Properties of Populations

Age structure

Density

Fertility
What is a population?

• A group of organisms of the same species that occupy a well defined geographic region and exhibit reproductive continuity from generation to generation; ecological and reproductive interactions are more frequent among these individuals than with members of other populations of the same species.
Real populations are messy

- Broken up into populations
- But divisions are not entirely clear
In the real world, defining populations isn’t simple

• Populations often do not have clear boundaries

• Even in cases with clear boundaries, movement may be common
An extreme example... *Ensatina* salamanders

Not only are populations continuous, but so are species!
Metapopulations make things even more complicated

- Occur in fragmented habitats
- Connected by limited migration
- Characterized by extinction and recolonization → populations are transient
Glanville Fritillary in the Åland Islands

The glanville fritillary

Red dots indicate occupied habitat and white dots empty habitat in 1993.

Picture by Timo Pakkala
1) Density – The number of organisms per unit area

2) Genetic structure – The spatial distribution of genotypes

3) Age structure – The ratio of one age class to another

4) Growth rate – (Births + Immigration) – (Deaths + Emigration)
Describing populations I – Population density

United States at night

Population density shapes:

- Strength of competition within species
- **Spread of disease**
- Strength of interactions between species
- Rate of evolution

\[ \rho_i = \frac{N_i}{A_i} \]
Population density and disease, *Trypanosoma cruzi* (Chagas disease)

*Trypanosoma cruzi* (protozoan)

“Assassin bug” (vector)

Currently infects between 16,000,000 and 18,000,000 people and kills about 50,000 people each year
Population density and disease, *Trypanasoma cruzi*

A case study from the Brazilian Amazon

- Since 1950, human population has increased ≈ 7 fold
- Since 1950, the number of infections has increased ≈ 30 fold
- Suggests that rates of infection are increasing with human density

Emerging infectious diseases. 7: 100-112.
Describing populations II – Genetic structure

Imagine a case with 2 alleles: A and a, with frequencies $p_i$ and $q_i$, respectively.

Population 1

- $p_1 = .9$
- $q_1 = 2/20 = .1 = 1 - p_1$

Population 2

- $p_2 = .1$
- $q_2 = 18/20 = .9 = 1 - p_2$

These populations exhibit genetic structure!
## Sickled cells and malaria resistance

### Genotype vs Phenotype

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Phenotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>AA</td>
<td>Normal red blood cells, malaria susceptible</td>
</tr>
<tr>
<td>Aa</td>
<td>Mostly normal red blood cells, malaria resistant</td>
</tr>
<tr>
<td>aa</td>
<td>Mostly sickled cells, very sick</td>
</tr>
</tbody>
</table>

![Malaria in red blood cells](image1)

![A ‘sickled’ red blood cell](image2)
The frequency of the sickle cell gene is higher in populations where Malaria has been prevalent historically.
Describing populations III – Age structure

(a) Mexico

(b) United States

(c) Sweden
What determines a population’s age structure?

• Probability of death for various age classes

• Probability of reproducing for various age classes

• These probabilities are summarized using life tables
Mortality schedules: the probability of surviving to age $x$

We can quantify mortality schedules using life table
Quantifying mortality using life tables

<table>
<thead>
<tr>
<th>Age class</th>
<th>Number alive at age x</th>
<th>Proportion surviving to age x</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1000</td>
<td>1.000</td>
</tr>
<tr>
<td>2</td>
<td>916</td>
<td>.916</td>
</tr>
<tr>
<td>3</td>
<td>897</td>
<td>.897</td>
</tr>
<tr>
<td>4</td>
<td>897</td>
<td>.897</td>
</tr>
<tr>
<td>5</td>
<td>747</td>
<td>.747</td>
</tr>
<tr>
<td>6</td>
<td>426</td>
<td>.426</td>
</tr>
<tr>
<td>7</td>
<td>208</td>
<td>.208</td>
</tr>
<tr>
<td>8</td>
<td>150</td>
<td>.150</td>
</tr>
<tr>
<td>9</td>
<td>20</td>
<td>.020</td>
</tr>
</tbody>
</table>

How could you collect this data in a natural population?

Now let’s work through calculating the entries
Calculating entries of the life table: $l_x$

The proportion surviving to age class $x = $ The probability of surviving to age class $x$

$$l_x = \frac{N_x}{N_0}$$

Follow a single ‘cohort’

<table>
<thead>
<tr>
<th>$x$</th>
<th>$N_x$</th>
<th>$l_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1000</td>
<td>1.000</td>
</tr>
<tr>
<td>2</td>
<td>916</td>
<td>$= \frac{N_2}{N_1} = \frac{916}{1000} = .916$</td>
</tr>
<tr>
<td>3</td>
<td>897</td>
<td>$= \frac{N_3}{N_1} = \frac{897}{1000} = .897$</td>
</tr>
<tr>
<td>4</td>
<td>897</td>
<td>$= \frac{N_4}{N_1} = \frac{897}{1000} = .897$</td>
</tr>
<tr>
<td>5</td>
<td>747</td>
<td>$= \frac{N_5}{N_1} = \frac{747}{1000} = .747$</td>
</tr>
<tr>
<td>6</td>
<td>426</td>
<td>$= \frac{N_6}{N_1} = \frac{426}{1000} = .426$</td>
</tr>
<tr>
<td>7</td>
<td>208</td>
<td>$= \frac{N_7}{N_1} = \frac{208}{1000} = .208$</td>
</tr>
<tr>
<td>8</td>
<td>150</td>
<td>$= \frac{N_8}{N_1} = \frac{150}{1000} = .150$</td>
</tr>
<tr>
<td>9</td>
<td>20</td>
<td>$= \frac{N_9}{N_1} = \frac{20}{1000} = .020$</td>
</tr>
</tbody>
</table>
What determines a population’s age structure?

- Probability of death for various age classes ✓
- # of offspring produced by various age classes
- These probabilities are summarized using life tables
Fecundity schedules: # of offspring produced at age $x$

$m_x = \text{The expected number of daughters produced by mothers of age } x$

Fecundity can also be summarized using life tables.
Summarizing fecundity using a life table

<table>
<thead>
<tr>
<th>$x$</th>
<th>$l_x$</th>
<th>$m_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>.8</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>.6</td>
<td>.5</td>
</tr>
<tr>
<td>4</td>
<td>.4</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>.2</td>
<td>5</td>
</tr>
</tbody>
</table>

This entry designates the EXPECTED # of offspring produced by an individual of age 4.

In other words, this is the AVERAGE # of offspring produced by individuals of age 4.
If $l_x$ and $m_x$ do not change, populations reach a stable age distribution

As long as $l_x$ and $m_x$ remain constant, these distributions would never change!
Describing populations IV – Growth rate

A population’s growth rate can be readily estimated *** if a stable age distribution has been reached ***
Why is a stable age distribution important?
Using life tables to calculate population growth rate

<table>
<thead>
<tr>
<th>$x$</th>
<th>$l_x$</th>
<th>$m_x$</th>
<th>$l_xm_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1*0 = 0</td>
</tr>
<tr>
<td>2</td>
<td>.75</td>
<td>0</td>
<td>.75*0 = 0</td>
</tr>
<tr>
<td>3</td>
<td>.5</td>
<td>1</td>
<td>.5*1 = .50</td>
</tr>
<tr>
<td>4</td>
<td>.25</td>
<td>4</td>
<td>.25*4 = 1</td>
</tr>
</tbody>
</table>

The first step is to calculate $R_0$:

$$R_0 = \sum l_x m_x$$

This number, $R_0$, tells us the expected number of offspring produced by an individual over its lifetime.

- If $R_0 < 1$, the population size is decreasing
- If $R_0 = 1$, the population size is steady
- If $R_0 > 1$, the population size is increasing

$$R_0 = \sum l_x m_x = 1*0 + .75*0 + .5*1 + .25*4 = 1.5$$
Using life tables to calculate population growth rate

<table>
<thead>
<tr>
<th>$x$</th>
<th>$l_x$</th>
<th>$m_x$</th>
<th>$l_x m_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>.75</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>.5</td>
<td>1</td>
<td>.50</td>
</tr>
<tr>
<td>4</td>
<td>.25</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>

The second step is to calculate $G$

$$G = \frac{\sum_{x=1}^{k} l_x m_x x}{\sum_{x=1}^{k} l_x m_x}$$

This number, $G$, is a measure of the generation time of the population, or more specifically, the expected (average) age of reproduction.

$$G = \frac{\sum_{x=0}^{k} l_x m_x x}{\sum_{x=0}^{k} l_x m_x} = \frac{1*0*1+.75*0*2+.5*1*3+.25*4*4}{1*0+.75*0+.5*1+.25*4} = \frac{5.5}{1.5} = 3.67$$
Using life tables to calculate population growth rate

The last step is to calculate \( r \)

\[
r \approx \frac{\ln(R_0)}{G} = \frac{\ln(1.5)}{3.67} = .110
\]

This number, \( r \), is a measure of the population growth rate.

Specifically, \( r \) is the probability that an individual gives birth per unit time minus the probability that an individual dies per unit time.

\[ \Rightarrow \text{Population growth rate depends on two things:} \]

1. Generation time, \( G \)
2. The number of offspring produced by each individual over its lifetime, \( R_0 \)
The importance of generation time

Imagine two different populations, each with the same $R_0$:

<table>
<thead>
<tr>
<th>Population 1</th>
<th>x</th>
<th>$l_x$</th>
<th>$m_x$</th>
<th>$l_xm_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>.75</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>.5</td>
<td>1</td>
<td>.50</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>.25</td>
<td>4</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Population 2</th>
<th>x</th>
<th>$l_x$</th>
<th>$m_x$</th>
<th>$l_xm_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>.75</td>
<td>.667</td>
<td>.5</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>.5</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>.25</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

$R_{0,1} = 1.5$

$G_1 = 3.67$

$r_1 = .110$

$R_{0,2} = 1.5$

$G_2 = 1.33$

$r_2 = .305$

The growth rate of population 2 is almost three times greater, even though individuals in the two populations have identical numbers of offspring!
Using $r$ to predict the future size of a population

The change in population size, $N$, per unit time, $t$, is given by this **differential equation**:

\[
\frac{dN}{dt} = rN
\]

\[
\int \frac{1}{N} dN = \int r dt
\]

\[
\ln N = rt
\]

\[
N_t = N_0 e^{rt}
\]

One of the most influential equations in the history of biology
What are the consequences of this result?

For population size to remain the same, the following must be true:

\[ N_t = N_0 e^{rt} \]

This can only be true if ???

This is the concept of an equilibrium
What are the consequences of this result?

\[ N_t = N_0 e^{rt} \]

If \( r \) is anything other than 0 (\( R_0 \) is anything other than 1), the population goes extinct or becomes infinitely large.
A real example of exponential population growth…

\[ N_t = N_0 e^{rt} \]

From 0-1500: Human population increases by \( \approx 1.0 \) billion

From 1500-2000: Human population increases by \( \approx 10.0 \) billion

This observation had important historical consequences…
Using life tables: A practice question

A team of conservation biologists is interested in determining the optimum environment for raising an endangered species of flowering plant in captivity. For their purposes, the optimum environment is the one that maximizes the growth rate of the captive population allowing more individuals to be released into the wild in each generation. To this end, they estimated life table data for two cohorts (each of size 100) of captive plants, each raised under a different set of environmental conditions. Using the data in the hypothetical life tables below, answer the following questions:

<table>
<thead>
<tr>
<th>Population 1 (in environment 1)</th>
<th>Population 2 (in environment 2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>x</td>
<td>N&lt;sub&gt;x&lt;/sub&gt;</td>
</tr>
<tr>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>1</td>
<td>100</td>
</tr>
<tr>
<td>2</td>
<td>50</td>
</tr>
<tr>
<td>3</td>
<td>25</td>
</tr>
<tr>
<td>4</td>
<td>10</td>
</tr>
</tbody>
</table>

A. Using the data from the hypothetical life tables above, calculate the expected number of offspring produced by each individual plant over its life, R<sub>0</sub>, for each of the populations.

B. Using the data in the life tables above, calculate the generation time for each of the populations.

C. Using your calculations in A and B, estimate the population growth rate, r, of the two populations. Which population is growing faster? Why?

D. Assuming the populations both initially contain 100 individuals, estimate the size of each population in five years.

E. If the sole goal of the conservation biologists was to maximize the growth rate of the captive population, which conditions (those experienced by population 1 or 2) should they use for their future programs?

*** We will work through this problem during the next class. Be prepared***