Matrix Modelling

An approach for modelling dynamics of species with age and/or stage structure

One of the most influential approaches in population ecology.

COMPADRE and COMADRE illustrate how widely this approach has been used: Databases containing matrix representations of demography for 345 animal species and 650 plant species.

Why matrix modelling?

- The models we have considered so far (i.e. Ricker and Hassell & Comins) assume that population has no age or size structure.
- However, survival and reproduction often differ among individuals of different ages.
- Consideration of age-specific vital rates can be critical in many areas of wildlife conservation: translocations and reintroductions, harvesting, population viability analysis (PVA), control of invasive species.
- How do we include age-specific survival and fecundity into population models for wildlife species?

Matrix Modelling … let's start!

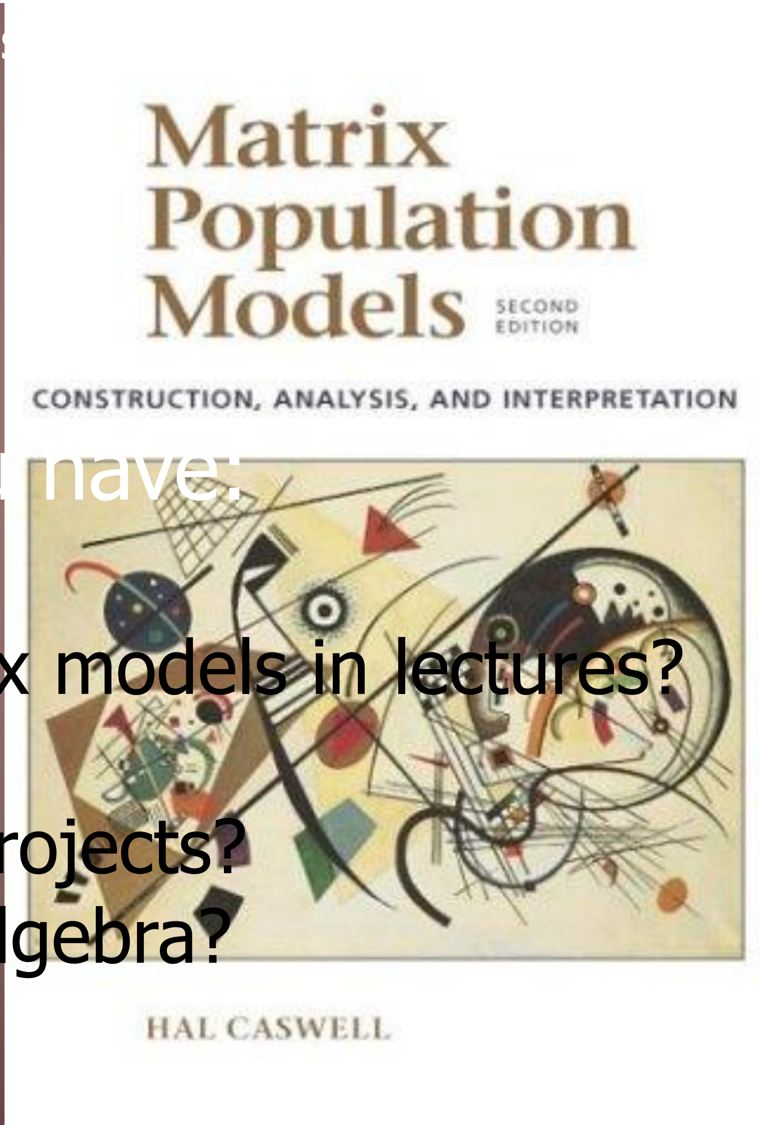
Population growth can be analysed us

Theory of matrices can be found in books such as this of Caswell (1989).

&

Documentation on MyAberdeen

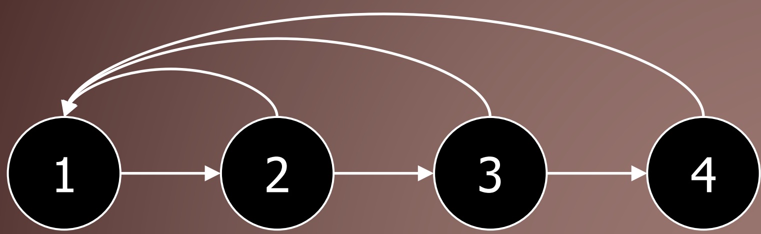
Including in RangeShifter manual…



How many of you have:

1. Heard of age/stage based matrix models in lectures?
2. Used such models in practicals?
3. Used such models in research projects?
4. Remember some (any) matrix algebra?

Life Cycles:



Matrix algebra also provides the opportunity to analyse populations which are structured according to other criteria than age, for example according to "stage" or "size"

Age classified model

Size classified model

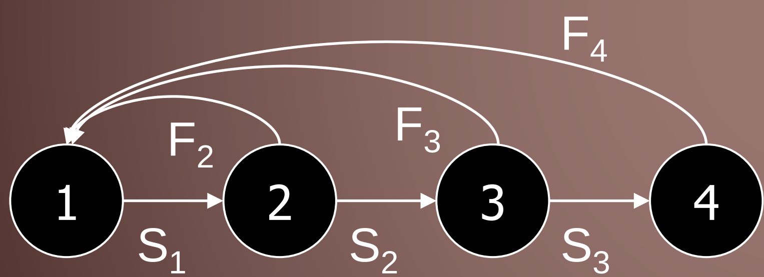
Difference is that individuals can NOT go back in, or stay the same age, but they can in characteristics such as size or weight.

1 2 3 4 Age-class / Size-class

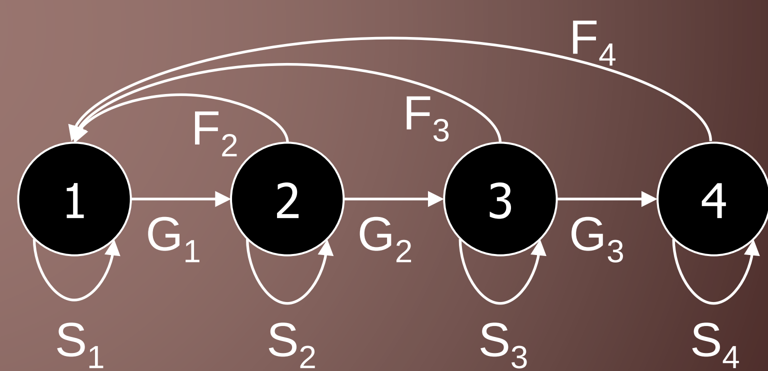
0 1 2 3 4 Age (e.g. in years)

Life cycles: females only! (or know sex ratios)

A life cycle can be broken down into Growth and/or Survival and reproduction (Fecundity). How do these factors, affect population growth and population structure of an unlimited population?



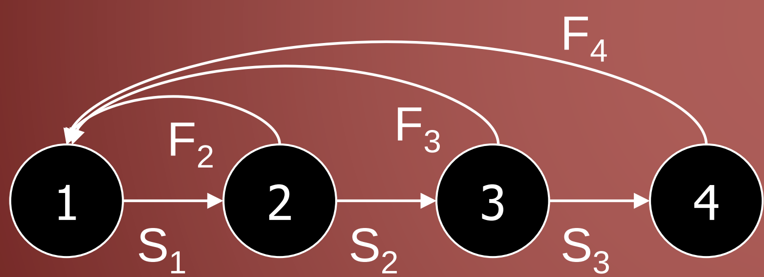
Age classified model



Size/Stage classified model

Matrix Modelling

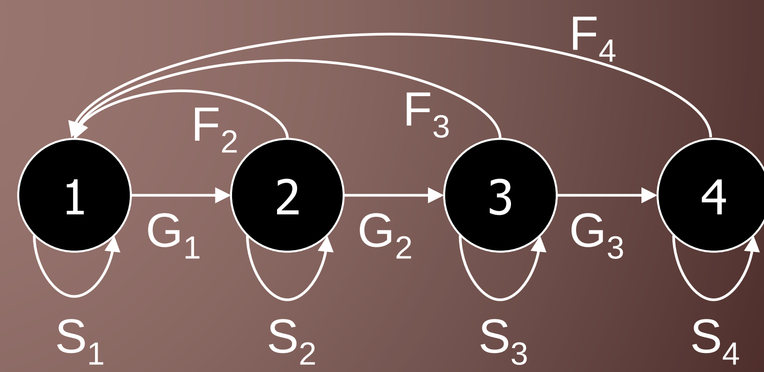
$$M = \begin{pmatrix} 0 & F_2 & F_3 & F_4 \\ S_1 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 \\ 0 & 0 & S_3 & 0 \end{pmatrix}$$



Age classified model

Leslie matrix

$$M = \begin{pmatrix} S_1 & F_2 & F_3 & F_4 \\ G_1 & S_2 & 0 & 0 \\ 0 & G_2 & S_3 & 0 \\ 0 & 0 & G_3 & S_4 \end{pmatrix}$$



Size/Stage classified model

Lefkovitch matrix

Basic Matrix Algebra

A vector is a column of numbers: $\begin{pmatrix} 100 \\ 10 \\ 1 \end{pmatrix}$

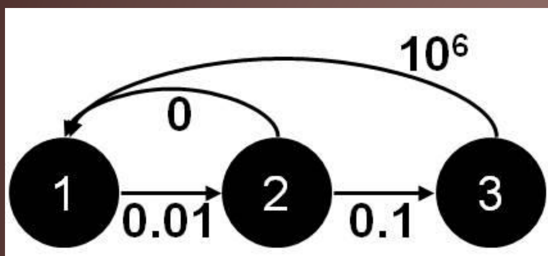
- **Seeds**
- **Juvenile plants**
- **Reproductive adult plants**

In a vector you can easily show population composition. **Stage based population**

Assume, for example the vector above shows the population of a plant species. The top number (100) is the number of seeds per m^2, the middle number (10) is the number of juvenile plants per m^2, and the bottom number (1) is the number of adult, reproducing plants.

Basic Matrix Algebra

Life cycle:



Transition or Projection matrix:

$$\begin{pmatrix} 0 & 0 & 10^6 \\ 0.01 & 0 & 0 \\ 0 & 0.1 & 0 \end{pmatrix}$$

We can interpret the numbers in a transition matrix column by column.

$$\begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix} \rightarrow \begin{pmatrix} 0 \\ 0.01 \\ 0 \end{pmatrix}$$

A population with 1 seed per m^2 exists the next year as juvenile plants with a density of 0.01 m^{-2}.

$$\begin{pmatrix} 0 \\ 1 \\ 0 \end{pmatrix} \rightarrow \begin{pmatrix} 0 \\ 0 \\ 0.1 \end{pmatrix}$$

A population with 1 juvenile plant per m^2 turns into a population of 0.1 reproductive plant in the next year.

$$\begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix} \rightarrow \begin{pmatrix} 10^6 \\ 0 \\ 0 \end{pmatrix}$$

A population with one adult reproductive plant per m^2 turns into a population of one million seeds per m^2 in the next year.

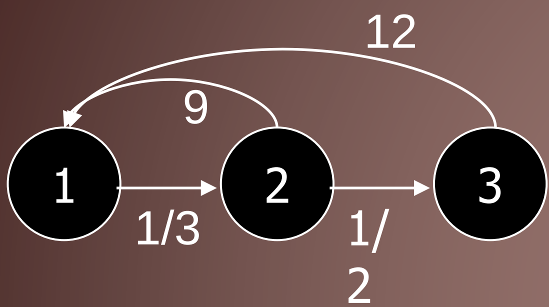
Matrix Multiplication

For any given current population, we can calculate the number of individuals that will be in each class the following time step. Imagine that at a given time the population is made of ***a*** individuals in class 1, ***b*** individuals in class 2 and ***c*** individuals in class 3:

$$\begin{pmatrix} 0 & 0 & 10^6 \\ 0.01 & 0 & 0 \\ 0 & 0.1 & 0 \end{pmatrix}\begin{pmatrix} a \\ b \\ c \end{pmatrix}$$

$$\rightarrow \begin{pmatrix} 0 \times a + & 0 \times b + & 10^6 \times c \\ 0.01 \times a + & 0 \times b + & 0 \times c \\ 0 \times a + & 0.1 \times b + & 0 \times c \end{pmatrix}$$

Example



$$M = \begin{pmatrix} 0 & 9 & 12 \\ 1/3 & 0 & 0 \\ 0 & 1/2 & 0 \end{pmatrix}$$

If the initial population is $(0, 0, 1)^T$ what will be the population structure after 1 year?

$$M = \begin{pmatrix} 0 & 9 & 12 \\ 1/3 & 0 & 0 \\ 0 & 1/2 & 0 \end{pmatrix} \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix} = \begin{pmatrix} 0\text{x}0 & + 9\text{x}0 & + 12\text{x}1 \\ (1/3)\text{x}0 & + 0\text{x}0 & + 0\text{x}1 \\ 0\text{x}0 & + (1/2)\text{x}0 & + 0\text{x}1 \end{pmatrix} = \begin{bmatrix} 12 \\ 0 \\ 0 \end{bmatrix}$$

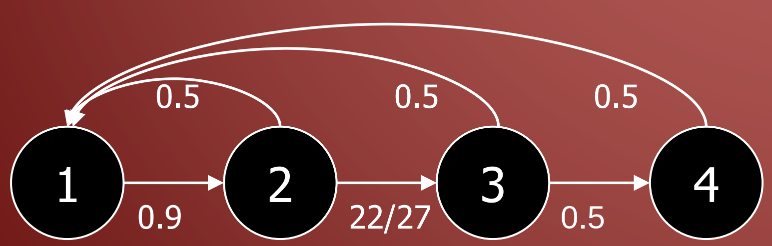
Matrix Multiplication

$$\begin{pmatrix} 0 & 0.5 & 0.5 & 0.5 \\ 0.9 & 0 & 0 & 0 \\ 0 & 22/27 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{pmatrix}\begin{pmatrix} 90 \\ 0 \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ 81 \\ 0 \\ 0 \end{pmatrix}$$

$$\rightarrow \left(\begin{pmatrix} 0 & 0.5 & 0.5 & 0.5 \\ 0.9 & 0 & 0 & 0 \\ 0 & 22/27 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{pmatrix}\begin{pmatrix} 0 \\ 81 \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} 40.5 \\ 0 \\ 66 \\ 0 \end{pmatrix}\right.$$

EXERCISE:

For a certain type of mammal, structured into age classes 0-1, 1-2, 2-3 and 3-4 the following life cycle applies:



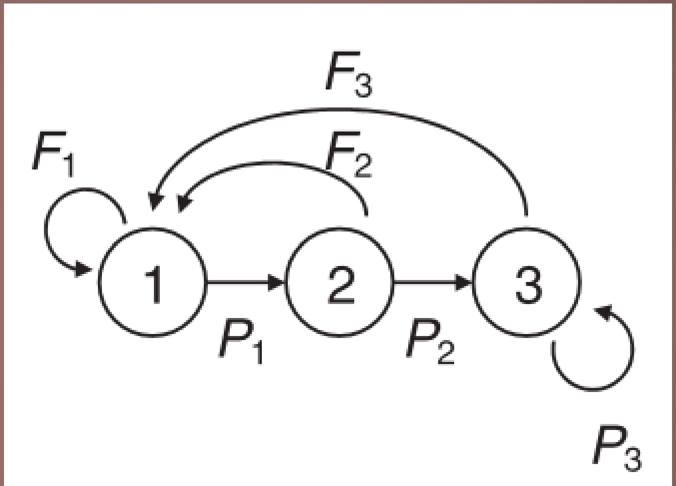
1. Construct a Leslie matrix.

2. If there are 90 individuals of 0 years old, what will be the age structure after 1 year and after 2 years?

Practise with life cycles: 1

Wild boar

Wild boar life cycle:



1 – juveniles
2 – yearlings
3 - adults

What does value P2 signify?
What is the mortality rate of adults?
How old does an individual need to be before it reproduces?

See Bieber & Ruf 2005. Journal of Applied Ecology 42: 1203-1213.

Let's construct the boar's matrix

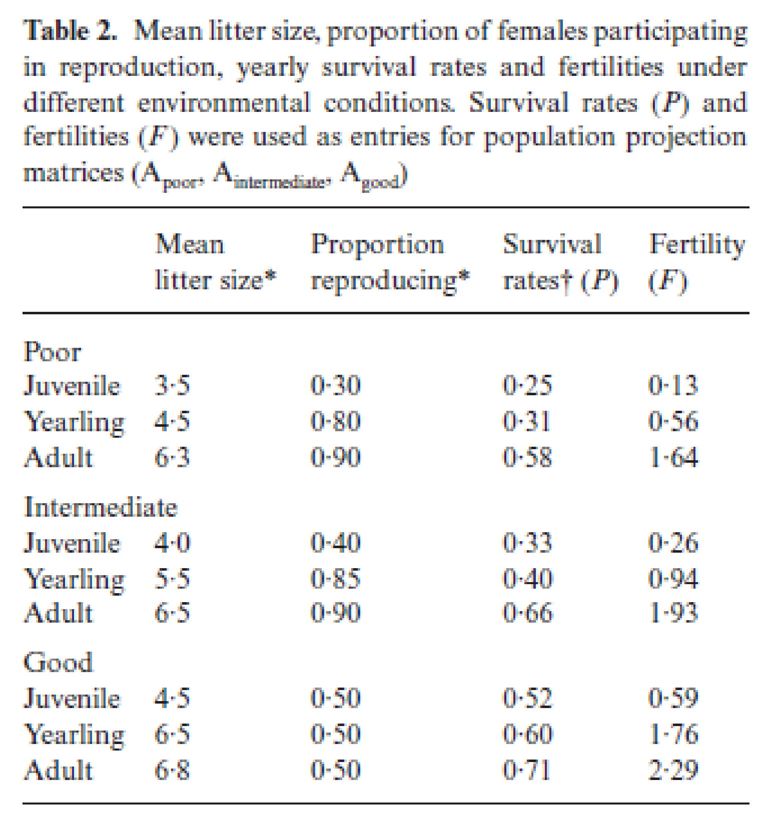


Table 2. Mean litter size, proportion of females participating in reproduction, yearly survival rates and fertilities under different environmental conditions. Survival rates (*P*) and fertilities (*F*) were used as entries for population projection matrices (A_{poor}, $A_{intermediate}$, A_{good})

	Mean litter size*	Proportion reproducing*	Survival rates† (*P*)	Fertility (*F*)
Poor				
Juvenile	3·5	0·30	0·25	0·13
Yearling	4·5	0·80	0·31	0·56
Adult	6·3	0·90	0·58	1·64
Intermediate				
Juvenile	4·0	0·40	0·33	0·26
Yearling	5·5	0·85	0·40	0·94
Adult	6·5	0·90	0·66	1·93
Good				
Juvenile	4·5	0·50	0·52	0·59
Yearling	6·5	0·50	0·60	1·76
Adult	6·8	0·50	0·71	2·29

What is the demographic matrix for good environmental conditions?

How big is the matrix?
Where are the non zero elements?
What values do they take?

0.59	**1.76**	**2.29**
0.52		
	0.60	0.71

Why the difference between mean litter size and fertility?

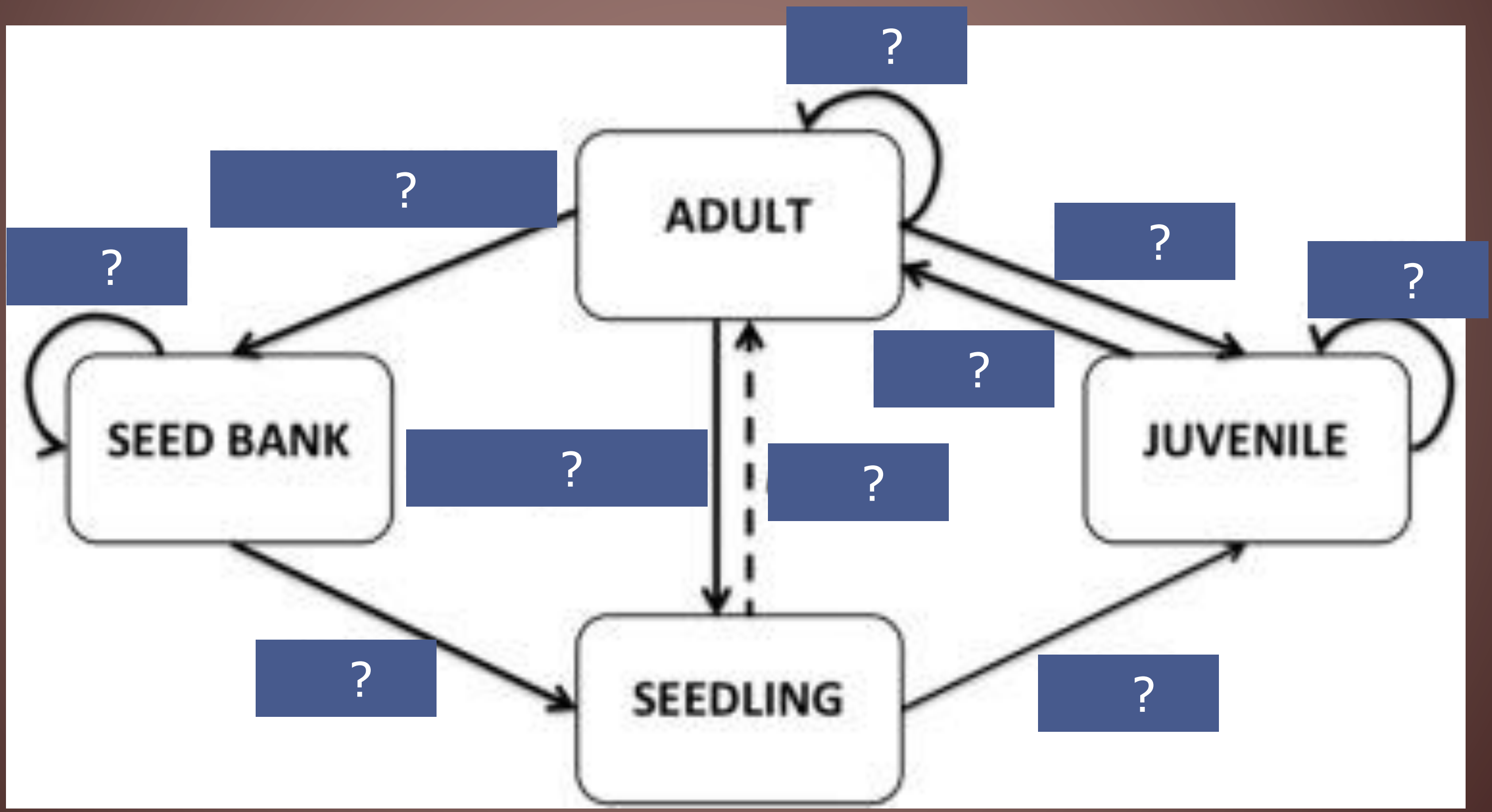
Practise with life cycles: 2

Astragalus bibullatus

Astragalus bibullatus' life cycle consists of three above ground stages, seedlings, juveniles and adults, and a seed stage. Seedlings are first-year plants identified by the presence of cotyledons and a single leaf. Juveniles are non-reproductive, one-stem plants. Adults are either reproductive or non-reproductive, multi-stemmed plants.

Survival of above ground stages (Ps, Pj & Pa) was calculated as the number of individuals still alive in a given stage divided by the total number of individuals originally tagged in that stage. Growth and stasis probabilities (Gs, Sj, & Sa)were conditional on survival
and calculated as the number of individuals that transitioned from a given stage to another (from time t to time t+1). The average number of seeds in the seed bank and seedlings produced per reproductive plant in each year were the product of several vital rates: the proportion of adult plants that reproduced (Rp), the number of fruits per reproducing adult (Fp), the number of seeds per fruit (Fs), annual seed survivorship (Vi), and the proportion of viable seeds that germinate in a single year (Em).

Practise constructing life cycles: 2



Bernardo et al. 2016: Biological Conservation, Volume 203, 2016, 243–251

Life cycles can be sex specific.

North Atlantic Right Whale

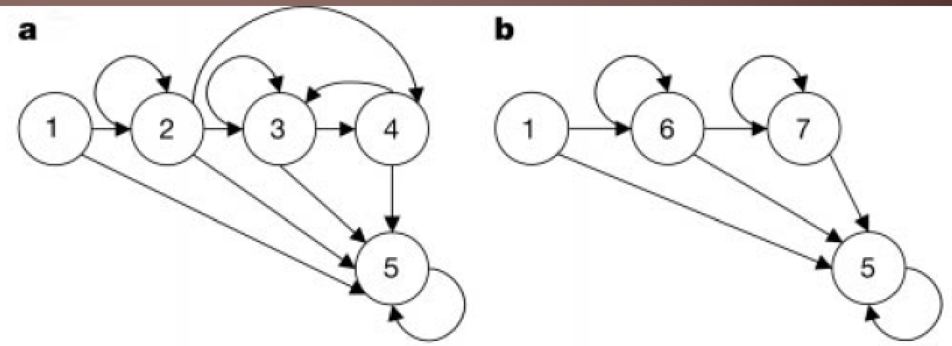


Figure 1 Life cycle graphs of female (**a**) and male (**b**) right whales. Numbers represent different stages: 1, calf; 2, immature female; 3, mature female; 4, mature females with newborn calves (mothers); 5, dead; 6, immature male; 7, mature male. Each arrow represents a possible transition in stage from one year to the next; the arrows going to stage 5 represent stage-specific mortalities. A calf is an individual that was sighted along with its mother. An immature is an individual known to be less than 9 years old. Mature individuals are known to be at least 9 years old, or in the case of females, have been sighted previously with a calf. Mothers are females that are sighted with a newborn offspring. If the sex of an individual is unknown, we assume it has an equal chance of being either female or male, as our data contain almost equal numbers of individuals (141 and 143) known to be female and male, respectively. Maturity status (whether an individual is immature or mature) is unknown in 22% of sightings. When maturity status was unknown, we estimated the probability that the individual was immature (0.30 for males, 0.87 for females) using the method described in ref. 10. These probabilities were used in stage-assignment matrices[10] for likelihood calculations.

See Fujiwara & Caswell 2001. Nature 414: 537-541.

Life cycles can be sex specific.

North Atlantic Right Whale

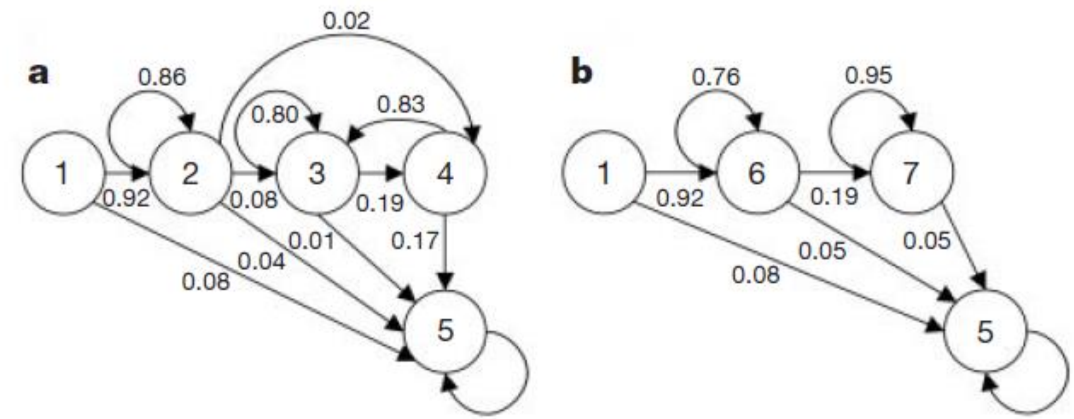


Figure 3 Constant transition probabilities estimated using the best sighting model (M_1). Life cycle graphs of female (**a**) and male (**b**) right whales. The numbers in the circles are the same as in Fig. 1.

What is the mortality rate of an immature male?
What is the probability a mature female will produce a calf?
What is the rate at which immature males become mature?
From these figures, what is the cost of reproduction for a female?

See Fujiwara & Caswell 2001. Nature 414: 537-541.

Leslie Matrix Model: standard assumptions

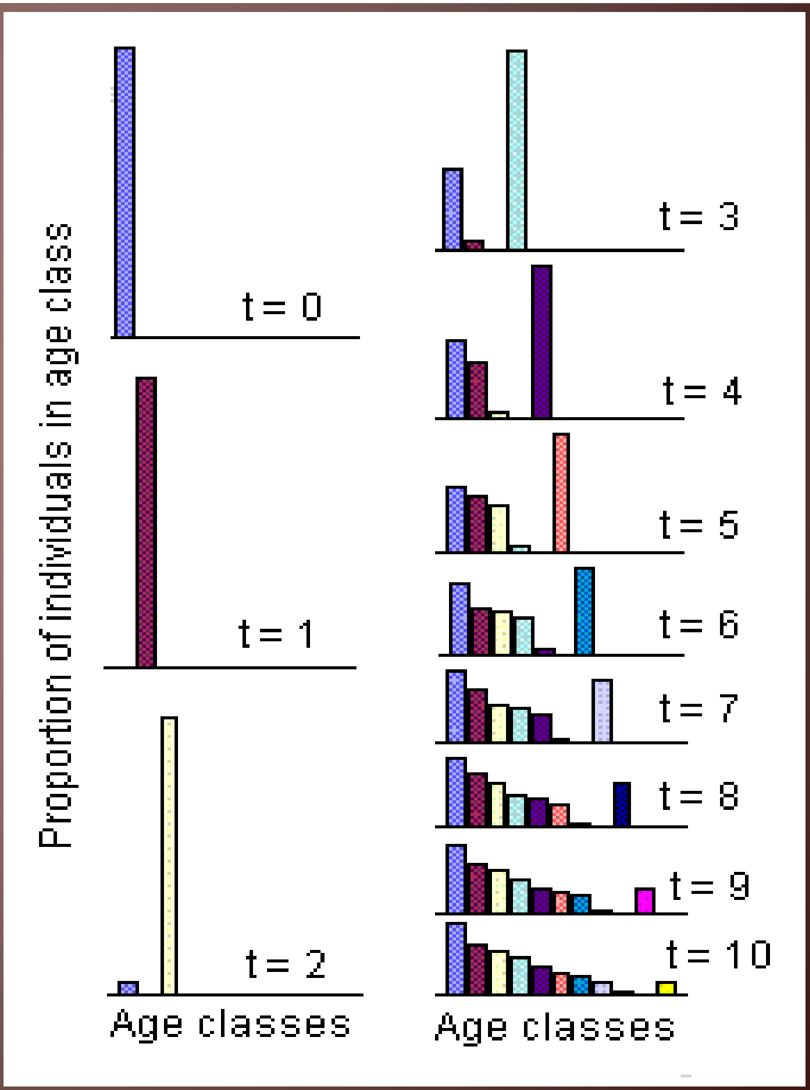
- Model both sexes or only females (e.g., fecundity is the number of daughters per adult female)
- Assume no variation among individuals ***within an age class***
- Normally no density dependence (but can be added)
- Normally no stochasticity (but stochastic matrix models can be built and analysed)
- Often assume closed population, but approach can be extended to include dispersal (or harvest)

Outputs from a matrix model: Stable age distributions

Major feature of Leslie Matrix Model:

Age distribution approaches a stable age

(Note this does not imply a stable population size!)



Stable age distribution

- Repeatedly multiplying an age distribution by a Leslie matrix eventually will produce a **stable age distribution** (i.e. given by the right eigenvector in matrix language).
- **Stable** means that the *proportion* of individuals in each age class does not vary.
- A population with a stable age distribution could be increasing or decreasing. That is, the relative abundances in each age class remain constant even if the absolute numbers change.
- A stable age distribution for a population that is neither increasing nor decreasing ($\lambda=1$) is termed a **stationary age distribution.**

Outputs: Equilibrium rate of growth.

- After a population reaches a stable age distribution, it will grow exponentially with rate equal to lambda.
- Lambda is termed the dominant eigenvalue of the projection matrix.
- Lambda is a long-term, deterministic measure of growth rate of a population in a constant environment.
- The stable age distribution and lambda are independent of the initial age distribution; they depend on the projection matrix.

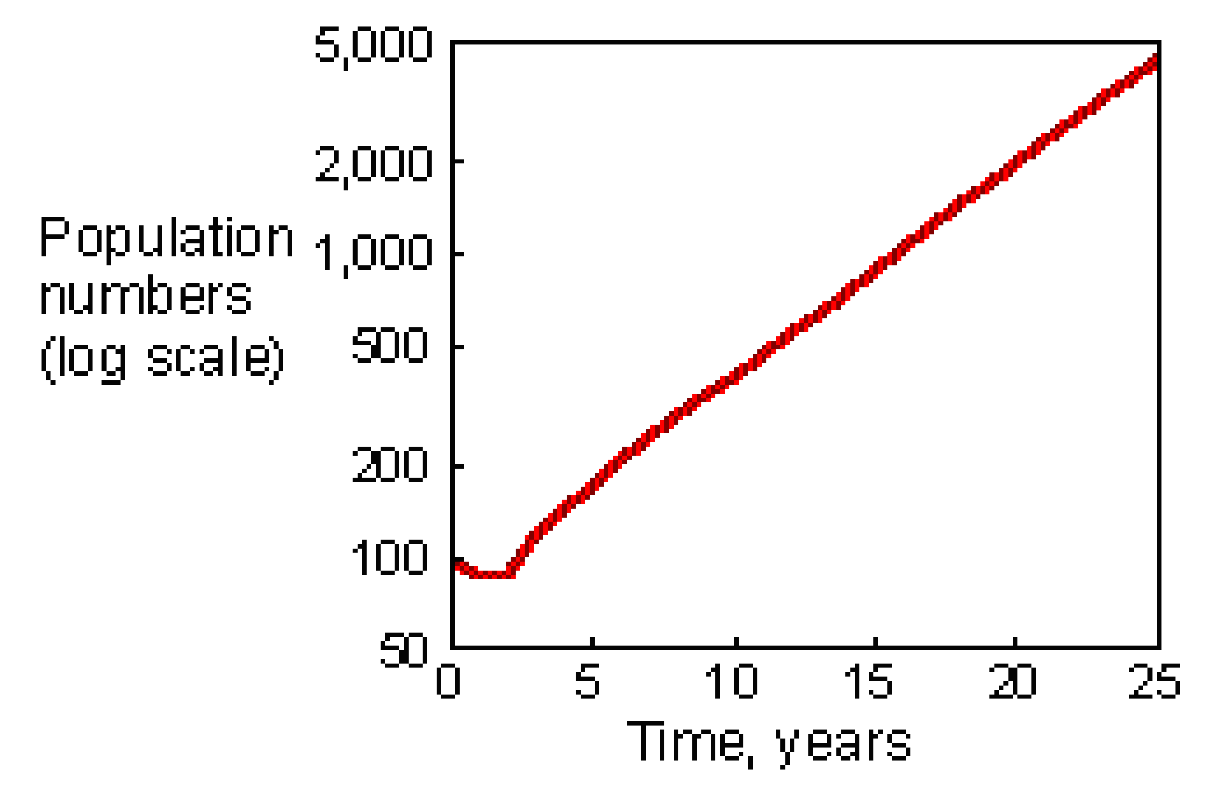
Reproductive Value

- Another useful measure that can be calculated from a Leslie matrix is reproductive value (the dominant left eigenvector).
- Reproductive value is the relative contribution to future population growth an individual in a certain age class is expected to make.

Matrix models

$$N_t = \lambda^t N_0$$

A few damping oscillations are followed by an exponential growth, determined by the dominant λ



Sensitivity Analysis

What happens to the population growth (lambda) when Matrix parameters are changed?

$$\begin{pmatrix} 0 & 9 & 12 \\ 1/3 & 0 & 0 \\ 0 & 1/2 & 0 \end{pmatrix}$$

Not every parameters is as important. Changes in some parameters have a large effect on lambda, while others have little effect. The sensitivity of lambda for changes in matrix parameters is as follows:

Sensitivity analysis

The sensitivity of lambda to all matrix parameters can be calculated and represented in a so-called sensitivity matrix: **S**.

$$\frac{1}{54} \times \begin{pmatrix} 24 & 4 & 1 \\ 144 & 24 & 6 \\ 144 & 24 & 6 \end{pmatrix} = \begin{pmatrix} 0.44 & 0.07 & 0.02 \\ 2.67 & 0.44 & 0.11 \\ 2.67 & 0.44 & 0.11 \end{pmatrix} \Rightarrow \boxed{\begin{pmatrix} - & 0.07 & 0.02 \\ 2.7 & - & - \\ - & 0.44 & - \end{pmatrix}}$$

Biologically impossible matrix parameters are often removed.

One can produce a new matrix **S** of sensitivities of population growth to shifts in all elements of **M**. This makes it possible to compare the importance of various elements (or life history components) for the population under study. BUT….

Sensitivity analysis

In our example population growth is most sensitive for changes in the survival of the first to the middle age class.

$$\begin{pmatrix} - & 0.07 & 0.02 \\ 2.7 & - & - \\ & 0.44 & - \end{pmatrix}$$

Sensitivity values on the sub-diagonal are much higher than the values of the reproduction values in the top row. For example a change of 0.2 in survival is big, while on reproduction of 9 or 12 it’s small.

$$\begin{pmatrix} 0 & 9 & 12 \\ 1/3 & 0 & 0 \\ 0 & 1/2 & 0 \end{pmatrix}$$

So a sensitivity matrix is **scale dependent**. Scale dependency is avoided using an **elasticity analysis**.

Elasticities take into account the fact that survival and fecundity are measured in different units:

In the elasticity analysis they calculate the *proportional changes* in λ as a result of *proportional changes* in the matrix elements

Define: e_{ij} the elasticity of λ to a change in a_{ij}.

Can be calculated from the eigenvectors of **M**

$$e_{ij} = \frac{\partial\lambda/\lambda}{\partial a_{ij}/a_{ij}} = \frac{\partial \ln \lambda}{\partial \ln a_{ij}} = \frac{a_{ij}}{\lambda} \times \frac{\partial\lambda}{\partial a_{ij}} = \frac{a_{ij}}{\lambda} \times s_{ij}$$

Elasticity Analysis

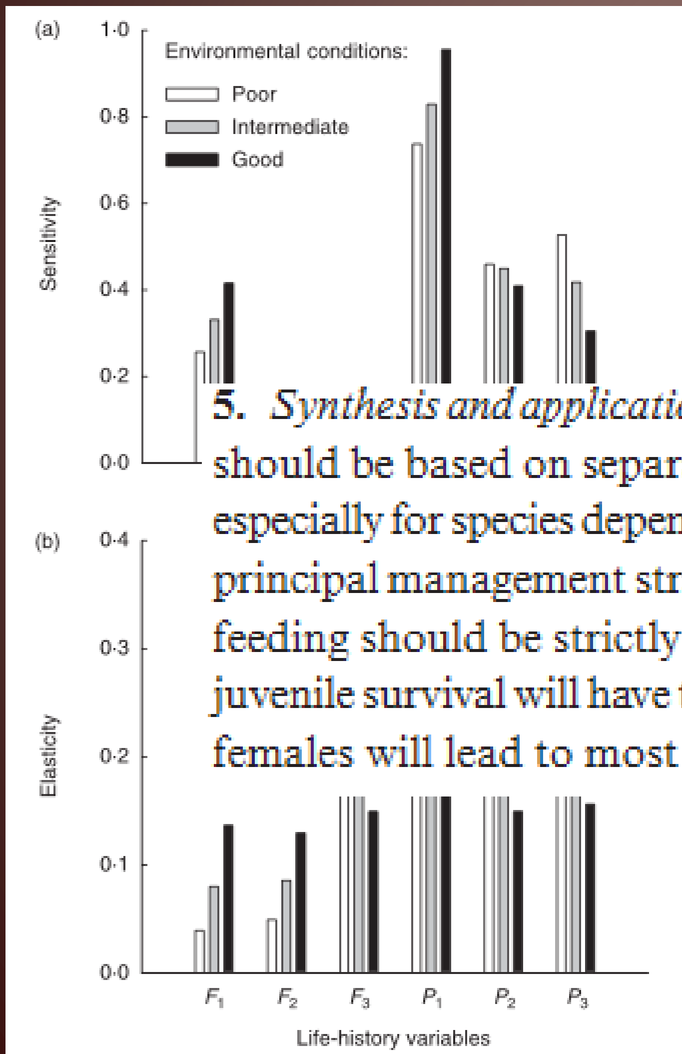
Elasticities of all elements sum to 1

One can produce a new matrix **E** of Elasticities of population growth to shifts in all elements of **M**. This makes possible to compare the importance of various elements (or life history components) for the population under study.

$$\frac{1}{54}\times\begin{pmatrix} 24\times\frac{0}{2} & 4\times\frac{9}{2} & 1\times\frac{12}{2} \\ 144\times\frac{1/3}{2} & 24\times\frac{0}{2} & 6\times\frac{0}{2} \\ 144\times\frac{0}{2} & 24\times\frac{1/2}{2} & 6\times\frac{0}{2} \end{pmatrix} = \frac{1}{108}\times\begin{pmatrix} 0 & 36 & 12 \\ 48 & 0 & 0 \\ 0 & 12 & 0 \end{pmatrix}$$

$$= \frac{1}{9}\times\begin{pmatrix} 0 & 3 & 1 \\ 4 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix}$$

Elasticities for the boar



F1=0.59	F2=1.76	F3=2.29
P1=0.52		
	P2=0.60	P3=0.71

5. *Synthesis and applications*. We suggest that, whenever possible, management strategies should be based on separate elasticity analyses for different environmental conditions, especially for species dependent on pulsed resources. For wild boar we suggest the following principal management strategies to stop further population increases: (i) supplementary feeding should be strictly avoided; (ii) under good environmental conditions, reducing juvenile survival will have the largest effect on λ, whereas strong hunting pressure on adult females will lead to most effective population control in years with poor conditions.

effective management, based on the elasticities?

Adult survival

Saving the North Atlantic Right Whale?

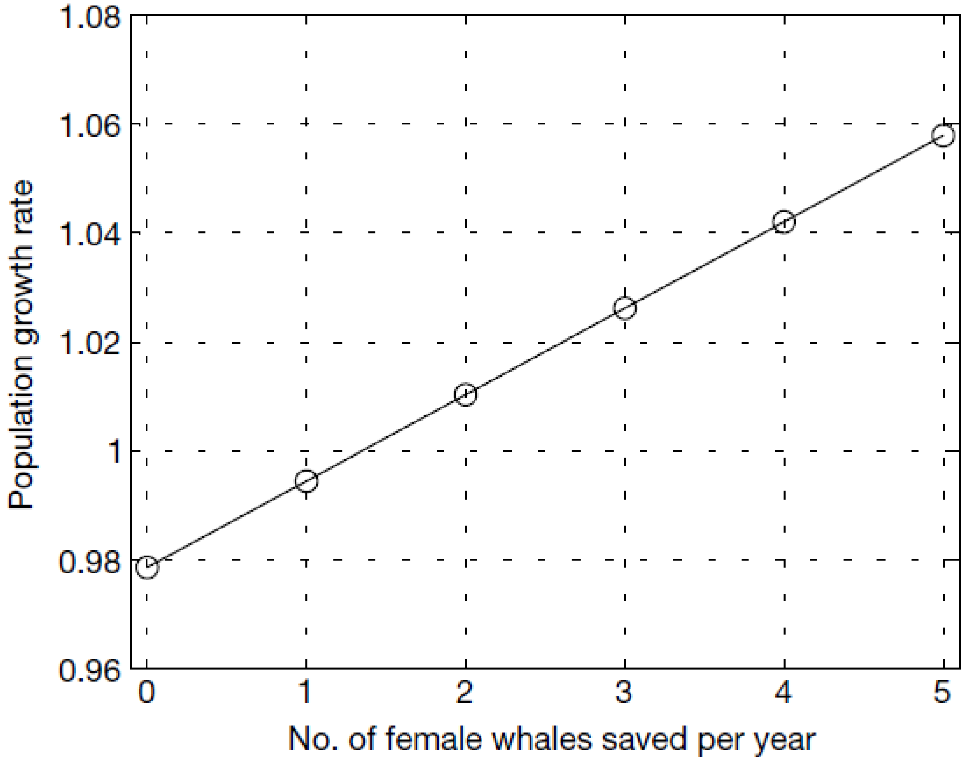


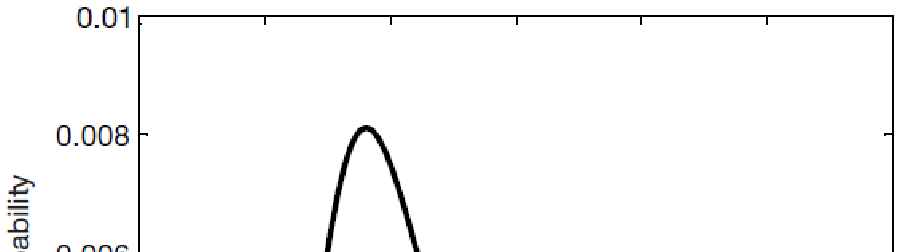
Figure 7 The predicted population growth rate that would result from preventing deaths of females regardless of their stage.

From these model results, how many female whales need to be saved from mortality (e.g. ship collision) to have a positive population growth rate?

Note that this model was run as a stochastic simulation with starting population size same as estimated in real world.

If population was twice as large how many whales would need to be saved?

Saving the North Atlantic Right Whale?



The mean time to extinction under demographic stochasticity is 208 years (similar to the estimate of 191 years in ref. 1). The deterministic time to extinction is 245 years. Thus demographic stochasticity reduces expected extinction time by 15%. Figure 6 gives the complete distribution of extinction times; there is a 5% chance of extinction within 130 years and a 25% chance of extinction within 165 years. These calculations exclude other factors such as continued declining survival trends, environmental stochasticity and Allee effects, all of which would hasten extinction. Thus the

Figure 6 The probability distribution of time to extinction assuming demographic stochasticity. The distribution was calculated from a multi-type branching process, treating transitions and reproduction as independent events (multinomial and Bernoulli, respectively; see ref. 5).

Because it is a stochastic model can gain a distribution of times to extinction.

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chasticity
on risk by

You have now heard how to…

- Incorporate age-specific survival and fecundity into population growth models using matrix models
- Construct and project a Leslie Matrix
- Introduced the terms eigenvectors and eigenvalues
- Calculate stable age distributions
- Calculate age specific reproductive value