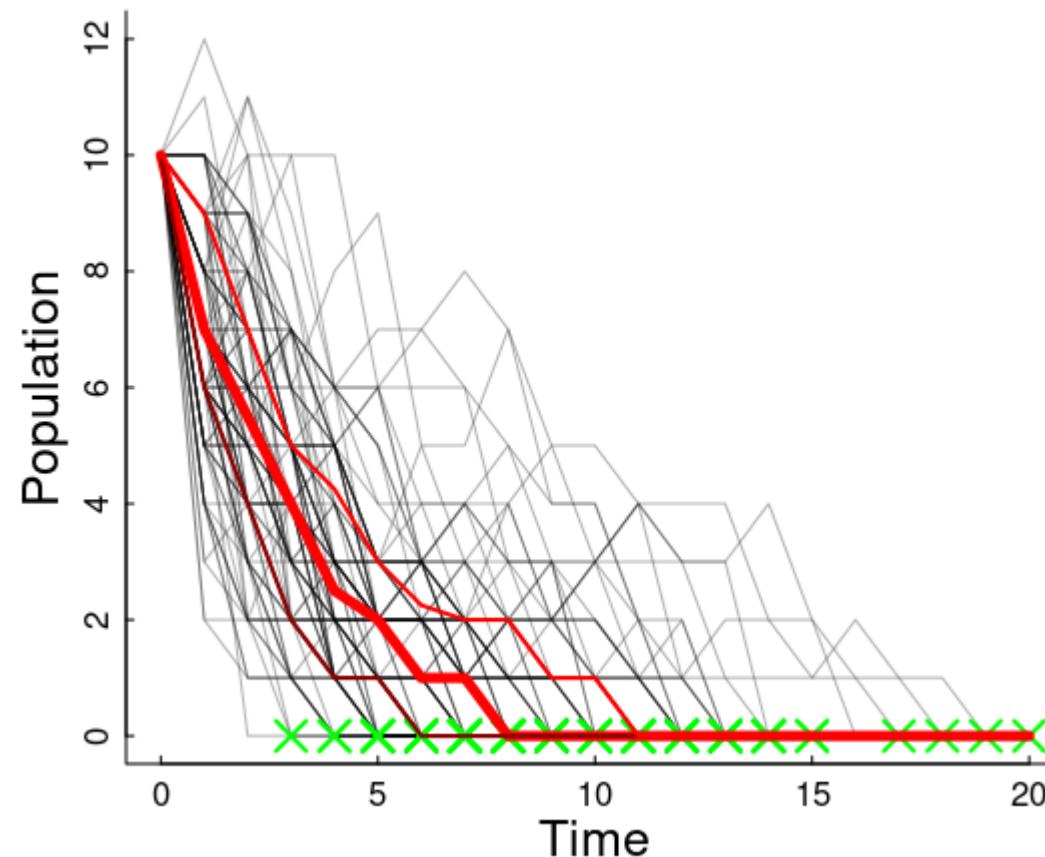
$$\widehat{\lambda} = p_s (1 + p_b) = 0.75$$

.

What does that mean for population growth!?

Cranking this experiment very many times.

Some predictions for a similar continuous model

Assume birth rate b and death rate d, and growth rate $r = b - d$.

The mean of the process is also exponential growth

$$E(N_t) = N_0 e^{rt}$$

If birth rate = death rate:

$$SD(N_t) \approx \sqrt{2N_0 b t}$$

Note, increases as square root of time. There's a somewhat more complex formula for births $\neq$ deaths.

More importantly:

$$P(extinction) = \begin{cases} \text{if } b > d; & (d/b)^{N_0} \\ \text{if } d > b; & 1 \end{cases}$$

Note that even when birth rate = death rate, $P(extinction) = 1$, i.e. eventual extinction is certain. This is very similar to the eventual probability of fixation for genetic drift.

Also, probability of extinction is lower for smaller N_0.

Environmental Stochasticity...

Some random aspect of the environment that influences r (whether via births or deaths or **both**) for the **entire population**.:

$$R \sim Dist(\mu_r, \sigma_r)$$

- μ_r is the *mean growth rate*
- σ_r is the *variability on the growth rate*

Can you think of some examples, e.g. for sea otters?

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Human Experiment

The **professor** IS the **environment**!

1. $$N_0 = 16$$

2. If the environment flips **Heads**, the population doubles.

3. If the environment flips **Tails**, the population halves.

Environmental Stochasticity: Analysis

This model can be written:

$$N_{t+1} = N_t \, 2^R$$

Where R is a random variable:

value	prob.
-1	1/2
+1	1/2

$$E(R) = \mu_r = 0$$

So population should not grow, on average.

$$E(N(r)) = N_0 e^{\mu_r t} = N_0$$

And:

$$SD(R) = \sigma_R = 1$$

- Are you doomed to extinction?
- Does this remind you of another process from earlier in class?

Experiment here: https://egurarie.shinyapps.io/StochasticGrowth

A stochastic population is a random variable!

$$N(t) \sim Dist(\mu_N(t), \sigma_N(t))$$

The mean / expectation is the same as for the exponential growth function, but with the mean growth rate substituted:

$$\mu_N(t) = N_0 e^{\mu_r t}$$

But the standard deviation of the function increases with time!
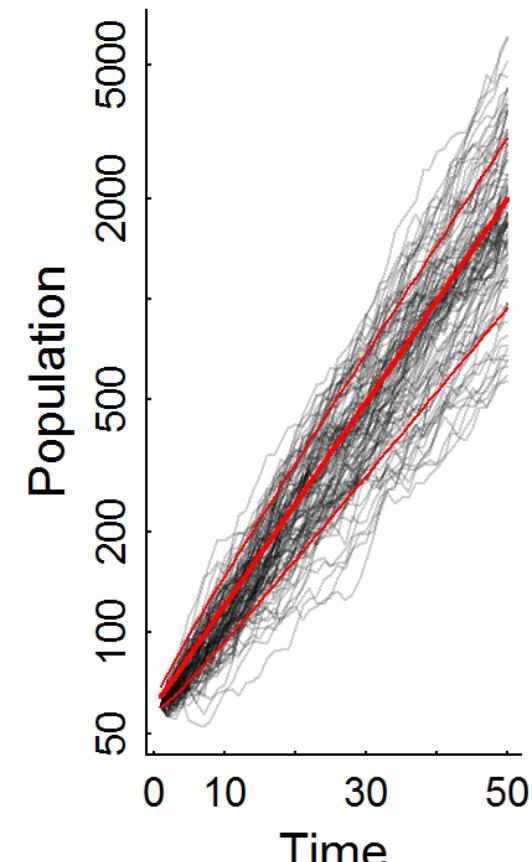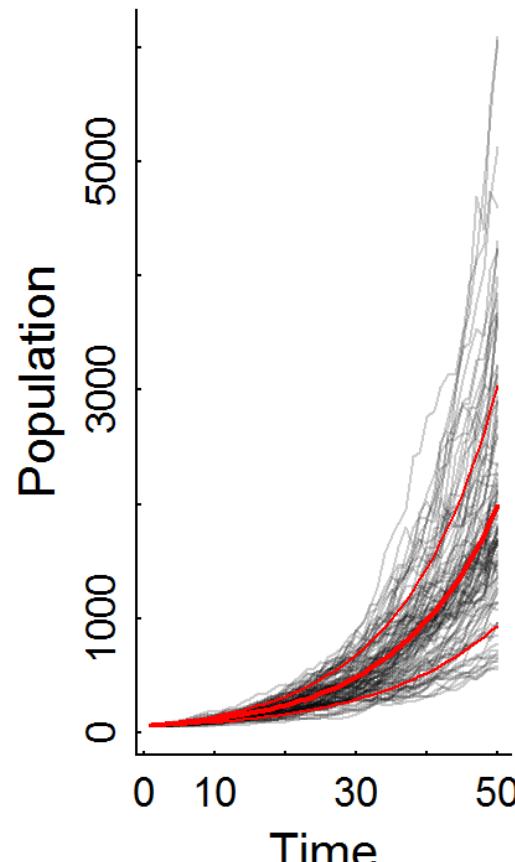
$$\sigma_N^2(t) \approx N_0 \, e^{\mu_r t} \sqrt{e^{\sigma_r^2 t} - 1}$$

Sea otter example, with $\mu_r = 0.07$ and $\sigma_r = 0.07$:
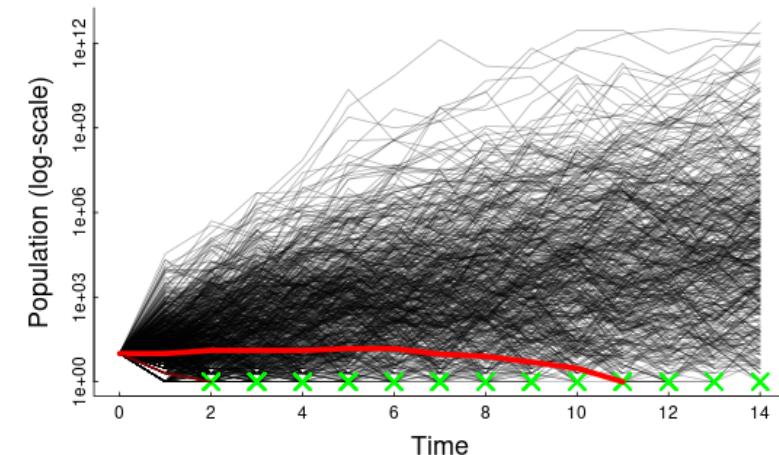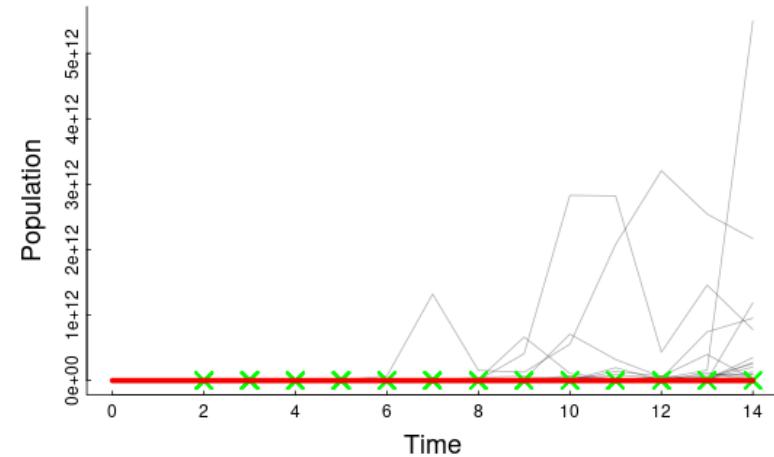
If things are TOO random that spells trouble!

According to theory, if:

$$\sigma_r > 2\mu_r$$

extinction is nearly certain - even if μ_r is positive and on average there is growth.

Experiment here:
https://egurarie.shinyapps.io/StochasticGrowth

Key Takeaways

1. Nature is a combination of **very complex** and **truly random**. So we have to get comfortable with randomness

2. **Demographic stochasticity** refers to **individual randomness**, and particularly effects **small populations**.

3. **Environmental stochasticity** affects **everyone similarly**, **big** or **small** populations, and too much randomness bodes ILL.