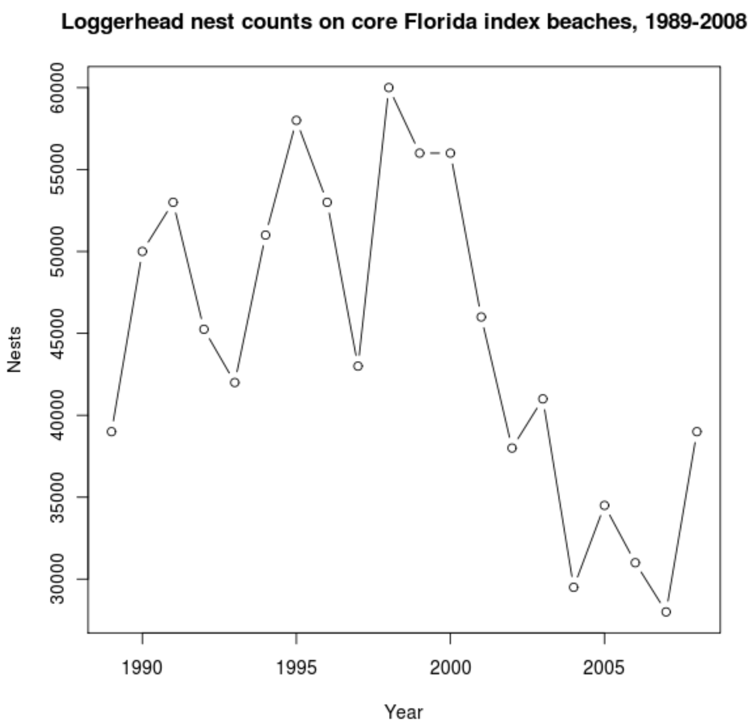
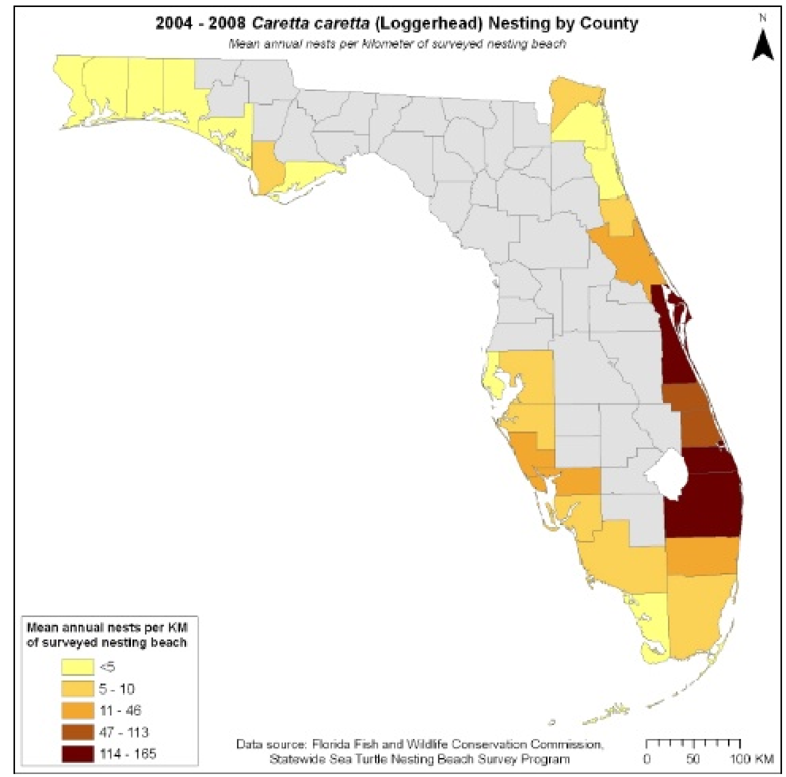
Demography of Structured Populations

8 September 2009

Loggerhead Sea Turtle (*Caretta caretta*)





Classified as Endangered by IUCN under criterion A

(observed, estimated, inferred, or suspected decline of 50% over three generations)

Listed by Convention on migratory species

Listed under CITES

Listed by the US Endangered Species Act as Threatened since 1978

Threats to Loggerhead sea turtle population viability

Population management
- Beach closures
- Turtle Excluder Devices (TEDs)

Life history of *Caretta caretta*

Maturation

- Mature size is attained between age 12 yrs and 35 yrs (most studies: 20-25 years)
- Captives animals mature in 16 to 17 years
- Reproductive life span (after reaching maturity) is estimated at about 32 years

Reproduction

- Clutch size varies from ~70 to ~150 eggs and is correlated with body size
- Migration interval is one to five years
- Development time of eggs is ~60 d
- One to seven nests per year

Survival

- Lifespan in wild is 30-60 years
- Estimates of survivorship vary widely
  - Eggs/hatchlings: 6%-80%
  - Juveniles: ~70%
  - Sub-adults ~ 75%
  - Adults: ~80%

Questions

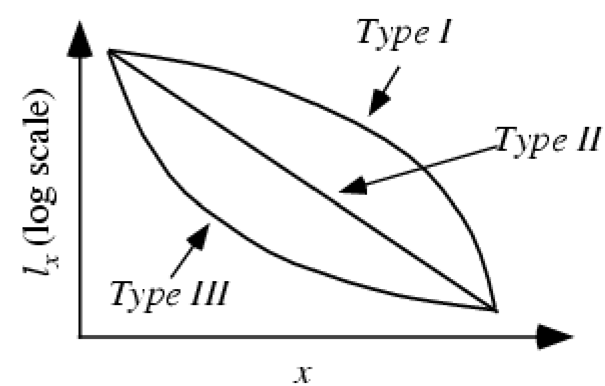
(1) What is the population growth rate?

(2) How do the different life stages contribute to population growth?

(3) How great an effect must interventions have to be successful?

The Leslie matrix and related models, vital rates

- A generalization of the density-independent discrete time population growth process
- State variables are abundance of each age or class
- Constants are the *vital rates*:
  - Survival/mortality
    - May be interpreted as rate, proportion, or probability
    - May also be interpreted as 1/(average lifespan)
  - Fecundity/Fertility
    - May be total offspring or total offspring living to next census
  - Growth rate
  - Regression



The Leslie matrix and related models, vital rates

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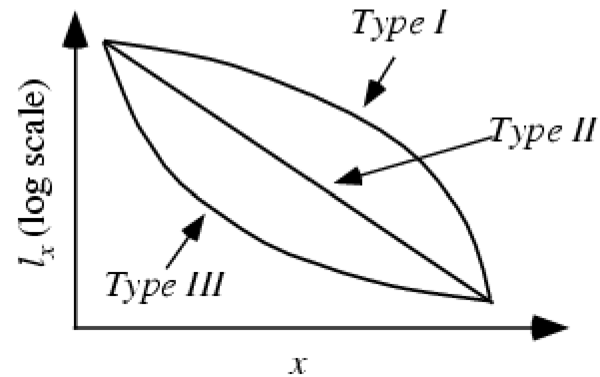
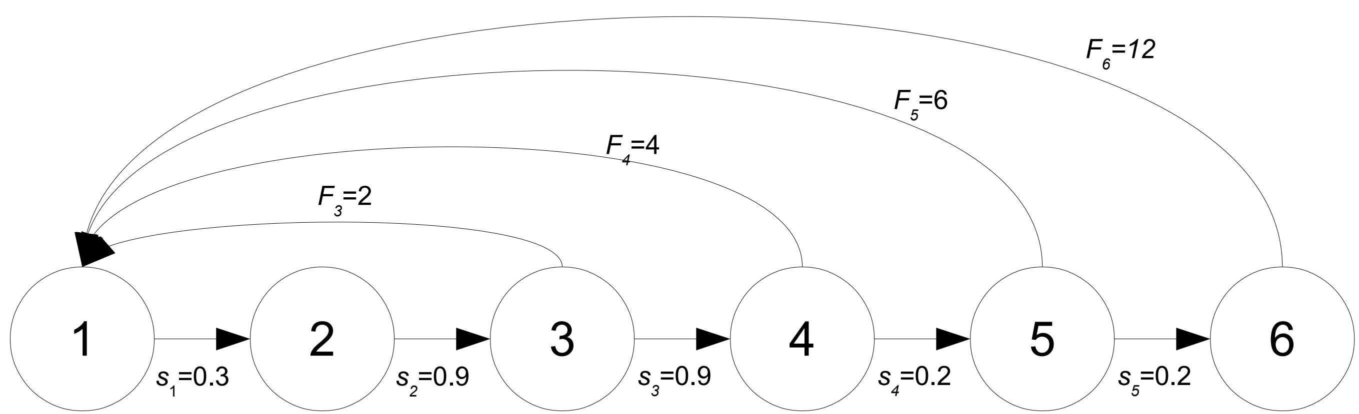


Note on notation: There are consistent patterns, but no universal notation

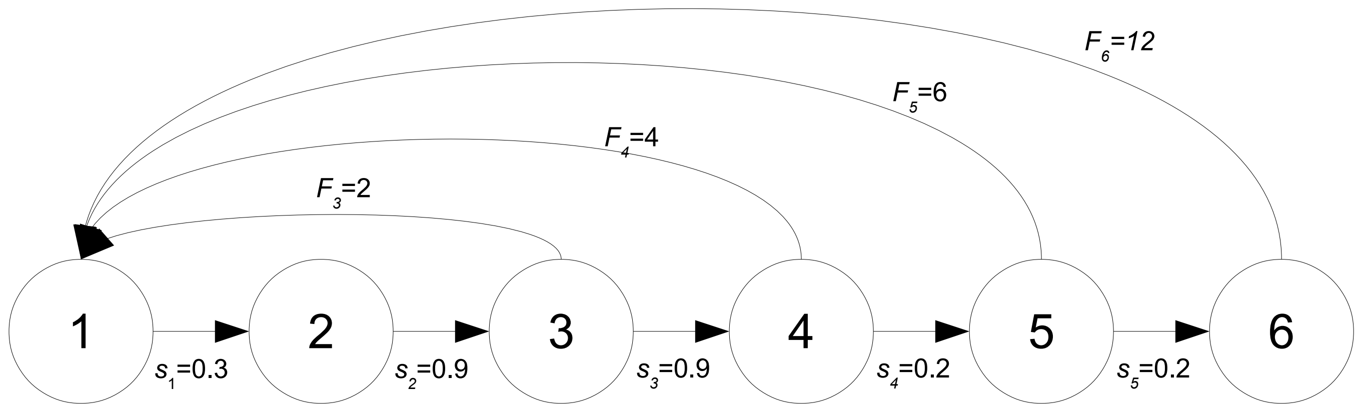
- death and mortality: μ, d, s=1-d, $l_x = s_1 s_2 s_3 \ldots s_x$
- birth and fecundity: f, F, β
- state variable: n, x
- projection matrix: **L**, **A**, Λ

The life history diagram

- Example
  - What is maximum lifespan?
  - What is age at first reproduction?
  - What type is the survival curve?



A model: a system of difference equations



n_0

n_1

n_2

n_3

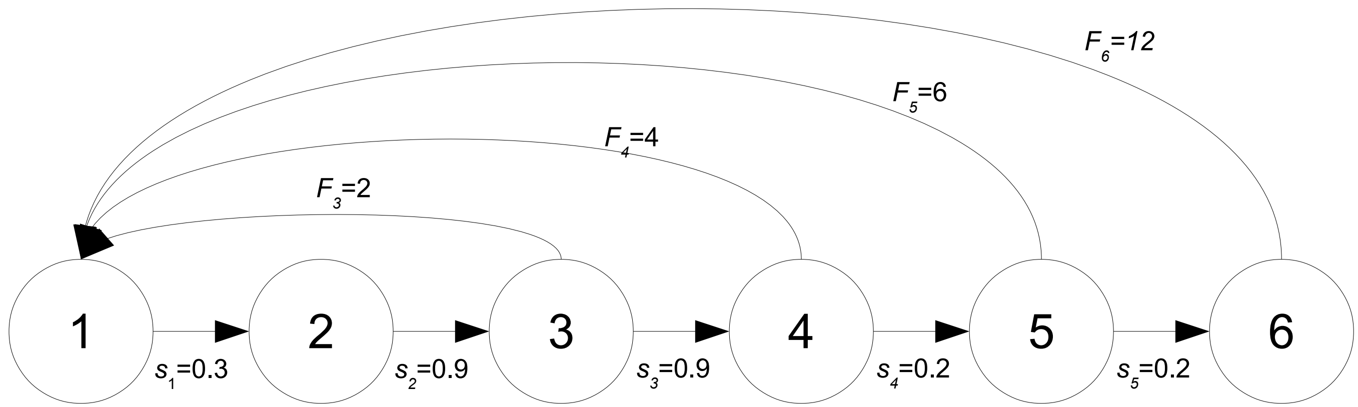
n_4

n_5

n_6

A vector of state variables represents *what we wish to represent:* size of the subpopulation at ages 0 through 6

A model: a system of difference equations



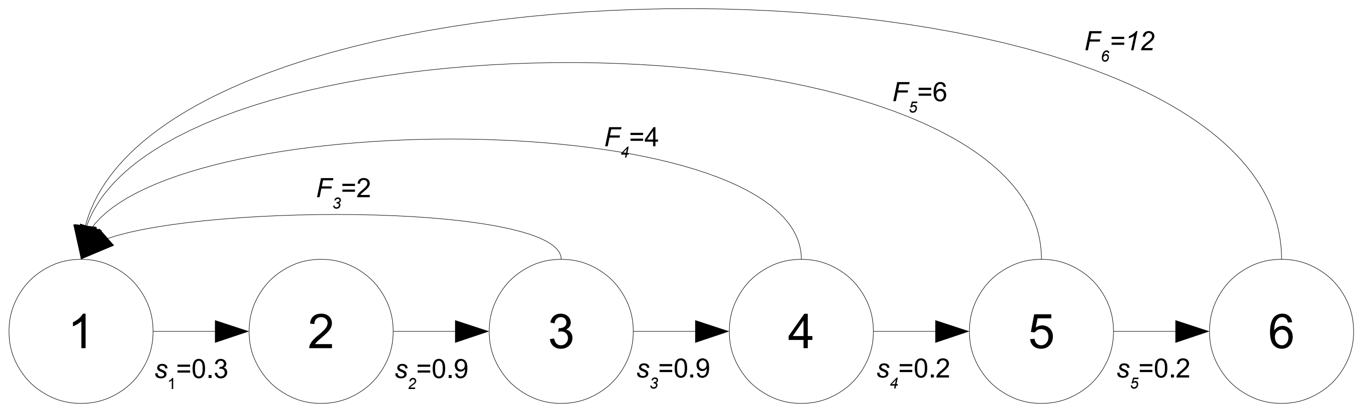
$$
\begin{aligned}
&n_0 \qquad\qquad n_0 = f_0(n_0, n_1, n_2, n_3, n_4, n_5, n_6)\\
&n_1 \qquad\qquad n_1 = f_1(n_0, n_1, n_2, n_3, n_4, n_5, n_6)\\
&n_2 \qquad\qquad n_2 = f_2(n_0, n_1, n_2, n_3, n_4, n_5, n_6)\\
&n_3 \qquad\qquad n_3 = f_3(n_0, n_1, n_2, n_3, n_4, n_5, n_6)\\
&n_4 \qquad\qquad n_4 = f_4(n_0, n_1, n_2, n_3, n_4, n_5, n_6)\\
&n_5 \qquad\qquad n_5 = f_5(n_0, n_1, n_2, n_3, n_4, n_5, n_6)\\
&n_6 \qquad\qquad n_6 = f_6(n_0, n_1, n_2, n_3, n_4, n_5, n_6)
\end{aligned}
$$

A set of *difference equations* relates population size to population size at the previous time

Here the equations are unspecified

More complete notation would have subscripts for *time indexing* – here it is understood that *n*'s on the left are one time step later than n's on the right

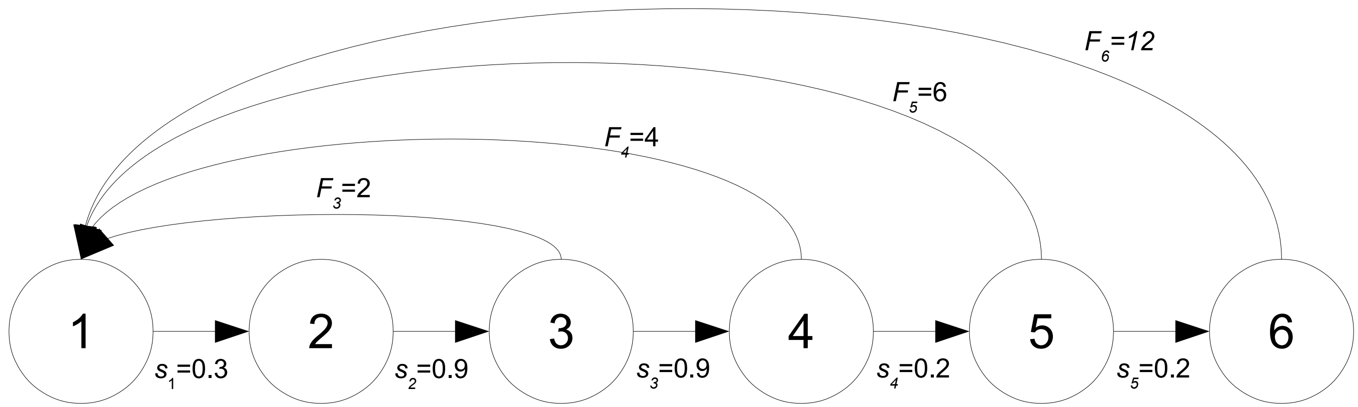
A model: a system of difference equations



n_0	$n_0 = f_0(n_0, n_1, n_2, n_3, n_4, n_5, n_6)$	$n_0 = f_0(\boldsymbol{n})$
n_1	$n_1 = f_1(n_0, n_1, n_2, n_3, n_4, n_5, n_6)$	$n_1 = f_1(\boldsymbol{n})$
n_2	$n_2 = f_2(n_0, n_1, n_2, n_3, n_4, n_5, n_6)$	$n_2 = f_2(\boldsymbol{n})$
n_3	$n_3 = f_3(n_0, n_1, n_2, n_3, n_4, n_5, n_6)$	$n_3 = f_3(\boldsymbol{n})$
n_4	$n_4 = f_4(n_0, n_1, n_2, n_3, n_4, n_5, n_6)$	$n_4 = f_4(\boldsymbol{n})$
n_5	$n_5 = f_5(n_0, n_1, n_2, n_3, n_4, n_5, n_6)$	$n_5 = f_5(\boldsymbol{n})$
n_6	$n_6 = f_6(n_0, n_1, n_2, n_3, n_4, n_5, n_6)$	$n_6 = f_6(\boldsymbol{n})$

More concise notion to represent population size as a *vector*

What are the equations? Combinations of multiplication and addition



$$n_0 = f_0(\boldsymbol{n})$$
$$n_1 = f_1(\boldsymbol{n})$$
$$n_2 = f_2(\boldsymbol{n})$$
$$n_3 = f_3(\boldsymbol{n})$$
$$n_4 = f_4(\boldsymbol{n})$$
$$n_5 = f_5(\boldsymbol{n})$$
$$n_6 = f_6(\boldsymbol{n})$$

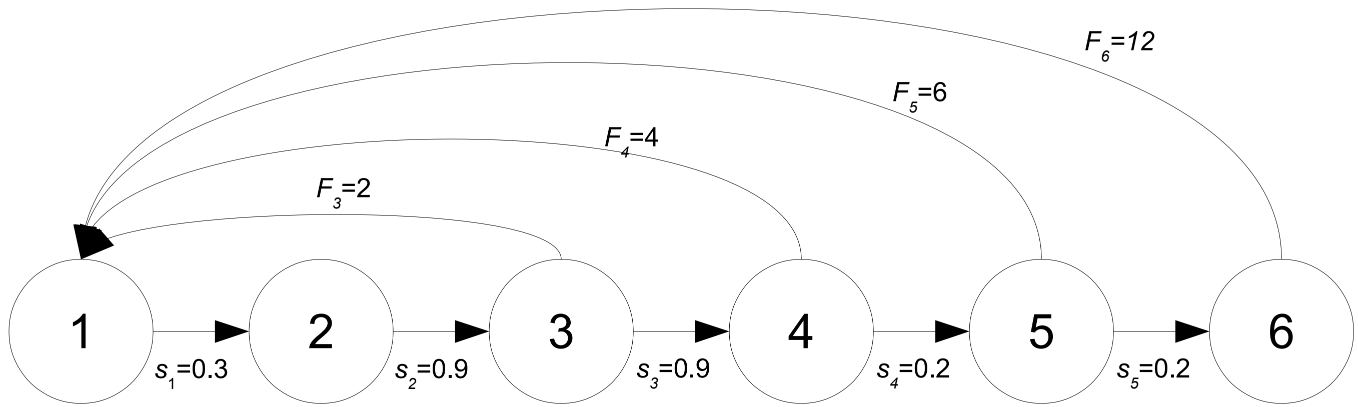
$$n_0 = f_0(\boldsymbol{n})$$
$$n_1 = f_1(\boldsymbol{n})$$
$$n_2 = f_2(\boldsymbol{n})$$
$$n_3 = f_3(\boldsymbol{n})$$
$$n_4 = f_4(\boldsymbol{n})$$
$$n_5 = f_5(\boldsymbol{n})$$
$$n_6 = s_5 n_5$$

Abundance of six-year-olds depends only on number of five-year-olds in the year before

$$n_0 = f_0(\boldsymbol{n})$$
$$n_1 = f_1(\boldsymbol{n})$$
$$n_2 = f_2(\boldsymbol{n})$$
$$n_3 = f_3(\boldsymbol{n})$$
$$n_4 = f_4(\boldsymbol{n})$$
$$n_5 = f_5(\boldsymbol{n})$$
$$n_6 = (0)n_0 + (0)n_1 + (0)n_2 + (0)n_3 + (0)n_4 + s_5 n_5 + (0)n_6$$

For the time being, we add in the remaining zeros

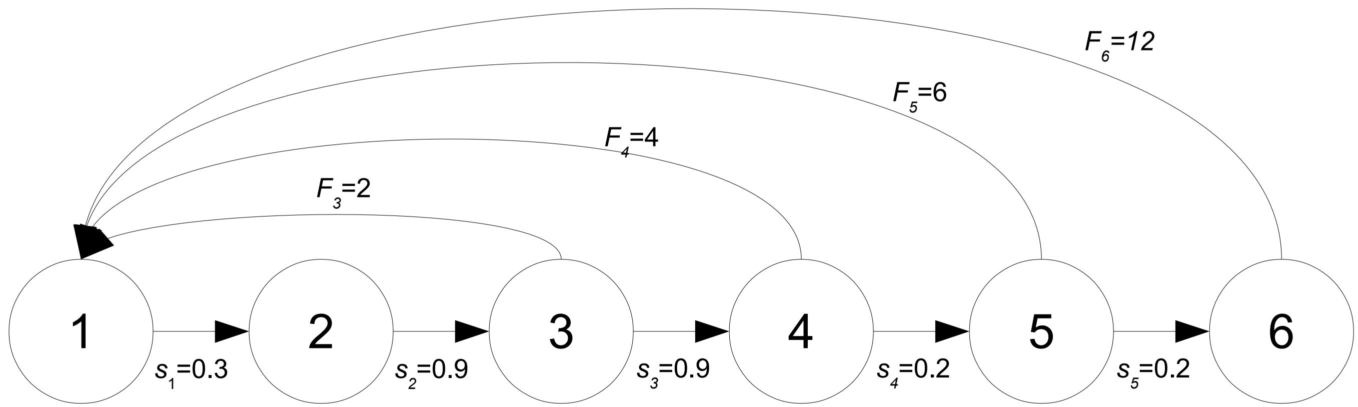
What are the equations? Combinations of multiplication and addition



A pattern emerges...

$$n_0 = f_0(\boldsymbol{n})$$
$$n_1 = f_1(\boldsymbol{n})$$
$$n_2 = (0)n_0 + s_1 n_1 + (0)n_2 + (0)n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
$$n_3 = (0)n_0 + (0)n_1 + s_2 n_2 + (0)n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
$$n_4 = (0)n_0 + (0)n_1 + (0)n_2 + s_3 n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
$$n_5 = (0)n_0 + (0)n_1 + (0)n_2 + (0)n_3 + s_4 n_4 + (0)n_5 + (0)n_6$$
$$n_6 = (0)n_0 + (0)n_1 + (0)n_2 + (0)n_3 + (0)n_4 + s_5 n_5 + (0)n_6$$

What are the equations? Combinations of multiplication and addition



The pattern is disrupted...

$$n_0 = f_0(\boldsymbol{n})$$
$$n_1 = \square + (0)n_1 + (0)n_2 + F_3 n_3 + F_4 n_4 + F_5 n_5 + F_6 n_6$$
$$n_2 = (0)n_0 + s_1 n_1 + (0)n_2 + (0)n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
$$n_3 = (0)n_0 + (0)n_1 + s_2 n_2 + (0)n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
$$n_4 = (0)n_0 + (0)n_1 + (0)n_2 + s_3 n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
$$n_5 = (0)n_0 + (0)n_1 + (0)n_2 + (0)n_3 + s_4 n_4 + (0)n_5 + (0)n_6$$
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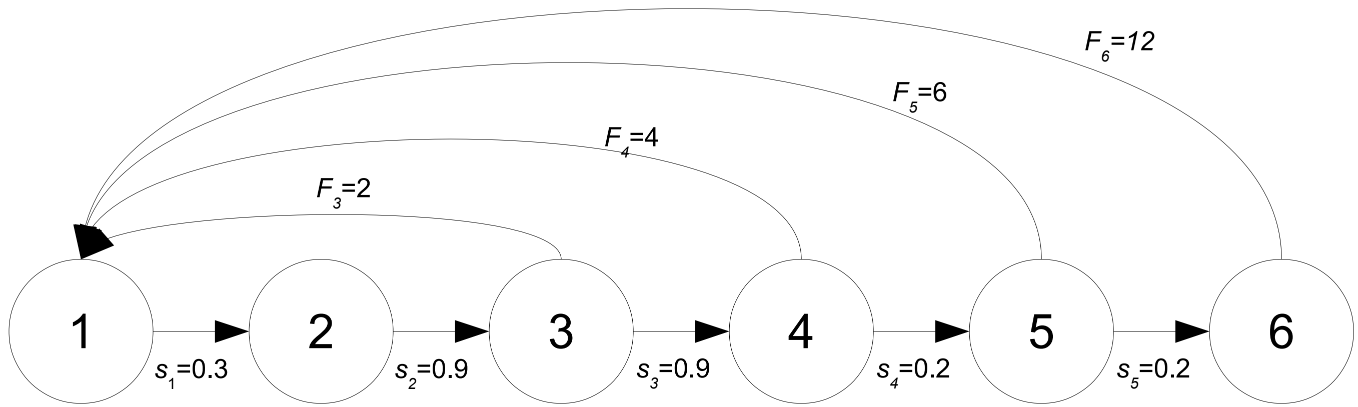
What are the equations? Combinations of multiplication and addition



Eliminate state variable n_0

Even though it exists it is never *observed* and is not *required to solve* any other equation – thus, it does not provide any additional *information* about the population growth process

Pre-reproductive census implies that F is *realized fecundity*

$$n_1 = (0)n_1 + (0)n_2 + F_3 n_3 + F_4 n_4 + F_5 n_5 + F_6 n_6$$
$$n_2 = s_1 n_1 + (0)n_2 + (0)n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
$$n_3 = (0)n_1 + s_2 n_2 + (0)n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
$$n_4 = (0)n_1 + (0)n_2 + s_3 n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
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Matrix Representation (cf. Appendix 2, p. 418)

- Linear algebra is the study of sets of linear equations and their transformations

Is our model a system of linear equations?

$$
\begin{aligned}
n_1 &= (0)n_1 + (0)n_2 + F_3 n_3 + F_4 n_4 + F_5 n_5 + F_6 n_6 \\
n_2 &= s_1 n_1 + (0)n_2 + (0)n_3 + (0)n_4 + (0)n_5 + (0)n_6 \\
n_3 &= (0)n_1 + s_2 n_2 + (0)n_3 + (0)n_4 + (0)n_5 + (0)n_6 \\
n_4 &= (0)n_1 + (0)n_2 + s_3 n_3 + (0)n_4 + (0)n_5 + (0)n_6 \\
n_5 &= (0)n_1 + (0)n_2 + (0)n_3 + s_4 n_4 + (0)n_5 + (0)n_6 \\
n_6 &= (0)n_1 + (0)n_2 + (0)n_3 + (0)n_4 + s_5 n_5 + (0)n_6
\end{aligned}
$$

Matrix Representation (cf. Appendix 2, p. 418)

- Linear algebra makes liberal use of matrix representation

$$n_1 = (0)n_1 + (0)n_2 + F_3 n_3 + F_4 n_4 + F_5 n_5 + F_6 n_6$$
$$n_2 = s_1 n_1 + (0)n_2 + (0)n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
$$n_3 = (0)n_1 + s_2 n_2 + (0)n_3 + (0)n_4 + (0)n_5 + (0)n_6$$
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$$n_5 = (0)n_1 + (0)n_2 + (0)n_3 + s_4 n_4 + (0)n_5 + (0)n_6$$
$$n_6 = (0)n_1 + (0)n_2 + (0)n_3 + (0)n_4 + s_5 n_5 + (0)n_6$$

Plus signs are implied

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{pmatrix} = \begin{pmatrix} (0)n_1 & (0)n_2 & F_3 n_3 & F_4 n_4 & F_5 n_5 & F_6 n_6 \\ s_1 n_1 & (0)n_2 & (0)n_3 & (0)n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & s_2 n_2 & (0)n_3 & (0)n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & (0)n_2 & s_3 n_3 & (0)n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & (0)n_2 & (0)n_3 & s_4 n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & (0)n_2 & (0)n_3 & (0)n_4 & s_5 n_5 & (0)n_6 \end{pmatrix}$$

Matrix × Matrix Multiplication

- The rule of matrix multiplication when a matrix is multiplied by another matrix
- Multiply row vectors by column vectors
- The multiplication of row *m* and column *n*, the vector product lives in element *m*,*n* of the product matrix

$$\boldsymbol{A}=\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \boldsymbol{B}=\begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix}$$

$$\boldsymbol{AB}=\begin{pmatrix} a_{11}b_{11}+a_{12}b_{21} & a_{11}b_{12}+a_{12}b_{22} \\ a_{21}b_{11}+a_{22}b_{21} & a_{21}b_{12}+a_{22}b_{22} \end{pmatrix}$$

- Tutorials
  - http://people.hofstra.edu/Stefan_Waner/realWorld/tutorialsf1/frames3_2.html
  - http://www.purplemath.com/modules/mtrxmult.htm
  - http://www.mai.liu.se/~halun/matrix/

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2×2 2×2

inner

outer

$$\boldsymbol{AB}=\begin{pmatrix} a_{11}b_{11}+a_{12}b_{21} & a_{11}b_{12}+a_{12}b_{22} \\ a_{21}b_{11}+a_{22}b_{21} & a_{21}b_{12}+a_{22}b_{22} \end{pmatrix}$$

It follows that to multiply two matrices the “inner” dimensions must be the same. The “outer” dimensions give the dimension of the product matrix. In this case two 2×2 matrices multiple to give a 2×2 matrix. Similarly, one can multiple a 4×2 matrix by a 2×3 matrix but not a 2×3 matrix by a 4×2 matrix.

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Vector × Vector Multiplication (a special case)

- The rule of vector multiplication
- Vectors must be same length
  - First vector a row
  - Second vector a column

$$\boldsymbol{a}=\begin{pmatrix} a_1 & a_2 & a_3 \end{pmatrix},\ \boldsymbol{b}=\begin{pmatrix} b_1 \\ b_2 \\ b_3 \end{pmatrix}$$

$$\boldsymbol{c}=\boldsymbol{ab}=\left(a_1 b_1+a_2 b_2+a_3 b_3\right)$$

Matrix × Vector Multiplication (another special case)

- The rule of matrix multiplication when a matrix is multiplied by a vector
- A vector is a special case of a matrix so matrix-vector multiplication is a special case of matrix multiplication

$$\boldsymbol{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \boldsymbol{b} = \begin{pmatrix} b_1 \\ b_2 \end{pmatrix}$$

$$\boldsymbol{Ab} = \begin{pmatrix} a_{11} b_1 + a_{12} b_2 \\ a_{21} b_1 + a_{22} b_2 \end{pmatrix}$$

Matrix × Vector Multiplication

- The rule of matrix multiplication when a matrix is multiplied by a vector

$$\boldsymbol{A}=\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \boldsymbol{b}=\begin{pmatrix} b_1 \\ b_2 \end{pmatrix}$$

$$\boldsymbol{Ab}=\begin{pmatrix} a_{11}b_1 & a_{12}b_2 \\ a_{21}b_1 & a_{22}b_2 \end{pmatrix}$$

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{pmatrix}=\begin{pmatrix} (0)n_1 & (0)n_2 & F_3 n_3 & F_4 n_4 & F_5 n_5 & F_6 n_6 \\ s_1 n_1 & (0)n_2 & (0)n_3 & (0)n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & s_2 n_2 & (0)n_3 & (0)n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & (0)n_2 & s_3 n_3 & (0)n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & (0)n_2 & (0)n_3 & s_4 n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & (0)n_2 & (0)n_3 & (0)n_4 & s_5 n_5 & (0)n_6 \end{pmatrix}$$

How can we take the right hand side of our equation and re-represent it in terms a a matrix product?

Matrix × Vector Multiplication

- We now have a representation which separates our constant from our state variables and will allow us to track the vector of size structured abundance over time

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{pmatrix} = \begin{pmatrix} (0)n_1 & (0)n_2 & F_3 n_3 & F_4 n_4 & F_5 n_5 & F_6 n_6 \\ s_1 n_1 & (0)n_2 & (0)n_3 & (0)n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & s_2 n_2 & (0)n_3 & (0)n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & (0)n_2 & s_3 n_3 & (0)n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & (0)n_2 & (0)n_3 & s_4 n_4 & (0)n_5 & (0)n_6 \\ (0)n_1 & (0)n_2 & (0)n_3 & (0)n_4 & s_5 n_5 & (0)n_6 \end{pmatrix}$$

Projected abundance (state variables)

Projection matrix (constants)

Past abundance (state variables)

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{pmatrix} = \begin{pmatrix} 0 & 0 & F_3 & F_4 & F_5 & F_6 \\ s_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_5 & 0 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{pmatrix}$$

Structure of the Leslie Matrix

- A projection matrix structured this way is commonly called a Leslie matrix after P.H. Leslie who worked with Charles Elton at the Oxford Bureau of Animal Population

Age-specific fecundity on the top line

Survivorship on the sub-diagonal

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{pmatrix} = \begin{pmatrix} 0 & 0 & F_3 & F_4 & F_5 & F_6 \\ s_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_5 & 0 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{pmatrix}$$

Zero everywhere else

Compact Notation

- We can now write a simple equation for structured population growth

$$\boldsymbol{n}_1 = \boldsymbol{L}\,\boldsymbol{n}_0$$

- Substituting, we extend to the next time step

matrix multiplication

$$\boldsymbol{n}_2 = \boldsymbol{L}\,\boldsymbol{n}_1 = \boldsymbol{L}(\boldsymbol{L}\,\boldsymbol{n}_0) = \boldsymbol{L}\,\boldsymbol{L}\,\boldsymbol{n}_0 = \boldsymbol{L}^2\,\boldsymbol{n}_0$$

- In general

$$\boldsymbol{n}_t = \boldsymbol{L}^t\,\boldsymbol{n}_0$$

Use this model to numerically solve structured population models

More insight...

- Note the similarity between the solutions of the unstructured model...

$$n_t = \lambda^t n_0$$

- And the structured model

$$\boldsymbol{n}_t = \boldsymbol{L}^t \boldsymbol{n}_0$$

λ is the dominant eigenvalue of the Leslie matrix

- Here we look for a deep connection between the structured and unstructured models
- This section follows pp. 66-72 in Case

λ is the dominant eigenvalue of the Leslie matrix

- Here we look for a deep connection between the structured and unstructured models
- This section follows pp. 66-72 in Case
- After *transient dynamics* no longer strongly affect the population the relative abundance of the different age classes stays the same – the so called *stable age distribution*
  - This can be proved mathematically (not required for this class)
  - In lab we will study this property numerically, particularly...
    - We will demonstrate to ourselves that the matrix operations and the original equations arrive at the same answer
    - We will study how deviations from the stable age distribution affect transient dynamics and how long these transients last

λ is the dominant eigenvalue of the Leslie matrix

- Our method will be to proceed by conjecture....
- CONJECTURE: There is some vector ***x*** such that multiplication by a *scalar* gives the same result as multiplication by ***L***

$$\boldsymbol{L}\,\boldsymbol{x} = \lambda\,\boldsymbol{x}$$

λ is the dominant eigenvalue of the Leslie matrix

- Our method will be to proceed by conjecture....
- CONJECTURE: There is some vector ***x*** such that multiplication by a *scalar* gives the same result as multiplication by ***L***

$$\boldsymbol{L}\,\boldsymbol{x} = \lambda\,\boldsymbol{x}$$

- If λ exists and ***x*** has properties such that the above equation is true, then we could replace our matrix equation

$$\boldsymbol{n}_t = \boldsymbol{L}^t\,\boldsymbol{n}_0$$

with

$$\boldsymbol{n}_t = g\,\lambda^t\,\boldsymbol{x}$$

g depends on the initial population vector

λ is the long run growth rate

x is the stable age distribution

λ is the dominant eigenvalue of the Leslie matrix

- It turns out that for a large class of matrices (of which all Leslie matrices are a subset) there is such a quantity – it is called the dominant eigenvalue
- The dominant eigenvalue λ of the Leslie matrix ***L*** gives the asymptotic geometric growth rate
  - For small matrices (two to three age classes) λ can be obtained analytically using the *characteristic equation* (not req'd for this course)
  - Otherwise, the dominant eigenvalue can be obtained numerically
    - In MATLAB use `eig`
    - In R use `eigen`
  - ***x*** (the stable age distribution is the (right) eigenevctor)
  - This rate is *asymptotic* because it is approached as time goes to infinity, in practice λ is achieved with tolerable precision within some tens of time steps
  - The left eigenvector ***v*** (the right eigenvector of the transpose of ***L***) gives *reproductive value*, i.e. $\boldsymbol{v}_i$ is the average number of future offspring of an individual of age *i*

From age-structured to stage-structured: the Lefkovich matrix

Stage-specific fecundity on the top line

Probability of “growth” on the sub-diagonal

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \end{pmatrix} = \begin{pmatrix} p_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\ g_1 & p_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & g_2 & p_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & g_3 & p_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & g_4 & p_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & g_5 & p_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & g_6 & p_6 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \end{pmatrix}$$

From age-structured to stage-structured: the Lefkovich matrix

Stage-specific fecundity on the top line

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \end{pmatrix} = \begin{pmatrix} p_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\ g_1 & p_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & g_2 & p_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & g_3 & p_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & g_4 & p_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & g_5 & p_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & g_6 & p_6 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \end{pmatrix}$$

Probability of remaining in the same class on the sub-diagonal

Also called “transition matrix”

All demographic transitions of the form “from—to” go in matrix element (*m*,*n*)

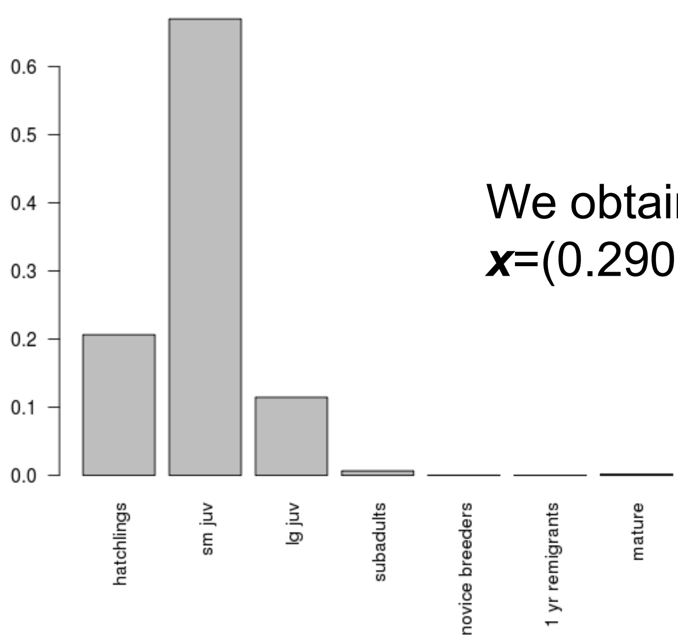
By the law of total probability

$$p_i + g_i + \mu_i = 1$$

Zero everywhere else

Growth rate of *Caretta caretta*

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0 & 127 & 4 & 80 \\ 0.6747 & 0.7370 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.0486 & 0.6610 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.0147 & 0.6907 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.0518 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.8091 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.8089 & 0.8089 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \end{pmatrix}$$



We obtain the dominant eigenvalue λ=0.945 and eigenvector ***x***=(0.2907, 0.9430, 0.1613, 0.0093, 0.0005, 0.0004, 0.0026)

Questions

(1) What is the population growth rate?

λ=0.945

(2) How do the different life stages contribute to population growth?

(3) How great an effect must interventions have to be successful?

How do the different life stages contribute to population growth?

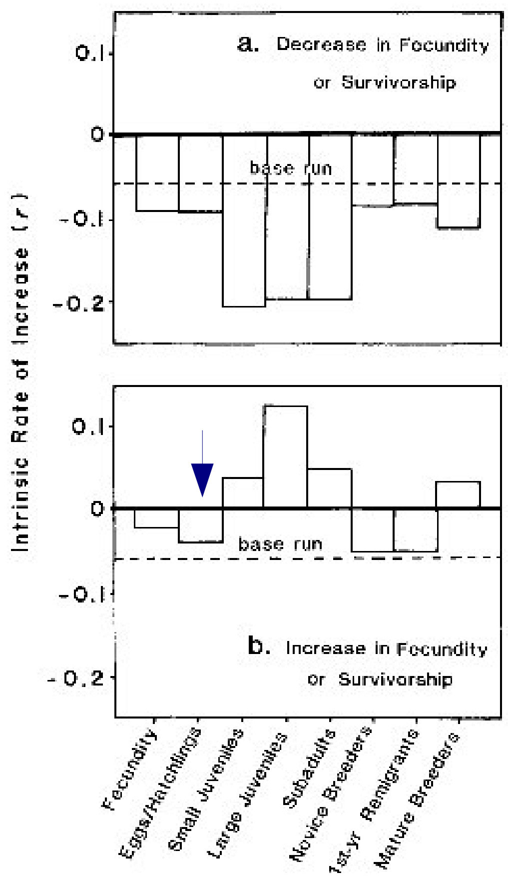
Sensitivity – rate of change of λ with respect to $\alpha_{i,j}$

Elasticity – Proportional rate of change of λ with respect to $\alpha_{i,j}$

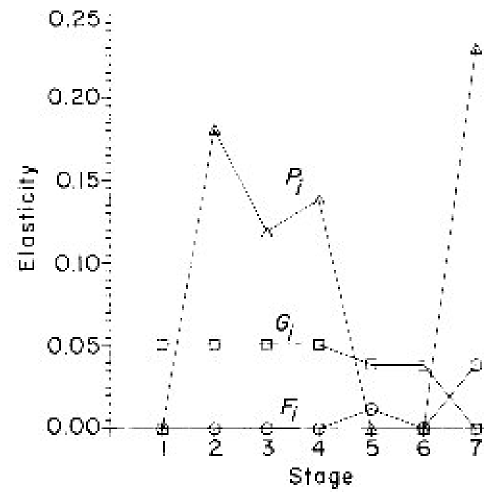
$$\frac{\partial \lambda}{\partial \alpha_{i,j}} = \frac{v_i w_j}{\langle \boldsymbol{w}, \boldsymbol{v} \rangle}$$

$$e_{i,j} = \frac{\alpha_{i,j}}{\lambda} \frac{\partial \lambda}{\partial \alpha_{i,j}} = \frac{\partial \log \lambda}{\partial \log \alpha_{i,j}}$$

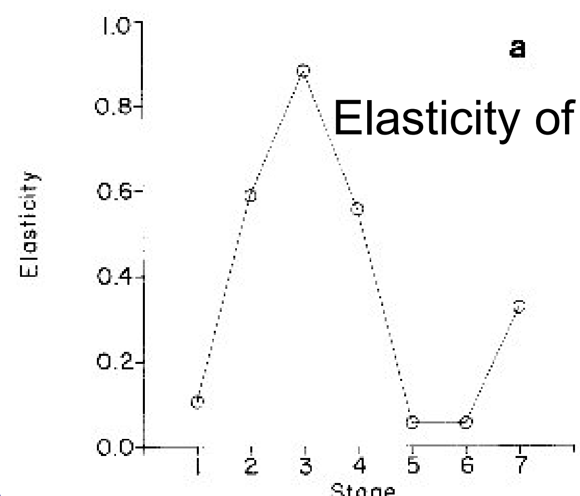
Elasticity of *Caretta caretta* growth



Decreasing hatchling survival to 0 does not prevent decline



Elasticity of matrix elements



Elasticity of age-specific survival

Questions

(1) What is the population growth rate?

λ=0.945

(2) How do the different life stages contribute to population growth?

Key life stages are juveniles and subadult

(3) How great an effect must interventions have to be successful?

Simulating effects of policy

Immature survivorship (nearshore bycatch) improved

Juvenile-Adult survivorship (TEDs) improved

Juvenile-Adult survivorship (TEDs) Improved, but less optimistic about hatchling survival

TABLE 6. Three management scenarios involving changes in mortality in various life stages of loggerhead sea turtles. For each scenario, the stages are listed along with the old and the new matrix elements* (P_i, G_i) and the resulting λ_m and r.

Change in initial matrix				Result	
Stage	Coefficient	Old	New	λ_m	r
Immature survivorship increased to 0.80					
2	P_2	0.7370	0.74695		
	G_2	0.0486	0.0531		
3	P_3	0.6610	0.7597	1.06	+0.06
	G_3	0.0147	0.0403		
4	P_4	0.6907	0.7289		
	G_4	0.0518	0.0710		
Large juveniles and subadults = 0.80; adults = 0.85					
3	P_3	0.6610	0.7597		
	G_3	0.0147	0.0403		
4	P_4	0.6907	0.7289		
	G_4	0.0518	0.0710	1.06	+0.06
5	G_5	0.8091	0.8500		
6	G_6	0.8091	0.8500		
7	P_7	0.8089	0.8500		
First-year = 0.33735; large juveniles, subadults = 0.80; adults = 0.85					
1	G_1	0.6747	0.33735		
3	P_3	0.6610	0.7597		
	G_3	0.0147	0.0403		
4	P_4	0.6907	0.7289		
	G_4	0.0518	0.0710	1.02	+0.02
5	G_5	0.8091	0.8500		
6	G_6	0.8091	0.8500		
7	P_7	0.8089	0.8500		

* P_i = the probability of survival while remaining in the same stage. G_i = the probability of surviving while growing to the next stage.

Questions

(1) What is the population growth rate?

λ=0.945

(2) How do the different life stages contribute to population growth?

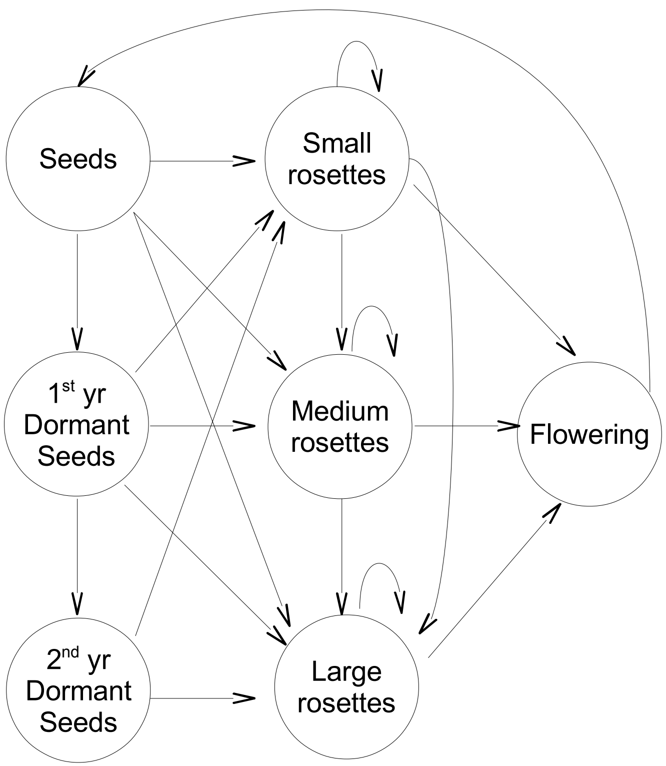
Key life stages are juveniles and subadult

(3) How great an effect must interventions have to be successful?

Even 100% survival of eggs/hatchlings would not cause λ to become greater than 1

A combination of beeach closures and increased survivorship (due to TEDs) could be effective

Life cycle of Teasel (*Dipsacus sylvestris*)



Two properties guarantee an asymptotic growth rate

- *Irreducibility* – The life cycle graph contains a path from every node to every other node
- *Primitivity* – A projection matrix is primitive if it become positive (every element >0) when raised to a sufficiently high power
  - A sufficient condition for primitivity is the existence of two adjacent classes with positive fertility

Summary

- Age- and stage-structured populations have a growth rate analogous to the growth rate of unstructured populations
  - This growth rate is given by the dominant eigenvalue of the population projection matrix
  - This growth rate is approached asymptotically
  - Transient dynamics may occur before the asymptotic growth rate is achieved
- Populations growing according to an age-structured model have a *stable age distribution*
- Sensitivity and elasticity analysis may be used to determine which ages/stages contribute most to population growth
- (The Lotka-Euler equation is the *characteristic polynomial* of the Leslie matrix and related age specific reproduction and cumulative survival to the growth rate λ)
- (The McKendrick-von Foerster model is a partial differential equation model for age-structured growth in continuous time)