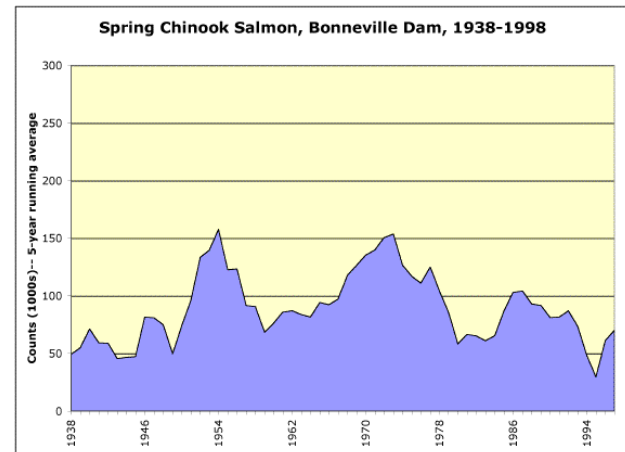
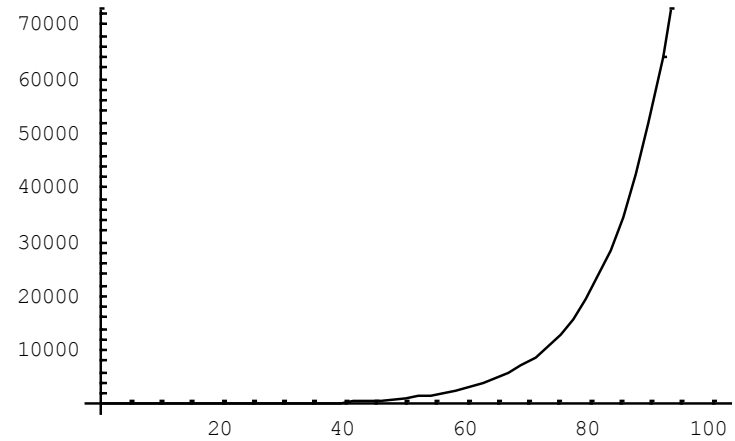


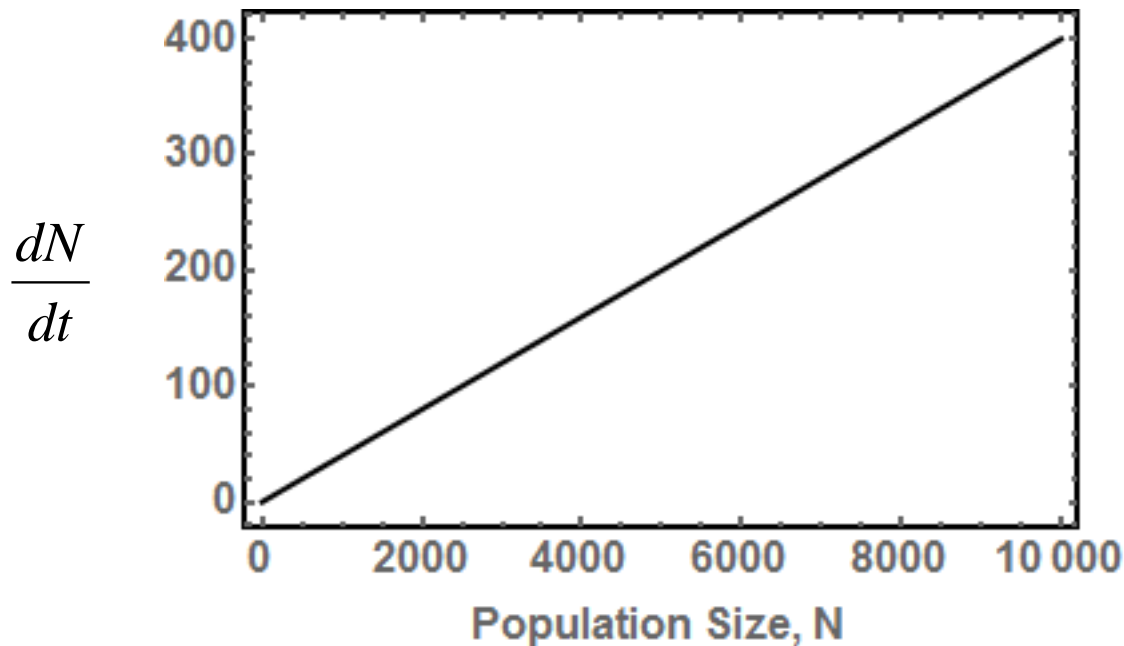
# Population growth

$$N_t = N_0 e^{rt}$$



# The simplest model of population growth

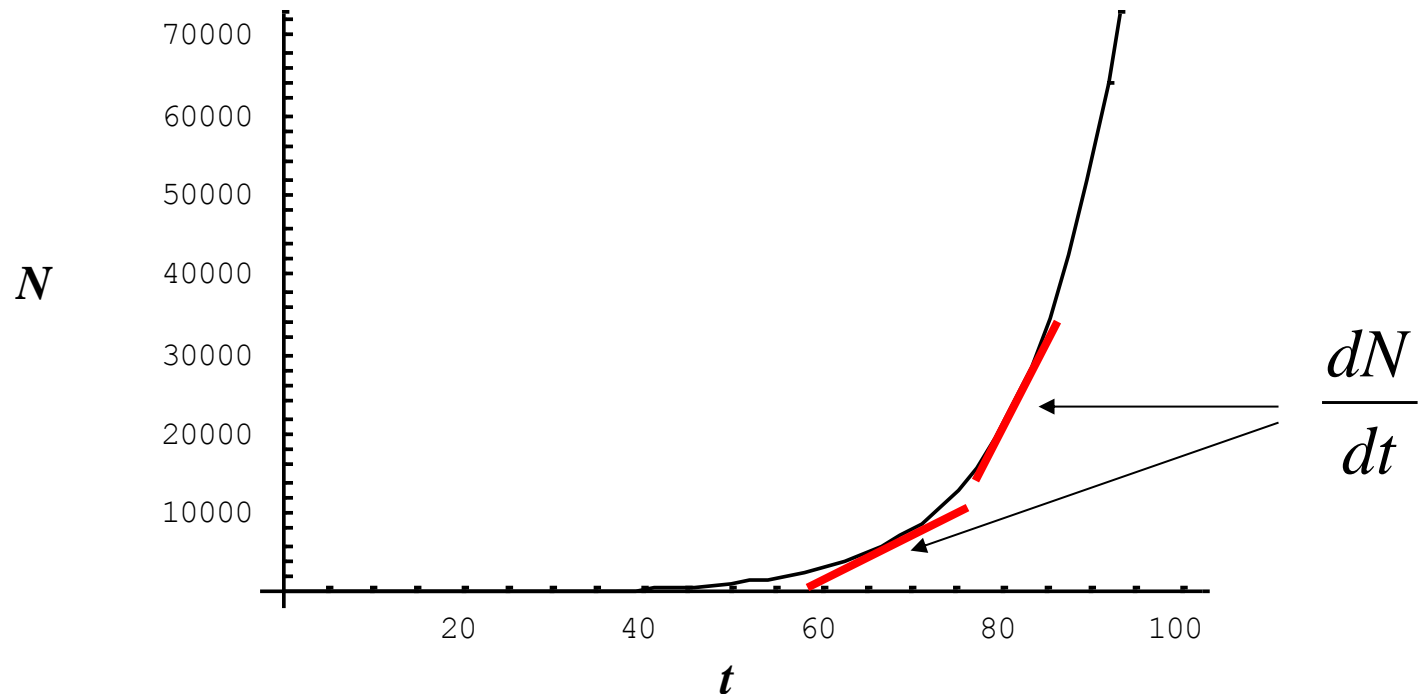
$$\frac{dN}{dt} = (b - d)N = rN$$



**What are the assumptions of this model?**

**We already saw that the solution is:**

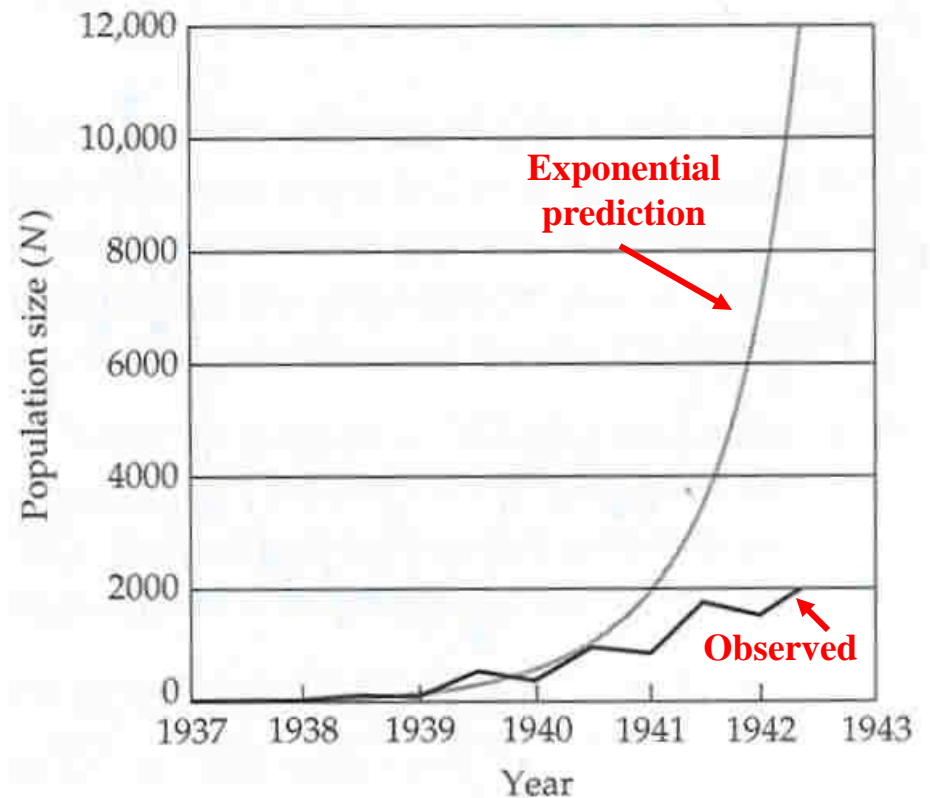
$$N_t = N_0 e^{rt}$$



**$r$  determines how rapidly the population will increase**

# A 'test' of the exponential model: Pheasants on Protection Island

- Abundant food resources
- No bird predators
- No migration
- 8 pheasants introduced in 1937



By 1942, the exponential model overestimated the # of birds by 4035

# Where did the model go wrong?

## Assumptions of our simple model:

1. No immigration or emigration
2. Constant  $r$ 
  - No random/stochastic variation
  - Constant supply of resources
3. No genetic structure (all individuals have the same  $r$ )
4. No age or size structure

# Stochastic effects

In real populations,  $r$  is likely to vary from year to year as a result of random variation in the per capita birth and death rates,  $b$  and  $d$ .

**This random variation can be generated in two ways:**

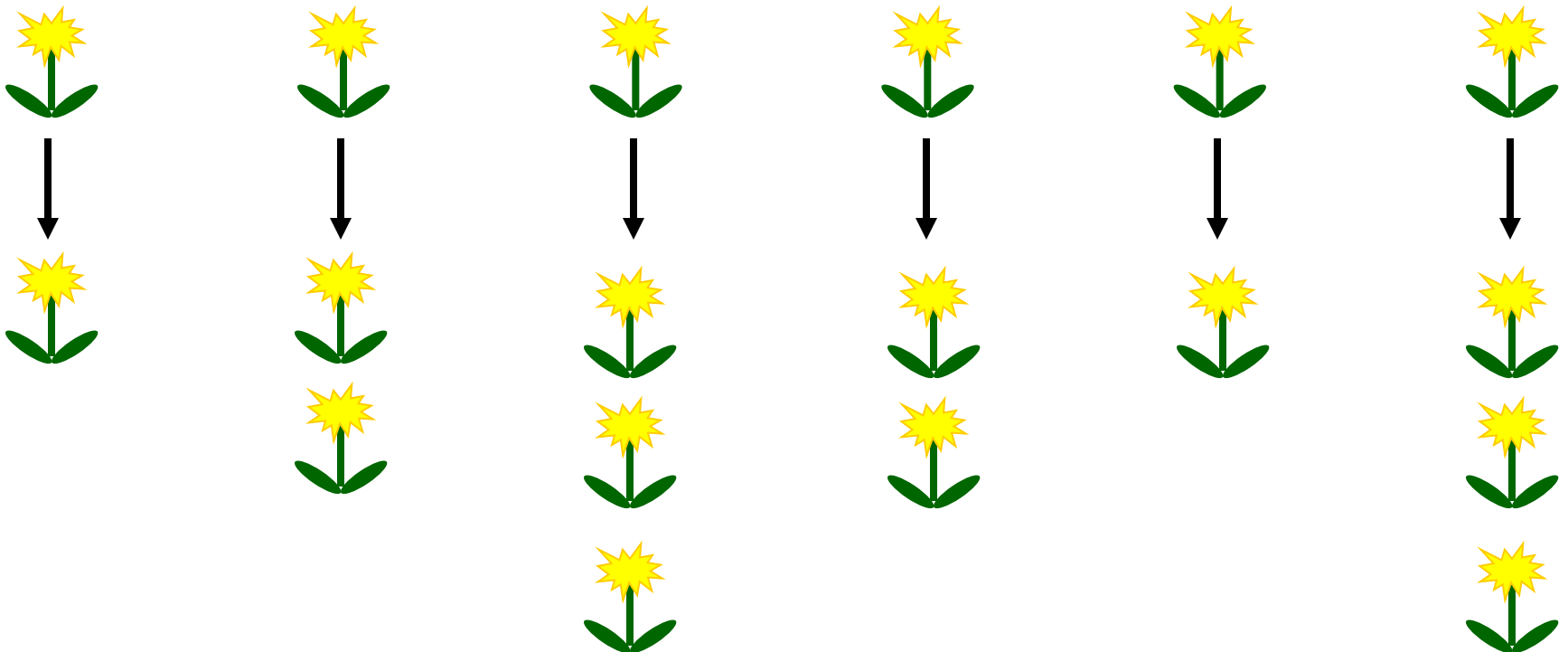
- 1. Demographic stochasticity – Random variation in birth and death rates due to sampling error in finite populations**
- 2. Environmental stochasticity – Random variation in birth and death rates due to random variation in environmental conditions**

# I. Demographic stochasticity

Imagine a population with an expected per capita birth rate of  $b = 2$  and an expected per capita death rate of  $d = 0$ .

In an INFINITE population, the average value of  $b$  is 2, even though some individuals have less than 2 offspring per unit time and some have more.

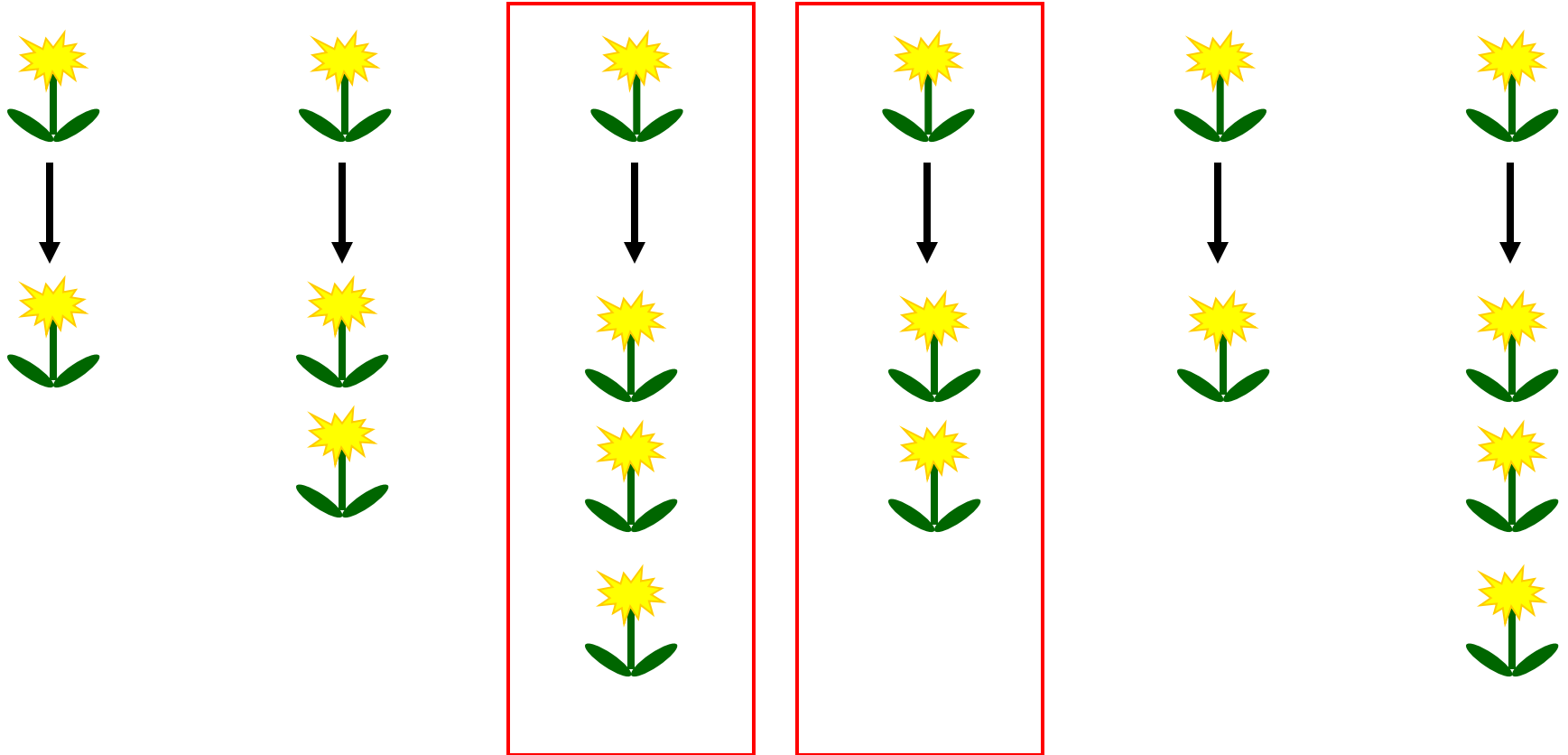
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# I. Demographic stochasticity

But in a **FINITE** population, say of size 2, this is not necessarily the case!

---



Here,  $b = 2.5$  (different from its expected value of 2) solely because of **RANDOM** chance!

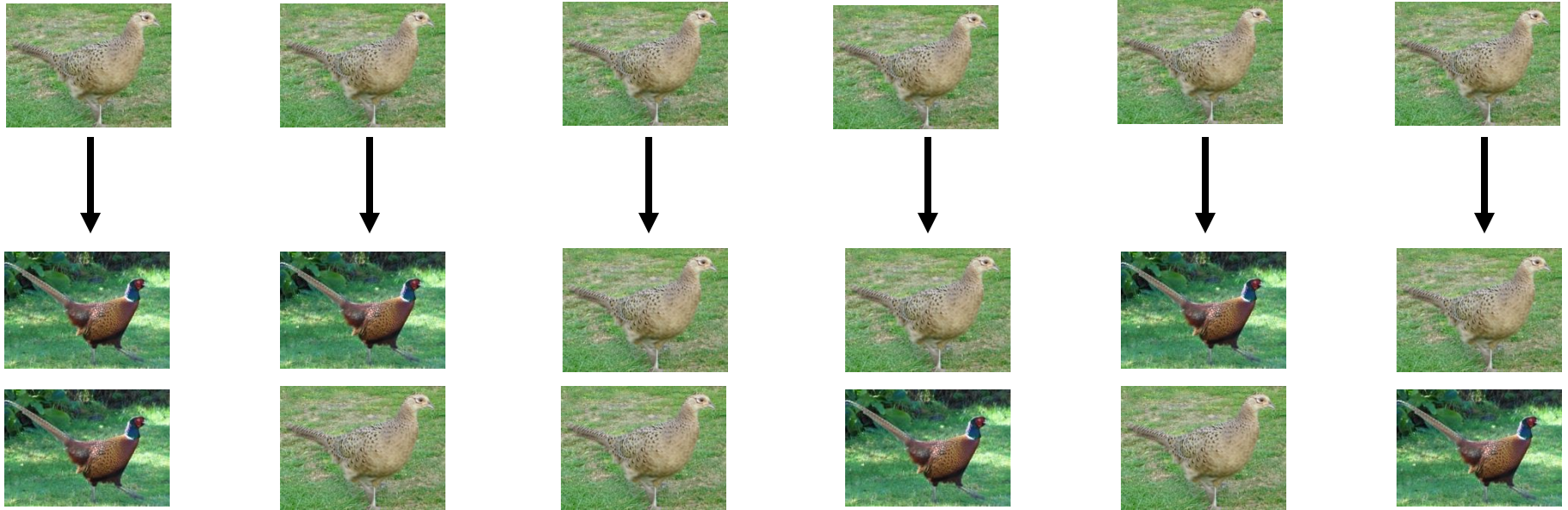


# I. Demographic stochasticity

Imagine a case where females produce, on average, 1 male and 1 female offspring.

In an INFINITE population the average value of  $b = 1$ , even though some individuals have less than 1 female offspring per unit time and some have more  $\rightarrow \Delta N = 0$

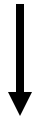
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# I. Demographic stochasticity

But in a FINITE population, say of size 2, this is not necessarily the case!

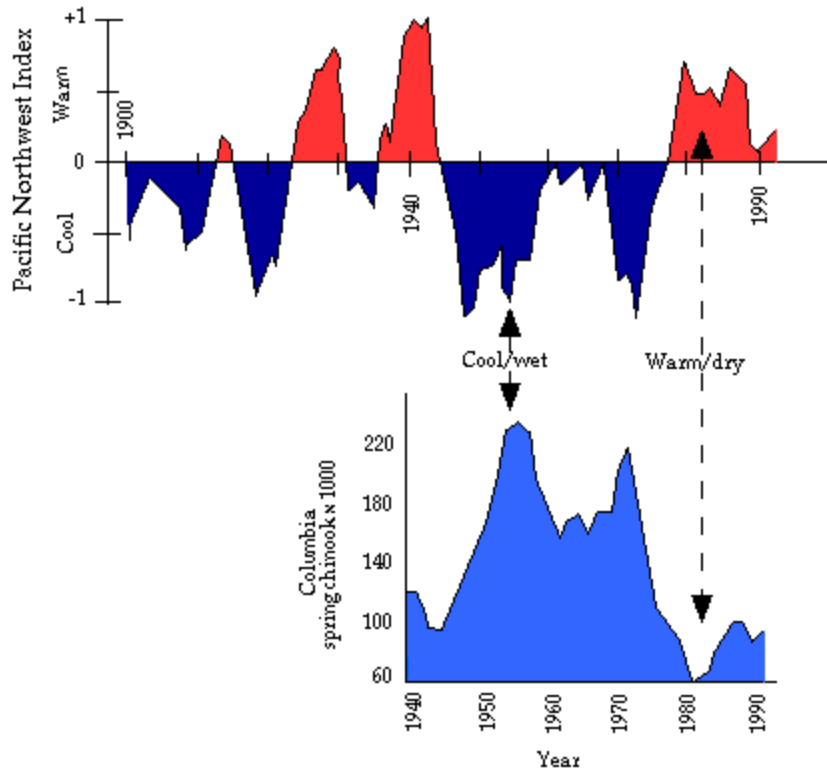
If the finite population  
were just these two



Here,  $b = .5$  (different from its expected value of 1) solely because of RANDOM chance!

## II. Environmental stochasticity

### Climatic Effects on Columbia River Chinook



Pacific Northwest Index and abundance of Columbia River upriver bright spring chinook track each other. Salmon and the PNI are 5 year running averages.

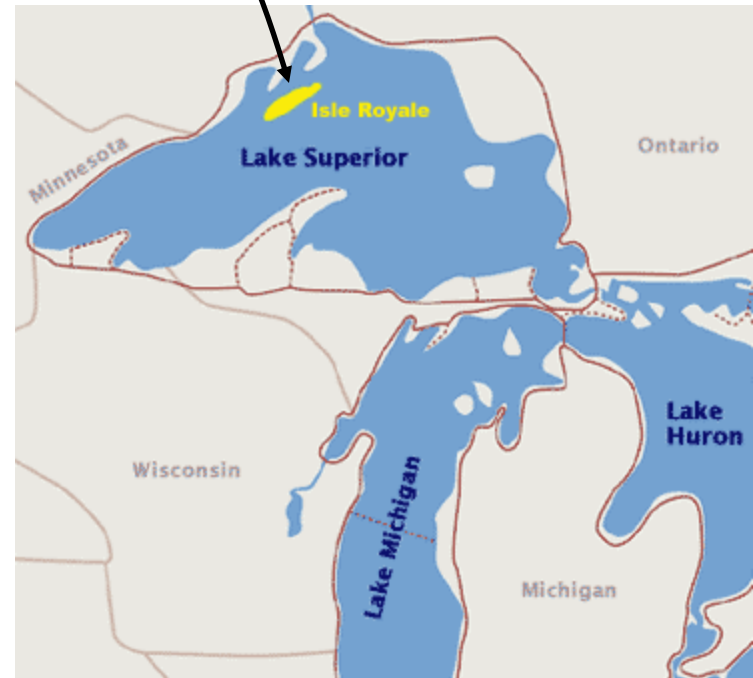
- $r$  is a function of current environmental conditions
- Does not require FINITE populations

Source:

Anderson, J.J. 1995. Decline and Recovery of Snake River Salmon. Information based on the CRiSP research project. Testimony before the U.S. House of Representatives Subcommittee on Power and Water, June 3.

# How important is stochasticity?

An example from the wolves of Isle Royale  
(Vucetich and Peterson, 2004)

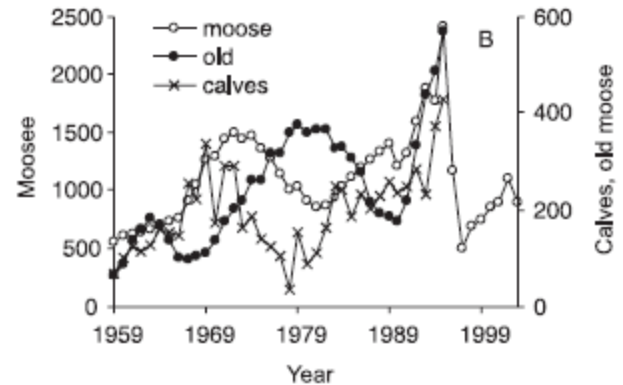


- **No immigration or emigration**
- **Wolves eat only moose**
- **Moose are only eaten by wolves**

# How important is stochasticity?

## An example from the wolves of Isle Royal

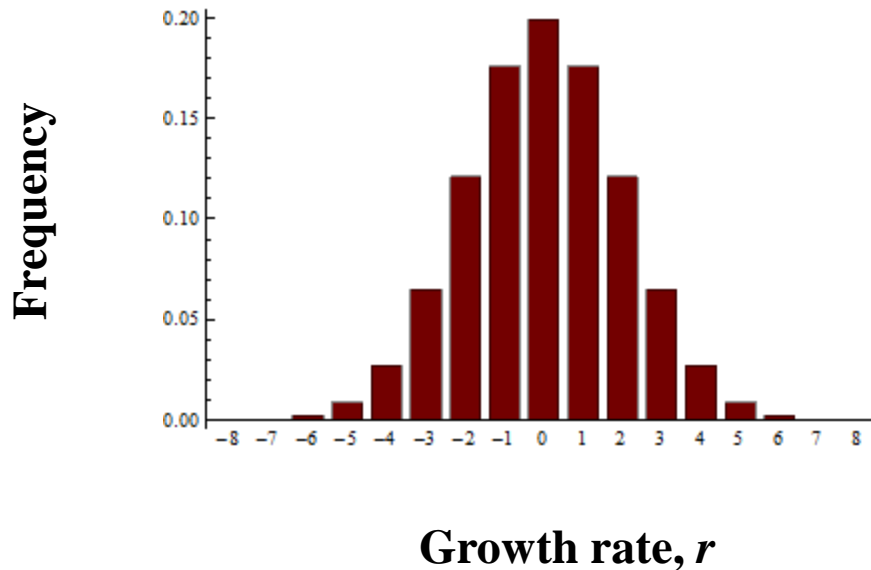
- Wolf population sizes fluctuate rapidly
- Moose population size also fluctuates
- What does this tell us about the growth rate,  $r$ , of the wolf population?



# How important is stochasticity?

## An example from the wolves of Isle Royal

The growth rate of the wolf population,  $r$ , is better characterized by a **probability distribution** with mean,  $\bar{r}$ , and variance,  $V_r$ .



What causes this variation in growth rate?

# **How important is stochasticity?**

## **An example from the wolves of Isle Royal**

**The researchers wished to test four hypothesized causes of growth rate variation:**

1. Snowfall (environmental stochasticity)
2. Population size of old moose (environmental stochasticity?)
3. Population size of wolves
4. Demographic stochasticity

**To this end, they collected data on each of these factors from 1971-2001**

**So what did they find?**

# How important is stochasticity?

An example from the wolves of Isle Royal

Cause	Percent variation in growth rate explained
Old moose	≈42%
Demographic stochasticity	≈30%
Wolves	≈8%
Snowfall	≈3%
Unexplained	≈17%

(Vucetich and Peterson, 2004)

- In this system, approximately 30% of the variation is due to demographic stochasticity
- Another 45% is due to what can perhaps be considered environmental stochasticity.

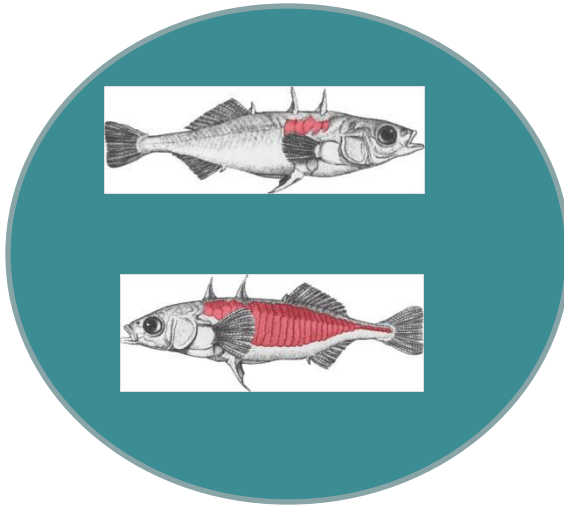
**\*\*\* At least for this wolf population, stochasticity is hugely important\*\*\***



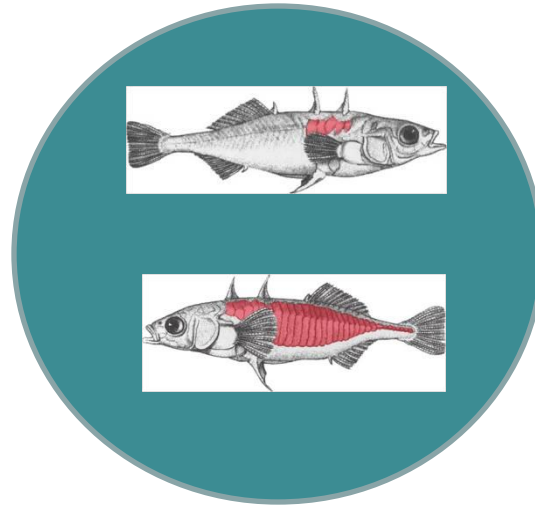
# Practice Problem:

You have observed the following pattern

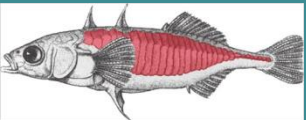
Lake 1



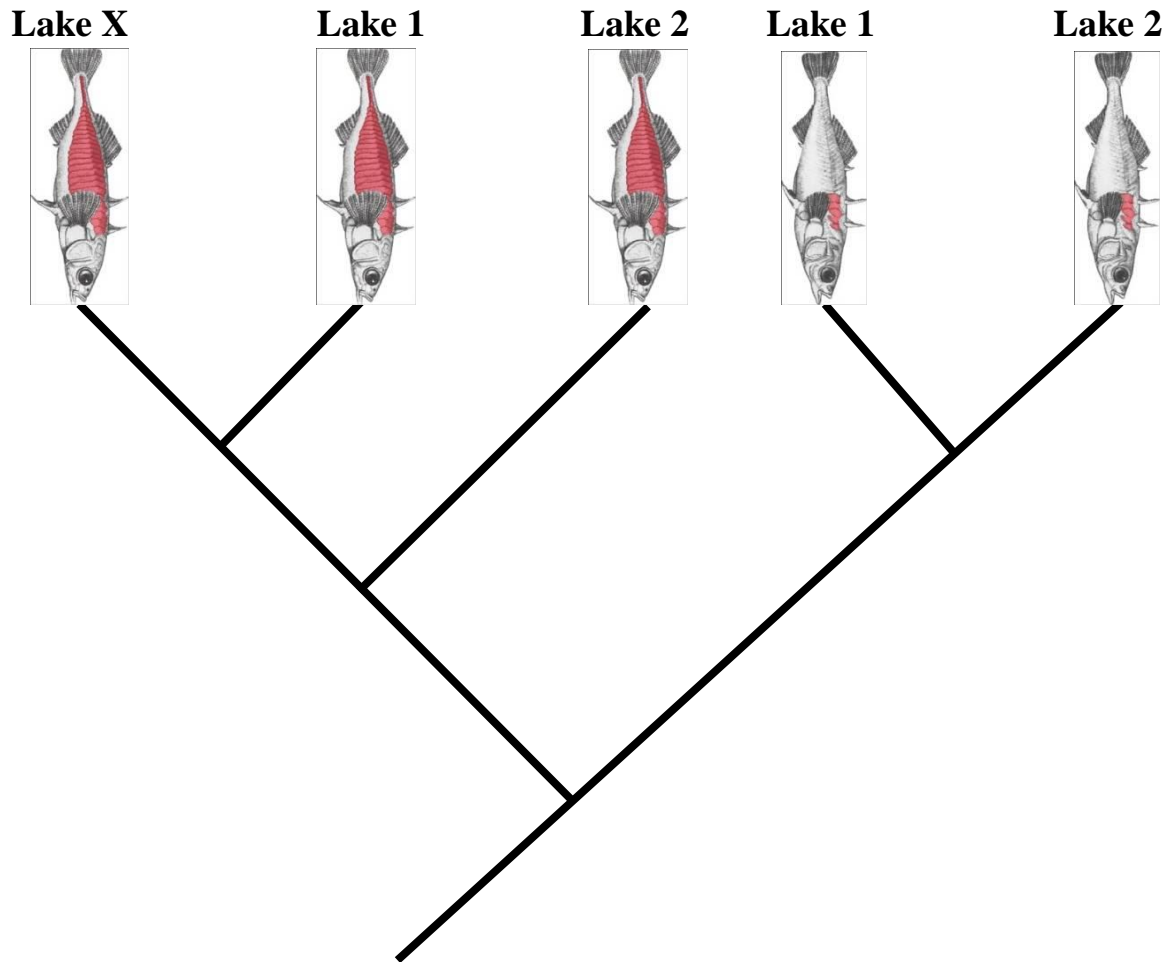
Lake 2



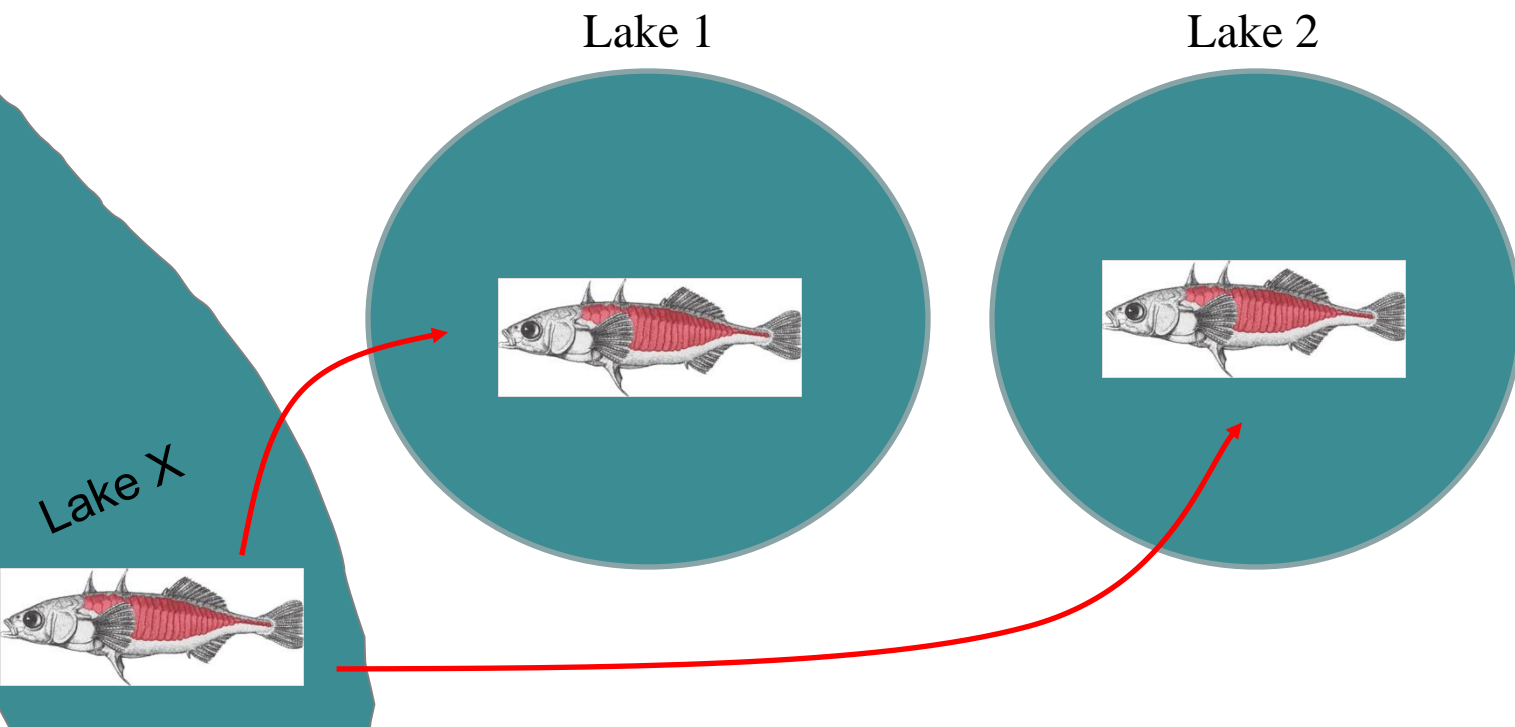
Lake X



In light of this phylogenetic data, how do you hypothesize speciation occurred?

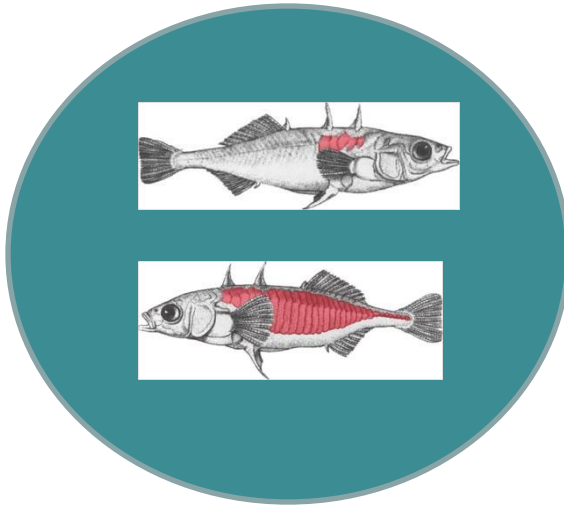


# A scenario consistent with the data

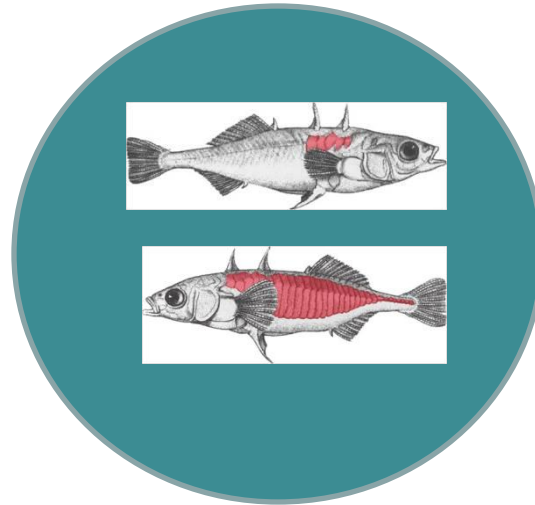


# A scenario consistent with the data

Lake 1



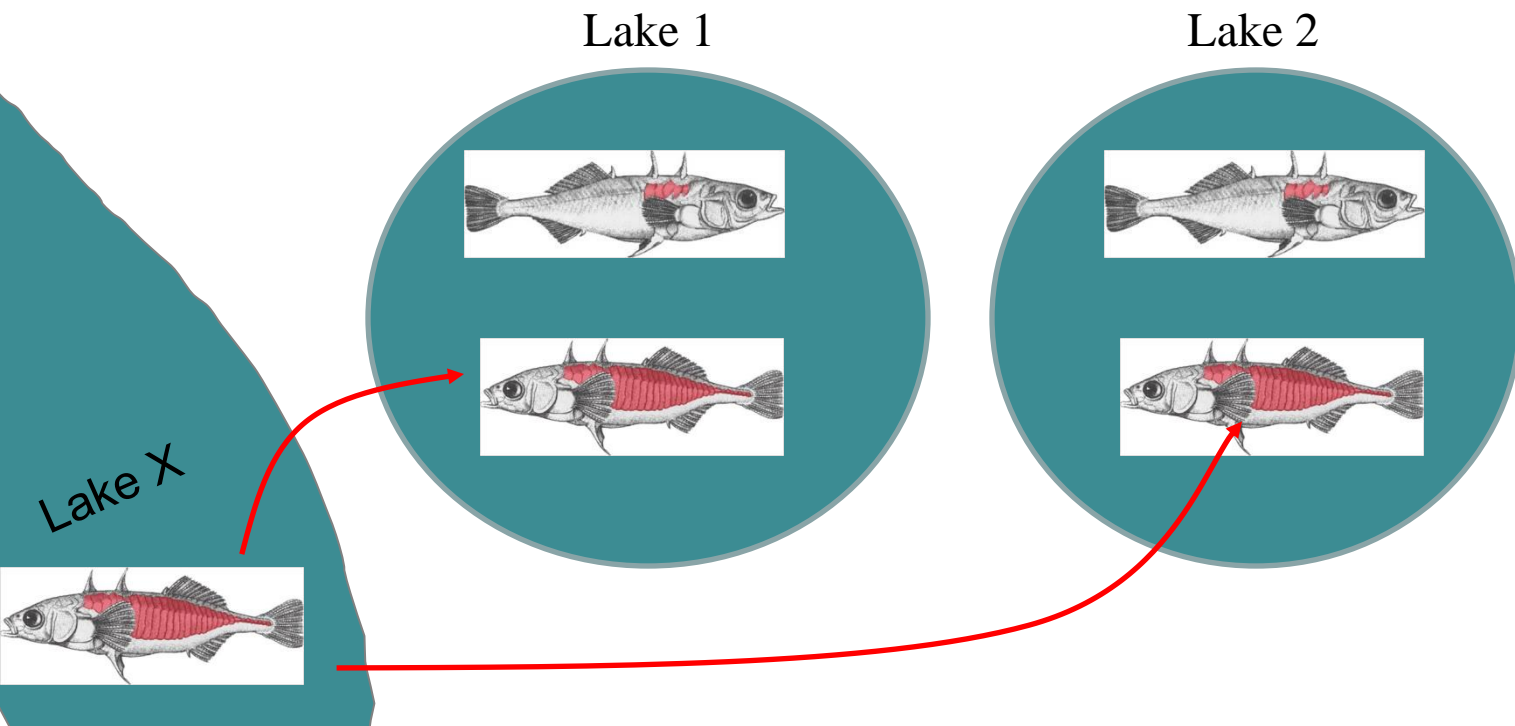
Lake 2



Lake X

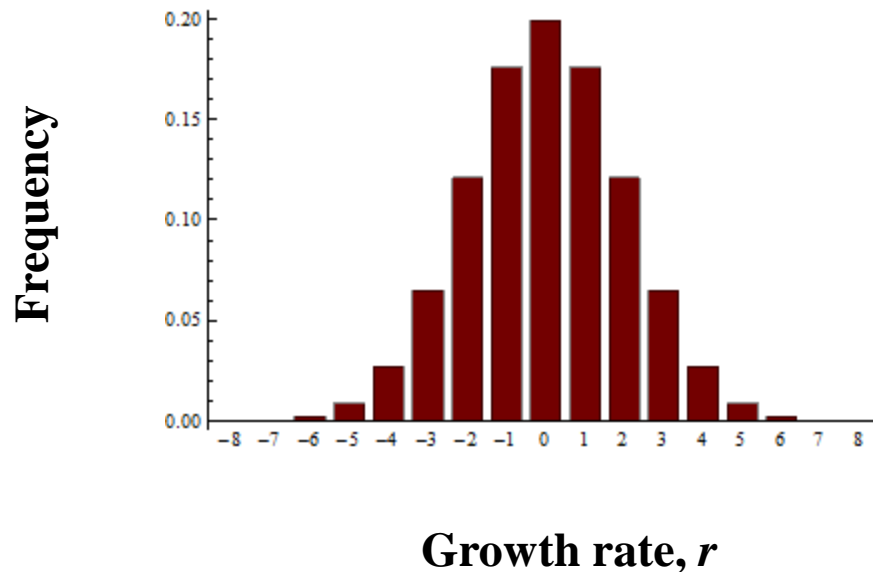


# A scenario consistent with the data



# Predicting population growth with stochasticity

Stochasticity is important in real populations; how can we integrate this into population predictions?

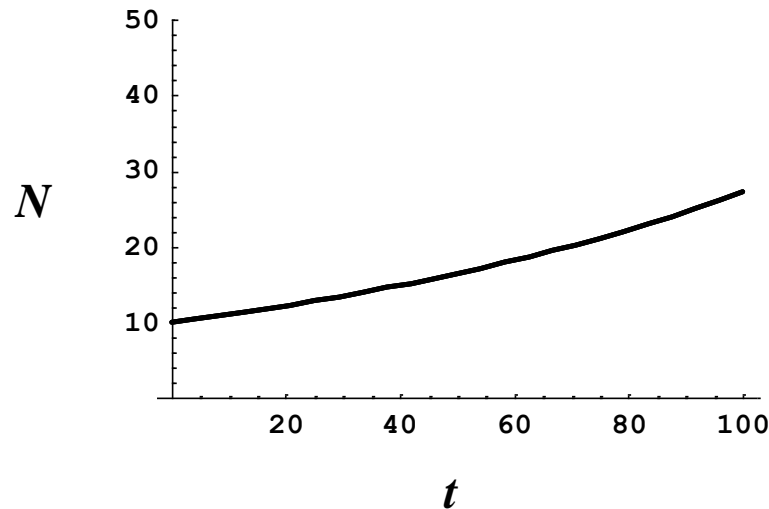


In other words, how do we integrate this distribution into:  $N_t = N_0 e^{rt}$

# Let's look at a single population

Imagine a population with an initial size of 10 individuals and an average growth rate of  $r = .01$

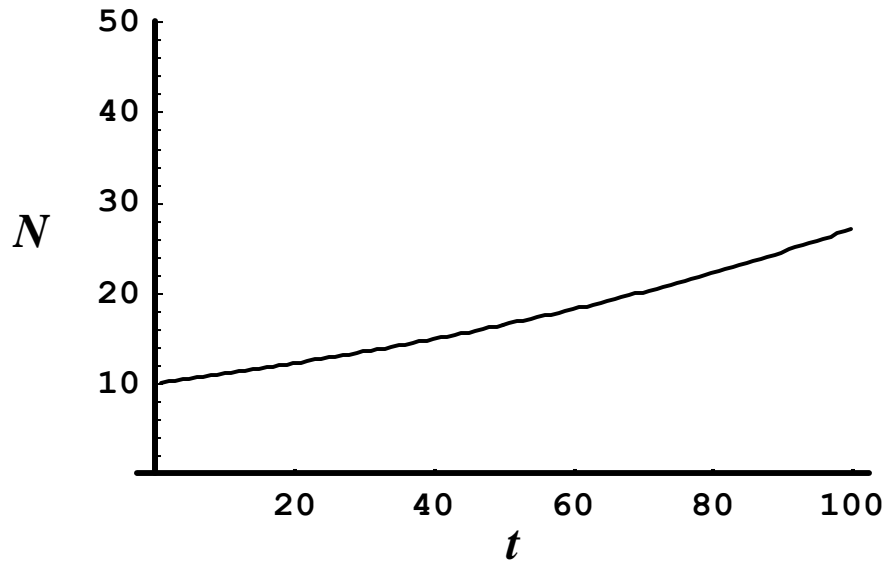
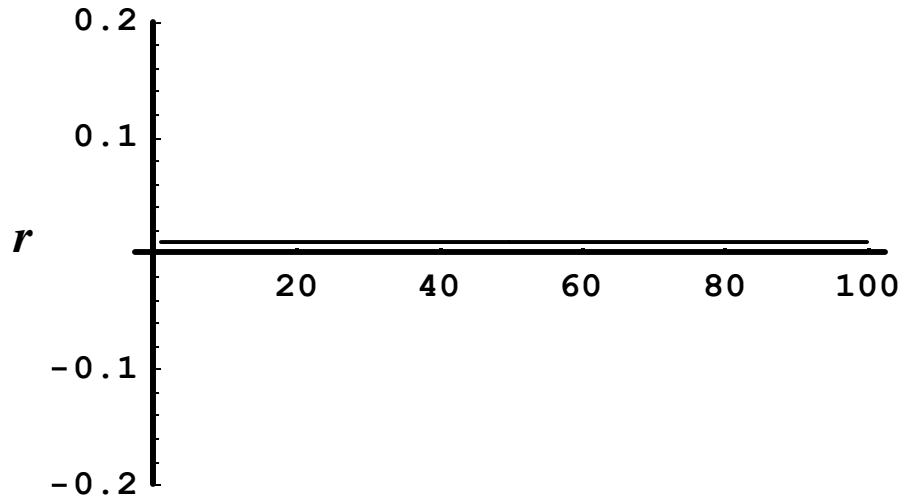
In the absence of stochasticity, our population would do this



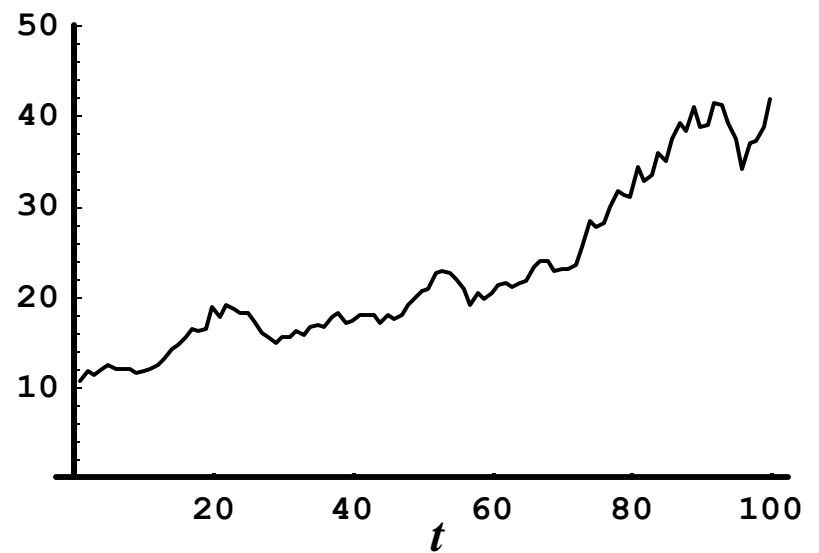
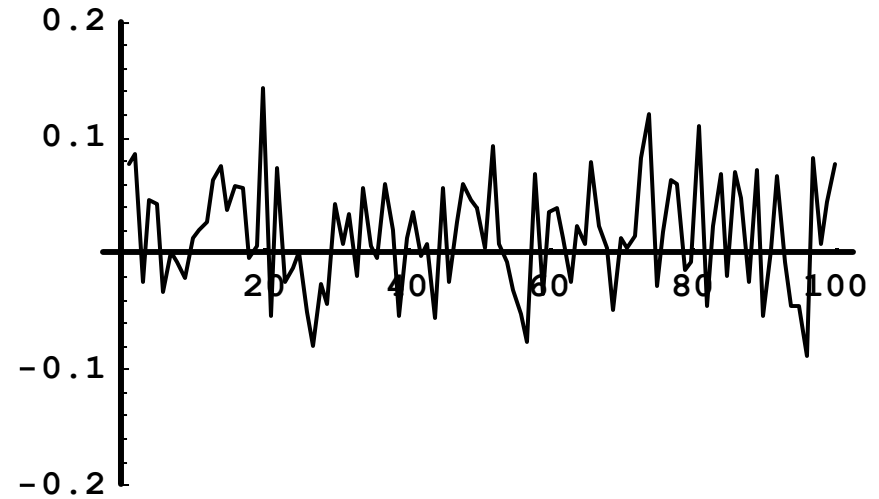
**The growth of this population is assured, there is no chance of extinction**

# But with stochasticity... we could get this

$$V_r = 0$$



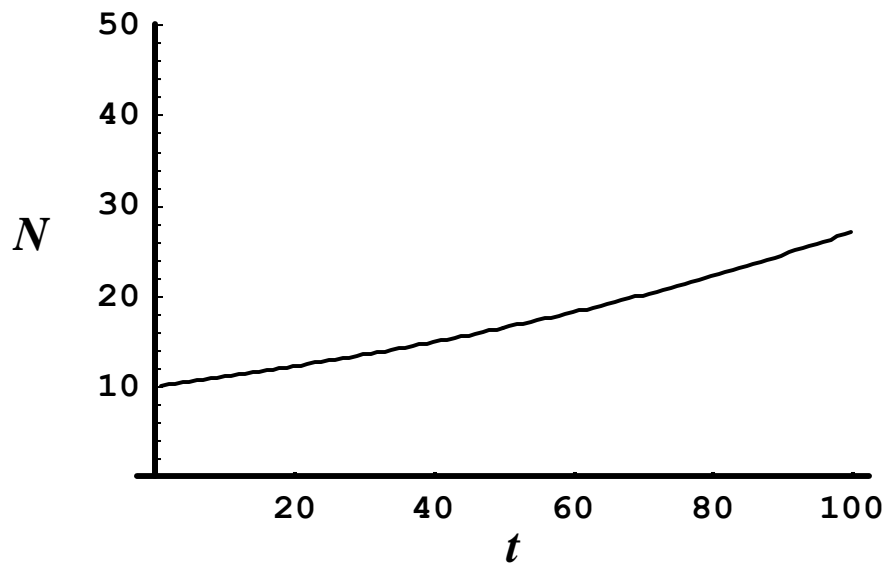
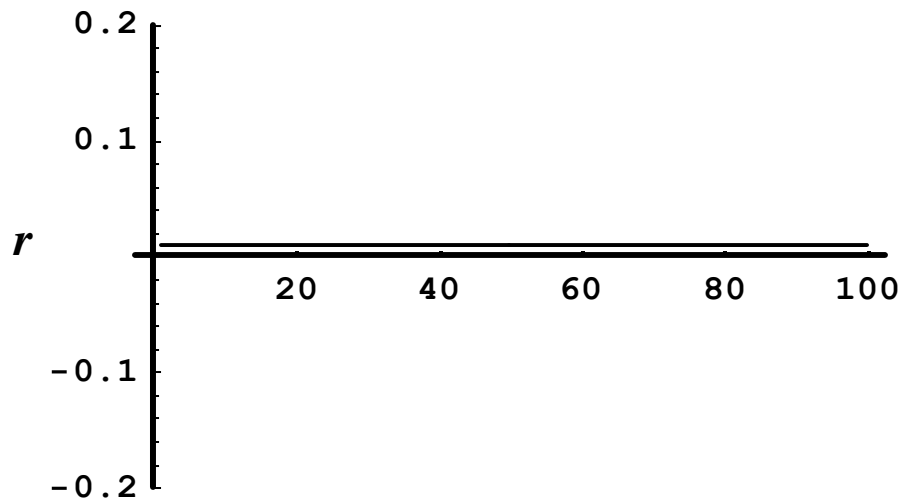
$$V_r = .0025$$



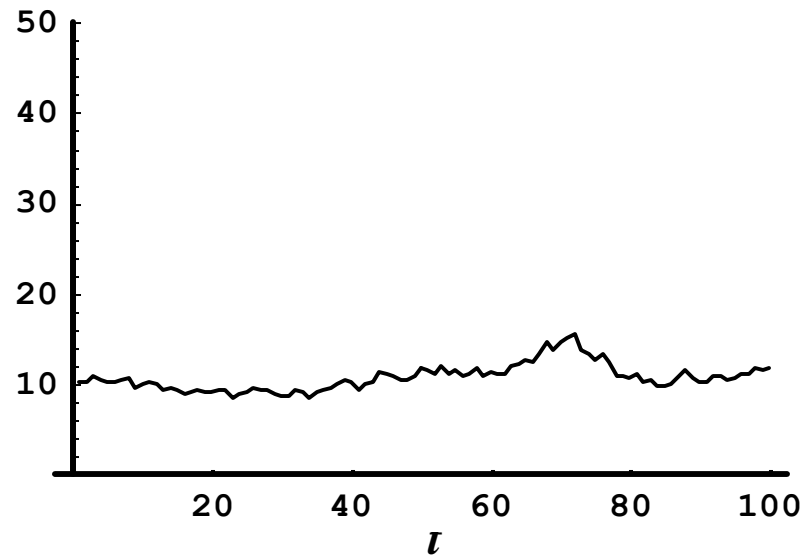
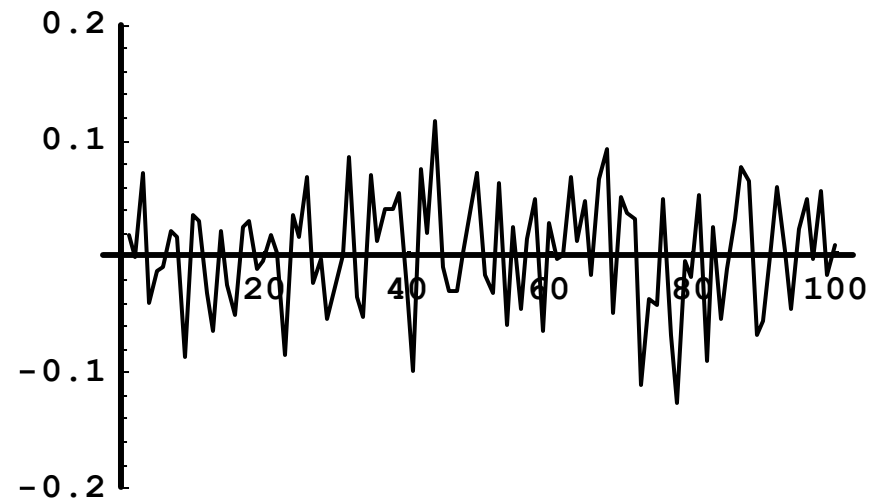


# Or this

$$V_r = 0$$

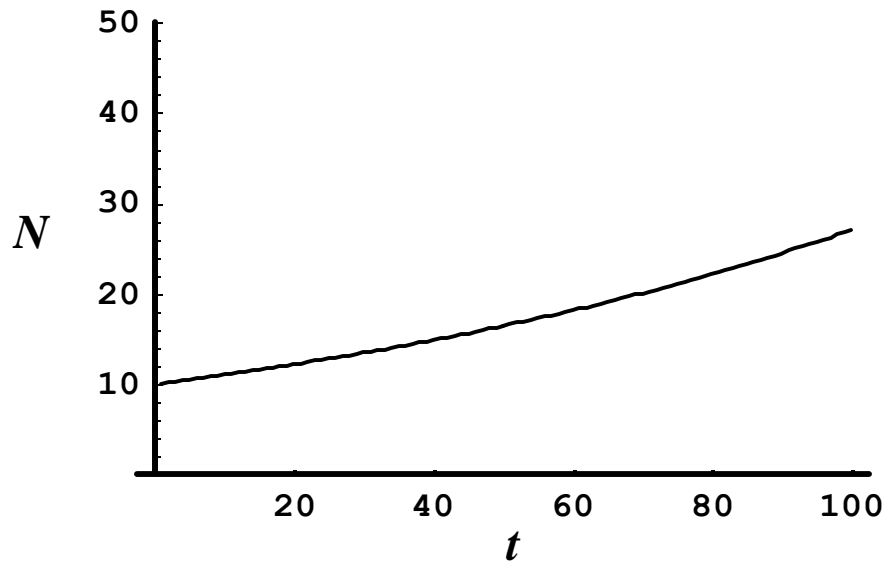
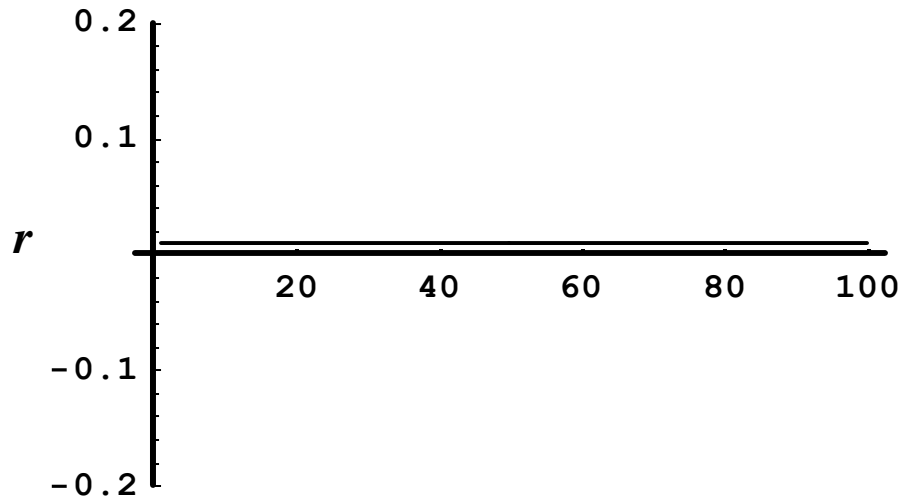


$$V_r = .0025$$

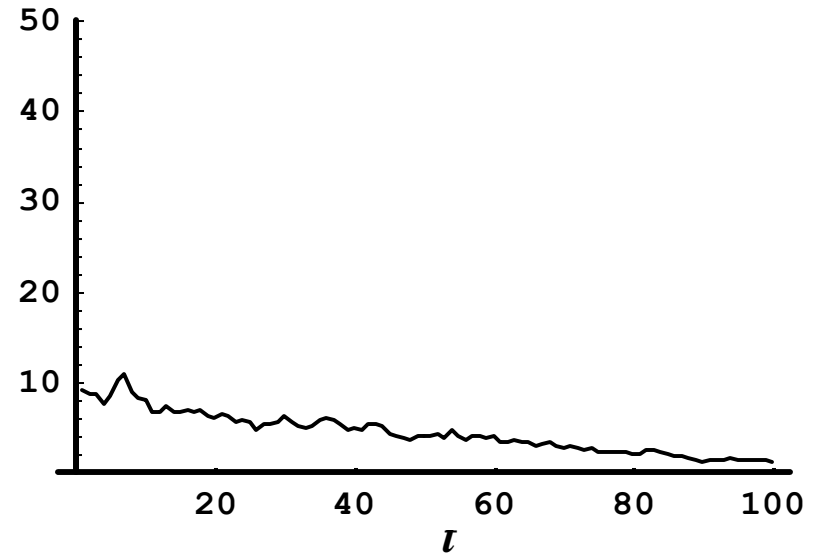
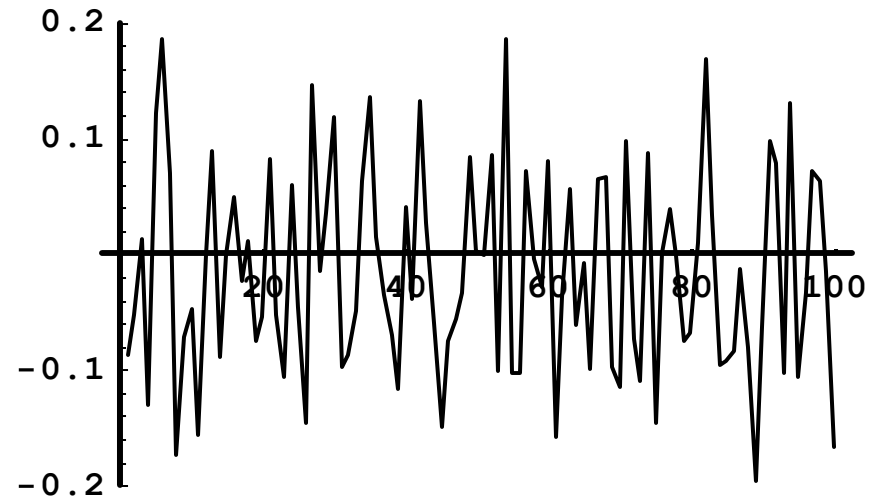


# Or even this...

$V_r = 0$



$V_r = .0025$



# Integrating stochasticity

**Generation 1: Draw  $r$  at random  $\rightarrow$  calculate the new population size**

**Generation 2: Draw  $r$  at random  $\rightarrow$  calculate the new population size**

•  
•  
•

**and so on and so forth**

The result is that we can no longer precisely predict the future size of the population. Instead, we can predict: 1) the **expected population size**, and 2) the **variance in population size**.

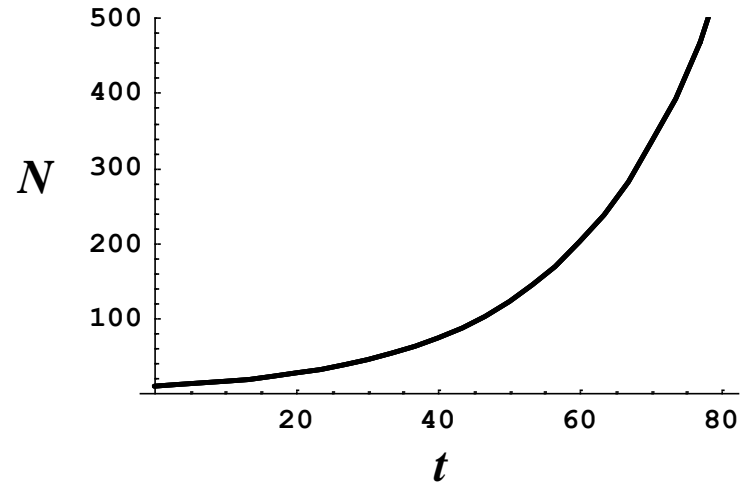
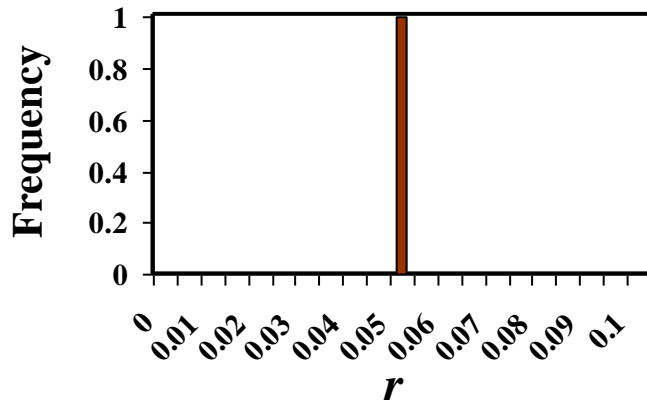
$$\bar{N}_t = N_0 e^{\bar{r}t}$$

$$V_{N_t} = N_0^2 e^{2\bar{r}t} (e^{V_r t} - 1)$$

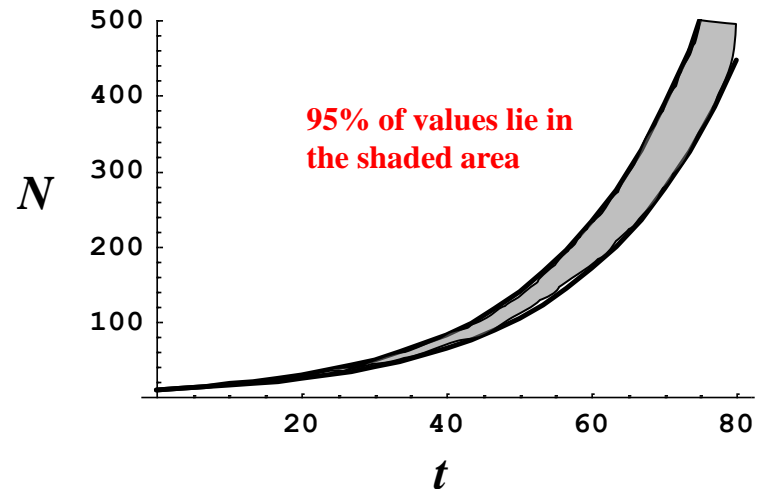
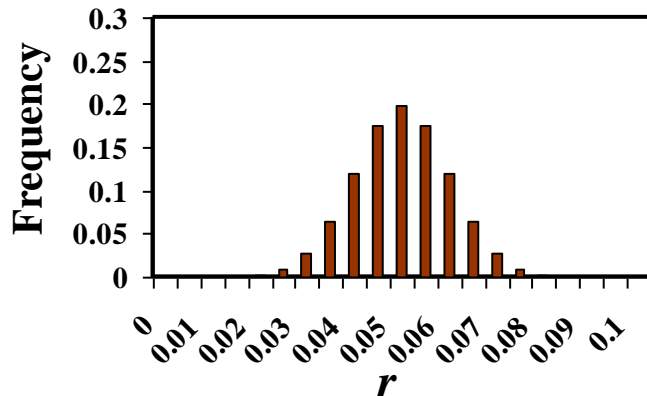
**Lets illustrate this with some examples...**

# Comparing two cases

Case 1: No stochasticity ( $\bar{r} = .05$   $V_r = 0$ )

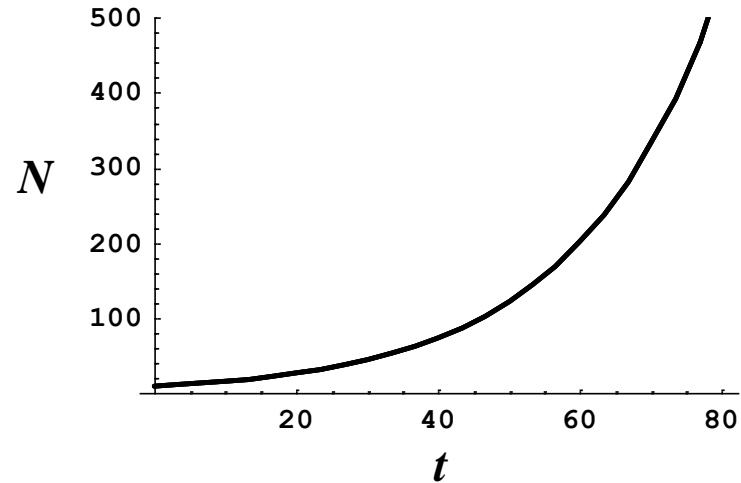
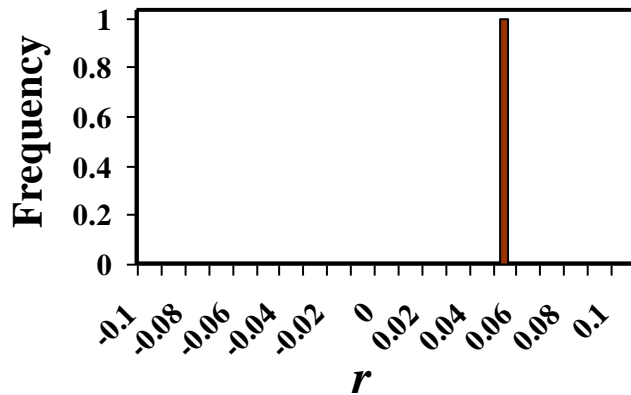


Case 2: Stochasticity ( $\bar{r} = .05$   $V_r = .0001$ )

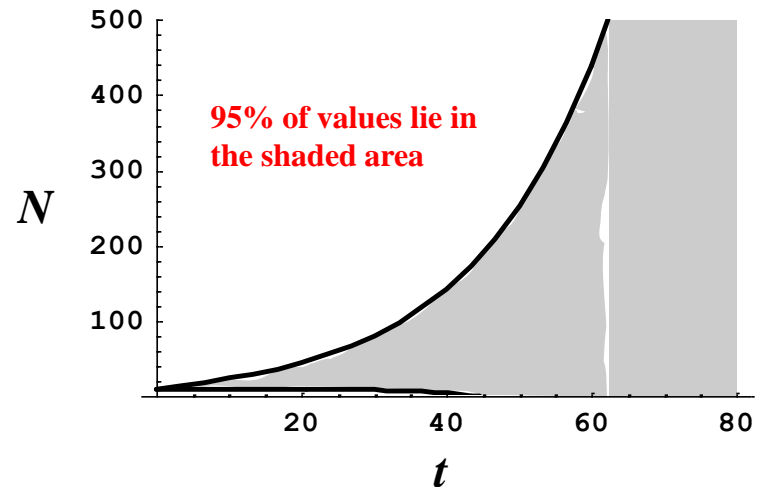
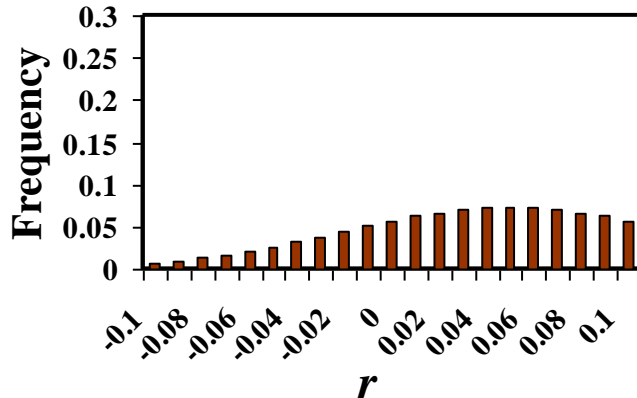


# What if the variance in $r$ is increased?

Case 1: No stochasticity ( $\bar{r} = .05$   $V_r = 0$ )



Case 2: Stochasticity ( $\bar{r} = .05$   $V_r = .005$ )



# How can we predict the fate of a real population?

$$\bar{N}_t = N_0 e^{\bar{r}t}$$

$$V_{N_t} = N_0^2 e^{2\bar{r}t} (e^{V_r t} - 1)$$

- What kind of data do we need?
- How could we get this data?
- How do we plug the data into the equations?
- How do we make biological predictions from the equations?

# A hypothetical data set

Replicate	r
1	0.10
2	0.15
3	0.05
4	0.00
5	-0.05
6	-0.02
7	0.05
8	-0.08
9	0.02
10	-0.05



Wolverine (*Gulo gulo*)

The question: How likely it is that a small ( $N_0 = 46$ ) population of wolverines will persist for 100 years without intervention?

The data: r values across ten replicate studies

# Calculation $\bar{r}$ and $V_r$

Replicate	$r$
1	0.10
2	0.15
3	0.05
4	0.00
5	-0.05
6	-0.02
7	0.05
8	-0.08
9	0.02
10	-0.05

$$\bar{r} = ?$$

$$V_r = ?$$



**Using estimates of  $\bar{r}$  and  $V_r$  in the equations**

$$\bar{N}_t = N_0 e^{\bar{r}t} = ?$$

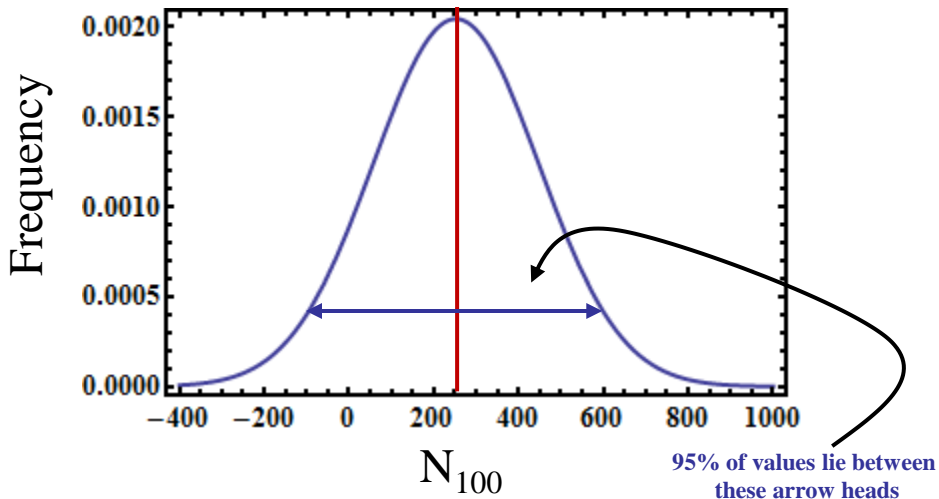
$$V_{N_t} = N_0^2 e^{2\bar{r}t} (e^{V_r t} - 1) = ?$$

# Translating the results back into biology

$$\bar{N}_{100} =$$

$$V_{N,100} =$$

OK, so what do these numbers mean?



- Remember that, for a normal distribution, 95% of values lie within 1.96 standard deviations of the mean
- This allows us to put crude bounds on our estimate for future population size
- What do we conclude about our wolverines?

# Practice Problem

Replicate	r
1	0.05
2	0.17
3	0.01
4	0.00
5	-0.07
6	-0.04
7	0.01
8	-0.08
9	0.02
10	-0.07



Wolverine (*Gulo gulo*)

The question: How likely it is that a small ( $N_0 = 36$ ) population of wolverines will persist for 80 years without intervention?

The data: r values across ten replicate studies