Matrix population models

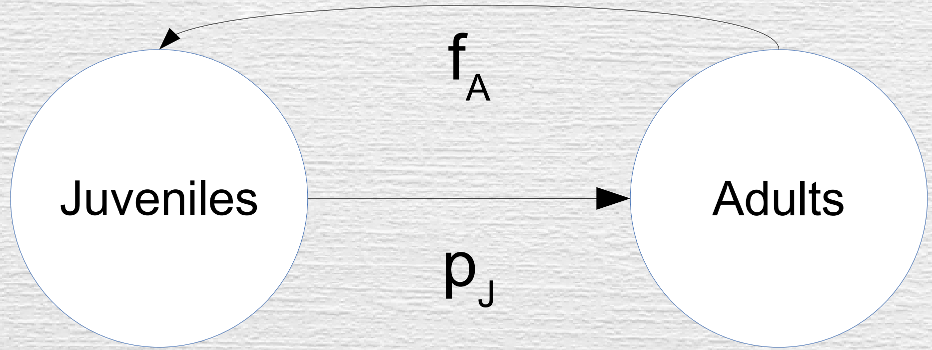
Population trend from survival and reproduction

Trend from demography

- Matrix population models allow us to estimate population growth rate (trend) from demographic rates
  - Like life tables, but do not require long time periods (cohort) or unattainable assumptions (period)
- Matrix models have many advantages
  - Amenable to using survival and reproductive rates from field studies, over relatively short periods
  - Information rich:
    - Estimates of demographic rates are also measures of status
    - Can identify the most important demographic rates and age classes for population growth
    - Can calculate stable age (stage) distribution

A simple age-structured population

- Imagine a species which is born, spends one year growing to maturity
  - Probability of surviving to maturity is p_J
  - Only adults reproduce, and once they reproduce they die
- Newborn females that survive to the next year, per female, is fecundity, f_A
- In a population you will have some adults that are reproducing, and some juveniles that are growing to adulthood



Next year's population

Next year's juveniles

$$J_{t+1} = f_A A_t$$

Total

$$N_{t+1} = f_A A_t + p_J J_t$$

Next year's adults

$$A_{t+1} = p_J J_t$$

Each age class is predicted separately, and then they are combined for a total population size

Next year's population projected

Next year's juveniles

$$f_A A_t = 10 \times 33 = 330$$

Next year's adults

$$p_J J_t = 0.4 \times 66 = 26.4$$

Total

$$N_{t+1} = 356.4$$

Same model, different representation

$$f_J J_t + f_A A_t = J_{t+1}$$

$$p_J J_t + p_A A_t = A_{t+1}$$

This is the same set of equations because…

No reproduction in juveniles, so f_J is 0

No survival of adults, so p_A is 0

Separate the demographic rates from the population sizes

Leslie matrix

Population vectors

$$\begin{bmatrix} f_J & f_A \\ p_J & p_A \end{bmatrix} \times \begin{bmatrix} J_t \\ A_t \end{bmatrix} = \begin{bmatrix} J_{t+1} \\ A_{t+1} \end{bmatrix}$$

This year's population *Next year's population*

Leslie matrix = matrix of demographic rates, describing transitions between adults and juveniles from one year to the next

L is multiplied by a vector of population sizes for each age at time t, but not in the way you think...

Matrix algebra

- Data that can be held in a matrix (rows and columns) can be manipulated using matrix algebra
- We can extract useful information from matrices
  - Growth rate
  - Stable age structure
- But, the rules for working with matrices are different from the arithmetic you are used to
- We'll learn just as much as you need for now...

Matrices

- Made up of rows and columns
- A 2x2 matrix has two rows, two columns
- Each entry is an **element**
  - a, b, c and d are elements
- Can refer to elements
  by row and column
  index – row and column number
  - thus, element 2,1 is c
  - a had index 1,1
- Matrices symbolized by bold, capital letters

$$\boldsymbol{A} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

Our matrix of demographic rates

$$\begin{array}{r c} & \begin{array}{cc} \textit{From this year's juveniles} & \textit{From this year's adults} \end{array} \\ \begin{array}{r} \textit{To next year's juveniles} \\ \textit{To next year's adults} \end{array} & \begin{bmatrix} f_J & f_A \\ p_J & p_A \end{bmatrix} \end{array}$$

Columns are this year's population, rows are next year's

Each element is a contribution by an age this year to an age next year

Our matrix of demographic rates

$$
\begin{array}{rc}
 & \begin{array}{cc} \textit{From this year's juveniles} & \textit{From this year's adults} \end{array} \\
\begin{array}{r} \textit{Have to be born into the juvenile age} \\ \textit{Have to survive being a juvenile to become an adult} \end{array} & \begin{bmatrix} 0 & f_A \\ p_J & 0 \end{bmatrix}
\end{array}
$$

Next year's juveniles produced only through reproduction by this year's adults

Next year's adults only come from this year's surviving juveniles

Estimating λ from a matrix model

- The brute force method
  - Project the population into the future
  - Once stable age distribution has been reached, divide N_{t+1} by N_t to estimate λ
- The mathematically elegant way
  - Calculate the growth rate (λ) and stable age distribution directly from the Leslie matrix

Projecting with a matrix model

- To use the model, we need to **matrix multiply** the Leslie matrix by the population vector
- Matrix multiplication is different
  - Multiply across the columns of the left matrix (or vector), down the rows of the right matrix (or vector), sum the products
  - The output will have the number of rows of the left matrix, the number of columns of the right – two rows and one column

$$\begin{bmatrix} f_J & f_A \\ p_J & p_A \end{bmatrix} \times \begin{bmatrix} J_t \\ A_t \end{bmatrix} = \begin{bmatrix} J_{t+1} \\ A_{t+1} \end{bmatrix}$$

R1C1 of output – across R1 of first matrix, down C1 of second

Across row 1

Down column 1

Row 1, column 1 of the result

$$\begin{bmatrix} f_J & f_A \\ s_J & s_A \end{bmatrix} \times \begin{bmatrix} J_t \\ A_t \end{bmatrix} = \begin{bmatrix} f_J J_t + f_A A_t = J_{t+1} \\ \ldots \end{bmatrix}$$

R2C1 of output – across R2 of first matrix, down C1 of second

Across row 2 *Down column 1* *Row 2, column 1 of the result*

$$\begin{bmatrix} f_J & f_A \\ s_J & s_A \end{bmatrix} \times \begin{bmatrix} J_t \\ A_t \end{bmatrix} = \begin{bmatrix} f_J J_t + f_A A_t = J_{t+1} \\ p_J J_t + p_A A_t = A_{t+1} \end{bmatrix}$$

Calculating growth rate

$$\begin{bmatrix} f_J & f_A \\ p_J & p_A \end{bmatrix} \times \begin{bmatrix} J_t \\ A_t \end{bmatrix} = \begin{bmatrix} J_{t+1} \\ A_{t+1} \end{bmatrix}$$

$$N_t = J_t + A_t \qquad J_{t+1} + A_{t+1} = N_{t+1}$$

$\lambda = N_{t+1}/N_t$ is a natural growth rate measure for a matrix model

Now with parameters and starting population sizes

		From				
		Juveniles	Adults			Time 0
To	Juveniles	0	10	x	Juveniles	66
	Adults	0.4	0		Adults	33

Same calculation as before, but using matrix multiplication

t+1

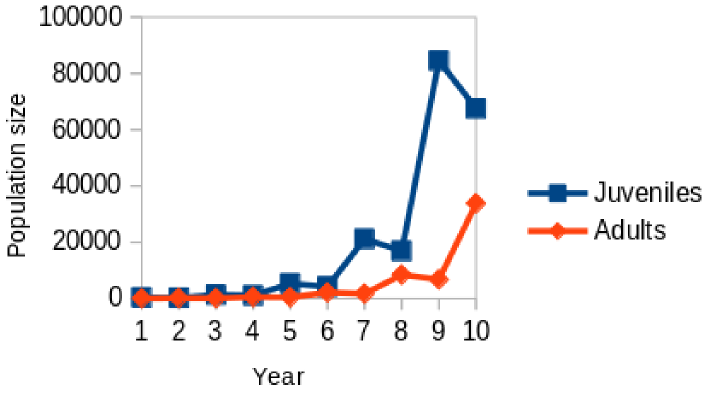
		From						
		Juveniles	Adults			Time 0		Time 1
To	Juveniles	0	10	x	Juveniles	66	=	330
	Adults	0.4	0		Adults	33		26.4
					Nt=0	99		356.4

So, λ = 356.4/99 = 3.6, right?

	A	B	C	D	E	F	G	H	I	J	K	L	M
1			From										
2			Juveniles	Adults			Time 0						
3	To	Juveniles	0	10	x	Juveniles	66						
4		Adults	0.4	0		Adults	33						
5													
6						Nt=0	99						
7													
8								Year					
9			Age	1	2	3	4	5	6	7	8	9	10
10			Juveniles	330	264	1320	1056	5280	4224	21120	16896	84480	67584
11			Adults	26.4	132	105.6	528	422.4	2112	1689.6	8448	6758.4	33792
12													
13			Nt	356.4	396	1425.6	1584	5702.4	6336	22809.6	25344	91238.4	101376
14													
15			λ	3.6	1.111111	3.6	1.111111	3.6	1.111111	3.6	1.111111	3.6	1.111111

Population size is not increasing steadily

Growth rate estimated with N_{t+1}/N_t is not the same every year



Why?

66 juvelines and 33 adults is not the stable age distribution

The mathematically elegant way

- λ can be calculated directly from the matrix **L**, without using the population vector
- Done by finding values that satisfy **Lw = λw**
- **λ** is a vector of **eigenvalues**, **w** is a matrix of **eigenvectors**
  - The largest non-negative element of **λ** is growth rate
  - The vector **w** that pairs with **λ** is the stable age distribution (sort of… more in a minute)
- Eigenvalues, **λ**, are found by solving:

$$det\left(L-\lambda I\right)=0$$

Some more matrix algebra:

$$det\left(L-\lambda\begin{bmatrix}1 & 0\\ 0 & 1\end{bmatrix}\right)=0$$

*I is the identity matrix – has the same property as 1 in arithmetic (a matrix multiplied by **I** gives you back the matrix)*

$$det\left(L-\begin{bmatrix}\lambda & 0\\ 0 & \lambda\end{bmatrix}\right)=0$$

Multiplying a scalar (i.e. a single number) by a matrix – multiply the scalar by each element

Matrix subtraction (or addition)

$$det\left(\begin{bmatrix} f_J & f_A \\ p_J & p_A \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix}\right) = 0$$

$$det\left(\begin{bmatrix} f_J - \lambda & f_A \\ p_J & p_A - \lambda \end{bmatrix}\right) = 0$$

Subtract each element from the right matrix from matching element in the left

$$det\left(\begin{bmatrix} f_J-\lambda & f_A \\ p_J & p_A-\lambda \end{bmatrix}\right)=0$$

Matrix determinant

$$(f_J-\lambda)(p_A-\lambda)-f_A p_J=0$$

$$\lambda^2+(-f_J-p_A)\lambda+(f_J p_A-f_A p_J)=0$$

$$\lambda^2+(0)\lambda+(0\,0-f_A p_J)=0$$

$$\lambda^2+(0)\lambda-f_A p_J=0$$

characteristic equation

Solutions are:

$$\frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

$$\begin{array}{c} \text{a} \\ (1) \end{array} \lambda^2 + \begin{array}{c} \text{b} \\ (0) \end{array} \lambda - \begin{array}{c} \text{c} \\ f_A p_J \end{array} = 0$$

$$\frac{-0 \pm \sqrt{0^2 - 4(1)(-(10 \times 0.4))}}{2(1)}$$

$$\lambda = \frac{4}{2}, -\frac{4}{2}$$

The largest positive eigenvalue is the finite rate of increase

Slightly less elegant way: use Solver to find the solutions

- Bigger matrices are hard to solve analytically
- We can get numeric solutions for growth rate and stable age distribution using Solver
- More during lab...

Stage-based models

- Leslie matrix is age-based – need a fecundity and survival probability for each year of life
- Many organisms become difficult to age once they reach adulthood
- Survival and fecundity values differ by stage instead of by age
  - Juvenile, adult
  - Between size classes
- Survivors take one of two possible paths
  - Survive and remain in the same stage
  - Survival and transition to the next stage
- A Lefkovitch matrix is stage-based

New life history

- Consider a species that:
  - Remains a juvenile for 2 years, with an annual survival probability of 0.4
  - Juveniles that survive become adults
  - Adults live multiple years, with a survival probability of 0.8
  - Adults do all the reproduction, with fecundity of 2 female offspring per female

Juvenile survival

d = duration = 5 years

p = annual survival probability = 0.4

P = survival and remaining juvenile

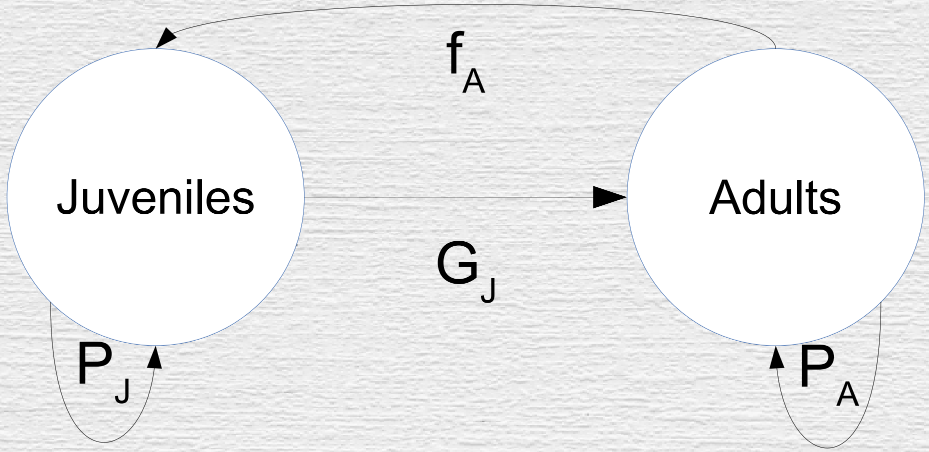
G = survival and growing to adulthood

$$P = \frac{\left(1 - p^{d-1}\right)}{1 - p^{d}}\, p = \frac{\left(1 - 0.4^{1}\right)}{\left(1 - 0.4^{2}\right)} 0.4 = 0.286$$

$$G = \frac{p^{d}\left(1 - p\right)}{1 - p^{d}} = \frac{0.4^{2}\left(1 - 0.4\right)}{\left(1 - 0.4^{2}\right)} = 0.114$$

Survival probability of 0.4 is divided between the two (0.286+0.114 = 0.4)

A life history diagram for this species



$$\begin{array}{r c}
 & \begin{array}{cc}\textbf{\textit{From juvenile}} & \textbf{\textit{From adults}}\end{array} \\
\begin{array}{r}\textbf{\textit{To juvenile}} \\ \textbf{\textit{To adults}}\end{array} & \begin{bmatrix} P_J & f_A \\ G_J & P_A \end{bmatrix}
\end{array}
\qquad
\begin{bmatrix} 0.286 & 2 \\ 0.114 & 0.8 \end{bmatrix}$$

Growth rate

The characteristic equation

$$(1)\lambda^2 - (P_J + P_A)\lambda + (P_J P_A - f_A G_J) = 0$$

$$\frac{(P_J + P_A) \pm \sqrt{(-(P_J + P_A))^2 - 4(1)(P_J P_A - f_A G_J)}}{2(1)}$$

$$\begin{bmatrix} P_J & f_A \\ G_J & P_A \end{bmatrix} = \begin{bmatrix} 0.286 & 2 \\ 0.114 & 0.8 \end{bmatrix}$$

$$\lambda = 1.0852, 0.0007$$

Stable age distribution – eigenvector for λ

- Using the relationship:

  Lw = λw

- The vector, w, that gives the same result when multiplied by either the Lefkovitch matrix (L) or by the growth rate (λ) is the right eigenvector of L for λ
- There is not a unique solution – any constant multiple of **w** is also an eigenvector
- Once w is found it isn't the stable age distribution yet – divide each element by the sum of the elements to get stable age distribution
- Finding w analytically is a little more complicated… we'll do this numerically in Excel

$$\boldsymbol{w} = \begin{bmatrix} -0.928 \\ -0.371 \end{bmatrix}$$

Sum = -1.299

$$\boldsymbol{w} = \begin{bmatrix} 0.715 \\ 0.285 \end{bmatrix}$$

Wrap-up

- The life history of species that live multiple years can be represented in a matrix
  - Leslie matrix = age-specific demographic rates
  - Lefkovitch matrix = stage-specific demographic rates
- We can calculate growth rate from one of these matrices alone
  - Do not need to know population sizes
  - Do not need the population to be at stable age distribution