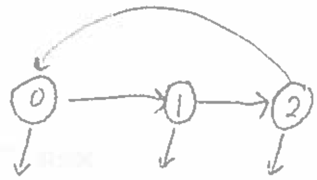
# Age-structured models

$N_{0,t+1} = b N_{2,t}$

$N_{1,t+1} = s_{01} N_{0,t}$

$N_{2,t+1} = s_{12} N_{1,t}$




No individuals survive to be > 2 y.

$b = 2 \qquad s_{01} = 0.5 \qquad s_{12} = 0.2$

$s_{ij}$ fraction of individuals aged $i$ that survive to age $j$.

$N_{0,0} = 3$

$N_{1,0} = 2$

$N_{2,0} = 1$

$b$ the number of offspring produced by 2 year olds

$N_{i,t}$ the number of age $i$ individuals at time, $t$.

What is the number of individuals of each age at $t = 1$ ?

$N_{0,1}, N_{1,1}, N_{2,1}$ ?

Let $t = 0$. Then

$N_{0,1} = b N_{2,0} \qquad N_{0,1} = 2 \times 1 = 2$

$N_{1,1} = s_{01} N_{0,0} \qquad N_{1,1} = 0.5 \times 3 = 1.5$

$N_{2,1} = s_{12} N_{1,0} \qquad N_{2,1} = 0.2 \times 2 = 0.4$

Matrix notation

We can rewrite this problem in matrix notation. This will enable us to more quickly calculate the future popn size, but also to calculate the intrinsic rate of growth and the stable age distribution.

We can write our model as:

$$N_{0,t+1} = 0 \times N_{0,t} + 0\, N_{1,t} + b\, N_{2,t}$$

$$N_{1,t+1} = s_{01} N_{0,t} + 0\, N_{1,t} + 0\, N_{2,t}$$

$$N_{2,t+1} = 0\, N_{0,t} + s_{12} N_{1,t} + 0\, N_{2,t}$$

and in matrix notation.

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \end{bmatrix} = \underbrace{\begin{bmatrix} 0 & 0 & b \\ s_{01} & 0 & 0 \\ 0 & s_{12} & 0 \end{bmatrix}}_{\text{Projection matrix / transition matrix.}} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \end{bmatrix}$$

Practice question

$$N_{0,t} = b_1 N_{1,t} + b_2 N_{2,t}$$

$$N_{1,t} = s_{01} N_{0,t}$$

$$N_{2,t} = s_{12} N_{1,t} + s_{22} N_{2,t}$$

# ...ltiplying matrices and vectors

**...tep 1** Determine the size of your answer.

$$\begin{bmatrix} & & \\ & & \\ & & \end{bmatrix} \begin{bmatrix} \\ \\ \\ \end{bmatrix} = \begin{bmatrix} \\ \\ \\ \end{bmatrix}$$

3 rows x 3 cols 3 rows x 1 col. 3 rows x 1 column.

must be the same

dimensions of answer

**...ep 2**

$$\begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix} = \begin{bmatrix} a_{11}N_1 + a_{12}N_2 + a_{13}N_3 \\ a_{21}N_1 + a_{22}N_2 + a_{23}N_3 \\ a_{31}N_1 + a_{32}N_2 \quad a_{33}N_3 \end{bmatrix}$$

$3 \times 3$ $3 \times 1$ $3 \times 1$

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix} = \begin{bmatrix} a_{11}N_1 + a_{12}N_2 \\ a_{21}N_1 + a_{22}N_2 \end{bmatrix}$$

$2 \times 2$ $2 \times 1$ $2 \times 1$

First row is contribution each age class makes to $N_{0,t+1}$

every age class can potentially contribute to $N_{0,t+1}$

Ex.

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & b \\ S_{01} & 0 & 0 \\ 0 & S_{12} & 0 \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \end{bmatrix} = \begin{bmatrix} 0N_{0,t} + 0N_{1,t} + bN_{2,t} \\ S_{01}N_{0,t} + 0N_{1,t} + 0N_{2,t} \\ 0N_{0,t} + S_{12}N_{1,t} + 0N_{2,t} \end{bmatrix}$$

this was the model just before we turned it into a matrix

Third row contribution each age class makes to $N_{2,t}$

$$= \begin{bmatrix} bN_{2,t} \\ S_{01}N_{0,t} \\ S_{12}N_{1,t} \end{bmatrix}$$

A population of frogs has the following projection matrix

$$\begin{bmatrix} 0.5 & 5 \\ 0.8 & 0 \end{bmatrix}$$

ne number of young of the year frogs is $N_{0,t}$. The number f 1 year old frogs is $N_{1,t}$. The popn model is

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \end{bmatrix} = \begin{bmatrix} 0.5 & 5 \\ 0.8 & 0 \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \end{bmatrix}$$

ppose we currently have 50 young of the year rogs and 20 1 year old frogs how many ogs will there be next year.

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \end{bmatrix} = \begin{bmatrix} 0.5 & 5 \\ 0.8 & 0 \end{bmatrix} \begin{bmatrix} 50 \\ 20 \end{bmatrix} = \begin{bmatrix} \overbrace{0.5 \times 50}^{\text{births from YOY frogs}} + \overbrace{5 \times 20}^{\text{births from 1 yr old frogs}} \\ \underbrace{0.8 \times 50}_{\text{maturation of YOY}} + \underbrace{0 \times 20}_{\text{survivorship of 1 year olds}} \end{bmatrix}$$

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \end{bmatrix} = \begin{bmatrix} 125 \\ 40 \end{bmatrix}$$

, figure out the meaning of the values in the [pro]jection matrix. for the frogs.

$$\begin{array}{c|c} & \begin{array}{cc} \text{YOY} & \text{1 yr} \end{array} \\ \begin{array}{c} \text{YOY} \\ \text{1 yr} \end{array} & \begin{bmatrix} 0.5 & 5 \\ 0.8 & 0 \end{bmatrix} \end{array}$$

5 is the number of YOY frogs produced by each 1 year old.

0.5 is the number of YOY frogs produced by each YOY frog.

0.8 is the prob. that a YOY frog survives to be 1 year old.

In general where $i$ is a row index and $j$ is a column index the entry in the projection matrix is the number of $i$-type individuals produced by a $j$-type individual.

Skills

1) From a model be able to write down the projection / transition matrix.

2) Use projection matrix to predict on time step into the future for a population with 2 or 3 different age classes

3) Know the meaning of the different elements of the projection matrix / transition matrix / Leslie matrix.

4) Calculate eigenvalues for 2x2 model, determine pop^n is increasing.

Question

...ppose the frog population has a projection matrix of

$$\begin{bmatrix} 0.5 & 2 & 3 \\ 0.8 & 0 & 0 \\ 0 & 0.8 & 0 \end{bmatrix}$$

Suppose we initially start with 50 young of the year frogs, 10 1 year old, and 10 2 year old frogs. What will be the number of frogs next year? In two years?

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \end{bmatrix} = \begin{bmatrix} 0.5 & 2 & 3 \\ 0.8 & 0 & 0 \\ 0 & 0.8 & 0 \end{bmatrix} \begin{bmatrix} 50 \\ 10 \\ 10 \end{bmatrix} = \begin{bmatrix} 25 + 20 + 30 \\ 40 + 0 + 0 \\ 0 + 8 + 0 \end{bmatrix}$$

$$= \begin{bmatrix} 75 \\ 40 \\ 8 \end{bmatrix}$$

$$\begin{bmatrix} N_{0,t+2} \\ N_{1,t+1} \\ N_{2,t+1} \end{bmatrix} = \begin{bmatrix} 0.5 & 2 & 3 \\ 0.8 & 0 & 0 \\ 0 & 0.8 & 0 \end{bmatrix} \begin{bmatrix} 75 \\ 40 \\ 8 \end{bmatrix} = \begin{bmatrix} 37.5 + 80 + 24 \\ 60 + 0 + 0 \\ 0 + 4.8 + 0 \end{bmatrix}$$

$$= \begin{bmatrix} 141.5 \\ 60 \\ 4.8 \end{bmatrix}$$

to determine if the population will increase.

To calculate the future population size, we multiply the vector of current population sizes by the projection matrix (on the right).

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \end{bmatrix}$$

Now we ask, is there a number, $\lambda$, that we could multiply the vector of initial population sizes by that would give the same result

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \end{bmatrix} = \lambda \begin{bmatrix} N_{0,t} \\ N_{1,t} \end{bmatrix} ?$$

he answer, in general, is no because the different age classes uld increase by different amounts, but we know from Lab 6 at eventually the population approaches a stable age structure. hen the stable age structure is reached then all age classes o increase by the same factor, $\lambda$, each time step. As such.

$$\begin{bmatrix} 0.5 & 5 \\ 0.8 & 0 \end{bmatrix} \begin{bmatrix} \hat{N}_{0,t} \\ \hat{N}_{1,t} \end{bmatrix} = \lambda \begin{bmatrix} \hat{N}_{0,t} \\ \hat{N}_{1,t} \end{bmatrix}$$

ere $\hat{N}_{0,t}$ is the number of young of the year frogs and $\hat{N}_{1,t}$ is the of 1 year old frogs such that $\frac{\hat{N}_{0,t}}{\hat{N}_{0,t}+\hat{N}_{1,t}}$ is the fraction of frogs when the stable age distribution is reached.

For a 2×2 matrix, λ, is calculated as,

$$\text{Det}\begin{bmatrix} a_{11}-\lambda & a_{12} \\ a_{21} & a_{22}-\lambda \end{bmatrix} = 0$$

$$(a_{11}-\lambda)(a_{22}-\lambda) - a_{21}a_{12} = 0$$

$$\lambda^2 - (a_{11}+a_{22})\lambda + a_{11}a_{22} - a_{21}a_{12} = 0$$

Use quadratic formula

$$\lambda = \frac{a_{11}+a_{22} \pm \sqrt{(a_{11}+a_{22})^2 - 4(a_{11}a_{22}-a_{21}a_{21})}}{2}$$

This gives two solutions. The dominant eigenvalue is the one that is biggest in absolute value. If the dominant If the absolute value of the dominant eigenvalue is bigger than 1, the population will increase. If the dominant eigenvalue is less than 1 in absolute value the population will decrease

Example

$$\begin{bmatrix} 0.5 & 5 \\ 0.8 & 0 \end{bmatrix} \qquad a_{11} = 0.5 \qquad a_{12} = 5$$

$$a_{21} = 0.8 \qquad a_{22} = 0.$$

$$x = \frac{0.5 + 0 \pm \sqrt{(0.5+0)^2 - 4(0 - 5 \times 0.8)}}{2}$$

$$= \frac{0.5 \pm \sqrt{0.25 + 16}}{2}$$

$$= \frac{0.5 \pm 4.03}{2}$$

$$= \frac{4.53}{2} \quad \text{and} \quad \frac{-3.53}{2}$$

The $\left|\frac{4.53}{2}\right| > \left|-\frac{3.53}{2}\right|$ so $\lambda = \frac{4.53}{2}$ is the dominant eigenvalue. The absolute value of the eigenvalue is $> 1$ so the population is increasing.

Leslie matrices have a common structure

\# of offspring produced by age j individuals.

$$\begin{bmatrix} b_0 & b_1 & \cdots & & b_n \\ s_{01} & 0 & \cdots & & 0 \\ 0 & s_{12} & 0 & \cdots & 0 \\ 0 & 0 & s_{23} & 0 & 0 \\ \vdots & & \vdots & & 0 \\ 0 & & 0 & & s_{n-1\,n} \end{bmatrix}$$

subdiagonal: survival probabilities

The intrinsic rate of growth for an age-structured model is calculated as the dominant/ leading eigenvalue of the projection matrix.

ii) The long-term dynamics of an ~~[illegible]~~ age-structured model are dominated by the dominant/ leading eigenvalue.

iii) An $n \times n$ dimensional projection matrix has $n$ eigenvalues. The ~~leading eigen~~ leading or dominant eigenvalue, for a discrete-time model, is the one with largest absolute value.

iv) The age-structured population will increase if the absolute value of the leading eigenvalue is $> 1$.

v) The age-structured population will decrease if the absolute value of the leading eigenvalue is less than 1.

vi) The stable age structure is given by the right eigenvector of the projection matrix. The stable age structure is the fraction of individuals in each age class. If a sufficient amount of time has passed this fraction doesn't change.

tice , (stage-structured popn).

$$\begin{bmatrix} 0 & 2 \\ 0.5 & 0.1 \end{bmatrix} \qquad a_{11} = 0 \qquad a_{12} = 2$$

$$a_{21} = 0.5 \qquad a_{22} = 0.1$$

$$\lambda_1 = \frac{a_{11} + a_{22} + \sqrt{(a_{11} + a_{22})^2 - 4(a_{11}a_{22} - a_{12}a_{21})}}{2}$$

$$= \frac{0.1 + \sqrt{0.1^2 + 4(1)}}{2}$$

$$= \frac{0.1 + \sqrt{4.01}}{2}$$

$$= \frac{2.1}{2}$$

$$= 1.05$$

$$\lambda_2 = \frac{a_{11} + a_{22} - \sqrt{(a_{11} + a_{22})^2 - 4(a_{11}a_{22} - a_{12}a_{21})}}{2}$$

$$= \frac{0.1 - \sqrt{0.1^2 + 4(1)}}{2}$$

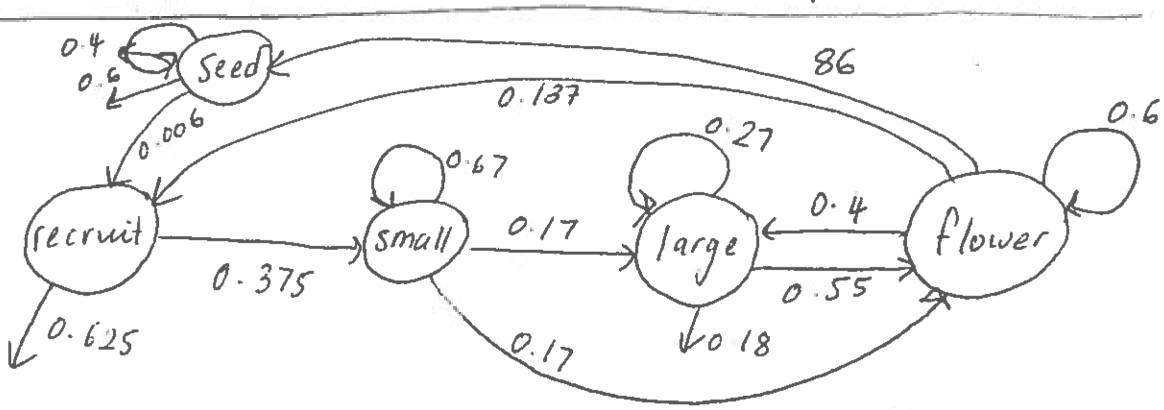
$$= \frac{-1.9}{2}$$

$$= -0.95$$

The dominant eigenvalue is $\lambda_1 = 1.05$. The popn is growing since $|\lambda_1| = 1.05 > 1$.

ge-structured models don't have this special structure.

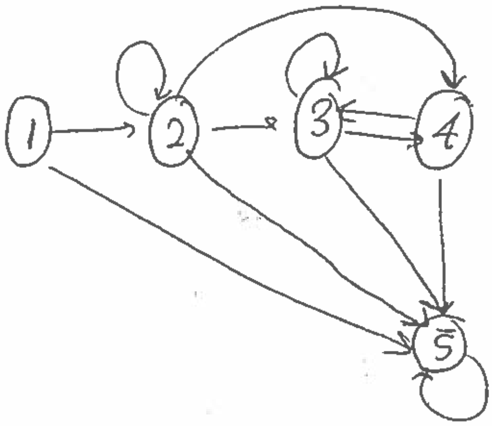
e.




Aquelegia chrysontha.

$$
\begin{array}{c|ccccc}
 & \text{seeds} & \text{recruits} & \text{small} & \text{large} & \text{flower} \\
\hline
\text{seeds} & 0.4 & 0 & 0 & 0 & 86 \\
\text{recruits} & 0.0006 & 0 & 0 & 0 & 0.14 \\
\text{small} & 0 & 0.375 & 0.67 & 0 & 0 \\
\text{large} & 0 & 0 & 0.17 & 0.27 & 0.4 \\
\text{flower} & 0 & 0 & 0.17 & 0.55 & 0.6
\end{array}
$$

Female North Atlantic Right whales




$$
\begin{bmatrix}
0 & F_2 & F_3 & 0 \\
P_{21} & P_{22} & 0 & 0 \\
0 & P_{32} & P_{33} & P_{34} \\
0 & P_{42} & P_{43} & 0
\end{bmatrix}
$$

1. calf
5. dead.
2. immature female
3. mature female.
4. mothers