

# Age-Structured Models

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Overview: The three computer labs in this series (5, 6 & 7) will gradually build up a hypothetical (but not totally unrealistic) scenario of a marine mammal population that feeds on a fish population, which is harvested commercially. The labs are straightforward but not prescriptive. This means that they allow several ways to achieve the same result. You will be provided with factual background information about the study system (section 1). You will also be given refreshers on the relevant ecological and mathematical theory (sections 2 & 3). A brief section on R commands (section 4) will provide you with all the raw ingredients (commands and syntax) necessary for writing a computer simulation for the system. Note that these are simply the ingredients that I have used for my particular implementation. You should not feel obliged to use all, or any, of them. The main teaching outcome from these labs is for you to meet the objectives in section 5 by putting together the diverse information in the preceding sections. Note that, as is usually the case, not all background information will be relevant. In this lab we will develop a stochastic model for a stage-structured population and use simulation to investigate the sensitivity of numerical output to assumptions and parameter values.

## 1. The Study System

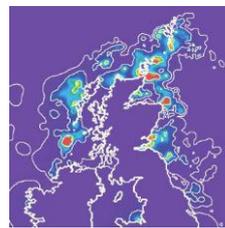
We will base this practical loosely around facts and figures pertaining to the British population of grey seals (*Halichoerus grypus*). The grey seal is the larger of the two species of seal that breed around the British Isles. It is found across the North Atlantic Ocean and in the Baltic Sea. There are two centres of population in the North Atlantic; one in Canada centred on Nova Scotia and the Gulf of St Lawrence and the other around the coast of the UK, especially in Scottish coastal waters. The largest population is in Canada. Populations in Canada, UK and the Baltic are increasing, although numbers are still relatively low in the Baltic where the population was drastically reduced by human exploitation.



Grey seal bull



Grey seal mother and pup



UK distribution



Isle of Rona

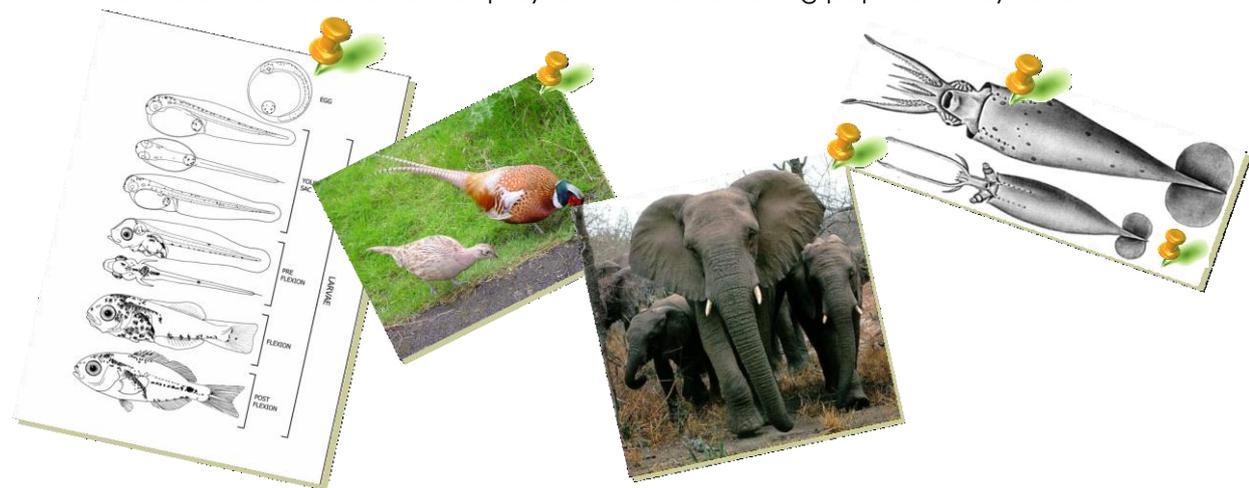
There are clear indications of a slowing down in population growth in UK and Canadian populations in recent years. In Europe, grey seals come ashore on remote islands and coastlines to give birth to their pups in the autumn, to moult in spring, and at other times of the year to haul out and rest between foraging trips to sea. Each mature female grey seal gives birth to a single white-coated pup, which is nursed for about three weeks before being weaned and moulting into its adult coat. About 45% of the world population of grey seals is found in Britain and over 90% of British grey seals breed in Scotland, the majority in the Hebrides and in Orkney. There are also breeding colonies in Shetland, on the north and east coasts of mainland Britain and in Devon, Cornwall and Wales. Although the number of pups born at colonies in the Hebrides has remained approximately constant since 1992, the total number of pups born throughout Britain has grown steadily since the 1960s when records began. Adult male grey seals may weigh up to 350 kg and grow to over 2.3 m in length. Females are smaller, reaching a maximum of 250 kg in weight and 2 m in length.

Grey seals are long-lived animals. Males may live for over 20 years and begin to breed from about age 10. Females often live for over 30 years and begin to breed at the end of their 5th year. Under good conditions about 90% of adult females will come on shore to breed. Little is known about the sex ratio in the population but current estimation methods assume (probably incorrectly) that there is an approximately equal number of males and females. Pup survival is about 70%, lower than the survival rates of approx 90%, estimated for sub-adults and adults.

Grey seals feed mostly on fish that live on, or close to the seabed. In the UK their diet is composed primarily of sandeels, whitefish (cod, haddock, whiting, ling), and flatfish (plaice, sole, flounder, dab) but varies seasonally and from region to region. Food requirements depend on the size of the seal and fat content (oiliness) of the prey. Grey seals often haul out on land, especially on outlying islands and remote coastlines exposed to the open sea. Tracking of individual seals has shown that they can feed up to several hundred kilometres offshore during foraging trips lasting several days. Individual grey seals based at a specific haulout site often make repeated trips to the same region offshore but will occasionally move to a new haulout and begin foraging in a new region. Movements of grey seals between haulouts in the North Sea and the Outer Hebrides have been recorded. The species breeds colonially on mainland shores and small islands and the numbers of pups born on the major colonies have been counted by SMRU annually since the late sixties by land-based surveys and aerial photography. These results are used to provide formal advice to government.

## 2. ecological theory

It is a commonplace notion that individuals are unique. However, traditional mathematical models of populations have tended to ignore individual variation. Any model that recognises differences between population members is called **structured**. Models may be structured by several phenotypic attributes, such as sex, age, size, physiological condition or life history stage. It is also possible to develop population genetics models which have a genotypic structure. Introducing structure into a population model makes it harder to analyse. So, although it is true that individuals are unique, before incorporating any of their biological attributes into a population model, we need to be sure that these attributes play a role in determining population dynamics.



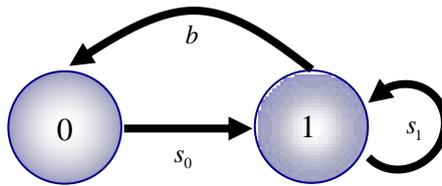
## 3. mathematical theory

An example of a state-structured model for a population with only two stages (mature and juvenile) can be written as follows

$$\begin{aligned} N_{0,t+1} &= bN_{1,t} \\ N_{1,t+1} &= s_1N_{1,t} + s_0N_{0,t} \end{aligned} \quad (1)$$

where  $N_{0,t}$  and  $N_{1,t}$  are, respectively the juvenile and mature individuals in the population and  $b, s_0, s_1$  are terms for fecundity and survival.

This is the simplest stage-structured model possible because it only has two stages and involves no sex. So, the population is either asexual or has a 1:1 sex ratio. We can visualise the life history of the species using a diagram where the states feature as nodes and the demographic processes of birth and death, feature as arrows.



Those of you with memories of matrix notation will notice that the model can also be written as follows:

$$\begin{bmatrix} 0 & b \\ s_0 & s_1 \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \end{bmatrix} = \begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \end{bmatrix} \quad (2)$$

This is called a **Leslie matrix model**. The operation between the two matrices on the left hand side of the equation, is matrix multiplication. Note that the state variables for different years are collected in column vectors (shown in black) and the vital rates (fecundity and survival) are collected in a square matrix (in this case a 2x2 matrix, shown in blue). Clearly therefore, matrix notation is useful as a bookkeeping device. Especially because matrices can be given shorthand names (usually printed in boldface notation). Hence eq. (2) above can be written simply,

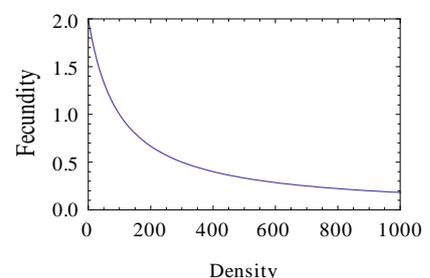
$$\mathbf{L}\mathbf{N}_t = \mathbf{N}_{t+1} \quad (3)$$

Note that all the characteristics of the demography of this system (vital rates and number of states) are captured by the Leslie matrix  $\mathbf{L}$ . If the demographic parameters of the system are constant, the population grows or declines exponentially. The real power of matrix algebra is in its ability to manipulate large data structures. For example, it can be shown that the intrinsic growth rate of the population can be obtained as a standard summary value of square matrices known as the *dominant eigenvalue*. Corresponding to this, there is a list of values called the *dominant eigenvector*. In models of exponentially increasing (or declining), state-structured populations, this list of values gives the relative sizes of states in the population.

The elements of the Leslie matrix can be constant numbers, unknown parameters or functions. This is particularly handy when we want to formulate mathematically the effect of biological processes on demographic rates. A prime example is **density dependence**: consider a population in which some limiting resource gets exploited and deplete, increasingly so with increasing population size. As animals fail to satisfy their requirements for this resource, their performance will suffer. If this impact becomes first apparent in fecundity, then we might choose to formulate  $b$  as a density dependent function. The one shown below is called a **Beverton-Holt function**:

$$b(n) = \frac{b_{\max}\beta}{\beta + n} \quad (4)$$

In this expression,  $b_{\max}$  is the maximum per capita rate of birth,  $n$  is population density (or an index of population density) and  $\beta$  is a parameter that can be interpreted as the value of population density at which the rate of birth has dropped to half of its maximum value. Let's have a look at the graph of this function for  $b_{\max} = 2, \beta = 100$ . As density increases, fecundity declines gradually towards zero. Notice that fecundity has dropped to 50% when density equals 100. Also notice that it takes much greater increases in density to further suppress fecundity.



Another useful extension of the basic model in eq (3) is the addition of demographic stochasticity. The term is used to describe the fact that birth and death are random processes.

Hence, when we are told that an average animal of age 5 or above has an annual survival probability of 0.9, this only means that it is expected to survive with this probability. In a population containing 100 such animals, the survivors from any particular year to the next could be modelled as a Binomial process  $B(0.9,100)$ .

This has an expected value of 90 individuals but this does not mean that exactly 90 individuals will always survive in any given year. Of the standard probability distributions, the Binomial is the one most often used to model survival and the Poisson is most easily employed for birth processes. The binomial may also be used for births in species which are known to give a maximum of one offspring.

## 4. R Ingredients

■ *Matrices* are two-dimensional tables that can be manipulated via the various operations of matrix algebra. A matrix is declared as `matrix(x, nrow= , ncol= )` where `x` is a vector of values (the elements of the matrix) and `nrow, ncol` are the dimensions of the matrix. For example, to construct the following matrix

$$\mathbf{a} = \begin{bmatrix} 1 & 4 \\ 2 & 5 \\ 3 & 6 \end{bmatrix} \quad (5)$$

we would use the statement `a<-matrix(c(1,2,3,4,5,6), nrow=3, ncol=2)` or, more simply `matrix(1:6, 3, 2)`. Matrix multiplication (should you know what it is and want to use it) between two matrices `a` and `b` of suitable dimensions is written as `a%*%b`. However, be warned that some parts of the practical will become harder if you take this route.

■ *Arrays* are similar to matrices but are predominantly used as storage devices and can be used to store higher-dimensional data structures. An array is declared as `array(x, dim= )` where `x` is a list of data values and `dim` is a vector of dimensions. For example, the matrix in eq. (5) can be constructed as an array by using the command `a<-array(1:6, c(3,2))`. To calculate the row or column totals of an array you can use the commands `rowSums()` and `colSums()` respectively.

■ *Element extraction*: is done in the same way for arrays and matrices. Here are some useful examples from the matrix/array in eq. (5). Try them out if you want.

If you want...	You type...	This gives you...
...the third element of <code>a</code>	<code>a[3]</code>	3
...the second row of <code>a</code>	<code>a[2,]</code>	2 5
...the first column of <code>a</code>	<code>a[,1]</code>	1 2 3
...the first four elements of <code>a</code>	<code>a[1:4]</code>	1 2 3 4

■ *Eigenvalues/eigenvectors*: Given a square matrix with the appropriate properties (we will not discuss what these are), R will give you the dominant eigenvalue by using the command `abs(eigen(L)$values[1])`. The corresponding eigenvector is given as `abs(eigen(L)$vectors[,1])`. Note that this is not automatically standardised to give proportions. Therefore, you need to make it add up to 1. In doing this, the command `sum()` will be useful. This, calculates the sum of a list of values.

■ *Simulating values from the Binomial and Poisson*: Consider the random variable  $X \sim B(N, p)$ . You can generate `r` random realisations of this with the command `rbinom(r, N, p)`. Similarly, `r` draws of the Poisson variate  $X \sim \text{Poisson}(\lambda)$  can be simulated by the command `rpois(r, lambda)`.

## 5. practical tasks

- 1 Read carefully the material in sections 1-3 above.
- 2 Read through the tasks in this section
- 3 Decide on the important and useful facts from sections 1-3 that you will need in dealing with the tasks

- 4■ Give names and values to the parameters you will need to use in your code (e.g. pup survival could be `s0`, fecundity could be `b`, etc). Keep those in a separate section of your code (preferably somewhere at the top).
- 5■ Decide on an appropriate data structure to store the sizes (in numbers of individuals) of the different population components.

Model 1: Deterministic model of unrestricted growth

- 6■ Sketch out your population model. In doing this, it may help to ignore explicitly modelling males but you will need to justify this assumption in your report.
- 7■ Consider a population that, in year 1 of the study was founded by 3 adult females and an unknown number of males.
- 8■ Write a bit of code that generates deterministic population trajectories of up to 50 years.
- 9■ Calculate the theoretical intrinsic growth rate of this population
- 10■ Calculate the theoretical stable stage structure for this population and plot it as a histogram
- 11■ Generate a histogram of the observed stage structure at year 50
- 12■ Check that your model/code are performing as they must by comparing the histograms from the two previous steps
- 13■ Generate a time series plot for total population size during the 50 years of the simulation

Model 2: Deterministic model of density-limited growth

- 14■ Copy-paste your original model in a new document. Add a density dependence term to fecundity by assuming the following: Fecundity is affected by the total population size in the current year. Specifically, fecundity drops to 50% of its maximum value when the total population reaches 50 individuals.

Model 3. For a single realisation of the stochastic model of unrestricted growth:

- 15■ Copy-paste your original model in a new document. Add demographic stochasticity to the model by using appropriate probability distributions for fecundity and survival (Note that the population trajectory will now be different every time you run the model!)

## 6. Assessment

Write a report no longer than 3 pages of A4 (single-spaced, Times Roman, 12pt) containing the following:

Model 1. For the deterministic model of unrestricted growth:

- 1■ A mathematical and diagrammatic description of your population model.
- 2■ A table of symbols used for your code, each with an explanation. If they are parameters, then also site a value or plausible range of values.
- 3■ The population's intrinsic growth rate and a histogram of its state-structure after 50 years
- 4■ A time series plot of total population size during the 50 years

Model 2. For the deterministic model of density-limited growth:

- 5■ A histogram of the population's state-structure after 50 years
- 6■ A time series plot of total population size during the 50 years
- 7■ Briefly comment on how the output of this model differs from that of Model 1

Model 3. For a single realisation of the stochastic model of unrestricted growth:

- 8■ A histogram of the population's state-structure after 50 years
- 9■ A time series plot of total population size during the 50 years
- 10■ Briefly comment on how the output of this model differs from that of Model 1
- 11■ Attach your code at the end of the 3 pages as an Appendix.