Advanced Topics in Population and Community Ecology and Conservation

Lecture 1

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Overview

Today we will...

- **Revise the concept of population**

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- Revise the concept of population
- **Introduce demographic concepts**

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- Introduce demographic concepts
- **Matrix population models**

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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 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 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

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A quick review

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- B = the number of births

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A quick review

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- D = the number of deaths

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A quick review

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Where:

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- $D =$ the number of deaths
- $I =$ the number of immigrants

A quick review

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- B = the number of births
- D = the number of deaths
- I = the number of immigrants
- E = the number of emigrants

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A quick review

This is often simplified to

$$N_{t+1} = \lambda N_t$$

Where:

- λ summarises $B - D + I - E$

$$\frac{dN}{dt} = rN$$

Where:

- $r = lnN$- the intrinsic rate of increase

A quick review

This is often simplified to

$$N_{t+1} = \lambda N_t$$

Where:

- λ summarises $B - D + I - E$
- λ is the net reproductive rate - the number of organisms next year per organism this year

$$\frac{dN}{dt} = rN$$

Where:

- $r = lnN$- the intrinsic rate of increase

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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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A quick review

Describing mortality and fecundity

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- 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 $s = N - d$ survive and the probability of dying, $p = \frac{d}{N}$

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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

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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

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

Data collection

What if data are not complete?

Year	1	2	3	4	5	6	7	8
Capture history	1	0	1	0	1	1	0	0

- Animal seen known to be alive (1)

Data collection

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Capture history	1	0	1	0	1	1	0	0

- 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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Year	1	2	3	4	5	6	7	8
Capture history	1	0	1	0	1	1	0	0

- 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)

Analysis of capture histories to estimate survival

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

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- Can do this for each year, for each class of animal (age, size, phenotype genotype)

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- 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

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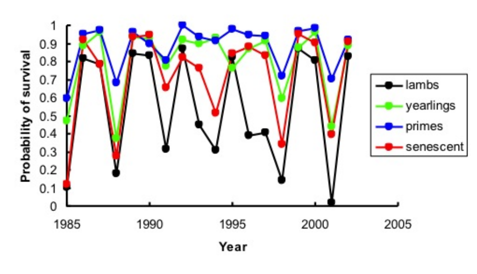
Mark Recapture Analysis

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)

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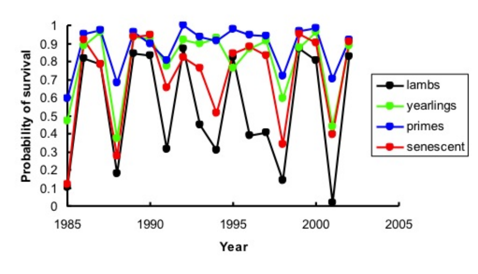

- In long-lived animals, variability in vital rates is greatest in young and old individuals (e.g. Soay sheep)
- Density-dependent and independent processes can interact to influence demography (At low density, climate doesn‘t influence survival, but at high density, climate does influence survival e.g. 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

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A quick review

Population growth

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- 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)

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A quick review

Exponential growth

- All populations have the potential to increase exponentially

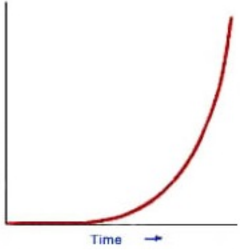

Figure 1. Exponential growth

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A quick review

Exponential growth

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

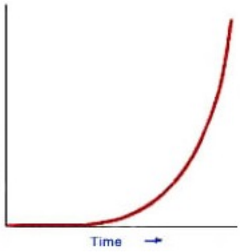

Figure 1. Exponential growth

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?

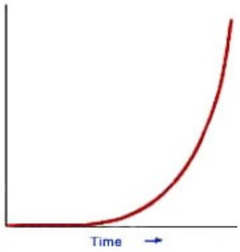

Figure 1. Exponential growth

Limitations of exponential growth

Limits to exponential growth

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

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Limitations of exponential growth

Limits to 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
- Extrinscic 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)

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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

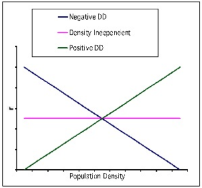

Figure 2. Density dependence

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Density dependence

How does it affect population fluctuations?

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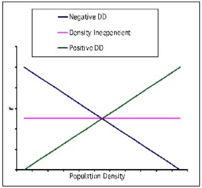
- If the per capita growth rate changes as density varies it is said to be density dependent



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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
- 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

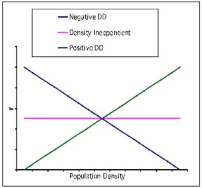

Figure 2. Density dependence

Density dependence

Density Dependence can help us answer many questions

- Why do populations fluctuate in size?

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- Why do populations fluctuate around a mean?

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- Why do populations fluctuate around a mean?
- In common species the mean is high, in rare species the mean is low

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
- Why are the fluctuations different? Large animals often appear to have stable populations, small animals fluctuate variably with huge peaks and troughs

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Density dependence

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)

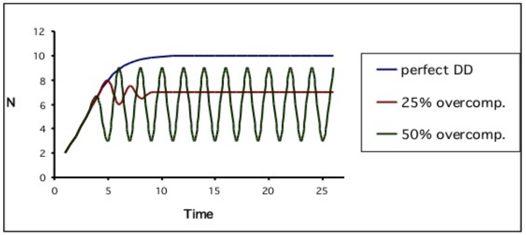

Figure 3. Overcompensation due to density dependence

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)

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"

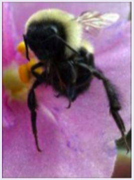

Figure 5. Carpenter bee (Xylocopa micans) on Vitex sp.

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Populations are structured

Models when individuals differ

- What are we trying to explain?

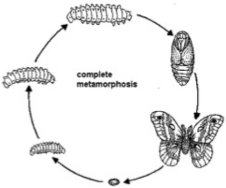
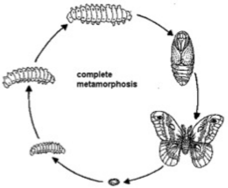


Figure 6. Dark Green Fritillary (Argynnis aglaja) life cycle

Populations are structured

Models when individuals differ

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



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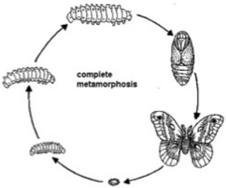

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Populations are structured

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

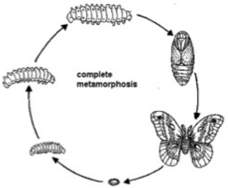


Figure 6. Dark Green Fritillary (Argynnis aglaja) life cycle

Start with a life cycle

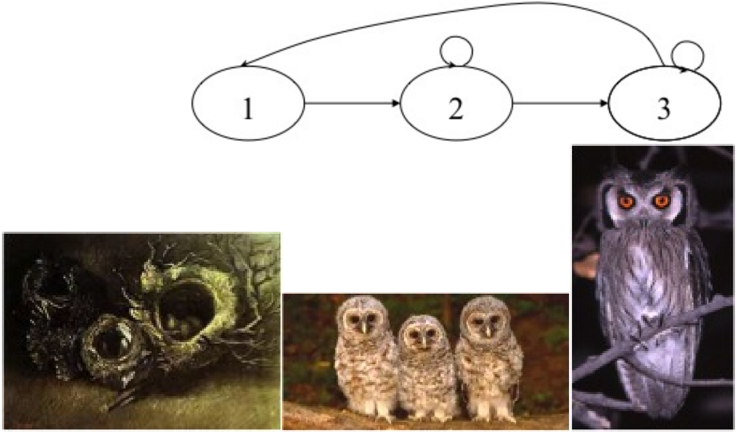
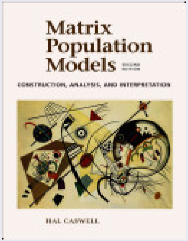


Figure 7. Stage cycle

Matrix models

What they are...

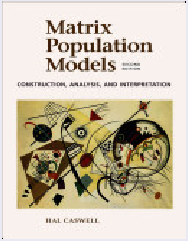
- Matrix population models are a specific type of population model that uses matrix algebra



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



Using vectors to describe the number of invividuals

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

$$\begin{pmatrix} 184 \\ 42 \\ 97 \end{pmatrix} = \text{Population model} * \begin{pmatrix} 276 \\ 57 \\ 118 \end{pmatrix}$$

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

Matrices

Using vectors to describe the number of inviduals

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

$$\begin{pmatrix} 184 \\ 42 \\ 97 \end{pmatrix} = \text{Population model} * \begin{pmatrix} 276 \\ 57 \\ 118 \end{pmatrix}$$

- **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**

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Matrices are an ideal model to describe transitions

Using vectors to describe the number os inviduals

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

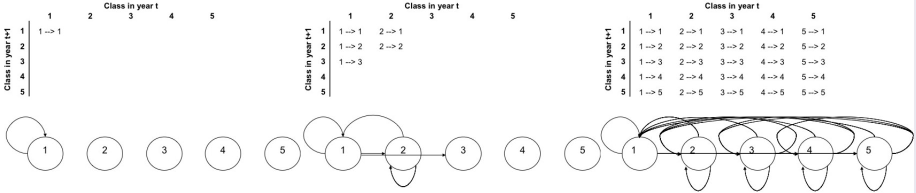
$$\begin{pmatrix} 184 \\ 42 \\ 97 \end{pmatrix} = \begin{pmatrix} 0 & 0 & 1.56 \\ 0.15 & 0 & 0 \\ 0 & 0.17 & 0.74 \end{pmatrix} \begin{pmatrix} 276 \\ 57 \\ 118 \end{pmatrix}$$

$$\mathbf{n_{t+1}} = \mathbf{A} \,.\, \mathbf{n_t}$$

- 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



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Matrices are an ideal model to describe transitions

Biological relevance of matrix elements

Class in year t+1	Class in year t: 1	2	3	4	5	
1	1 --> 1	2 --> 1	3 --> 1	4 --> 1	5 --> 1	= recruitment
2	1 --> 2	2 --> 2	3 --> 2	4 --> 2	5 --> 2	
3	1 --> 3	2 --> 3	3 --> 3	4 --> 3	5 --> 3	
4	1 --> 4	2 --> 4	3 --> 4	4 --> 4	5 --> 4	
5	1 --> 5	2 --> 5	3 --> 5	4 --> 5	5 --> 5	

- Lets 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

Matrices are an ideal model to describe transitions

Biological relevance of matrix elements

Class in year t

Class in year t+1	1	2	3	4	5	
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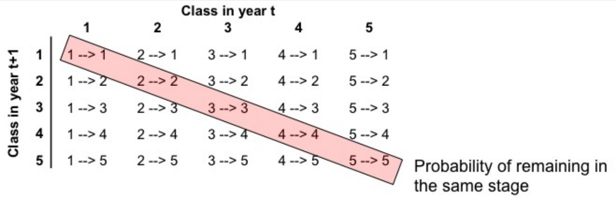
- Lets assume the matrix describes a yearly time step and the population census is conducted just before breeding occurs. The top row represents the per capita number of offspring that are nearly one year old at time t+1 produced by individuals in each class at time t
- For example, if there were 112 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 $283 / 112 = 2.527$

Matrices are an ideal model to describe transitions

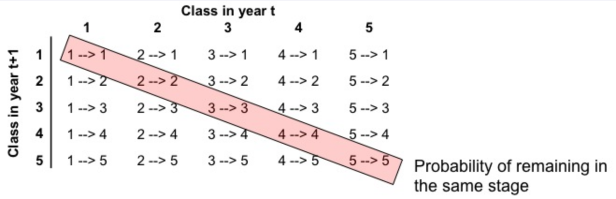
Biological relevance of matrix elements



- 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

Matrices are an ideal model to describe transitions

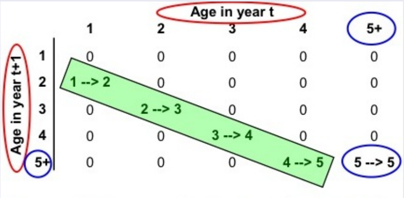
Biological relevance of matrix elements



- 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
- 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

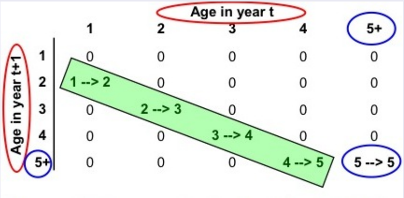
Biological relevance of matrix elements



- Now considering an age structured model individuals can only increase in age

Matrices are an ideal model to describe transitions

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

Matrices are an ideal model to describe transitions

Biological relevance of matrix elements

Age in year t+1 \ Age in year t	1	2	3	4	5+
1	0	0	0	0	0
2	1 --> 2	0	0	0	0
3	0	2 --> 3	0	0	0
4	0	0	3 --> 4	0	0
5+	0	0	0	4 --> 5	5 --> 5

- 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

$$N_{t+1} = N_{t,a} x S_a + N_{t,i} x R_i x S_i$$

Where:

- $N_{t,a}$ = number of adult females at time t

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Matrices are an ideal model to describe transitions

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Where:

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- S_a = annual survival of adult females from time t to time t+1

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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

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Matrices are an ideal model to describe transitions

In a matrix notation

$$\begin{pmatrix} N_{t+l_i} \\ N_{t+l_a} \end{pmatrix} = \begin{pmatrix} S_i R_i & S_a R_i \\ S_i & S_a \end{pmatrix} \begin{pmatrix} N_{t_i} \\ N_{t_a} \end{pmatrix} \quad .$$

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$$\begin{pmatrix} N_{t+l_1} \\ N_{t+l_2} \\ N_{t+l_3} \end{pmatrix} = \begin{pmatrix} F_1 & F_2 & F_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & 0 \end{pmatrix} \begin{pmatrix} N_{t_1} \\ N_{t_2} \\ N_{t_3} \end{pmatrix} \quad .$$

- Each row in the first and third matrices corresponds to animals within a given age range (0 to1 years, 1 to 2 years and 2 to 3 years).

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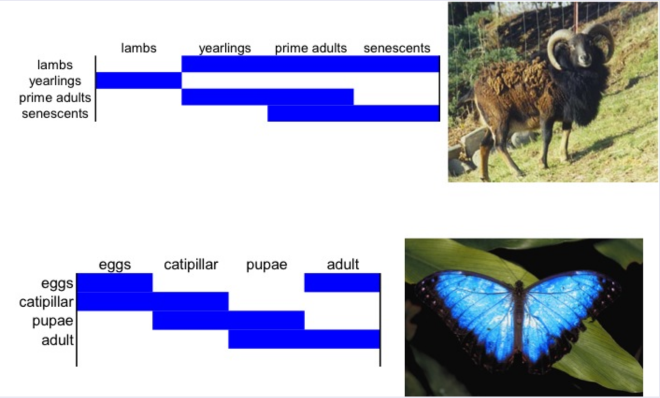
- These models can give rise to interesting cyclical or seemingly chaotic patterns in abundance over time when fertility rates are high
- The terms F_i and S_i can be constants or they can be functions of environment, such as habitat or population size. Randomness can also be incorporated into the environmental 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

$$w = \Sigma(n_{t+1}) \,/\, \Sigma(n_t)$$

$$\underbrace{\begin{pmatrix} 184 \\ 42 \\ 97 \end{pmatrix}}_{\Sigma(n_{t+1}) = 323} = \begin{pmatrix} 0 & 0 & 1.56 \\ 0.15 & 0 & 0 \\ 0 & 0.17 & 0.74 \end{pmatrix} \underbrace{\begin{pmatrix} 276 \\ 57 \\ 118 \end{pmatrix}}_{\Sigma(n_t) = 451}$$

$w = 323 / 451 =$ **0.716**

- Observed (average per capita) population growth rate

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- 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)

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- $\lambda =$ 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.

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- $\omega =$ per capita population growth rate given an observed population vector 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

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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

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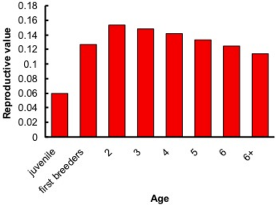
- The right eigenvector w is the stable (st)age distribution or the long term equilibrium states
- The left eigenvector (v) is the reproductive value for the population at equilibrium
- Reproductive value (Fisher 1930): "To what extent will persons of this age, on the average, contribute to the ancestry of future generations? This question is of some interest, since the direct action of Natural Selection must be proportional to this contribution"

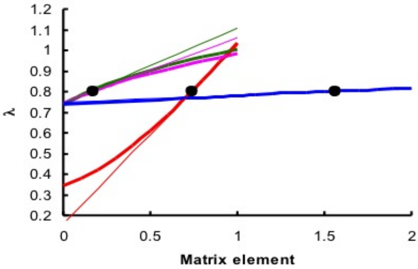
Reproductive value

- Function of both recruitment and survival probability. For most vertebrates reproductive value peaks with young breeding adults



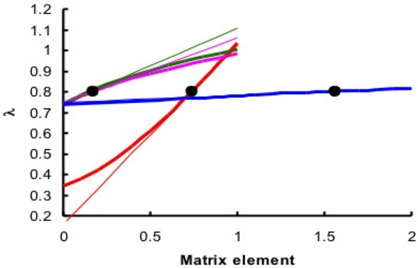
Sensitivity

- The association between a matrix element and λ. What would happen to λ if a matrix element was perturbed?



Sensitivity

- The association between a matrix element and λ. What would happen to λ if a matrix element was perturbed?
- Black dots representλ for the unperturbed matrix. Thick lines = actual consequences. Thin lines = linear approximations



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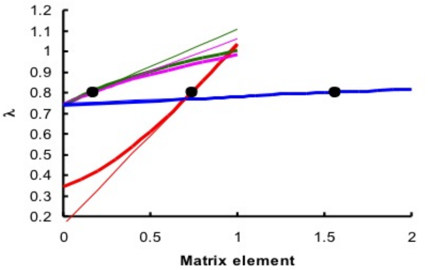
Sensitivity and Elasticity

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



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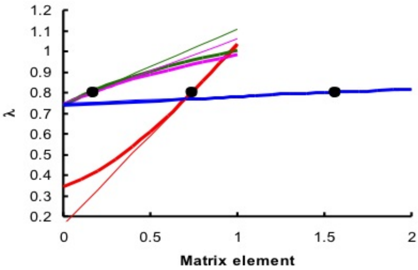

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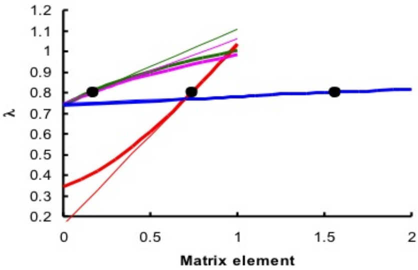
Sensitivity and Elasticity

- Straightforward to approximate sensitivities analytically however, they assume a small perturbation to the matrix as the approximations are linear
- Elasticities = proportional sensitivities (i.e. they sum to one)
- To identify the key demographic rate associated with λ can target demographic rates with high sensitivites / 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)

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Limitations of matrices

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- No variation is demographic rates

Ways to get around this

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

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Stochastic matrices

- What if demographic rates vary with time?

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- Also see papers by Tuljapurkar et al.

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Summary

- Basic concepts of population and demography

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- Structured populations

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- Modelling framework for age or stage structured populations

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