Today we will...

- Revise the concept of population
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- Revise the concept of population
- **Introduce demographic concepts**
Today we will...

- Revise the concept of population
- Introduce demographic concepts
- **Matrix population models**
A quick review

A population is...

- A group of individuals of one species that can be defined as a single unit, distinct from other such units
A population is...

- A group of individuals of one species that can be defined as a single unit, distinct from other such units
- A cluster of individuals with a high probability of mating with each other, compared to their probability of mating with members of another population
A quick review

Fundamental equation of population change

\[ N_{t+1} = N_t + B - D + I - E \]

Where:

- \( N_t \) = the number of organisms now
A quick review

Fundamental equation of population change

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Where:

- \( N_t \) = the number of organisms now
- \( N_{t+1} \) = the number of organisms in the next time step per year per generation
A quick review

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Fundamental equation of population change

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A quick review

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- \( I \) = the number of immigrants
- \( E \) = the number of emigrants
A quick review

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A quick review

This is often simplified to

\[ N_{t+1} = \lambda N_t \]

Where:

- \( \lambda \) summarises \( B - D + I - E \)

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

Where:

- \( r = \ln N \) - the intrinsic rate of increase
This is often simplified to

\[ N_{t+1} = \lambda N_t \]

Where:
- \( \lambda \) summarises \( B - D + I - E \)
- \( \lambda \) is the net reproductive rate - the number of organisms next year per organism this year

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

Where:
- \( r = \ln N \) - the intrinsic rate of increase
A quick review

Describing mortality and fecundity

- Fecundity is often expressed on a per capita basis, which means dividing the total fecundity by population size

Mortality is often expressed as a proportion or percentage dying in a time interval. If \( d \) individuals die in a population of \( N \) individuals, then

\[
\text{survive} = N - d
\]

The probability of dying, \( p \), is

\[
p = \frac{d}{N}
\]
Describing mortality and fecundity

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A quick review

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- If $d$ individuals die in a population of $N$ individuals, then $s = N - d$ survive and the probability of dying, $p = \frac{d}{N}$. 

Easiest way to collect such data is from marked individuals.
A quick review

Describing mortality and fecundity

- Fecundity is often expressed on a per capita basis, which means dividing the total fecundity by population size.
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- If \( d \) individuals die in a population of \( N \) individuals, then \( s = N - d \) survive and the probability of dying, \( p = \frac{d}{N} \).
- Easiest way to collect such data is from marked individuals.
How to collect data that is useful

- Follow individuals throughout their lives recording birth data, breeding attempt data and movement and death data
Data collection

How to collect data that is useful

- Follow individuals throughout their lives recording birth data, breeding attempt data and movement and death data
- In practice it is nearly always impossible to do this. Bighorn sheep at Ram Mountain offer one exception
What if data are not complete?

- Animal seen known to be alive (1)

<table>
<thead>
<tr>
<th>Year</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capture history</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Data collection

What if data are not complete?

- Animal seen known to be alive (1)
- Animal not seen, but not dead as seen in a later census- either alive but not seen and living in study area or temporarily emigrated (0)

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<tr>
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<td>1</td>
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<td>0</td>
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<td>1</td>
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Data collection

What if data are not complete?

- Animal seen known to be alive (1)
- Animal not seen, but not dead as seen in a later census- either alive but not seen and living in study area or temporarily emigrated (0)
- Animals not seen now or in later census- either alive but not seen and living in the study or emigrated or dead (Last two zeros)
Mark Recapture Analysis

Mark Recapture Analysis: estimates survival probabilities from recapture histories by examining what the probability of sighting an animal in a specific demographic class is, given that it has to be alive.
Analysis of capture histories to estimate survival

Mark Recapture Analysis

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- Mark Recapture Analysis: estimates survival probabilities from recapture histories by examining what the probability of sighting an animal in a specific demographic class is, given that it has to be alive.
- Uses this information to determine when a “0” is likely to mean an animal has in fact died.
- Can do this for each year, for each class of animal (age, size, phenotype genotype).
- Can then use this information to estimate when a “0” with no following resightings means death.
Some insights from mark-recapture analyses

- In long-lived animals, variability in vital rates is greatest in young and old individuals (e.g. Soay sheep)
Mark Recapture Analysis

Some insights from mark-recapture analyses

- In long-lived animals, variability in vital rates is greatest in young and old individuals (e.g. Soay sheep)
- Density-dependent and independent processes can interact to influence demography (At low density, climate doesn‘t influence survival, but at high density, climate does influence survival e.g. Mouse opossum: Lima et al. 2001 Proc. Roy. Soc. B 268, 2053-2064)
A quick review

Population growth
- Populations grow when birth rate > death rate

Growth rate
- Growth is the number of births - number of deaths in a population
A quick review

Population growth
- Populations grow when birth rate > death rate
- Stay the same when equal

Growth rate
- Growth is the number of births - number of deaths in a population
- Birth rate is number of births/1000 individuals (sometimes expressed as a proportion)
A quick review

Population growth

- Populations grow when birth rate $>$ death rate
- Stay the same when equal
- Decline when birth rate $<$ death rate

Growth rate

- Growth is the number of births - number of deaths in a population
- Birth rate is number of births/1000 individuals (sometimes expressed as a proportion)
- Death rate is number of deaths/1000 individuals (sometimes expressed as a proportion)
A quick review

Exponential growth

- All populations have the potential to increase exponentially

Figure 1. Exponential growth
A quick review

Exponential growth

- All populations have the potential to increase exponentially
- This has been realised since Malthus and Darwin

Figure 1. Exponential growth
A quick review

Exponential growth

- All populations have the potential to increase exponentially
- This has been realised since Malthus and Darwin
- But, for the most they do not... Why?

Figure 1. Exponential growth
Limitations of exponential growth

Some factors that affect birth and death rates are dependent on the size of the population (density-dependent factors).

Larger populations may mean less food/individual, fewer resources for survival or reproduction.

Extrinsic factors can also cause populations to fluctuate (independent of population size) such as weather patterns, disturbance or habitat alterations, interspecific interactions (you will learn more about these in the community part of the lectures).
Limitations of exponential growth

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Limits to exponential growth

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Density dependence

How does it affect population fluctuations?

- The per capita rate of increase of a population will in general depend on density

Figure 2. Density dependence
Density dependence

How does it affect population fluctuations?

- The per capita rate of increase of a population will in general depend on density.
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Figure 2. Density dependence
Density dependence

How does it affect population fluctuations?

- The per capita rate of increase of a population will in general depend on density.
- If the per capita growth rate changes as density varies it is said to be density dependent.
- The concept of density dependence is fundamental to population dynamics. We can use these graphs to determine stability.

Figure 2. Density dependence
Density Dependence can help us answer many questions

- Why do populations fluctuate in size?
Density dependence

Density Dependence can help us answer many questions

- Why do populations fluctuate in size?
- Why do populations fluctuate around a mean?
Density dependence

Density Dependence can help us answer many questions

- Why do populations fluctuate in size?
- Why do populations fluctuate around a mean?
- In common species the mean is high, in rare species the mean is low
Density Dependence can help us answer many questions

- Why do populations fluctuate in size?
- Why do populations fluctuate around a mean?
- In common species the mean is high, in rare species the mean is low
- Why are the fluctuations different? Large animals often appear to have stable populations, small animals fluctuate variably with huge peaks and troughs
Density dependence can help us answer many questions

- Density-dependence is a powerful force in regulating populations
 Density dependence

Density Dependence can help us answer many questions

- Density-dependence is a powerful force in regulating populations
- Simple models can generate a range of patterns
Density dependence

Fluctuations

- Overcompensation (If DD is not perfect its effects may overcompensate for current population levels)

Figure 3. Overcompensation due to density dependence
Density dependence

Examples of overcompensation

- Cinnabar moths on ragwort: the caterpillars eat the plants on which they are dependent entirely and the most of the local population can fail to reach a size sufficient to pupate, thus, most die.

Figure 4. Cinnabar moth caterpillar (Tyria jacobaeae) on ragwort (Jacobaea vulgaris)
Density dependence

Examples of overcompensation

- Nest site competition in bees: some solitary bee species will fight to the death to secure a nest site. The corpse of the victim effectively blocks the hole for the victor and removes this resource from the "game".

Figure 5. Carpenter bee (Xylocopa micans) on Vitex sp.
Models when individuals differ

- What are we trying to explain?

Figure 6. Dark Green Fritillary (Argynnis aglaja) life cycle
Populations are structured

Models when individuals differ

- What are we trying to explain?
- Need a value (or function) describing dynamics of each class

Figure 6. Dark Green Fritillary (Argynnis aglaja) life cycle
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- Need to combine these into a single model

Figure 6. Dark Green Fritillary (Argynnis aglaja) life cycle
Populations are structured

Models when individuals differ

- What are we trying to explain?
- Need a value (or function) describing dynamics of each class
- Need to combine these into a single model
- We will focus on: population size, growth rate and structure

Figure 6. Dark Green Fritillary (Argynnis agrilla) life cycle
Start with a life cycle

Figure 7. Stage cycle
Matrix models

What they are...

- Matrix population models are a specific type of population model that uses matrix algebra.
Matrix models

What they are...

- Matrix population models are a specific type of population model that uses matrix algebra
- Make use of age or stage-based discrete time data
Matrices

Using vectors to describe the number of individuals

- How do we get from population structure in year 1 to population structure in year 2 in terms of births and deaths?

\[
\begin{pmatrix}
184 \\
42 \\
97
\end{pmatrix} = \text{Population model} \times 
\begin{pmatrix}
276 \\
57 \\
118
\end{pmatrix}
\]

- Survey year 1: Total = 451 = 276 hatched chicks + 57 pre-reproductive juveniles + 118 adults
Matrices

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- Survey year 1: Total = 451 = 276 hatched chicks + 57 pre-reproductive juveniles + 118 adults
- Survey year 2: Total = 323 = 184 hatched chicks + 41 pre-reproductive juveniles + 97 adults
Matrices are an ideal model to describe transitions

Using vectors to describe the number of individuals:

- Vectors and matrices are referred to as bold, non-italicised letters.

\[
\begin{pmatrix}
184 \\
42 \\
97
\end{pmatrix} =
\begin{pmatrix}
0 & 0 & 1.56 \\
0.15 & 0 & 0 \\
0 & 0.17 & 0.74
\end{pmatrix}
\begin{pmatrix}
276 \\
57 \\
118
\end{pmatrix}
\]

\[n_{t+1} = A \cdot n_t\]

- So a matrix can describe how the population structure at one point in time is a function of the population structure in a previous point in time.
Matrices are an ideal model to describe transitions

Biological relevance of matrix elements
Matrices are an ideal model to describe transitions

### Biological relevance of matrix elements

Let's assume the matrix describes a yearly time step and the population census is conducted just before breeding occurs. The top row represents the per capita number of offspring that are nearly one year old at time \( t+1 \) produced by individuals in each class at time \( t \).

<table>
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<tr>
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<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Class in year ( t+1 )</td>
<td>1 --&gt; 1</td>
<td>2 --&gt; 1</td>
<td>3 --&gt; 1</td>
<td>4 --&gt; 1</td>
<td>5 --&gt; 1</td>
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<td></td>
<td>1 --&gt; 2</td>
<td>2 --&gt; 2</td>
<td>3 --&gt; 2</td>
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= recruitment

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Matrices are an ideal model to describe transitions

Biological relevance of matrix elements

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<th>4</th>
<th>5</th>
</tr>
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<tbody>
<tr>
<td>Class in year t</td>
<td>1 to 1</td>
<td>2 to 1</td>
<td>3 to 1</td>
<td>4 to 1</td>
<td>5 to 1</td>
</tr>
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<td>1</td>
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= recruitment

- Let's assume the matrix describes a yearly time step and the population census is conducted just before breeding occurs. The top row represents the per capita number of offspring that are nearly one year old at time t+1 produced by individuals in each class at time t.

- For example, if there were 112 individuals in class 3 at year t, and they produced 283 offspring (class 1 individuals) that were in the population at year t+1, the value for the 3 to 1 transition would be $\frac{283}{112} = 2.527$. 
Matrices are an ideal model to describe transitions.

**Biological relevance of matrix elements**

Continuing with the same pre-breeding model. The main diagonal represents the per capita production of individuals in a class in year $t+1$ by individuals in that class in year $t$.

![Matrix Diagram]

Probability of remaining in the same stage.
Matrices are an ideal model to describe transitions

Biological relevance of matrix elements

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- Continuing with the same pre-breeding model. The main diagonal represents the per capita production of individuals in a class in year $t+1$ by individuals in that class in year $t$
- Biologically this generally relates to the probability of individuals remaining within a class. Cell to 1, however, can represent individuals in class 1 that produce offspring that recruit to class 1 within a year
Matrices are an ideal model to describe transitions.

Biological relevance of matrix elements

- Now considering an age structured model, individuals can only increase in age.
Matrices are an ideal model to describe transitions

Now considering an age structured model, individuals can only increase in age.

- Group all individuals that are five years old and older into one element.
Matrices are an ideal model to describe transitions.

Biological relevance of matrix elements

- Now considering an age structured model, individuals can only increase in age.
- Group all individuals that are five years old and older into one element.
- Individuals ageing by one year (diagonal).
Matrices are an ideal model to describe transitions

Using the fundamental equation for each class

\[ N_{t+1} = N_{t,a} \times S_a + N_{t,i} \times R_i \times S_i \]

Where:

- \( N_{t,a} \) = number of adult females at time \( t \)
Matrices are an ideal model to describe transitions using the fundamental equation for each class:

\[ N_{t+1} = N_{t,a} \times S_a + N_{t,i} \times R_i \times S_i \]

Where:
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- \( N_{t,i} \) = number of immature females at time \( t \)
Matrices are an ideal model to describe transitions

Using the fundamental equation for each class

\[ N_{t+1} = N_{t,a} \times S_a + N_{t,i} \times R_i \times S_i \]

Where:

- \( N_{t,a} \) = number of adult females at time \( t \)
- \( N_{t,i} \) = number of immature females at time \( t \)
- \( S_a \) = annual survival of adult females from time \( t \) to time \( t+1 \)
- \( S_i \) = annual survival of immature females from time \( t \) to time \( t+1 \)
- \( R_i \) = ratio of surviving young females at the end of the breeding season per breeding female
Matrices are an ideal model to describe transitions.

Using the fundamental equation for each class

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- \( R_i \) = ratio of surviving young females at the end of the breeding season per breeding female
Matrices are an ideal model to describe transitions.

In a matrix notation

\[
\begin{pmatrix}
N_{t+l_t} \\
N_{t+l_a}
\end{pmatrix}
= 
\begin{pmatrix}
S_i R_i & S_a R_i \\
S_i & S_a
\end{pmatrix}
\begin{pmatrix}
N_{t_t} \\
N_{t_a}
\end{pmatrix}
\]
Matrices are an ideal model to describe transitions in population dynamics. In a matrix notation, each row in the first and third matrices corresponds to animals within a given age range (0 to 1 years, 1 to 2 years, and 2 to 3 years). The top row of the middle matrix consists of age-specific fertilities: \( F_1, F_2, \) and \( F_3. \) These models can give rise to interesting cyclical or seemingly chaotic patterns in abundance over time when fertility rates are high.

The terms \( F_i \) and \( S_i \) can be constants or they can be functions of environment, such as habitat or population size. Randomness can also be incorporated into the environmental component (as we will see tomorrow).

\[
\begin{pmatrix}
N_{t+l_1} \\
N_{t+l_2} \\
N_{t+l_3}
\end{pmatrix}
=
\begin{pmatrix}
F_1 & F_2 & F_3 \\
S_1 & 0 & 0 \\
0 & S_2 & 0
\end{pmatrix}
\begin{pmatrix}
N_{t_1} \\
N_{t_2} \\
N_{t_3}
\end{pmatrix}.
\]
Matrices are an ideal model to describe transitions in a matrix notation.

Each row in the first and third matrices corresponds to animals within a given age range (0 to 1 years, 1 to 2 years and 2 to 3 years).

The top row of the middle matrix consists of age-specific fertilities: F1, F2 and F3.

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\begin{pmatrix}
N_{t+l_1} \\
N_{t+l_2} \\
N_{t+l_3}
\end{pmatrix} =
\begin{pmatrix}
F_1 & F_2 & F_3 \\
S_1 & 0 & 0 \\
0 & S_2 & 0
\end{pmatrix}
\begin{pmatrix}
N_{t_1} \\
N_{t_2} \\
N_{t_3}
\end{pmatrix}.
\]
Matrices are an ideal model to describe transitions

### In a matrix notation

\[
\begin{pmatrix}
N_{t+1} \\
N_{t+2} \\
N_{t+3}
\end{pmatrix} = \begin{pmatrix}
F_1 & F_2 & F_3 \\
S_1 & 0 & 0 \\
0 & S_2 & 0
\end{pmatrix}
\begin{pmatrix}
N_t \\
N_{t+1} \\
N_{t+2}
\end{pmatrix}
\]

- Each row in the first and third matrices corresponds to animals within a given age range (0 to 1 years, 1 to 2 years and 2 to 3 years).
- The top row of the middle matrix consists of age-specific fertilities: F1, F2 and F3.
- These models can give rise to interesting cyclical or seemingly chaotic patterns in abundance over time when fertility rates are high.

The terms \(F_i\) and \(S_i\) can be constants or they can be functions of environment, such as habitat or population size. Randomness can also be incorporated into the environmental component (as we will see tomorrow).
Matrices are an ideal model to describe transitions

In a matrix notation

\[
\begin{pmatrix}
N_{t+t_1} \\
N_{t+t_2} \\
N_{t+t_3}
\end{pmatrix} =
\begin{pmatrix}
F_1 & F_2 & F_3 \\
S_1 & 0 & 0 \\
0 & S_2 & 0
\end{pmatrix}
\begin{pmatrix}
N_{t_1} \\
N_{t_2} \\
N_{t_3}
\end{pmatrix}
\]

- Each row in the first and third matrices corresponds to animals within a given age range (0 to 1 years, 1 to 2 years and 2 to 3 years).
- The top row of the middle matrix consists of age-specific fertilities: $F_1$, $F_2$ and $F_3$.
- These models can give rise to interesting cyclical or seemingly chaotic patterns in abundance over time when fertility rates are high.
- The terms $F_i$ and $S_i$ can be constants or they can be functions of environment, such as habitat or population size. Randomness can also be incorporated into the environmental component (as we will see tomorrow).
Matrices are an ideal model to describe this transition.

Examples of matrices from biological systems:

- **Blue parts of the matrices represent non-zero elements**
How do matrices work

How can we analyse matrices

\[ w = \frac{\sum(n_{t+1})}{\sum(n_t)} \]

\[
\begin{pmatrix}
184 \\
42 \\
97
\end{pmatrix}
= 
\begin{pmatrix}
0 & 0 & 1.56 \\
0.15 & 0 & 0 \\
0 & 0.17 & 0.74
\end{pmatrix}
\begin{pmatrix}
276 \\
57 \\
118
\end{pmatrix}
\]

\[ \sum(n_{t+1}) = 323 \]

\[ \sum(n_t) = 451 \]

\[ w = \frac{323}{451} = 0.716 \]

- Observed (average per capita) population growth rate
How do matrices work

How can we analyse matrices

\[
\begin{align*}
    w &= \frac{\sum(n_{t+1})}{\sum(n_t)} \\
    &= \frac{184}{0.15} \\
    &= 1.56 \\
    &= \frac{276}{0.17} \\
    &= 1.61 \\
    &= \frac{57}{0.74} \\
    &= 0.76 \\
    &= \frac{118}{0.74} \\
    &= 0.76 \\
    &\quad \\
    \end{align*}
\]

\[
\begin{align*}
    \Sigma(n_{t+1}) &= 323 \\
    \Sigma(n_t) &= 451 \\
    w &= \frac{323}{451} = 0.716
\end{align*}
\]

- Observed (average per capita) population growth rate
- In year \( t+1 \) the population is 71.6 % as large as it was in year \( t \). On average one individual in year \( t \) is only 0.716 individuals in year \( t+1 \) (hence the per capita bit)
How do matrices work

- $\lambda =$ per capita population growth rate when the population is at equilibrium or long-term population growth rate. This is the dominant eigenvalue of the matrix.

- If a population structure is at equilibrium, then $\lambda = \omega$. When $\lambda > 1$ the population is growing, $\lambda < 1$ the population is declining and $\lambda = 1$ the population is constant.
How do matrices work

- $\lambda =$ per capita population growth rate when the population is at equilibrium or long-term population growth rate. This is the dominant eigenvalue of the matrix.
- $\omega =$ per capita population growth rate given an observed population vector. If a population structure is at equilibrium, then $\lambda = \omega$.
How do matrices work

- $\lambda = \text{per capita population growth rate when the population is at equilibrium or long-term population growth rate. This is the dominant eigenvalue of the matrix.}$
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Reproductive value

- From the matrix model we can find the right \((w)\) and left \((v)\) eigenvectors of the matrix \(A\) associated with the dominant eigenvalue.
Reproductive value

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- The right eigenvector \(w\) is the stable (st)age distribution or the long term equilibrium states.
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- The left eigenvector \( (v) \) is the reproductive value for the population at equilibrium.

Reproductive value (Fisher 1930): “To what extent will persons of this age, on the average, contribute to the ancestry of future generations? This question is of some interest, since the direct action of Natural Selection must be proportional to this contribution.”
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Reproductive value (Fisher 1930): “To what extent will persons of this age, on the average, contribute to the ancestry of future generations? This question is of some interest, since the direct action of Natural Selection must be proportional to this contribution”
Reproductive value

- Function of both recruitment and survival probability. For most vertebrates reproductive value peaks with young breeding adults.
The association between a matrix element and $\lambda$. What would happen to $\lambda$ if a matrix element was perturbed?
Sensitivity

- The association between a matrix element and $\lambda$. What would happen to $\lambda$ if a matrix element was perturbed?
- Black dots represent $\lambda$ for the unperturbed matrix. Thick lines = actual consequences. Thin lines = linear approximations.
Sensitivity and Elasticity

- Straightforward to approximate sensitivities analytically, however, they assume a small perturbation to the matrix as the approximations are linear.

\[
\text{Elasticities} = \text{proportional sensitivities (i.e. they sum to one)}
\]

To identify the key demographic rate associated with \( \lambda \) can target demographic rates with high sensitivities / elasticities for conservation / bio-control.
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Limitations of matrices

- Most frequently used analysis assume the population is at equilibrium structure

Ways to get around this

- Demographic rates varying from year to year incorporating environmental variation (adding stochasticity)
Limitations of matrices

- Most frequently used analysis assume the population is at equilibrium structure
- No variation is demographic rates

Ways to get around this

- Demographic rates varying from year to year incorporating environmental variation (adding stochasticity)
• What if demographic rates vary with time?
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Instead of working with average lambda well want to work with the long-run stochastic growth rate
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Stochastic matrices

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- We will see an example tomorrow
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- Also see papers by Tuljapurkar et al.
Basic concepts of population and demography
Summary

- Basic concepts of population and demography
- Structured populations
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- Modelling framework for age or stage structured populations
Summary

- Basic concepts of population and demography
- Structured populations
- Modelling framework for age or stage structured populations
- Discrete time models are the most often used - especially matrices