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
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.
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 $\Rightarrow \Delta N=0$
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

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

Source:

How important is stochasticity?
An example from the wolves of Isle Royal
(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

<table>
<thead>
<tr>
<th>Cause</th>
<th>Percent variation in growth rate explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>Old moose</td>
<td>≈42%</td>
</tr>
<tr>
<td>Demographic stochasticity</td>
<td>≈30%</td>
</tr>
<tr>
<td>Wolves</td>
<td>≈8%</td>
</tr>
<tr>
<td>Snowfall</td>
<td>≈3%</td>
</tr>
<tr>
<td>Unexplained</td>
<td>≈17%</td>
</tr>
</tbody>
</table>

(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
In light of this phylogenetic data, how to you hypothesize speciation occurred?
A scenario consistent with the data
A scenario consistent with the data
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

\[ V_r = 0 \]

\[ V_r = 0.0025 \]
Or this

<table>
<thead>
<tr>
<th>$V_r = 0$</th>
<th>$V_r = .0025$</th>
</tr>
</thead>
<tbody>
<tr>
<td>[ r ]</td>
<td>[ N ]</td>
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<td>[ t ]</td>
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<tr>
<td>[ 0.2 ]</td>
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</table>
Or even this...

\[ V_r = 0 \]

\[ V_r = 0.0025 \]
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**.

\[
\overline{N}_t = N_0 e^{\bar{r}t}
\]

\[
V_{N_t} = N_0^2 e^{2\bar{r}t} (e^{V_{r,t}} - 1)
\]

Let's illustrate this with some examples...
Comparing two cases

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

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

95% of values lie in the shaded area
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?
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

<table>
<thead>
<tr>
<th>Replicate</th>
<th>$r$</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>0.10</td>
</tr>
<tr>
<td>2</td>
<td>0.15</td>
</tr>
<tr>
<td>3</td>
<td>0.05</td>
</tr>
<tr>
<td>4</td>
<td>0.00</td>
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<tr>
<td>5</td>
<td>-0.05</td>
</tr>
<tr>
<td>6</td>
<td>-0.02</td>
</tr>
<tr>
<td>7</td>
<td>0.05</td>
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<tr>
<td>8</td>
<td>-0.08</td>
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<tr>
<td>9</td>
<td>0.02</td>
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<tr>
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Wolverine (*Gulo gulo*)
Calculation $\bar{r}$ and $V_r$

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$\bar{r} = ?$

$V_r = ?$
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

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

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Wolverine (*Gulo gulo*)