Age- and stage-structured population models



Today's topics

Motivation

Birth and death rates usually depend on age.

Growth rates will differ between populations with different age structures.

Some age classes contribute more to population growth than others.

This has important management implications.

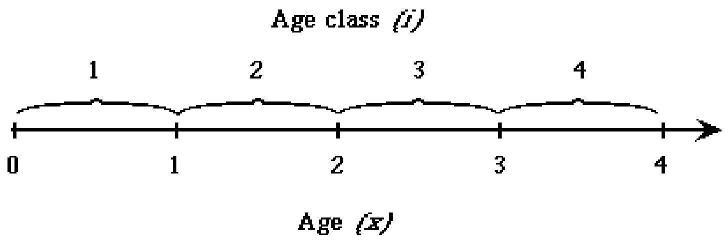
Matrix models vs life tables

Matrix models

- Age is discrete
- Age class is denoted by i
- Each age class can have its own vital rates

Life tables

- Age is continuous
- Actual age is denoted by x
- Each age can have its own vital rates

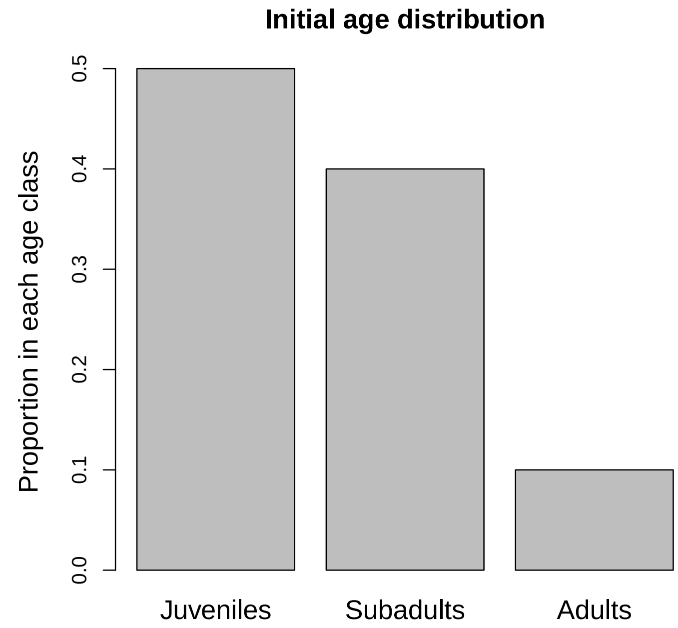


Age-class abundance and age distribution

- $n_{i,t}$ is abundance of age class i in year t
- Suppose initial abundance in the 3 age classes is:
  - $n_{1,0} = 50$ (Age class 1, juveniles)
  - $n_{2,0} = 40$ (Age class 2, subadults)
  - $n_{3,0} = 10$ (Age class 3, adults)
- This implies an initial age distribution of:
  - $c_{1,0} = n_{1,0}/N_0 = 0.5$
  - $c_{2,0} = n_{2,0}/N_0 = 0.4$
  - $c_{3,0} = n_{3,0}/N_0 = 0.1$

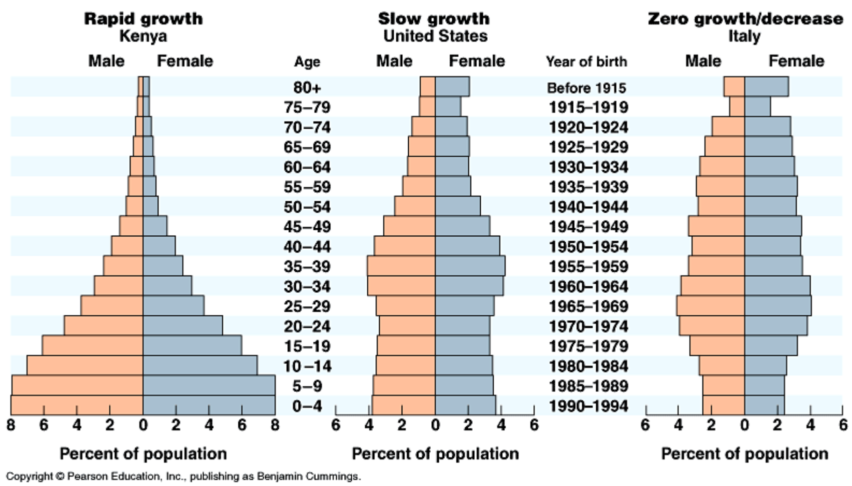
An age distribution describes the proportion of individuals in each age class

Age distribution



Age distribution

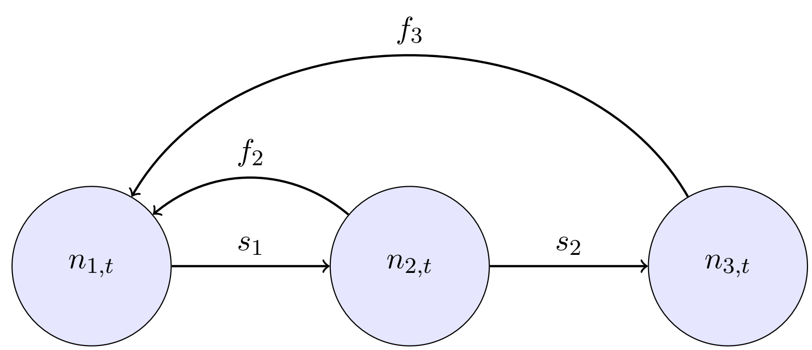
Declining populations have relatively more old individuals than growing populations



Three age class example

We need a model for $n_{i,t+1}$, abundance of each age class in next time step

- Depends on age class survival rates s_i
- And age class birth rates b_i
- Fecundity is often defined as the product of birth rate and offspring survival, $f_i = b_i \times s_0$



How does this population grow?

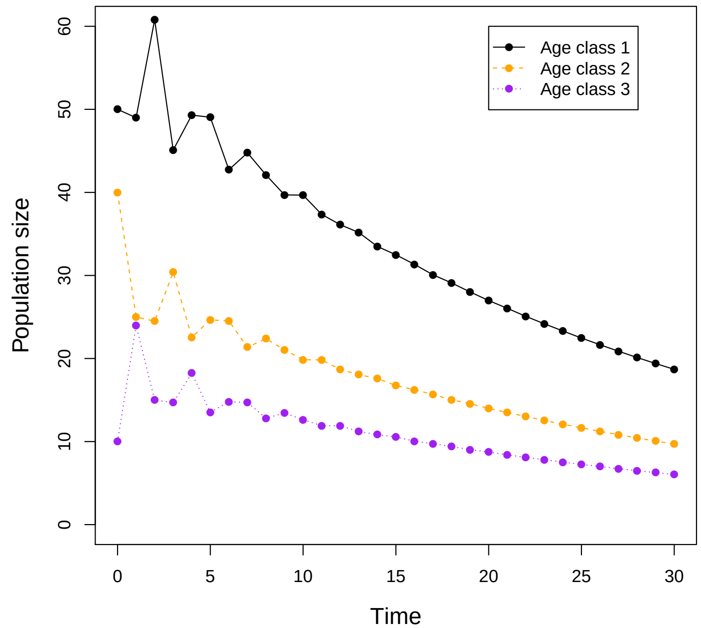
Age class	Equation
1	$n_{1,t+1} = n_{1,t} \times f_1 + n_{2,t} \times f_2 + n_{3,t} \times f_3$
2	$n_{2,t+1} = n_{1,t} \times s_1$
3	$n_{3,t+1} = n_{2,t} \times s_2$

Example

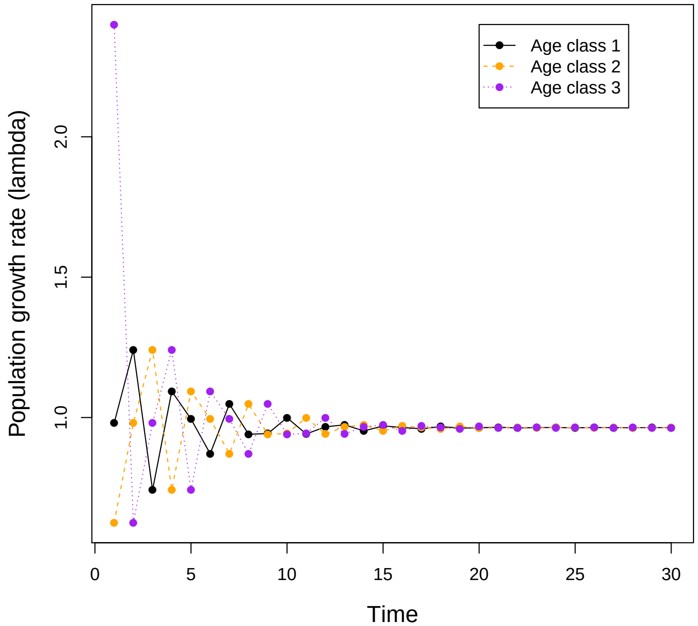
Let's choose values of s_i and f_i

Age class	Initial population size $n_{i,0}$	Survival probability s_i	Fecundity rate f_i
1	50	0.5	0.0
2	40	0.6	0.8
3	10	0.0	1.7

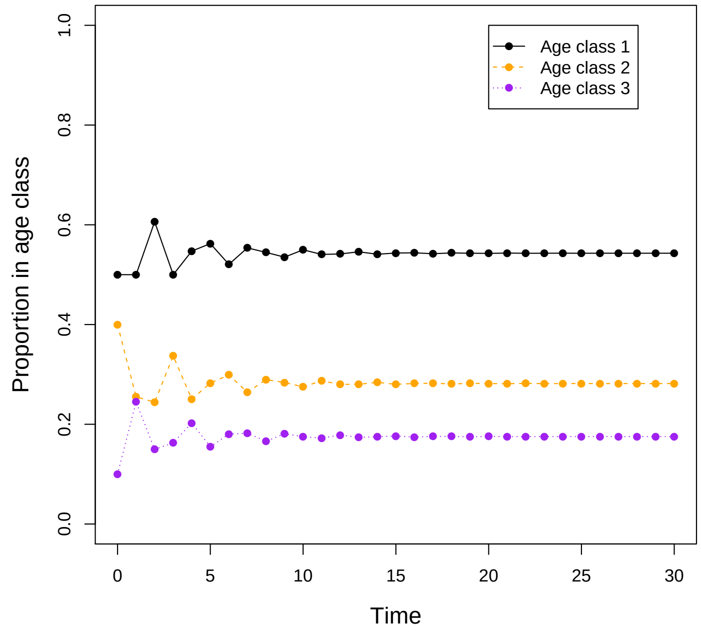
Population size, $n_{i,t}$



Growth rates, $n_{i,t+1}/n_{i,t} = \lambda_{i,t}$



Age distribution, $c_{i,t}$



Important things to note

Age distribution converges to a **stable age distribution** when survival and fecundity rates are constant.

Stable age distribution is the proportion of individuals in each age class when the population converges.

Growth rates of each age class differ at first, but converge once the stable age distribution is reached.

Asymptotic growth rate is λ (without subscript).

Growth rate at the stable age distribution is the same for all age classes, and it is geometric!

Matrix models

Matrix models aren't actually "new" models.

They are the same old models we have been talking about.

But, they make it much easier to compute important quantities like λ and *reproductive value*.

What is a matrix?

Definition: A matrix is a rectangular array of numbers

- Usually denoted by an uppercase, bold letter
- Either square or rounded brackets are used
- Usually, rows are indexed by i, columns by j

Example of a 3×4 matrix:

$$\mathbf{A} = \begin{bmatrix} a_{1,1} & a_{1,2} & a_{1,3} & a_{1,4} \\ a_{2,1} & a_{2,2} & a_{2,3} & a_{2,4} \\ a_{3,1} & a_{3,2} & a_{3,3} & a_{3,4} \end{bmatrix}$$

Leslie matrix

What is it?

- Square matrix
- Fertilities on first row
- Survival probs on lower off-diagonal

Example:

$$\mathbf{A} = \begin{bmatrix} f_1 & f_2 & f_3 & f_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix}$$

How do we use a Leslie matrix?

These two expressions are equivalent:

Age class	Equation
1	$n_{1,t+1} = n_{1,t} \times f_1 + n_{2,t} \times f_2 + n_{3,t} \times f_3$
2	$n_{2,t+1} = n_{1,t} \times s_1$
3	$n_{3,t+1} = n_{2,t} \times s_2$

AND

$$\mathbf{n}_{t+1} = \mathbf{A} \times \mathbf{n}_t$$

Matrix multiplication

$$\begin{bmatrix} aw + bx + cy + dz \\ ew + fx + gy + hz \\ iw + jx + ky + lz \\ mw + nx + oy + pz \end{bmatrix} = \begin{bmatrix} a & b & c & d \\ e & f & g & h \\ i & j & k & l \\ m & n & o & p \end{bmatrix} \times \begin{bmatrix} w \\ x \\ y \\ z \end{bmatrix}$$

Matrix multiplication and Leslie matrix

$$\begin{bmatrix} n_{1,t+1} \\ n_{2,t+1} \\ n_{3,t+1} \\ n_{4,t+1} \end{bmatrix} = \begin{bmatrix} f_1 & f_2 & f_3 & f_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} \times \begin{bmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \end{bmatrix}$$

Reproductive Value

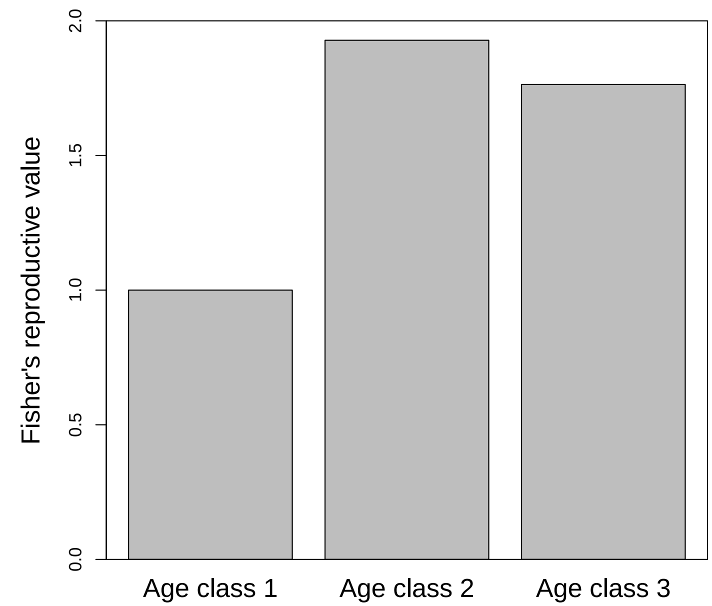
Definition: The extent to which an individual in age class i will contribute to the ancestry of future generations.

$$v_i = \sum_{j=i}^{I} \left(\prod_{h=i}^{j-1} s_h \right) f_j \lambda^{i-j-1}$$

Fact: A post-reproductive individual will have a reproductive value of zero

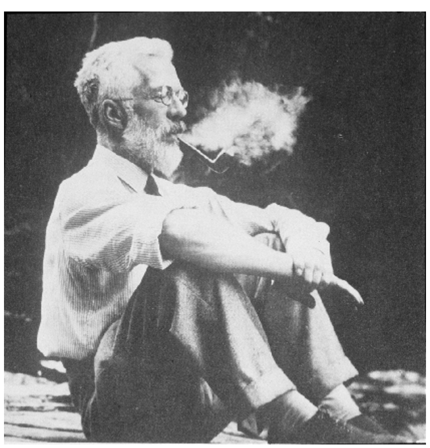
Question: Will a first-year individual have a higher or lower reproductive value than a second-year individual?

Reproductive value for previous example



Reproductive value

Sir Ronald Aylmer Fisher was central to the development of the idea of reproductive value.



Other important quantities

Net reproductive rate

The expected number of individuals produced by an individual over its lifetime

$$R_0 = \sum_{i=1}^{I} f_i \prod_{j=1}^{i-1} s_j$$

Generation time

The time required for a population to increase by a factor of R_0

$$T = \frac{\log(R_0)}{\log(\lambda)}$$

Other properties of the Leslie matrix[1]

The dominant eigenvalue of $\mathbf{A}$ is the growth rate λ.

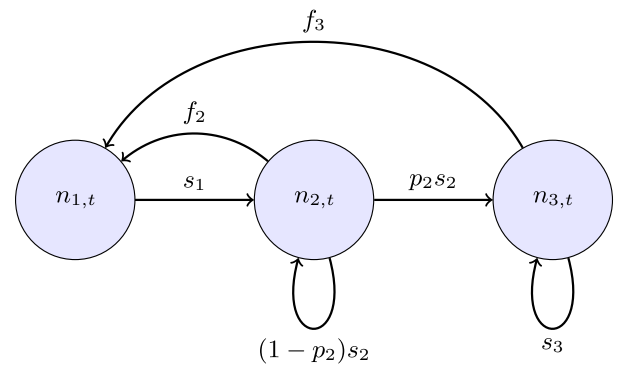
The right eigenvector is the **stable age distribution**.

The left eigenvector is **Fisher's reproductive value**.

[1] This is for graduate students only

Stage-structured population models

- Age isn't always the best way to think about population structure
- For some populations, it is much more useful to think about size structure or even spatial structure.
- These "stage-structured" models differ from age-structured models in that individuals can remain in a stage class (with probability $1 - p_i$) for multiple time periods.



Stage-structured population models

In stage-structured models, individuals transition from one stage to the next with probability p_i.

We can add these transition probabilities to our projection matrix like this:

$$\mathbf{A} = \begin{bmatrix} f_1 & f_2 & f_3 & f_4 \\ s_1 & s_2(1-p_2) & 0 & 0 \\ 0 & s_2 p_2 & s_3(1-p_3) & 0 \\ 0 & 0 & s_3 p_3 & s_4 \end{bmatrix}$$

Summary

Vital rates (s and f) are usually age-specific.

Population growth will depend on age distribution.

If vital rates are constant, population will reach stable age distribution with constant growth rate λ.

Reproductive value indicates which age class contributes the most to population growth.

Matrix models are a convenient method used to work with age-structured populations.